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Effect of volcanic ash deposition on length and radial growths of a deciduous montane tree (*Nothofagus pumilio*)

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Abstract Extreme environmental events such as volcanic eruptions can trigger plant responses that largely exceed those recorded for moderate-intensity disturbances. We assessed the effects of the June 2011 eruption of the Puyehue – Cordón Caulle volcano on the length and radial growths of juvenile *Nothofagus pumilio* trees at two sites located 20 (with >40 cm ash accretion) and 75 (without ash) km from the volcano. Variations in length and radial growth were evaluated for the periods 1999–2013 and 1993–2013 respectively; pre- and post-eruption growth rates were computed. The length growth of the *N. pumilio* trees located close to the volcano increased significantly after the eruption: shoot extensions during the growing season after the eruption were, on average, two to three times longer than average according to ontogenetic growth trends. Variations in radial growth after the eruption were comparatively less noticeable than those in length growth. No significant effects of the eruption were observed in those trees located 75 km from the volcano. In order to explain the exceptionally positive response of *N. pumilio*'s length growth to the volcanic eruption, three non-exclusive explanations were proposed: (i) thick ash layers increase water retention in the soil; (ii) volcanic ash facilitates the access of plants to nutrients; and (iii) volcanic ashes decrease herbivory and competition. The comparatively lower sensitivity of radial growth to this extreme volcanic event is also noteworthy. These findings highlight the need to further examine how large-scale volcanic events influence structure and/or functioning of ecosystem in the Patagonian forest.

Key words: disturbance, length growth, *Nothofagus pumilio*, radial growth, volcanic eruption.

INTRODUCTION

Volcanic eruptions may have dramatic consequences on ecosystems and, like other extreme events, may have played a vital role in the evolution of physiological and ecological traits of organisms and populations (Gutschick & BassiriRad 2003; Kitzberger 2013). Due to their unpredictability and low frequency but high magnitude, volcanic eruptions can modify the acclimation capacities of organisms beyond typical boundaries (Gutschick & BassiriRad 2003). Consequently, after such an episode, organisms or whole populations exhibit physiological and developmental responses to the new environment that significantly differ from normal acclimation (Gutschick & BassiriRad 2003). Therefore, the structure and/or functioning of ecosystems could pass through a generally slow recovery phase, where several species die and others benefit by colonizing the disturbed environment (Gutschick & BassiriRad 2003; Kitzberger 2013). Lava, mud or pyroclastic flows in combination with widespread tephra fall (Swanson & Major 2005) are damaging factors often linked to volcanic eruptions. The intensity of these factors would subside gradually as distance to the volcano increases (Antos & Zobel 2005; Collini *et al.* 2013), so that their negative impact on organisms may also be thought to decrease in the same direction. Non-lethal responses of plants to volcanic events are known to vary enormously depending on the granulometry, chemical composition, and the amount of debris deposited on plants. These responses also depend on the plant species and their phenological and ontogenetic stages at the time of the eruption (Antos & Zobel 2005).

Ash deposition following volcanic eruptions modifies plant growth rates and productivity with direct and indirect effects on affected forest ecosystems (Yamaguchi 1983; Hinckley *et al.* 1984; Segura *et al.* 1995; Biondi *et al.* 2003; Lawrence 2005). Potential negative effects of ash deposition on plants include mechanical damage, change in foliage geometry, deterioration of the photosynthetic crown and disruption of the energy balance caused by high temperatures (Seymour *et al.* 1983; Yamaguchi 1983; Lawrence 2005). On the other hand, ash deposition may have positive effects on tree growth and leaf production by increasing soil-water availability due to a

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decrease in evapotranspiration (Black & Mack 1986), promoting biomass production through a mulching effect (Chapin *et al.* 1987), diminishing herbivory (Chaneton *et al.* 2014) and/or increasing nutrient availability (Dahlgren *et al.* 2004).

One of the methods for assessing non-lethal effects of volcanic events on plants consists in quantifying inter-annual variations in plant growth. The effects of volcanic eruptions on radial growth have commonly been evaluated by measuring annual variations in tree-ring increments over decades to centuries (Yamaguchi 1983, 1985; Biondi *et al.* 2003). In trees from temperate regions, the responses to volcanic events can also be addressed through the evaluation of the variations in annual increments in the length of the trunk and/or branches (i.e. length growth or primary growth). In these species, annual increments in length, often referred to as annual shoots, may be traced several decades back by using the morphological and architectural signals (Hallé *et al.* 1978; Barthélémy & Caraglio 2007). Although height is relevant in tree competition for light and consequently in successional changes (Goulet *et al.* 2000), the effects of volcanic eruptions on length growth have been rarely studied (but see, Zobel & Antos 1985). In the southern hemisphere, volcanic eruptions are moulding landscapes by shaping past and present ecological systems; however, few studies have addressed their impact on the dynamics of Patagonian forests (Veblen *et al.* 1996; Swanson *et al.* 2013). In this sense, understanding the responses of dominant species to a high-intensity but low-frequency disturbance event would provide new insights to forest dynamics in Patagonia.

