

Interannual variations in primary and secondary growth of *Nothofagus pumilio* and their relationships with climate

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Abstract

Key message The aim of this study is to evaluate the relationships between primary and secondary growth as well as the influences of climate variations on both types of growth.

Abstract The relationships between apical (or primary) and radial (or secondary) growth, and climatic influences on both types of growth, were evaluated for *Nothofagus pumilio* (Nothofagaceae), the dominant subalpine tree in Patagonia. We measured the spacing and number of nodes of annual shoots developed in the period 2001–2010 in 40 *N. pumilio* trees growing near the upper *treeline* in the northern Patagonian Andes (41°S). Variations in ring width at the base of each trunk were also recorded. Interannual variations in primary and secondary growth were significantly related to each other, and to several climate variables. Mean temperatures in winter and early spring (June–October) prior to the period of shoot extension were positively associated with both primary and secondary growth. In addition, total summer precipitation (December–March) was positively related to shoot extension, whereas mean summer temperature during the previous growth season

(January–March) was directly related to radial growth. These climatic influences on *N. pumilio* growth may play a major role in regulating the expressions of preformation and neoformation.

Keywords Tree growth · Treeline · Precipitation · Temperature · Preformation · Neoformation

Introduction

Abundant evidence indicates that the unusual climatic conditions recorded during recent decades have altered forest structure and composition (Andreu et al. 2007; Allen et al. 2010; Anderegg et al. 2013). Temperature and precipitation departures from historical patterns of variability are undoubtedly affecting the growth of plants (Valladares et al. 2006; Villalba et al. 2012). For some regions, these climate variations are leading to changes in plant distribution and community structure (Parmesan 2006; IPCC 2007; Hamann and Wang 2006). The effects of climate changes on plants should be more evident near the limits of their distributions (Parmesan 2006). In this context, it is accepted that forests close to their high-altitude limits are excellent sources of proxy climate information, since these populations are highly sensitive to environmental variations (Fritts 1976; Villalba et al. 1997).

The clear seasonality of climate in temperate regions generates anatomical, morphological and architectural marks on the stem, which allow the assessment of annual increases in the height of trees, often referred to as primary growth (Kozłowski 1971; Hallé et al. 1978; Barthélémy and Caraglio 2007). Similarly, variations in radial growth during the year, also called secondary growth, result in tree-ring formation in the stem of most trees from

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temperate and cold climates (Evert 2008; Beck 2010). It is widely accepted that interannual variations in both primary and secondary growth are related to ontogenetic and environmental factors (Barthélémy and Caraglio 2007). Dendrochronology has traditionally studied the influence of climate on secondary growth (Fritts 1976). The effects of climate variations on primary growth have rarely been assessed. Previous knowledge on the architecture and ontogeny of a specific species is necessary to identify annual increments in primary growth (Passo et al. 2002; Heuret et al. 2006; Magnin et al. 2012). Since primary and secondary growth in species from temperate and cold climates occur mainly in spring and summer, variations in the growth of these species are often contrasted with environmental conditions in these seasons (Fritts 1976). However, it is known that plant growth also involves differentiation processes at the cellular level, which often occur prior to shoot-extension or radial-increase phases, and may thus be affected by environmental conditions preceding the spring–summer period (Fritts 1976). For primary growth, those organs in which the differentiation phase is clearly separated in time from the extension phase are described as preformed organs. In contrast, when both processes are simultaneous, the resulting organs are described as neoformed (Hallé et al. 1978). Axis segments derived from primary growth may consist entirely of preformed organs or neoformed organs, or may include both kinds of organs (Barthélémy and Caraglio 2007). Studies concerning climate influences on primary growth should therefore take into account that differentiation and extension processes could be affected by different environmental factors at different times, depending on whether the organs are preformed or neoformed (Guédon et al. 2006). Similarly, the influences of climate on radial growth could be limited to the current growth season when the ring is formed, but more frequently growth may reflect climate influences during the current and previous growth seasons (Fritts 1976).

