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ORIGINAL ARTICLE

Spatial and temporal variation in *Nothofagus pumilio* growth at tree line along its latitudinal range (35°40′–55° S) in the Chilean Andes

Antonio Lara[1]*, Ricardo Villalba[2], Alexia Wolodarsky-Franke[1], Juan Carlos Aravena[3,4], Brian H. Luckman[4] and Emilio Cuq[1]

[1]*Laboratorio de Dendrocronología, Instituto de Silvicultura, Universidad Austral de Chile, Valdivia, Chile,* [2]*Departamento de Dendrocronología e Historia Ambiental, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, IANIGLA, Mendoza, Argentina,* [3]*Centro de Estudios Cuaternarios, Universidad de Magallanes, Punta Arenas, Chile and* [4]*Department of Geography, University of Ontario, London, Ontario, Canada*

*Correspondence: Antonio Lara, Laboratorio de Dendrocronología, Instituto de Silvicultura, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.
E-mail: antoniolara@uach.cl

ABSTRACT

Aim To identify the dominant spatial and temporal patterns of *Nothofagus pumilio* radial growth over its entire latitudinal range in Chile, and to find how these patterns relate to temperature and precipitation variation from instrumental records.

Location This study comprises 48 tree line or high elevation *N. pumilio* sites in the Chilean Andes between 35° 36′ and 55° S. *Nothofagus pumilio* is a deciduous tree species that dominates the upper tree line of the Chilean and Argentinean Andes in this latitudinal range.

Methods At each of the sampled sites, two cores from 15 to 40 living trees were collected using increment borers. Cores were processed, tree rings were measured and cross-dated, using standard dendrochronological procedures. Radii from nearby sites were grouped into 13 study regions. A composite tree-ring width chronology was developed for each region in order to capture and integrate the common growth patterns. For the identification of the dominant patterns of growth, as well as temperature and precipitation variation, we used principal components (PCs) analysis. Correlation analysis was used for the study of the relationship of *N. pumilio* tree-ring growth with temperature and precipitation records.

Results *Nothofagus pumilio* tree line elevation is 1600 m in the northernmost region and gradually decreases to 400 m in the southernmost region. Despite local differences along the transect, the decrease in tree line elevation is fairly constant, averaging *c.* 60 m per degree of latitude (111 km). Tree growth at the northernmost regions shows a positive correlation with annual precipitation (PC1-prec) and negative correlation with mean annual temperature (PC2-temp), under a Mediterranean-type climate where water availability is a major limiting factor. Conversely, tree growth is positively correlated with mean annual temperature (PC1-temp) in the southern portion of the gradient, under a relatively cooler climate with little seasonality in precipitation.

Main conclusions Our findings indicate that temperature has a spatially larger control of *N. pumilio* growth than precipitation, as indicated by a significant ($P < 0.05$) either positive or negative correlation of tree growth and PC1-temp and/or PC2-temp for nine of the 13 regional chronologies (69.2% of the total), whereas precipitation is significantly correlated with only two chronologies (15.4% of the total). Temporal patterns of *N. pumilio* tree growth reflected in PC1-growth for the period between 1778 and 1996 indicate an increasing trend with above the mean values after 1963, showing high loadings in the southern

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part of the gradient. This trend may be explained by a well-documented increase in temperature in southern Patagonia. Ongoing and future research on *N. pumilio* growth patterns and their relationship to climate covering the Chilean and Argentinean Andes will improve the understanding of long-term climate fluctuations of the last three to four centuries, and their relationship to global change at a wide range of spatial and temporal scales.

Keywords

Chile, climate change, dendrochronology, latitudinal gradient, *Nothofagus*, Patagonia, precipitation, temperature, tree growth, tree line.

RESUMEN

Objetivo Identificar los principales patrones espaciales y temporales de crecimiento radial de *Nothofagus pumilio* a lo largo del gradiente latitudinal completo de estos bosques en Chile, y encontrar como estos patrones se relacionan con las variaciones de temperatura y precipitación provenientes de registros instrumentales.

Ubicación Este estudio comprende 48 sitios de *N. pumilio* ubicados en el límite altitudinal arbóreo (*tree line*) o cerca de éste en los Andes de Chile entre los 35°36′ y los 55° S. *N. pumilio* es una especie arbórea caducifolia que domina los limites altitudinales de Chile y Argentina en este rango latitudinal.

Métodos En cada uno de los sitios muestreados se colectaron dos tarugos (testigos) de 15–40 árboles vivos usando taladros de incremento. Los tarugos fueron procesados usando técnicas dendrocronológicas estándar. Los radios de sitios cercanos fueron agrupados para definir 13 regiones de estudio. Para cada una de estas regiones se desarrolló una cronología compuesta de tal manera de capturar e integrar los patrones de crecimiento comunes dentro de cada región. Se usó análisis de componentes principales (PC) para la identificación de los patrones dominantes de variación del crecimiento, temperatura y precipitación. Las relaciones entre crecimiento de *N. pumilio* con los registros de temperatura y precipitación fueron estudiadas mediante análisis de correlación.

Resultados La altitud del límite superior arbóreo es 1.600 metros para la región de estudio ubicada en el extremo norte y disminuye gradualmente hasta alcanzar 400 metros en el extremo sur. A pesar de variaciones locales a lo largo del transecto, la disminución en la altitud del límite arbóreo es relativamente constante, a una tasa promedio de 60 metros por grado de latitud (111 km). El crecimiento radial en las regiones de estudio ubicadas en el extremo norte del gradiente muestra una correlación positiva con precipitación anual (PC1-prec), y una correlación negativa con temperatura media anual (PC2-temp), bajo un clima de tipo mediterráneo donde la disponibilidad de agua es el factor limitante para el crecimiento. Por el contrario, en la porción sur del gradiente latitudinal el crecimiento radial está positivamente correlacionado con la temperatura media anual (PC1-temp), bajo un clima relativamente más frío con una menor estacionalidad en las precipitaciones.