On June 4 2011, the eruption of the *Puyehue – Cordón Caulle Volcanic Complex* (PCCVC) caused the massive death of forests in the immediate vicinity of the crater and impacted, mostly through ash accumulation, more than 240 000 km^2 across Argentinean territories in northern Patagonia (Gaitán *et al.* 2011). This eruption provided an opportunity to examine the effects of an extreme event on the growth of *Nothofagus pumilio* (Poepp. et Endl.) Krasser, the most abundant tree species in the upper mountain slopes of the Patagonian Andes (Donoso 2006). Given its large ecological amplitude, *N. pumilio* presents a variety of morphological types and regenerative dynamics, mostly associated with the frequency and magnitude of disturbance regimes (such as windstorms, woodfires, avalanches, landslides or natural falling trees, Veblen *et al.* 1996; Donoso 2006). However, the effect of a large-scale disturbance, such as volcanic eruptions on growth patterns of *N. pumilio* has rarely been studied. Previous works have assessed the variations in radial and length growth of *N. pumilio* over decades to centuries in relation to regional climatic fluctuations (Villalba *et al.* 1997; Lara *et al.* 2001; Passo *et al.* 2002; Magnin *et al.* 2014), but none of these studies reported the effects of volcanic ash deposition on tree growth. In this study, we retrospectively assessed inter-annual variations in length and radial growth of *N. pumilio* at a site in Argentina located 20 km from the PCCVC, where ash deposits reached over 40 cm in depth, and contrasted with those recorded at a *N. pumilio* stand in the same region but unaffected by ash accretion (70 km from the PCCVC) (Magnin *et al.* 2014). We hypothesized that the occurrence of ash deposition from the PCCVC eruption had a negative effect on the length and radial growth of trees closer to the volcano (20 km from the PCCVC), whereas trees located far from the volcano should not exhibit notable changes in their typical growth variations over time. Narrow or missing growth rings and/or short or missing internodes were expected in trees located closer to the PCCVC.

METHODS

The June 2011 PCCVC eruption

Two major eruptions (1921–1922 and 1960), and other six minor eruptions (1905, 1914, 1919, 1929, 1934 and 1990), have been recorded for the PCCVC during the 20th century (Collini *et al.* 2013). The most recent eruption of the PCCVC in the south-eastern sector of the Lake Region of Chile (40°34′S, 72°07′W, 2236 m altitude) started on June 4, 2011, and caused substantial landscape changes in northern Patagonia (Ruggiero & Kitzberger 2014). Pumice and ash were expelled from that date up to March 12, 2012, although the largest proportion of volcanic material was deposited during the first days of the eruption (Villarosa & Outes 2013). Ashes were distributed mainly eastwards due to the occurrence of persistent westerly winds over the region (Gaitán *et al.* 2011; Collini *et al.* 2013). Most plants in the close vicinity of the PCCVC (within about 15 km) died after the eruption, probably as a consequence of the deep layer of debris that caused physical and/or chemical damage to their buds and leaves. The impact of the eruption on plants located farther away from the volcano was more variable depending on terrain slope and wind direction, which modified the depth of the deposited ash layer (Puntieri *et al.* 2013).

Species and study sites

Nothofagus pumilio is a deciduous tree that dominates subalpine forests in the southern Andes of Argentina and Chile between 36° and 55°S. This species is adapted to grow under a great variety of soils, slopes and environmental conditions (Schlatter 1994). At some localities, it can reach up to 30 m in height and 1.7 m in diameter (González *et al.* 2006), but becomes a creeping shrub at the upper elevational treeline (Dimitri 1972). The soils of *N. pumilio* forests are predominantly andisoles or basaltics formed during the Quaternary, mostly covered by post-glacial volcanic ashes (Schlatter 1994; Gerding & Thiers 2002). In this region, the Andes Cordillera constitutes a barrier to westerly winds; consequently the climate is dominated by a sharp west-east decreasing rainfall gradient (from 4500 mm on the western side to 700 mm or less on the eastern side, Conti 1998). The climate of the region is characterized by a marked seasonality in temperature and precipitation, with cold and wet winters (over 70% of precipitation occurring between May and October, mainly as snow above 1000 m), and mild and dry summers. *Nothofagus pumilio* can grow under extreme temperatures, from a mean annual temperature of 3.5 to 7°C at upper and lower elevations respectively (Schlatter 1994).