Nothofagus pumilio (Poepp. et Endl.) Krasser (Nothofagaceae) is a deciduous species that dominates the high-elevation forests along the Patagonian Andes from 35°S to 55°S (Dimitri 1972). In addition to timber production, this species provides important ecological services in relation to water regulation and nutrient conservation on the steep Andean slopes (Rusch 1993; Frangi et al. 2005). Predicted vegetation changes due to global warming (Parmesan 2006; Hamann and Wang 2006; IPCC 2007) indicate major impacts on *N. pumilio* forests, since upper-elevation tree-lines appear to be especially sensitive to climate changes (Hill and Dettmann 1996). Dendrochronological studies that evaluated the influence of climate on the growth of *N. pumilio* at the upper treeline show that interannual variations in radial growth are inversely related to precipitations

in the winter–early spring period (June–October) and directly related to mean temperatures in the late spring–summer period (September–March; Villalba et al. 1997, 2003; Lara et al. 2005). However, there is marked variability in tree responses to climate depending on aspect, slope steepness, and microsite conditions. A better understanding of these relationships could be reached by simultaneously studying the environmental effects on primary and secondary growth.

The main objective of this work was to evaluate the relationships between primary and secondary growth in a population of *N. pumilio* near the treeline, and examine the influences of temperature and precipitation on primary and secondary growth over a 10-year period.

Materials and methods

Study site

The study was carried out on a *N. pumilio* stand at Monte Tronador, Parque Nacional Nahuel Huapi, northwestern Patagonia, Argentina (41°11'S, 71°47'W, 1,411 m). The climate in the region is characterized by a sharp west-to-east precipitation gradient, from 4,000 mm to less than 700 mm per year on the main Cordillera and the Patagonian forest-steppe border, respectively (Conti 1998; Villalba et al. 2003). There is a marked seasonality in both temperature and precipitation. Winters are cold with abundant precipitation, whereas summers are mild with a substantial decrease in precipitation (Fig. 1). The total annual precipitation recorded 13.4 km to the east of the study site is 1,447 mm (Hotel Tronador, 41°16'S, 71°39'W, 815 m, period 2000–2011; Fig. 1). Seventy-two percentage of the total annual precipitation occurs between May and October; at elevations above 1,000 m, precipitation normally occurs as snow. Over the period 2000–2011, the mean annual temperature recorded on a Hobo datalogger at the study site (1,411 m) is 4.6 °C (Fig. 1).

Tree sampling

Samples were collected in April 2011 at the end of the 2010–2011 growth season. We selected 40 individuals from a homogeneous and healthy-looking *N. pumilio* stand in advanced juvenile stage covering an area of approximately two ha. The stand is characterized by individuals with a mean height (\pm SE) of 4.0 ± 0.1 m, a mean diameter of 5.6 ± 0.2 cm, and a mean age (\pm SE) of 33.2 ± 0.2 years (determined by ring counting of basal trunk sections, see following section). No obvious signs of recent stand disturbance were recorded. From each sampled tree, we collected the main axis of the trunk