Conclusiones principales Nuestro estudio muestra que la temperatura tiene una importancia relativa mayor sobre el crecimiento de *Nothofagus pumilio* que la precipitación, indicado por una correlación estadísticamente significativa ($P < 0.05$) de signo positivo o negativo entre crecimiento arbóreo y PC1-temp y/o PC2-temp para 9 de las 13 cronologías regionales (69.2% del total), mientras que la precipitación (PC1-prec) está correlacionada significativamente sólo con dos cronologías (15.4% del total). Los patrones temporales del crecimiento radial de *N. pumilio* reflejados en el PC1 de crecimiento para el periodo 1778–1996 indican una tendencia al aumento con valores sobre la media a partir de 1963, con altos valores en los autovectores resultantes del análisis de componentes principales para la porción sur del gradiente. Esta tendencia puede ser explicada por el aumento de temperaturas para la Patagonia Sur, el cual está bien documentado por otros estudios. Los estudios en marcha y la futura investigación en los patrones de crecimiento de *N. pumilio* y su relación con el clima abarcando los Andes de Chile y Argentina mejorará nuestro entendimiento de las fluctuaciones climáticas de los últimos 3–4 siglos y su relación con el cambio global en un amplio rango de escalas espaciales y temporales.

INTRODUCTION

Tree-ring records provide important information for understanding the spatial and temporal patterns of tree-growth variability and their implications for the management of natural resources. Tree-ring records from tree line and other high elevation sites, although often of difficult access, are highly sensitive to climate variations and thus provide early evidence of changes in forest structure and composition. In addition, these sites are less disturbed by logging and human-set fires and may therefore provide long records to monitor environmental changes at a variety of time-scales (Luckman, 1990; Villalba *et al.*, 1997).

Nothofagus pumilio is a deciduous tree species that dominates the upper tree line of the Chilean and Argentinean Andes between 35°36′ and 55° S (Donoso, 1993). Studies using *N. pumilio* tree rings for temperature and precipitation reconstruction have been carried out for several regions. In Argentina, tree-ring chronologies have been developed for northern Patagonia (39–41° S, Villalba *et al.*, 1997; Schmelter, 2000) and southern Patagonia (54–55° S, Boninsegna *et al.*, 1989; Roig *et al.*, 1996). In Chile, tree-ring chronologies of *N. pumilio*, and climate reconstructions from its northernmost limit in the central Chilean Andes (35°36′–38°38′ S) and from southern Patagonia (51–55° S) have been developed (Lara *et al.*, 2001; Aravena *et al.*, 2002). Tree rings from both sides of the Andes have recently been used for the analysis of the temperature patterns of the twentieth century in the context of the last 400 years for northern and southern Patagonia (Villalba *et al.*, 2003). Other studies have addressed the dynamics of *N. pumilio* tree line in northern Patagonia (40°44′–41°15′ S), analysing seedling establishment and growth at krummholz stands in both Chile and Argentina (Daniels, 2000; Daniels & Veblen, 2003, 2004). Recently, studies on the dynamics of *N. pumilio* tree lines have also been conducted in Tierra del Fuego in Chile (54°30′ S, Cuevas, 1999, 2000, 2002).

Available research on *N. pumilio* growth at tree lines has been specific to different regions. Therefore, a comprehensive analysis of the spatial and temporal patterns of *N. pumilio* radial growth at tree lines and their relationship through its entire latitudinal gradient is needed. The aim of this paper is to identify the dominant spatial and temporal patterns of *N. pumilio* radial growth at tree line and upper-elevation sites over the entire latitudinal range of the species in Chile (35°36′–55° S), covering 2200 km. We also analyse the spatial and temporal patterns of temperature and precipitation variations in southern South America from instrumental records and we study the spatial and temporal relationships of the *N. pumilio* tree-ring growth with instrumental records of climate.

STUDY AREA

Sample sites

Between 1997 and 2000, we sampled *N. pumilio* at 48 tree line and high elevation sites along the 2200-km latitudinal transect from Vilches (35°36′ S) to Navarino Island (55° S, Table 1). These sites were grouped into 13 study regions covering the entire latitudinal range of this tree species (Fig. 1). The elevation of sites varies significantly along the transect. The tree line of *N. pumilio* is 1600 m in the two northernmost regions (Vilches and Laguna del Laja) and decreases southwards to 400 m in Tierra del Fuego. A composite chronology was developed for each of these 13 regions, including one to nine sites, to capture and integrate the regional environmental variation in tree growth (Table 1). The number of sites varied due to the relative abundance and accessibility of *N. pumilio* forests in each region.

Most soils along the sampled transect are of volcanic origin with different degrees of development. Soils of *N. pumilio* forests range from 0.3 to 1.0 m deep, decreasing with elevation and latitude. They tend to be loamy or sand-loamy in texture, with pH ranging between 4.5 and 5.8 (Schlatter, 1994; Thiers, 1997). In Laguna del Laja, Conguillío, Antillanca and Yates, soils are more poorly developed with sandy textures, mixed with coarse volcanic ash deposited from recent (twentieth century) eruptions (Lara *et al.*, 2001).

Forest composition and structure vary considerably in the different regions studied (Table 1). The northernmost site sampled in Vilches is a mixed *N. pumilio*–*N. obliqua* stand, formed by erect trees from 15 to 20 m in height. Sites sampled at Laguna del Laja were pure *N. pumilio* stands. In Conguillío, *N. pumilio* typically grows in mixed stands often overtopped by the long-lived conifer *Araucaria araucana* (Table 1). In Yates, *N. pumilio* occurs with *Fitzroya cupressoides*. Further south, sampled sites are in pure *N. pumilio* stands, except for one *N. antarctica* stand in Tierra del Fuego (Table 1). Thirty-nine of the sampled sites corresponded to old-growth tree line stands with erect trees averaging 10–12 m in height but