Two stands of juvenile trees of *N. pumilio* (i.e. trees that had not reached the stage of sexual reproduction) were sampled in northwestern Patagonia, Argentina (Table 1). One stand was located on the slope of Cerro Pantojo (Parque Nacional Nahuel Huapi, 40°43′S, 71°54′W, 1200 m; Fig. 1; hereafter Pantojo stand), about 20 km from the PCCVC. The second stand was located on the slope of Cerro Tronador (Parque Nacional Nahuel Huapi, 41°11′S, 71°47′W, 1400 m; Fig. 1; hereafter Tronador stand), some 75 km from the PCCVC. Both *N. pumilio* stands originated after disturbances. The Pantojo stand established after the construction of route N° 231, whereas the Tronador stand developed after large tree fall gaps. At both sites, there were about five juvenile trees of *N. pumilio* per square metre; these trees showed vigorous growth and were homogeneous in height. Following the June 2011 PCCVC eruption, a volcanic ash layer about 40 cm thick with particles of different sizes (from 62 μm to 32 mm, Villarosa & Outes 2013) accumulated at Pantojo stand. At Tronador stand, ash accumulation after the June 2011 PCCVC eruption was <0.2 cm thick (Fig. 1a, Gaitán *et al.* 2011).

Table 1. Characteristics of the studied stands

	Pantojo	Tronador
Age (years)	50.4 ± 0.2	32.2 ± 0.2
Height (m)	8.2 ± 0.2	4.0 ± 0.1
DBH (cm)	7.8 ± 0.3	5.6 ± 0.2

DBH, diameter at breast height. Values represent the mean and ±1 standard error.

Study material and sampling

Samplings were conducted on April 2012 and April 2013 (autumn), upon completion of the corresponding growing season (spring-summer). Twenty-five and 40 *N. pumilio* trees were selected at Pantojo and Tronador stands respectively (Fig. 1b). Both tree stands showed good health conditions and no obvious damage by herbivory (Table 1). The main vertical axis (i.e. the trunk) of each individual was identified (Fig. 2a). Boundaries between successive annual shoots constituting the trunk were identified through morphological markers, from the distal towards the proximal part of the trunk (Fig. 2b, Barthélémy *et al.* 1999; Puntieri *et al.* 1999). These morphological markers are hidden by secondary growth and self-pruning over the years, making the identification of inter-shoot limits inaccurate for long sequence analysis. Hence, we identified shoots corresponding to the most recent 12 and 15 years at the Tronador and Pantojo stands, respectively. Length and number of internodes were registered for the annual shoots

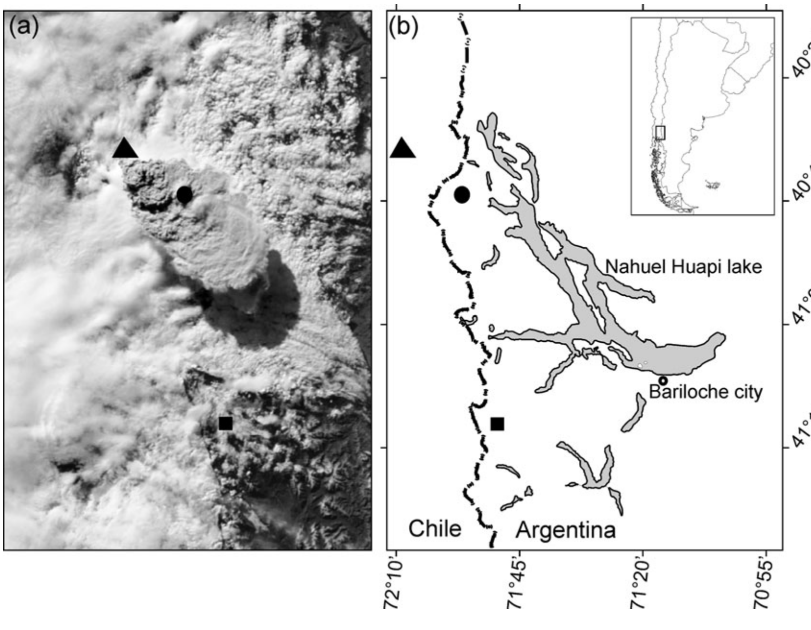

Fig. 1. Study area. (a) MODIS-Aqua image taken on 4 June 2011 (NASA-GSFC) few minutes after the eruption; the ash plume reaches about ~40 km in south-east direction. (b) Locations of the volcanic complex Puyehue – Cordón Caulle (PCCVC; ▲) and the Pantojo (●) and Tronador (■) study sites are indicated.