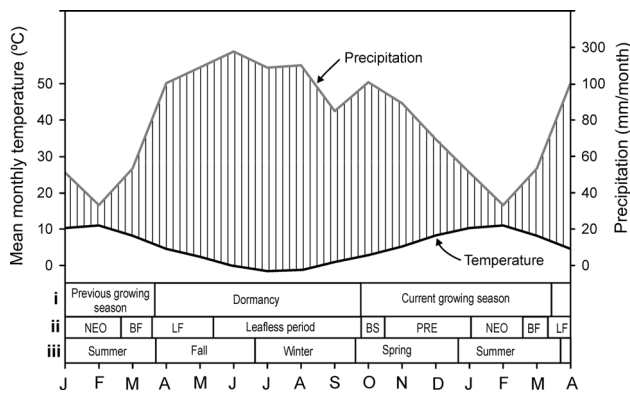


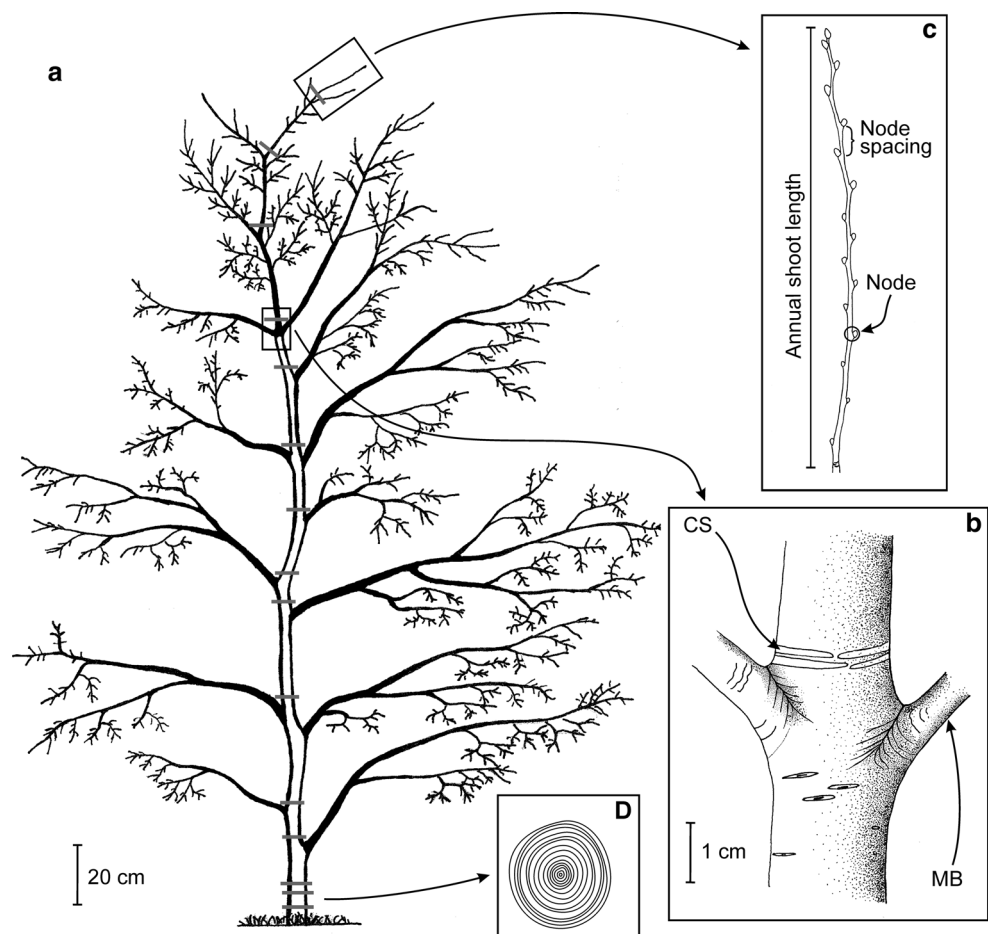
Fig. 1 Climatic diagram of the study area, according to Walter and Lieth (1960). Monthly total precipitation and mean temperature over the period 2001–2010 from Hotel Tronador (precipitation) and La Almohadilla (temperature) weather records. The area between the curves of temperature and precipitation (*vertical lines*) highlights the variations in moisture availability throughout the year, with the lowest level in summer. Below the curves are indicated: *i* growth and dormancy periods for *N. pumilio*, *ii* phenological stages of *N. pumilio* shoots based on previous studies (Rusch 1993; García et al. 2006), and *iii* seasons of the year for the Southern Hemisphere. Periods of extension of neoformed organs (NEO), bud formation (BF), leaf fall (LF), bud sprouting (BS), extension of preformed organs (PRE) are indicated

containing at least the ten most recently extended annual shoots. The identification of inter-shoot limits was based on the positions on the trunk of cataphyll scars and main branches (Fig. 2a, b; 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, which is why only a series of shoots corresponding to 10 consecutive years was evaluated in this study. For each annual shoot the length and number of nodes were registered (Fig. 2c). In forestry literature, the term “node” is often used to define the region of stem where long shoots or branch whorls are attached (Kozłowski 1971). In contrast, in this work the term node is used in its strict botanical sense, i.e., the point of leaf insertion on the stem (Bell 2008).