Table 1 Description of the 13 study regions

Study region						Number of sample sites per forest structure type		
Code	Name	Latitude (S)	Longitude (W)	Elevation range (m a.s.l.)	Dominant tree species*	Krummholz	Old growth with erect trees	Total
VIL	Vilches	35°36′	71°00′	1530	NP–NO		1	1
LAJ	Laguna del Laja	37°27′	71°11′	1500–1720	NP		4†	4
CON	Conguillío	38°42′	71°33′	1490–1650	NP–AA	1	2	3
ANT	Antillanca	40°42′	72°15′	1000–1300	NP		4	4
YAT	Volcán Yate	41°48′	72°19′	1300	NP–FC		1	1
FUT	Futaleufú	43°07′	71°45′	1230–1350	NP		2	2
CIS	Cisnes	44°39′	71°42′	1000–1200	NP	1	2	3
COC	Cochrane	47°12′	72°24′	800–1180	NP	1	8	9
OHI	O'Higgins	48°30′	72°30′	1200	NP		1	1
PAI	Torres del Paine	50°57′	72°54′	650–980	NP		5	5
ARE	Punta Arenas	53°00′	71°00′	350–600	NP	1	2	3
FUE	Tierra del Fuego	54°17′	68°45′	200–600	NP	2	4	6
					NA	1		
NAV	Navarino	54°57′	67°30′	300–600	NP	2	4	6
Total						8	40	48

NP, *Nothofagus pumilio*; NO, *Nothofagus obliqua*; AA, *Araucaria araucana*; FC, *Fitzroya cupressoides*; NA, *Nothofagus antarctica*.
*Nomenclature follows: Rodríguez, R., Matthei, O. & Quezada, M. *Flora Arbórea de Chile* (1983). Editorial de la Universidad de Concepción, Concepción, Chile.
†One site is a second-growth forest.

exceptionally reaching 22–26 m, depending on soil characteristics, aspect, wind exposure and elevation. Eight of the sites studied were *N. pumilio* krummholz that were 2–6 m tall, growing at more stressed tree line sites or south-facing slopes with relatively short growing seasons due to a long snow cover period (Table 1). One of the sampled sites in Laguna del Laja is a post-fire second growth stand. All sampled stands have a dense canopy (crown cover > 75%), forming a sharp upslope boundary with the alpine meadows and scrublands. Detailed descriptions of the northern regions (Vilches, Laguna del Laja Conguillío) and southern ones (Torres de Paine, Punta Arenas, Tierra del Fuego and Isla Navarino) are given in Lara *et al.* (2001) and Aravena *et al.* (2002), respectively.

Climate

The study area spans almost 20° of latitude and several different climatic regimes. In the northern part (35°40′–38° S), the climate is of Mediterranean-type with dry summers (Miller, 1976). Annual precipitation increases from north to south and becomes more equitably distributed over the year with decreasing interannual variability due to the increasing influence of moist Pacific air-masses (Miller, 1976). Interannual climate variability in the central Andes and northern Patagonia is significantly affected by the El Niño-Southern Oscillation (ENSO), which strongly influences precipitation and temperature patterns over wide areas of Chile and Argentina, with a high temporal instability (Aceituno, 1988; Daniels & Veblen, 2000; Montecinos & Aceituno, 2003). For example, at Concepción (36°46′ S) mean annual temperature is 12.2 °C and the annual precipitation is 1210 mm, with > 70% of the precipitation falling in the fall and winter (Pezoa, 2003). In Puerto Montt (41°25′ S), mean annual temperature is 9.9 °C and the annual precipitation is 1783 mm, with 41% of the precipitation falling in spring and summer (Pezoa, 2003). Further south in Punta Arenas (53° S), the climate is cooler with a mean temperature of 5.9 °C and 416 mm of annual precipitation evenly distributed through the year (Pezoa, 2003). Precipitation increases with elevation at any given latitude. For example at 36–37° S, annual precipitation increases from 1210 mm in Concepción (at 10 m a.s.l.) to 2145 mm in Bullileo, located at 600 m (Pezoa, 2003).

METHODS

Tree-ring growth patterns

At each of the 48 sampled sites, two cores from 15 to 40 living trees were collected using increment borers. Cores were mounted, sanded and cross-dated following standard dendrochronological procedures (Stokes & Smiley, 1968). For dating purposes, we followed Schulman's (1956) convention for the Southern Hemisphere, which assigns to each tree ring the date of the year in which tree growth started. Cross-dating consists of assigning a calendar year to each ring in every sample by comparing the growth patterns among the different cores from one site (Fritts, 1976). Ring widths were measured to the nearest 0.001 mm under a microscope with a Bannister-type measuring stage connected to a computer (Robinson & Evans, 1980), using a measuring program developed at Universidad

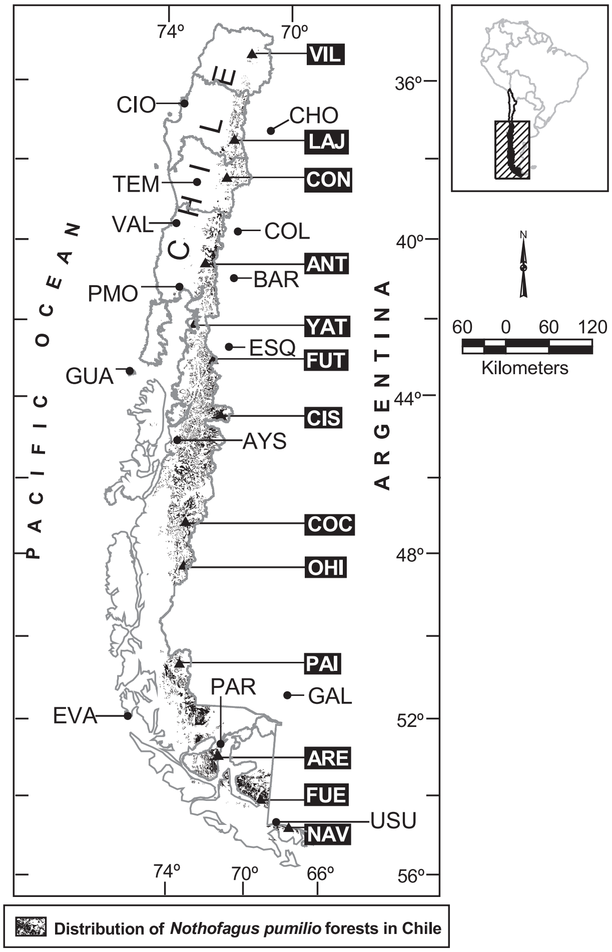

Figure 1 Location of the study regions for which regional tree-ring chronologies were developed (▲), meteorological stations (●). Distribution of *Nothofagus pumilio* forests in Chile shown with a shaded pattern. Codes for study regions and meteorological stations are given in Tables 1 and 2, respectively.