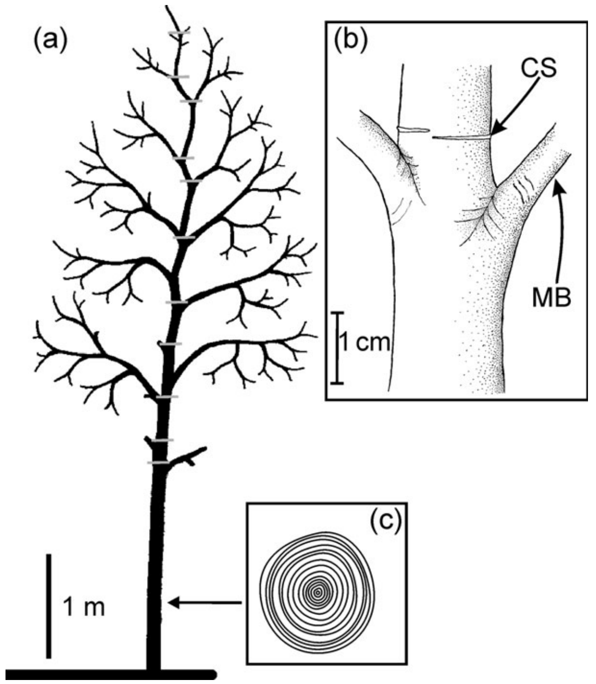

Fig. 2. (a) Semi-schematic drawings of juvenile *Nothofagus pumilio* trees similar to those selected for this study. Horizontal gray lines across the trunk indicate the boundaries between annual shoots. In the scheme at upper right box are shown the morphological makers (b). Cross-section at the base of the trunk is indicated in the lower right box (c). CS, cataphylls scares; MB, main branch.

developed during 2001–2012 (Tronador stand) and 1999–2013 (Pantojo stand) for the selected trees. From each tree, a core was taken at breast height (1.3 m) using an increment borer (Fig. 2c). In the laboratory, cores were polished and measured following the procedures described in Stokes and Smiley (1968). After a precise definition of the growth rings, a calendar year was assigned to each annual growth ring under a stereo-microscope with magnifications between 6× and 50×. Ring dating followed Schulman's convention (Schulman 1956) for the southern hemisphere, which assigns to each annual ring the date of the year in which growth began. Ring widths corresponding to the years 1993–2013 at Pantojo stand, and to the years 2001–2012 at Tronador stand, were measured to the nearest 0.001 mm using a Velmex machine. Chronologies from ring widths were produced using the TURBO ARSTAN software (Cook 1985). This program generates chronologies combining the standardized series of ring widths with a robust estimate of the mean values. The standardization adjusts the observed data series to an exponential curve or trend line and generates a dimensionless index by dividing the observed value by the expected value. In consequence, those trees with the highest rates of growth did not dominate the final mean chronology. To reduce autocorrelation and increase the common signal of individuals of the stand, standardized series were modelled using autoregressive methods (Cook 1985). The use of the autoregressive residuals highlights the high frequency or inter-annual variability in tree-ring variations.

Data analyses

Variations in length and number of internodes of the annual shoots and in width of tree rings were compared over time (1999–2013 for length and number of internodes, and 1993–2013 for tree-ring widths), using repeated-measures ANOVA with one factor (time). The assumptions of sphericity, normality and homoscedasticity of the measurements were checked before each analysis.

Variations in number of internodes and length of annual shoots, as well as in tree-ring widths, were compared between sites (Pantojo and Tronador stands) for the 2001–2012 period, which was common for both sites. In order to compensate for inter-individual differences in the absolute values of the growth attributes, relative values (*xr*) were computed as:

$$xr_i = \left(\frac{x_i}{\sum_j^i x} \cdot 100 \right)$$

where x is the absolute value, i indicates the first value in the sequence and j the last value. For each attribute, repeated-measures ANOVA on two factors was applied; the effects of time (repeated measure), site, and the interaction between them were evaluated. Additional comparisons, for tree-ring width, between pre- and post-eruption periods (3 years before and after) were performed using a *t*-test. A significance level of $\alpha = 0.05$ was adopted in all comparisons.