Sample preparation and analysis of dendro-architectural chronologies

In the laboratory, the cross sections taken at trunk bases (Fig. 2d) were polished and measured following the procedures described in Stokes and Smiley (1968). After a precise definition of the growth rings, the samples were

Fig. 2 Diagram of a *N. pumilio* juvenile tree similar to those selected for this study (a). Horizontal gray lines across the stem indicate the boundaries between annual shoots. Marks on the trunk indicating an annual limit are shown in the scheme at the lower right box (b). The most recently extended shoot is indicated in the upper right box (c). The cross section at the base of the trunk is indicated in the lower left box (d). CS cataphyll scar, MB main branch



dated (i.e., assigning a calendar year to each annual growth ring) under a stereomicroscope with magnifications between $6\times$ and $50\times$. The dating procedure followed Schulman's convention (1956) for the Southern Hemisphere, which assigns each annual ring the date of the year in which growth began. Ring widths were measured to the nearest 0.001 mm using a Velmex machine.

Chronologies from ring width, number of nodes and annual shoot length were produced by the TURBO ARSTAN software (Cook 1985). This program generates chronologies combining the standardized series of rings width, number of nodes and annual shoot length with a robust estimate of the mean values. This standardization adjusts the observed data series to a curve or a 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 avoid introducing artificial tendencies in each time series, a linear adjustment to the mean value of the series was adopted for standardization. The chronologies in this study represent time series of interannual variations in the primary and secondary growth of *N. pumilio* along a sequence of 10 consecutive years.

Since both primary growth attributes (length and number of nodes of annual shoots) exhibited similar trends over the time sequence ($r = 0.98$, $p < 0.001$), we used the number of nodes as the primary growth variable to relate with climatic variations. The variable "length" was included in the calculation of the length/number of nodes ratio, which represents the average distance between two consecutive nodes of an annual shoot, hereafter called "node spacing". To compare the mean variations of primary and secondary growths simple Pearson correlations were calculated along the 2001–2010 time sequence.

The strength of the relationships between growth attributes (primary and secondary) and climate was estimated by determining the correlation coefficients between tree-ring width, number of nodes and node spacing, with monthly precipitation and temperature records. The precipitation and temperature variables most closely related to tree growth in a particular year were identified by averaging the individual monthly values over 2–4 consecutive months starting in January of the previous growth season (year^{-1}), and ending in May of the current growth season (Fig. 1). Finally, the percentages of variation in the attributes of primary and secondary growth that were explained by climate were established using stepwise multiple linear regressions (value for including an independent variable: $F \geq 4.0$; value for excluding an independent variable: $F < 4.0$). Monthly total precipitations are from the Hotel Tronador weather station, whereas temperature data are