Austral de Chile. The computer program COFECHA (Holmes, 1983) was used to detect measurement and cross-dating errors. Radii from nearby sites with a high correlation among them were grouped into study regions. This analysis produced 13 study regions, and we developed a composite tree-ring chronology for each region. For this purpose, we selected those tree-ring series from the sites included in each region that were longer than 100 years and had a correlation coefficient ≥ 0.32 with the corresponding regional master series computed by the COFECHA program. These composite chronologies were created to capture the common growth patterns from each region.

Each ring-width series was standardized and averaged with other series to produce 13 mean regional composite chronologies (Fritts, 1976). Standard chronologies were produced using the ARSTAN program (Cook & Holmes, 1984; Cook, 1985). We used a negative exponential curve, linear regressions of negative slope or a horizontal line as theoretical curves of standardization. This process reduces the variance among cores and transforms ring widths into dimensionless index values. It also removes or reduces the influence of disturbance and changes in tree growth with age, but preserves a large portion of the low-frequency variations in the tree-ring series.

In order to assess the temporal variability in the strength of the common variation in each regional chronology, which we infer reflects common responses to climatic influences, we used the running series of average correlations (Rbar) and expressed population signal (EPS) statistics (Briffa, 1995). Rbar is the mean correlation coefficient for all possible pairings among tree-ring series from individual cores, computed for a specific common time interval (Briffa, 1995). The running EPS statistic is computed from Rbar and is a measure of the similarity between a given tree-ring chronology and a hypothetical chronology that has been infinitely replicated from the individual radii included in the given chronology for a specific common time interval (Briffa, 1995). Running EPS values were calculated over a 50-year window with a 25-year overlap. Following Wigley *et al.* (1986), a threshold value for EPS ≥ 0.85 for any given regional chronology and running period was considered adequate to reflect a common growth signal.

Temporal patterns in tree-growth were analysed from the tree-ring indices of each regional chronology. In order to emphasize the low-frequency variation in each chronology, we generated a smoothed line using the filter defined by Essenwanger (1986). Smoothed lines were generated for the analysis of the low-frequency long-term trends in the temporal patterns of tree growth as well as temperature and precipitation records, identifying periods of increasing, decreasing or stable trends.

We conducted principal components (PCs) analysis (Cooley & Lohnes, 1971) of the 13 regional composite chronologies for the common interval 1878–1996 in order to identify the dominant spatial and temporal patterns in tree growth of *N. pumilio*. The spatial variations in tree growth of *N. pumilio* across the Andes were analysed by plotting the eigenvalues for the first three PCs of each regional chronology, using the program SURFER (Golden Software Inc., 1999). Isolines of eigenvalues were calculated using the kriging interpolation procedure (Golden Software Inc., 1999).

Spatial and temporal patterns of temperature and precipitation variation

We compiled the data from those climate stations with the longest and most complete instrumental temperature and precipitation records within the latitudinal range of this study in Chile and Argentina (Table 2). This included nine records for temperature and 11 for precipitation. In order to identify the dominant spatial and temporal patterns of climate variation throughout the study area, we conducted PCs analysis of the annual temperatures and precipitation instrumental records from the climate stations located in Chile and Argentina from 38–55° S, for the common interval 1932–86. The computation of the annual means considered the monthly records of April of a given year through March of the following year. The spatial patterns of temperature and precipitation variability were analysed using the program SURFER, as described for growth patterns.

Table 2 Meteorological records used for comparing radial growth with spatial and temporal climatic variations

Station	Code	Country	Latitude (S)	Longitude (W)	Elevation (m)	Record period	Parameter	Source
Concepción	CIO	CH	36°46′	73°03′	12	1892–1987	P	Rosenblüth *et al.* (1997)
Chosmalal	CHO	AR	37°23′	70°17′	862	1904–96	P	Ser.Met.Nac.
Temuco	TEM	CH	38°45′	72°35′	114	1912–91	T, P	Rosenblüth *et al.* (1997)
Valdivia	VAL	CH	39°48′	73°14′	19	1912–91	P	Rosenblüth *et al.* (1997)
Collun-có	COL	AR	39°58′	71°12′	875	1912–89	T, P	Ea. Collun-có
Bariloche	BAR	AR	41°09′	71°16′	825	1905–90	P	Ser.Met.Nac.
Pto. Montt	PMO	CH	41°25′	73°05′	85	1912–91	T, P	Rosenblüth *et al.* (1997)
Esquel*	ESQ	AR	42°54′	71°20′	785	1905–88	T, P	Ser.Met.Nac.
Guafo	GUA	CH	43°34′	74°45′	140	1908–89	T	Rosenblüth *et al.* (1997)
Aysén	AYS	CH	45°20′	72°40′	11	1931–92	T, P	Rosenblüth *et al.* (1997)
Río Gallegos	GAL	AR	51°36′	68°18′	50	1931–90	T	Ser.Met.Nac.
Faro Evangelistas	EVA	CH	52°24′	75°06′	60	1905–92	P	Rosenblüth *et al.* (1997)
Punta Arenas	PAR	CH	53°00′	70°51′	37	1905–92	T, P	Rosenblüth *et al.* (1997)
Ushuaia	USU	AR	54°40′	68°10′	40	1911–86	T	Ser.Met.Nac.

CH, Chile; AR, Argentina; P, precipitation; T, temperature; Ser.Met.Nac., Servicio Meteorológico Nacional; Ea. Collun-có, Estancia Collun-có.
*The period for precipitation at Esquel is 1896–1990.

Growth–climate spatial and temporal relationships

The influence of temperature and precipitation on *N. pumilio* tree-ring growth and the spatial variation of this influence along the latitudinal gradient was analysed using correlation analysis between the regional tree-ring standard chronologies and the amplitude of the first three PCs for temperature and precipitation (Blasing *et al.*, 1984).

The analysis of growth–climate temporal relationships was performed in two stages. First, correlation analysis was used to examine the relationships between the PCs of tree growth and PCs of temperature and precipitation for the 1932–86 period, when both tree-ring and instrumental records were available. Secondly, we selected the PCs for tree-growth and instrumental records that were highly correlated and plotted them in order to assess visually their variation through time.