RESULTS

Temporal variation in tree growth

At Pantojo stand, annual shoot length and number of internodes showed small variations over the period 1999–2010 (Fig. 3a,b). For the first growing season following the eruption (2011–2012), sharp increases in both variables were registered (Fig. 3a, b). On average, annual shoots reached two to three times the length and number of internodes of shoots before the eruption (for variation in the period 1999–2013; $F = 20.9$ for length, and $F = 43.8$ for number of internodes; $P < 0.001$). In the two subsequent growth seasons (2012–2013 and 2013–2014), the annual shoot length and number of internodes decreased, but were still significantly higher than those recorded before the eruption (Fig. 3a,b).

Following the 2011 eruption, variations in tree-ring widths at Pantojo stand were not as large as those recorded for shoot length and number of internodes (Fig. 4; for the period 1993–2013; $F = 1.5$, $P > 0.05$). Although a slight increase in tree-ring width indices could be graphically visualized for the first two growing seasons after the eruption, no statistical difference was found when tree-ring width

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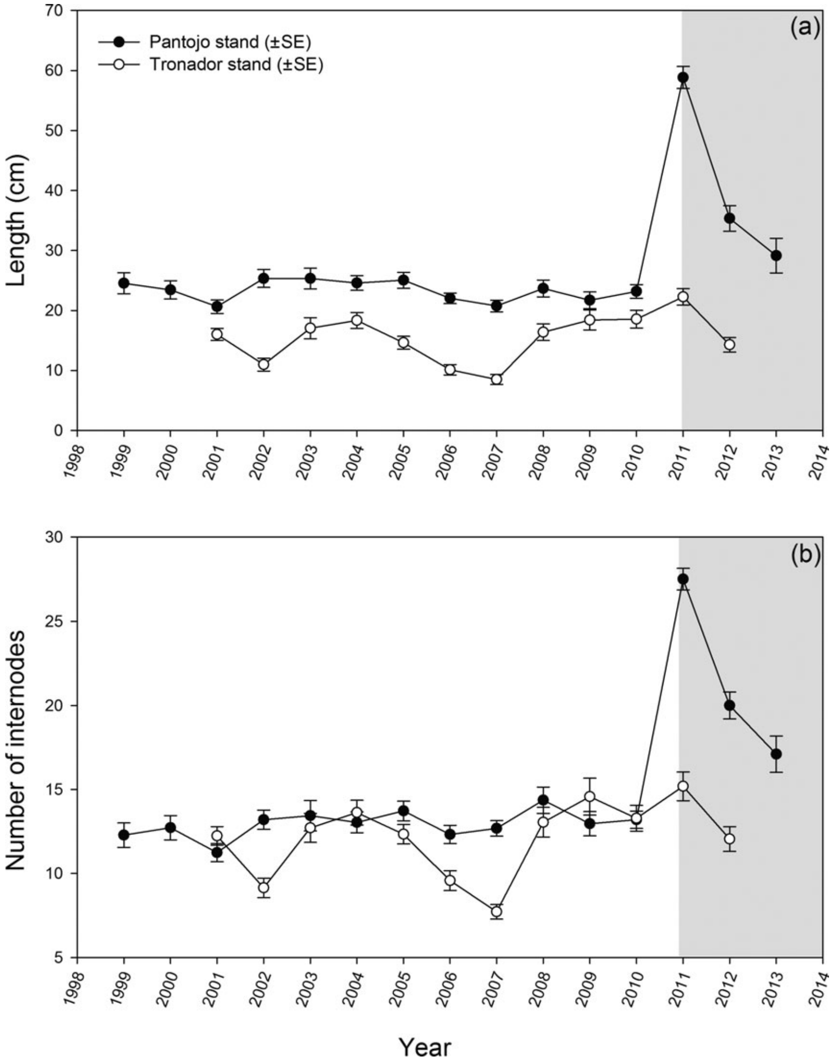

Fig. 3. Inter-annual variations in trunk shoot length (a) and number of internodes (b) for *Nothofagus pumilio* trees developed at Pantojo (black circles) and Tronador stands (white circles). The shaded area indicates the post-eruption period. Mean values ± 1 SE are presented for each growth attribute.

indexes were compared between the 3 years preceding and the 3 years following the eruption ($t = 1.1$, $P = 0.436$).