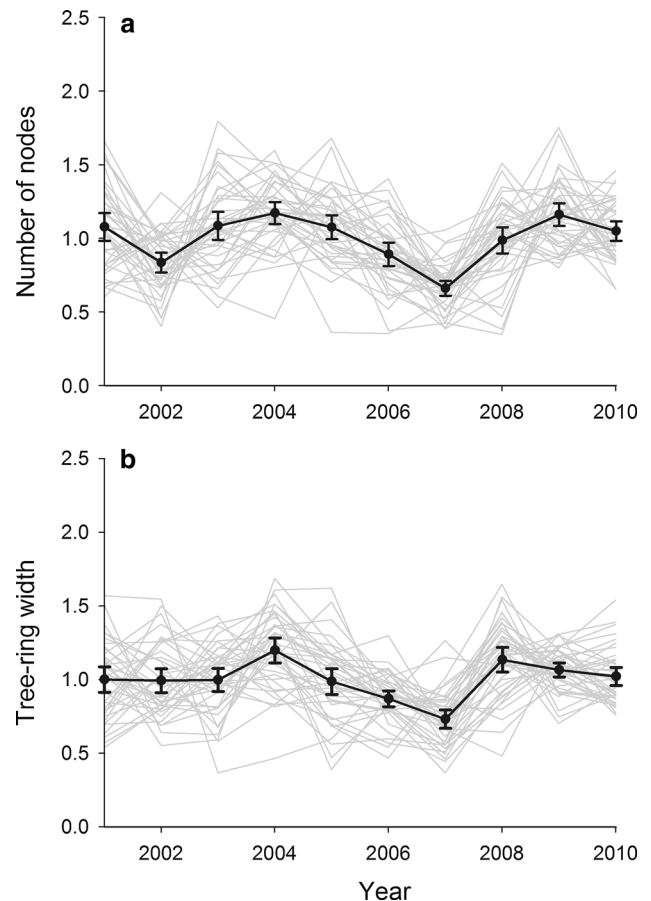


Fig. 3 Standardized interannual variations in number of nodes (a) and tree-ring width (b) for *N. pumilio* trees at La Almohadilla over the 2001–2010 period. Bold curves represent mean values (\pm the 95 % confidence interval) of these growth attributes

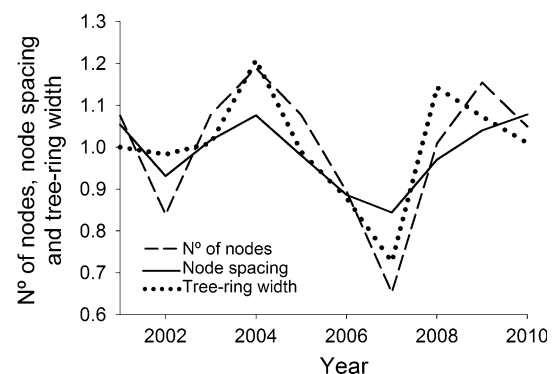


Fig. 4 Standardized interannual variations in primary (number of nodes and node spacing) and secondary growth (tree-ring width) for *N. pumilio* trees over the 2001–2010 period

expressed as deviations from the period mean over the interval 2001–2010, recorded by IANIGLA at the study site.

Table 1 Pearson correlation coefficients between standardized growth characteristics of *N. pumilio* and selected climate variables over the 2001–2010 interval

	Node spacing	Tree-ring width	Summer temperature (year ⁻¹)	Winter–early spring temperature	Summer precipitations
Number of nodes	0.98***	0.84**	0.31 ^{ns}	0.76**	0.69*
Node spacing		0.76**	0.20 ^{ns}	0.66*	0.66*
Tree-ring width			0.67*	0.73**	0.28 ^{ns}

Summer (year⁻¹) and winter–early spring temperatures are previous to the growth season and summer precipitations are concurrent with the growth season

Statistical significances between variables are indicated (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ^{ns} $p > 0.05$)

Results

Temporal variations in primary and secondary growth

The number of nodes per annual shoot and tree-ring widths of *N. pumilio* varied substantially over the period 2001–2010 (Fig. 3a). Variations in tree-ring width followed a similar pattern to the number of nodes, except that mean ring width did not decrease from 2001 to 2002 or increase from 2008 to 2009 (Fig. 3b).

Tree-ring width variations along the temporal sequence analyzed were positively correlated with the number and spacing of nodes, which were also positively correlated with each other (Fig. 4; Table 1).

Relationships between tree growth and climate

Variations in number and spacing of nodes per annual shoot were significantly correlated to summer precipitations (December–March) in the current growth season and to winter–early spring temperatures (June–October) at the beginning of the current growth season (Table 1). Variations in tree-ring width were significantly correlated to summer temperatures (January–March) during the previous growth season (year⁻¹) and to winter–early spring temperatures at the beginning of the current growth season (Table 1). Warmer temperatures during the winter–early spring period at the beginning of the growth season favored the formation of shoots with more and longer nodes as well as wider tree rings (e.g. 2004; Fig. 5). Opposite patterns were recorded after cold winter–early spring periods (e.g., 2007; Fig. 5). Above-average temperatures during the year⁻¹ summer were positively correlated with tree-ring width (Fig. 5c; Table 1), but not with the number and spacing of nodes of the annual shoots (Fig. 5a, b; Table 1). In contrast, total summer precipitations during the period of growth were positively correlated with the number and spacing of nodes (Fig. 5a, b; Table 1) but not with ring width (Fig. 5c; Table 1).