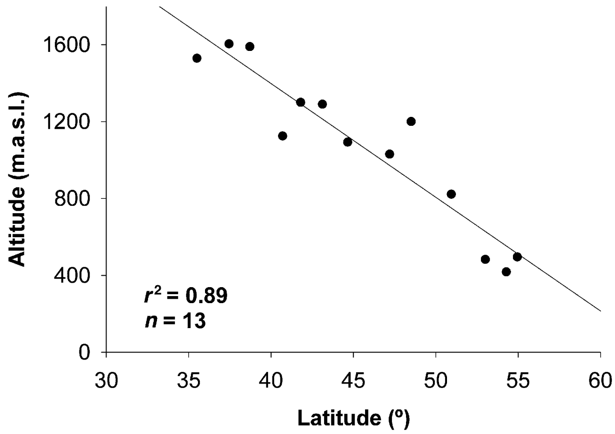

Figure 2 Relationship between latitude (° S) and altitude (m a.s.l.) for the different study regions.

RESULTS AND DISCUSSION

Tree-ring growth patterns

The 13 study regions show a considerable decrease in elevation of *N. pumilio* tree line along the latitudinal gradient, from 1600 m a.s.l. at 35°40′ to 400 m a.s.l. at 55° S. There is a significant correlation ($r^2 = 0.89$; $P < 0.05$) between latitude and elevation of the 13 study regions (Fig. 2). The slope of this regression line indicates an average north–south decrease in tree line elevation of 60 m per degree of latitude (111 km), as mean annual temperature decreases southwards.

Ten of the 13 regional tree-ring chronologies cover the 200-year period 1797–1996; the three shortest chronologies at Vilches, Antillanca and O'Higgins start in 1829, 1878 and 1851, respectively (Table 3). Mean sensitivity, characterizing the year-to-year variability in tree-ring records (Fritts, 1976), ranges between 0.15 and 0.28, whereas the standard deviation in tree rings ranges between 0.19 and 0.32 (Table 3). The mean sensitivity and the standard variation of the regional chronologies are generally lower than the values reported for individual sites in these regions (Table 3, Lara *et al.*, 2001; Aravena *et al.*, 2002). These differences reflect the fact that the composite chronologies average the regional environmental variation in tree growth, whereas the site chronologies for individual stands contain local environmental variability regarding elevation, slope, aspect as well as past disturbance.

Tree-growth patterns through time vary among the regional chronologies (Fig. 3). General patterns show that the chronologies located in the northern portion of the *N. pumilio* latitudinal range, between Vilches and Yates, have index values that fluctuate around the mean in the 1750–1996 period (Fig. 3). Conversely, the smoothing function of the

Table 3 Descriptive statistics for the 13 regional composite standard tree-ring chronologies for *Nothofagus pumilio*

Study region and chronology									
Code	Name	Period	No. of trees	No. of radii	Mean tree-ring width (mm)	Mean sensitivity*	SD	First-order autocorrelation†	Rbar‡
VIL	Vilches	1829–1996	43	49	1.44	0.17	0.21	0.48	0.20
LAJ	Laguna del Laja	1759–1996	94	94	1.09	0.15	0.19	0.48	0.21
CON	Conguillío	1739–1996	92	93	1.00	0.17	0.22	0.50	0.18
ANT	Antillanca	1878–1998	75	90	1.07	0.17	0.20	0.45	0.20
YAT	Volcán Yate	1754–1997	34	40	0.66	0.28	0.32	0.42	0.33
FUT	Futaleufú	1791–1997	40	52	1.07	0.16	0.20	0.49	0.18
CIS	Cisnes	1786–1997	52	54	0.88	0.18	0.23	0.55	0.15
COC	Cochrane	1720–1997	82	94	0.86	0.17	0.23	0.59	0.23
OHI	O'Higgins	1851–1999	17	24	0.81	0.22	0.28	0.49	0.38
PAI	Torres del Paine	1762–1996	72	94	0.87	0.20	0.24	0.54	0.22
ARE	Punta Arenas	1768–1996	73	93	0.92	0.23	0.27	0.53	0.19
FUE	Tierra del fuego	1752–1996	71	95	0.83	0.26	0.29	0.50	0.26
NAV	Navarino	1763–1996	56	69	0.94	0.23	0.26	0.48	0.24

*Mean sensitivity is the measure of the relative changes in ring width variations from year to year (Fritts, 1976).
†Autocorrelation is the serial correlation coefficient for the chronology at a lag of 1 year.
‡Rbar is the mean correlation coefficient for all possible pairings among tree-ring series from individual cores, computed for a specific common time interval. In this case we used a 50-year window with a 25-year overlap (Briffa, 1995).

chronologies in the southern portion of the latitudinal range (Punta Arenas to Navarino) show a long-term variation from values below the mean between 1750 and 1900, towards values above the mean starting in the 1950s and 1960s (Fig. 3). These southern chronologies also have a higher interannual variability in tree growth, which accounts for a relatively higher mean sensitivity and standard deviation compared with the northern ones (Fig. 3, Table 3).

Correlation patterns of the regional chronologies show, in general, greater similarity among chronologies that are geographically closer and an increasing difference between chronologies from distant sites (Fig. 4). The two northernmost chronologies were significantly correlated ($P < 0.05$) to each other (Vilches and Laguna del Laja), but did not correlate with the other regions. Similarly, the central–northern regional chronologies (Antillanca and Yates) correlated only to each other and the southernmost chronologies (Punta Arenas, Tierra del Fuego and Navarino) followed the same pattern (Fig. 4). Conguillío, Cisnes and O'Higgins do not show significant correlations with any other chronology (Fig. 4).

The mean Rbar for the different regional chronologies, representing the mean correlation among tree-ring series for overlapping 50-year periods, varies between 0.18 and 0.38 (Table 3). All the chronologies have EPS values above the threshold of 0.85 (Wigley *et al.*, 1986) after 1880 (Fig. 5). This indicates temporal stability, good quality and a strong common signal for all the chronologies during the past 100 years. The Vilches, Laja, Conguillio, Yates, Futaleufú and O'Higgins chronologies show values below this threshold in their early portions, mainly due to the low number of series included in this period (Fig. 5).