At Tronador stand, inter-annual variations in shoot length and number of internodes were remarkably more variable than those observed at Pantojo stand during the pre-eruption period. Both attributes exhibited low values for years 2002, 2006 and 2007. Compared to Pantojo stand, changes in annual shoot length and number of internodes after the eruption were less noticeable at Tronador stand, although the mean values recorded for 2011 were the highest values for the 2001–2012 period (Fig. 3a,b). Comparisons between sites for relative growth attributes over this period indicated significant differences in annual shoot length and number of internodes; both variables were higher for Pantojo than for Tronador stands (Table 2). Differences in ring width between stands were not significant. For all three attributes, significant time × site interactions indicated that temporal variations in these attributes did not follow a similar tendency at both stands. Nonetheless, length growth and number of internodes dropped in years 2006 and 2007 in both populations. Ring width reached its lowest values in these 2 years at Tronador stand, and in year 2009 at Pantojo stand.

DISCUSSION

Volcanic eruption and length growth

The *N. pumilio* trees at Cerro Pantojo stand, where ash accretion after the 2011 PCCVC eruption was >40 cm deep, exhibited a remarkable increase in

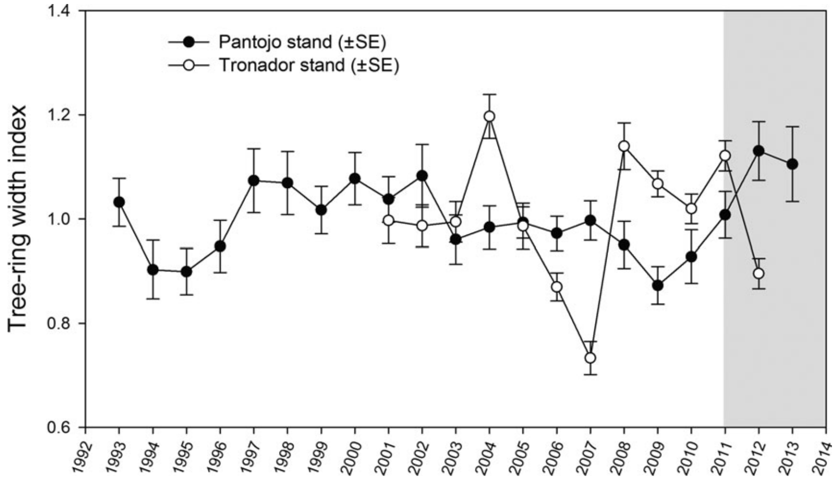

Fig. 4. Standardized inter-annual variations in tree-ring width for samples of *Nothofagus pumilio* developed at Pantojo and Tronador stands. The shaded area indicates the post-eruption period. Mean inter-annual values (±1 SE) are shown for each growth attribute.

Table 2. Effects of time (years 2001–2012), site of growth (Pantojo and Tronador stands) and the interaction between both factors (time × site) on shoot length and number of internodes, and tree-ring width through two-factor ANOVAS with repeated measures on one factor (time)

	Time		Site		Time × site	
	F	*P*	*F*	*P*	*F*	*P*
Length	47.8	***	257.9	***	23.9	***
No. of internodes	36.6	***	51.7	***	17.5	***
Tree-ring width	2.9	**	0.1	ns	5.1	***

Statistical significance is indicated: $^{***}P < 0.001$; $^{**}P < 0.01$; ns $P > 0.05$. *F*, Fisher's statistic; *P*, significance level. Length and number of internodes were relativized, and ring width was standardized.

trunk length growth during the growing seasons following the eruption. The retrospective evaluation of trunk growth made in this study, combined with information from a previous study on the same population (Passo *et al.* 2002), indicates that yearly trunk length growth was consistently lower in the 29-year period preceding the 2011 PCCVC eruption than in the 3 years after the eruption. We propose three non-exclusive hypotheses to explain this unexpected response:

1. *Thick ash layers increase water retention in the soil.* The >40 cm ash layer that accumulated after the eruption would have reduced the loss of soil water by evapotranspiration, as shown in other regions after eruption events (Black & Mack 1986; Edmonds & Erickson 1994; Antos & Zobel 2005). The 2011 PCCVC eruption occurred during the cold-wet period of the year: precipitations in that period had reached about 297 mm at the time of the eruption (snow-water equivalent from March to June; *Autoridad Interjurisdiccional de Cuencas*, Argentina). The fresh ash layer most likely retained the snowpack formed before the eruption and contributed to reduce the water deficit during the following growth period (i.e. spring-summer). Previous studies indicate that the growth of *N. pumilio* is affected by spring-summer droughts on the Argentinean sector of the Patagonian Andes (Villalba *et al.* 1997; Lara *et al.* 2001; Magnin *et al.* 2014; Rodríguez-Catón *et al.* 2015).
2. *Volcanic ash facilitates the access of plants to nutrients.* Volcanic ash leachates regularly lack nitrogen and most of its phosphorus content is usually not easily available (Hinkley & Smith 1987). However, nutrients may be released from the buried forest floor as ashes boost the decomposition of organic matter by buffering cold temperatures (Edmonds & Erickson 1994). In Patagonian broadleaf forests, nitrogen is the most limiting nutrient and sometimes, phosphorus is co-limiting (Diehl *et al.* 2003). Despite the low phosphorus availability in the Patagonian volcanic soils, the low phosphorus limitation is probably related to the high intensity of mycorrhizal infection (Diehl *et al.* 2008). An increase in soil phosphorus in the Patagonian forests following the eruption of the PCCVC has not yet been recorded. However, records from nearby lakes indicate that substantial releases of phosphorus from PCCVC volcanic ashes a few weeks after the eruption induced substantial growth of algal communities (Modenutti *et al.* 2013).

Hence, phosphorus released by leaching from ash deposition could also have induced an increase in growth of terrestrial plants.

3. *Volcanic ashes decrease herbivory and competition.* The significant post-eruption increase in length growth could be due, in part, to a decrease in herbivory and competition. In support of this idea, Chaneton *et al.* (2014) suggested that ash fall following the 2011 PCCVC eruption could act as a natural broad-spectrum and long-lasting insecticide on the canopy of *N. pumilio* at large spatial scales, which would help increasing canopy productivity (Schowalter 2006). Volcanic ash could induce a strong deterrent effect on feeding of herbivorous insects or even the death of the insects by adhesion of ash particles to the cuticle (Buteler *et al.* 2014). On the other hand, ash-accretion might have reduced competition from understory plants, and hence increased the relative availability of nutrients and water for *N. pumilio* trees."

Whatever the factor/s that induced the exceptional increase in the length growth of *N. pumilio* trees after the 2011 PCCVC eruption, a morphogenetic response was involved. Length growth in *Nothofagus* spp. includes preformation (i.e. the differentiation of leaf primordia that remain stocked in winter buds until spring) and, in some cases, neoformation (i.e. the simultaneous differentiation and extension of leaves; Guédon *et al.* 2006; and references therein). It has been shown that the filling of winter buds through preformation in *Nothofagus* ends up during autumn (March-April; Puntieri *et al.* 2000; Souza *et al.* 2000; García *et al.* 2006), so that it should be expected that the winter buds of *N. pumilio* trees had completed their preformation by the time of the volcanic eruption. Juvenile trees of *N. pumilio* usually produce, on average, no more than 16 leaf primordia per apical bud (Souza *et al.* 2000). Therefore, the trunk shoots produced during the growth season after the eruption should have included neoformation following the extension of the preformed organs. Although little is known about the factors actually triggering this morphogenetic process, neoformation in trees from temperate regions has been regarded as part of an opportunistic strategy of exploitation of unforeseen favourable environmental conditions (Guédon *et al.* 2006). In this regard, it has been demonstrated for *N. pumilio* that trunk shoots developed in years with rainy summers would be more likely to include neoformed organs (Magnin *et al.* 2014). The length growth reduction (length and number of internodes of annual shoots) in the growing season following 2011 could be explained (i) by the fact that there was no snowpack between the pre-eruption soil and the ash layer, and (ii) by an exceptionally high meristematic demand caused by increased lateral shoots derived from the previous growing season (2011). However, growth in the 2012 growing season was still high compared to the mean over the pre-eruption period.