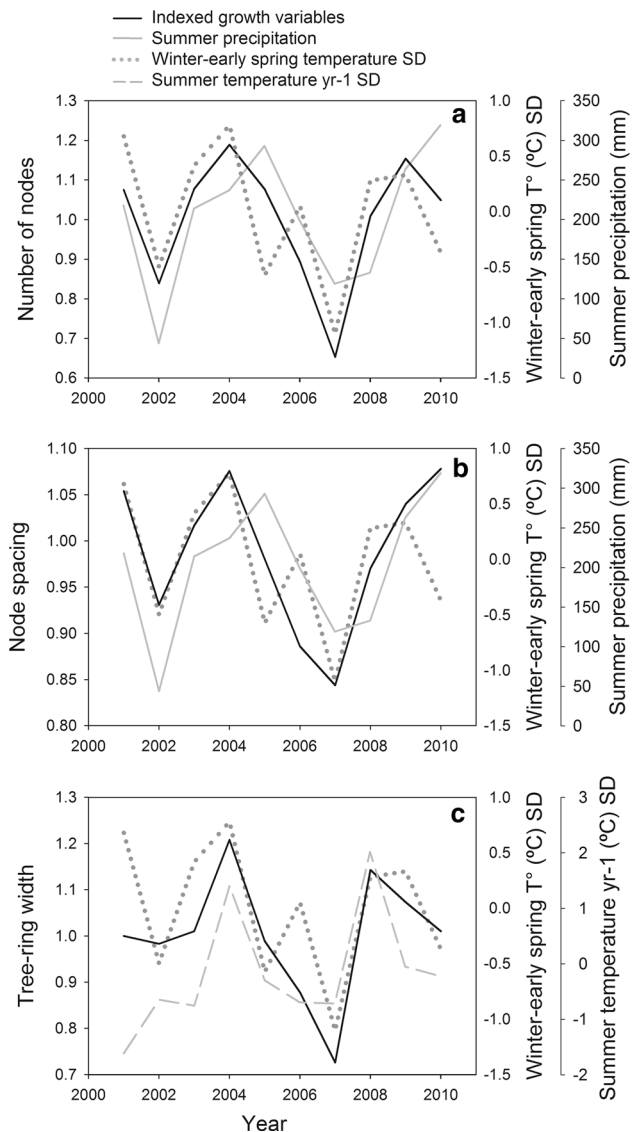


Fig. 5 Standardized growth attributes of *N. pumilio* trees: number of nodes (a), node spacing (b), and ring width for the trunk (c) over the 2001–2010 interval. Summer (year⁻¹) and winter–early spring temperatures (°C) previous to the growth season are expressed as standard deviations (SD) from the 2001–2010 period means; summer precipitations during the growth season are the total accumulated water (mm)

Regression models indicate that winter–early spring temperatures at the beginning of the growth season in combination with precipitations during the growth season accounted for 79 and 59 %, respectively, of the total variations in the number of nodes and node spacing over the 2001–2010 period (Table 2). Temperature variations in the year⁻¹ summer and winter–early spring accounted for 72 % of the total variation in tree-ring width over the same period (Table 2).

Discussion

To our knowledge, this study constitutes the first attempt to analyze the relationships between primary and secondary growth in *N. pumilio* and the effects of temperature and precipitation on both types of growth. At upper treeline, the growth of *N. pumilio* is influenced by climatic conditions preceding and concurrent with the growth season. The primary growth of *N. pumilio* is largely affected by winter–early spring temperatures at the beginning of growth, and summer precipitations in the growth season, whereas secondary growth is more sensitive to temperatures in the previous summer and in the winter–early spring period at the beginning of growth. In addition, wider tree rings are concurrent with the development of annual shoots with more nodes and longer internodes. Relationships between primary and secondary growth have rarely been explored (Paul-Victor and Rowe 2011; Cochard et al. 2005; Camarero et al. 2012; Colin et al. 2012). Some previous studies have evaluated the influence of primary growth (e.g., epicormic shoots) on the secondary growth of trees (Colin et al. 2012) and shown the influence of the physical environment (e.g., elevation, micro-topography and soil type) on both kinds of growth (Bret-Harte et al. 2002; Campioli et al. 2012). Nevertheless, the influences of temperatures and precipitations on both primary and secondary growth had not previously been considered.