Results from the PC analysis of the 13 *N. pumilio* regional chronologies show the spatial patterns of radial growth across the regions (Fig. 6). The first three PCs for growth (PC1-growth, PC2-growth and PC3-growth) for the common interval 1878–1996 account for 20.4%, 15.5% and 10.8% of the total variance, respectively (cumulative value 46.7%, Fig. 6). The southern chronologies have the highest loadings (> 0.6) in PC1-growth, with a clear pattern of decrease northwards, with loadings < 0.3 north of Torres del Paine (50°50′ S, Fig. 6). In contrast, the highest loadings of PC2-growth (> 0.6) are located in the northern end of the transect (Vilches and Laguna del Laja), and decrease southwards (Fig. 6). Antillanca and Yates have the highest loadings for PC3-growth (> 0.6), whereas the loading value for O'Higgins was > 0.3, with low positive values or negative values for most of the other regional chronologies along the latitudinal gradient (Fig. 6).

The dominant temporal patterns of *N. pumilio* radial growth are shown in Fig. 7. The long-term PC1-growth pattern reflected by the smoothed line shows values that remain below the mean from 1878 to 1939, have stayed close to the mean until 1963 and are above the mean thereafter (Fig. 7). This pattern is related to the southernmost chronologies (Punta Arenas, Tierra del Fuego and Isla Navarino), which have the highest PC1-growth loadings in Fig. 6. The smoothing function of PC2-growth indicates a gradual trend towards decreasing values, associated with the northernmost chronologies (Vilches and Laguna del Laja). The low frequency variation from the smoothed line of PC3-growth shows negative values from 1878 to 1900, and variations around the mean thereafter, associated with Antillanca and Yates (Fig. 7).

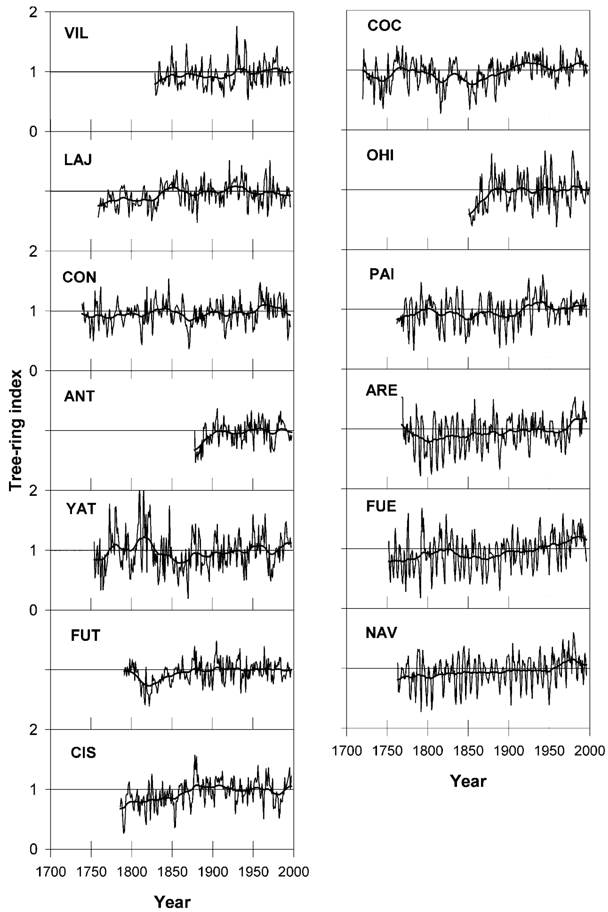

Figure 3 Standard composite tree-ring width chronologies for *Nothofagus pumilio* for the 13 study regions organized from north (top left) to south (bottom right). Tree-ring indices provide non-dimensional values that show changes in radial growth over time. A smoothed line generated using the filter defined by Essenwanger (1986) is drawn in order to emphasize the low-frequency variation for each chronology. Study region codes are explained in Table 1.

Spatial and temporal patterns of temperature and precipitation

The first two PCs for annual temperature departures (PC1-temp and PC2-temp) explain 40.6% and 28.2% of the variance, respectively (cumulative value 68.8%, Fig. 8). The two southernmost stations (Punta Arenas and Río Gallegos) have the highest loads for PC1-temp (> 0.8) with a decreasing trend northward (Fig. 8). PC2-temp shows the opposite trend with the highest loadings (> 0.6) in the northern stations (Temuco, Puerto Montt and Isla Guafo), and decreasing values southward with negative loadings for Punta Arenas and Ushuaia (Fig. 8).

The temporal patterns of temperature, reflected in PC1-temp and PC2-temp (Fig. 9) show opposite long-term trends, which are associated with the spatial distribution of the PC loadings (Fig. 8). PC1-temp shows a sustained increase throughout the period of the record (1932–86), which is highly influenced by Punta Arenas and Rio Gallegos (Fig. 9). Conversely, the smoothed line for PC2-temp shows a sustained decrease from the mid-1940s to the mid-1970s, an increase in 1976 and constant values thereafter (Fig. 9). This trend is reflecting the temperature variations at Temuco, Puerto Montt and Isla Guafo towards the north-west end of the study area (Fig. 8).

The first two PCs for precipitation departures (PC1-prec and PC2-prec) explain 53% and 14.5% of the total variance, respectively (cumulative value 67.5%, Fig. 10). PC1-prec loadings are highest (> 0.8) for Temuco, Collun-có and Chosmalal, located on the north-eastern extreme of the transect (Fig. 10). PC2-prec shows the highest loadings (> 0.7) for Punta Arenas and Faro Evangelistas, the two southernmost stations, with a decreasing gradient northward for stations located west and east of the Andean Divide (Fig. 10). The temporal patterns for PC1-prec are dominated by interannual variability and the smoothed line has remained close to the mean, with little fluctuations through the 1932–86 period (Fig. 11). In contrast, the long-term pattern for PC2-prec represented by the smoothing line, shows a steady decrease in precipitation, which intensifies after the 1960s (Fig. 11).

A regional decrease in precipitation registered at least since 1931 from instrumental records has been described for northern Chilean Patagonia (Rosenblüth *et al.*, 1997; Daniels & Veblen, 2000). Similarly, a steady decrease in precipitation in the 1931–2001 period recorded in most of the weather stations in Chile between 37° and 45° has also been described as the dominant regional precipitation pattern (Pezoa, 2003).