The increase in length growth following ash accretion at Pantojo stand contrasts with the lethal effect of this eruption on *N. pumilio* saplings, juvenile and adult trees located only 6 km closer to the PCCVC (S. Quiroga, unpublished data, 2015). Dead trees were affected by a similar amount of ash accretion at the same phenological stage as trees at the Pantojo stand (see, Gaitán *et al.* 2011), leaving an open question about the factors (e.g. ash temperature, particle size) that delimited the *N. pumilio* 'kill zone' around the PCCVC. Based on previous observations by Chaneton *et al.* (2014) for the same species in nearby areas affected by the PCCVC eruption, partial crown deaths of *N. pumilio* trees at Pantojo stand were expected after the eruption. However, we found no evidence of damage to buds, leaf primordia and branches caused by the eruption in Pantojo stand, which may be related to the fact that most of the expulsion of pyroclastic material from the PCCVC in 2011 occurred during the dormancy period of the deciduous *N. pumilio*. Morpho-anatomical traits of *N. pumilio* buds, such as their small size (<1 cm in length), scaly character, and the presence of resin-secreting colleters (Barthélémy *et al.* 1999), could be among the factors that facilitate the survival of this species at high-elevation environments with extreme climatic conditions. In contrast, we observed extensive death of leaves and branches, as well as breakages of branches and trunks in the evergreen *Nothofagus dombeyi*, which dominates forests located a few kilometres further east of the Pantojo site with less ash accumulation. Evergreeness implies a high death risk for plants living in areas where conditions adverse to leaf persistence frequently occur (see Givnish 2002). In this sense, the deciduous nature of *N. pumilio*, in addition to the aforementioned bud traits, would allow this species to survive the extreme conditions that occur during and after volcanic eruptions. Had the eruption occurred in a period when *N. pumilio* was in full leaf display, the effects of the eruption would have been more negative than those actually observed.

For the *N. pumilio* trees at Tronador, where ash accumulation was nil, the increases in the length and number of internodes of annual shoots in the growth season following the 2011 PCCVC eruption were far lower than those recorded at the Pantojo stand. Although these average values recorded for Tronador after the 2011 PCCVC eruption were the highest for these trees in the 2001–2012 period, these values cannot be considered atypical. Previous studies indicate that variations in temperature and precipitation explain most of the inter-annual changes in growth at

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Tronador (Magnin *et al.* 2014). This suggests that the exceptional values of annual length growth recorded at the Pantojo stand may have resulted from the interaction between the volcanic eruption and local environmental conditions during the growth season. According to our results, inter-annual variations in the growth of *N. pumilio* are largely modulated by local environmental conditions (mainly precipitation and temperatures) as suggested by significant time × site interactions (Table 2). In this sense, the low values in shoot length and number of internodes for the years 2002, 2006 and 2007 at Tronador stand are related to very cold winter temperatures (Magnin *et al.* 2014). Differences in tree age and size between both stands could also have affected these results.

Volcanic eruption and radial growth

Despite the notable increase in length growth after the 2011 eruption, statistical analyses indicated that ring widths were not significantly affected by the eruption. Nonetheless, a positive post-eruption change in ring width trends was visually evident (Fig. 4). The different responses in magnitude between length and radial growth after the 2011 PCCVC eruption may indicate that these two growth attributes have different sensitivities to environmental changes. It could also be argued that lateral tree axes, which also contribute to trunk thickening, may not have responded positively after the eruption, thus weakening the relationship between length growth and radial growth of the trunk. In any case, it is worth noticing that ring width, which is often employed to evaluate variations in past climatic conditions (Fritts 1976), may not be, at least in the short term and for this species, sensitive to an extreme event with lethal consequences for trees located at a relatively short distance from the sampled trees. In the vicinity of Mount St. Helens, in contrast, the 1980 eruption (which took place in early spring) had negative effects on the radial growth of evergreen conifers, sometimes resulting in the absence of annual growth rings (Seymour *et al.* 1983; Yamaguchi 1983; Segura *et al.* 1995). As in the case of length growth, the presence of green leaves at the time of the eruption may play a major role in the response of trees in terms of trunk thickness growth. In accordance with this idea, it was shown that the 1980 eruption of Mount St. Helens had a less notable effect on the growth of high-elevation trees, which had their buds still unopened at the time of the eruption (Crisafulli *et al.* 2005). However, low- and mid-altitude tree species, mostly evergreen conifers, retained varying amounts of ash in their leaves (Antos & Zobel 2005), which produced an inefficient heat exchange that killed extensive foliage masses (Seymour *et al.* 1983). The ash deposits led to several adverse effects for these species, the loss of leaves led to a reduction of the length and radial growths by decreasing shoot extension (Hinckley *et al.* 1984).

In conclusion, we have documented major changes in the length growth of subalpine *N. pumilio* forests affected by volcanic ash deposition. Volcanic ashes may have affected the structure and/or functioning of ecosystems by modifying biotic (herbivory, competition) and abiotic (nutrients and water availability) factors involved in the growth of *N. pumilio* trees. Our results highlight the need to further examine how large-scale eruptions events influence ecosystem function in the Patagonian Andes.

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