Our study indicates that tree-ring width in *N. pumilio* is strongly associated with temperatures in the previous summer and in the winter–early spring period at the beginning of growth. Previous dendrochronological studies in subalpine Patagonian forests demonstrated that variations in *N. pumilio* ring width are linked to seasonal and annual variations in temperature (Villalba et al. 1997, 2003; Lara et al. 2001, 2005; Boninsegna et al. 2009). In partial agreement with our results, these studies indicated that temperature in the spring–summer period of tree-ring formation is the climatic factor most closely associated to tree-ring width (Villalba et al. 1997; Lara et al. 2005). However, as pointed out by Villalba et al. (1997), temperature variations in other periods of the year also seem to be associated with the secondary growth of *N. pumilio* at

Table 2 Stepwise multiple regression (F to include = 4.0; F to exclude = 3.9) between primary (number of nodes and node spacing) and secondary growth (tree-ring width) using summer (year⁻¹) and winter–early spring temperatures previous to the growth season and summer precipitations concurrent with the growth season as predictor variables over the 2001–2010 period

Dependent Variables	F	p	R^2 (adj.)	Independent Variables
Number of nodes	18.4	0.002	0.79	Winter–Early Spring Temp. Summer precipitation
Node spacing	7.5	0.018	0.59	Winter–Early Spring Temp. Summer precipitation
Tree-ring width	12.4	0.005	0.72	Winter–Early Spring Temp. Summer Temp. (year ⁻¹)

All three dependent variables were standardized

The components of regression model were indicated: F Fisher's statistic, p significance level, and R^2 (adj.) adjusted coefficient of determination

upper treelines, which is consistent with the present study. In contrast to previous studies (Villalba et al. 1997; Lara et al. 2005), we did not find a significant relationship between secondary growth and concurrent summer precipitations. The absent of clear relationships between precipitation and secondary growth may reflect the lack of severe dry periods at the upper treeline in summer (Fig. 1). However, this difference could also be associated with the comparatively short chronology used here, and the different periods used for comparison with climate. The effects on growth of the climate in the previous growth season may be explained by arguing that photoassimilates generated by *N. pumilio* shoots in one growth season are assigned first to reserve tissues. Such reserves would be mobilized in the following growth season to contribute in the formation of conducting tissues, including those that compose the rings of stem xylem. Other species that inhabit high-altitude communities have been found to express delayed measurable responses to climatic factors (Kibe and Masuzawa 1992). More studies regarding resource storage and re-mobilization from storage tissues to growing points in *N. pumilio* are necessary.

Previous works analyzing the influence of environmental factors on the primary growth of *N. pumilio* have mainly focused on variations in the size of shoots and axes in contrasting environments (Stecconi et al. 2010). Passo et al. (2002) related architectural variations in *N. pumilio* with climate and showed that abundant precipitation during the driest period of the year (December–March) may increase annual shoot growth (measured as number and spacing of nodes). For years with very low summer precipitations,

these authors found remarkably low number and spacing of nodes per annual shoot. It has been documented that the largest shoots of young *N. pumilio* and *N. dombeyi* trees grow in spring through the extension of preformed organs, and in summer through the development of neoformed organs (Souza et al. 2000; Puntieri et al. 2000). Therefore, these species may respond to abundant summer precipitations through neoformation. Low humidity in summer may induce the death of the apex and some distal leaves in the shoots, thus limiting the expression of neoformation and, therefore, the number of nodes of the annual shoots in *N. pumilio* (Passo et al. 2002) and other South American *Nothofagus* species (Puntieri et al. 1998, 1999; Barthélémy et al. 1999). Although no summer water deficits were recorded over the study period (Fig. 1), water balance models reveal some stress during few weeks or even a month for some years (e.g., 2002 and 2007, unpublished data; see also Lara et al. 2005). Due to the low level of drought hardiness of recently extended leaves and internodes, primary growth could be more sensitive than secondary growth to short periods of water shortage during the growing season.