Growth–climate spatial relationships

Changes in the correlations along the latitudinal gradient indicate variations in the relative importance of temperature and precipitation as environmental controls of *N. pumilio* radial growth at tree line and high elevation sites (Fig. 12). PC1-temp has a positive correlation ($P < 0.05$) with all the tree-ring chronologies located between 48°30′ and 55° S including O'Higgins, Torres del Paine, Punta Arenas, Tierra del Fuego and Navarino regional chronologies (Fig. 12a). This represents 34% of the entire latitudinal gradient of *N. pumilio*. PC2-temp is positively correlated ($P < 0.05$) with Antillanca, Yates and O'Higgins, located discontinuously between 41 and 48° S, and is negatively correlated ($P < 0.05$) with Laguna del Laja and Conguillío, in the northern portion of the gradient (Fig. 12b). Conversely, tree growth has a positive correlation with precipitation (PC1-prec, $P < 0.05$) only at Laguna del Laja, in the northern portion of the gradient and has a negative correlation with Cochrane, located at 47° S (Fig. 12c). Although not significantly correlated at the 95% confidence level, the northernmost chronology at Vilches is also positively correlated with PC1-prec (Fig. 12c). No significant correlations were observed between PC2-prec and the regional chronologies.

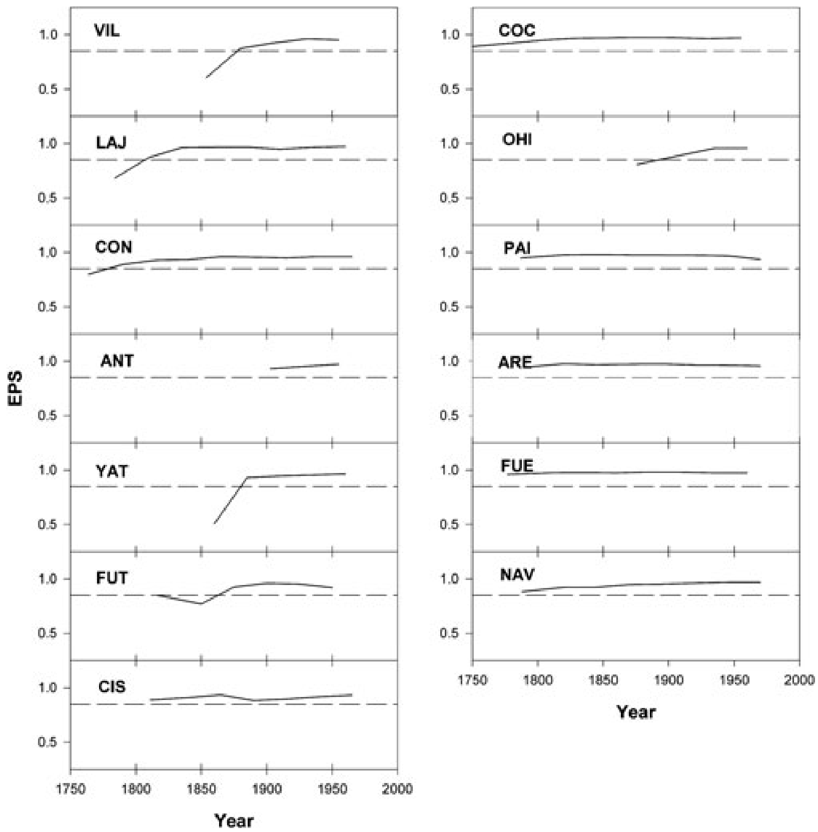

Figure 4 Expressed population signal (EPS) statistics for the 13 regional composite tree-ring width chronologies. EPS is a measure of the similarity between a given tree-ring chronology and a hypothetical chronology that has been infinitely replicated from the individual radii included for a specific common time interval (Briffa, 1995). Running EPS values were calculated over a 50-year window with a 25-year overlap. The dotted line is the threshold fixed at 0.85, considered adequate to reflect a common growth signal (Wigley *et al.*, 1986).

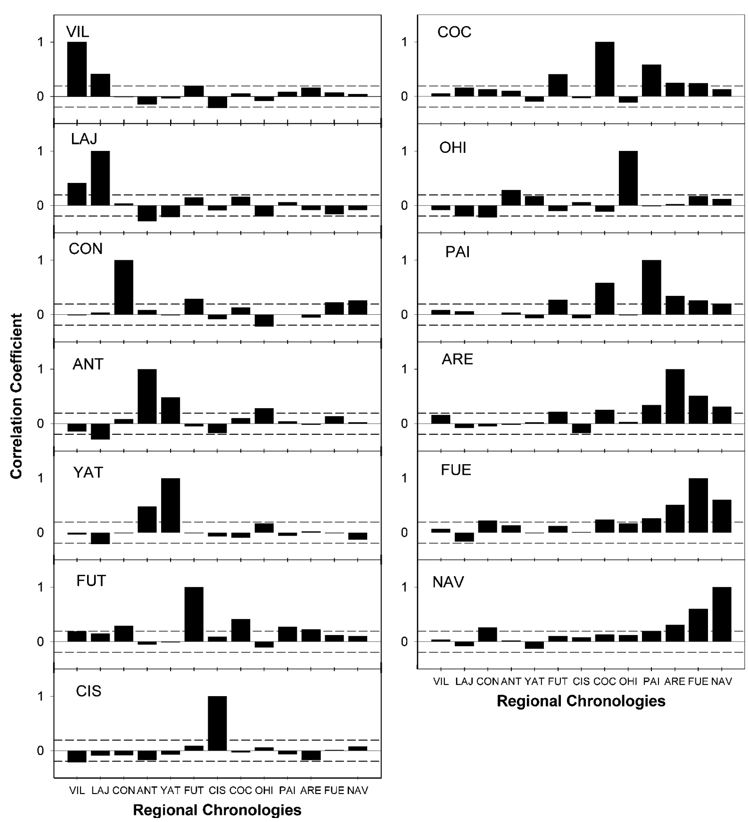

Figure 5 Correlation between the 13 regional tree-ring chronologies over the 1878–1996 common interval, organized from north (left) to south (right) along the *X*-axis. Dotted lines indicate the significance level ($P < 0.05$; $r > 0.194$ or $r < 0.194$). Study region codes are explained in Table 1.