The analysis of interannual variations in node spacing and its relationship with environmental conditions contributes to our understanding of the morphogenetic processes involved in primary growth. In this study, we showed that both summer precipitations and winter–early spring temperatures were positively correlated with the mean node spacing of annual shoots. In *N. pumilio*, shoots with a high mean node spacing have a high degree of neoformation, while shoots with low node spacing are entirely preformed (Souza et al. 2000). In consequence, the development of shoots with long node spacings in growth seasons with abundant precipitations (e.g., years 2004 and 2009; Fig. 5) would be indicative of high extents of neoformation, whereas the development of shoots with short node spacings in periods with low summer precipitation (e.g., 2002 and 2007; Fig. 5) would indicate a predominantly preformed nature of shoots. Our results support the idea that plants with the ability to add nodes by neoformation have developed a strategy for the exploitation of favorable environmental conditions during the growth season (Davidson and Remphrey 1994; Guédon et al. 2006). The relationship between winter–early spring temperatures and node spacing can be associated with a possible temperature mediated stimulus for the extension of preformed internodes and/or the activation of neoformation. Additional studies under controlled conditions are required for a more explicit evaluation of the role of environmental factors on the developmental processes involved in annual shoot growth. Likewise, the examination of node spacing along annual shoots is required to separate the preformed and neoformed parts in each shoot.

The positive influence of warmer winter–early spring temperatures on the primary and secondary growths of *N. pumilio* may be associated with early snowpack melting in subalpine *N. pumilio* forests. Villalba et al. (1997) showed that winter and spring temperatures control the snowpack duration on the ground, and therefore the length of the growing period, which is the most influential environmental factor modulating the growth of *N. pumilio* at the upper limit of its distribution. Specific local conditions at each site, such as solar radiation and wind exposure, influence snow accumulation and persistence (Wardle 1998), introducing individual differences in the responses of tree growth at similar elevations. Under cold spring conditions, the snowpack remains for a longer period, delaying bud sprouting and negatively affecting shoot extension and ring growth. Warmer winter–early springs result in the earlier onset and consequent extension of the growth season. In addition, warmer temperatures at the upper treeline favor stomata conductance, increase photosynthetic rate and carbon fixation (Srur et al. 2008).

For the Patagonian Andes, general circulation models of the atmosphere (GCMs) predict a mean summer temperature increase of 1.5–2.0 °C and a 10–20 % decrease in summer precipitation by the end of the 21st century (IPCC 2007). Based on this scenario, higher rates of growth in the upper *N. pumilio* treelines would be expected as shorter snowpack durations would lead to longer growth seasons. However, warmer and drier conditions during summer would increase water deficit, thus reducing neoformation and increasing the frequency of death in distal shoot portions. In consequence, longer growth periods would favor the primary growth of *N. pumilio* in the wettest areas of its distribution along the Andes. Similarly, although future warmer summers may increase secondary growth at the upper treeline, as indicated here, the increased water deficit at drier sites could be detrimental to radial growth, reducing the potentially beneficial effects of longer growth seasons. It would be expected that future environmental changes may affect the growth dynamics of the Andean–Patagonian forests through the introduction of deviations from the historical patterns of growth, changes in disturbance regimes, and shifts in forest distribution (Villalba and Veblen 1998; Villalba et al. 2005; Veblen et al. 2011). Our study illustrates how the modulation of *N. pumilio* growth by climatic variations is reflected in the plastic responses in growth patterns to environmental changes and provides insights as to how plant growth dynamics may be modified by future climate changes.

Author contribution statement Amaru Magnin: field work, sampling design, data analyses and manuscript writing. Javier Puntieri: field work, sampling design and manuscript writing. Ricardo Villalba: sampling design, data analyses and manuscript writing.

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Conflict of interest The authors declare that they have no conflict of interest.

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