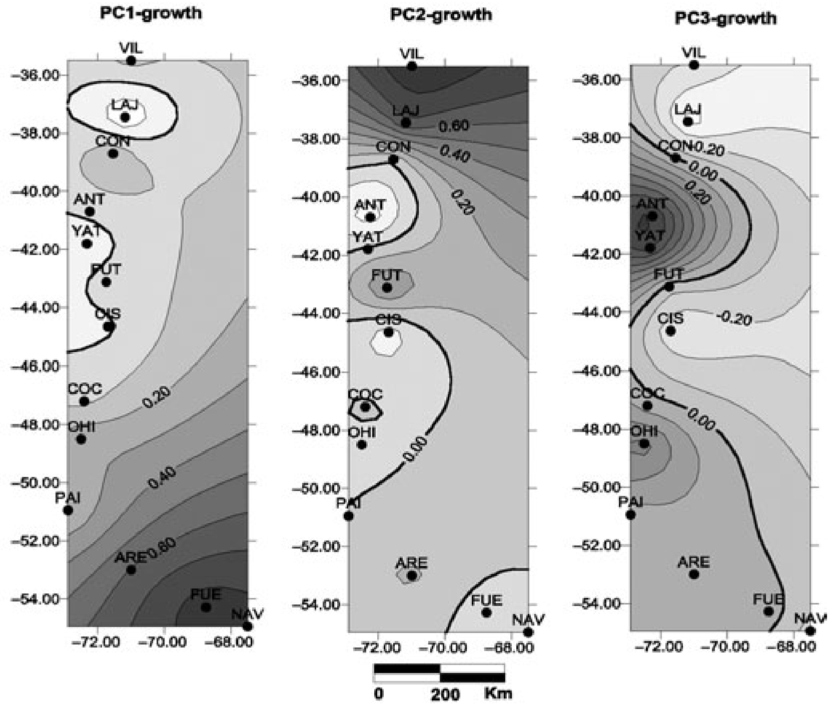

Figure 6 Spatial patterns of tree growth for the 13 *N. pumilio* regional chronologies along their geographical range, over the 1878–1996 common period. Chronologies are plotted in their longitudinal (*X*) and latitudinal (*Y*) locations. Isolines represent the factor scores for the first three principal components for radial growth (left box: PC1-growth, centre box: PC2-growth and right box: PC3-growth), which account for 20.4%, 15.5% and 10.8% of the total variance, respectively. Study region codes are explained in Table 1.

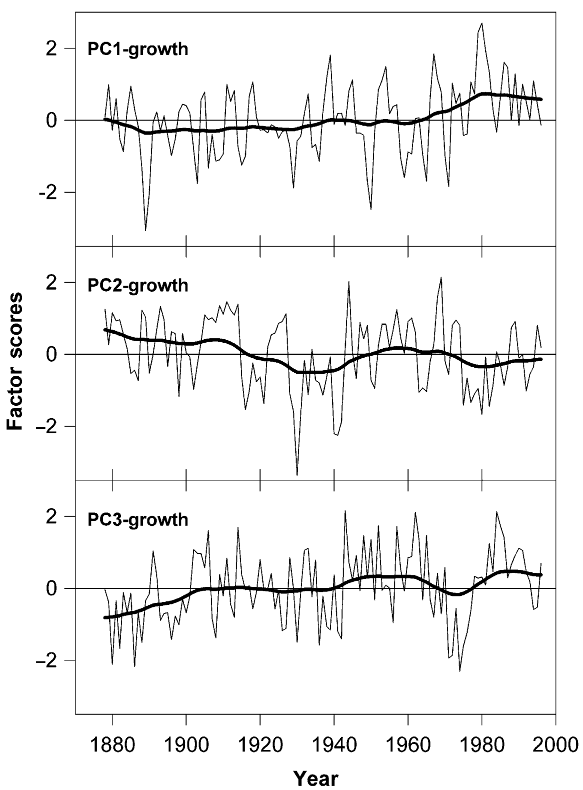

Figure 7 Temporal variations in the factor scores of the first three principal components of tree growth (from top to bottom: PC1-growth, PC2-growth and PC3-growth) extracted from the 13 *N. pumilio* regional chronologies over the 1878–1996 common period. A smoothed line, generated using the filter defined by Essenwanger (1986), is drawn in order to emphasize the low-frequency variations of tree growth.

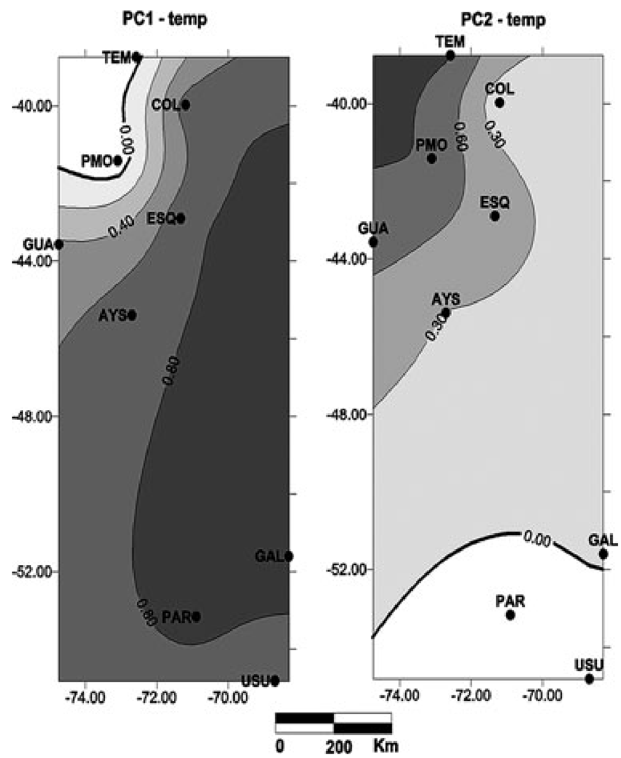

Figure 8 Spatial patterns of annual temperature variation for the nine instrumental records in the study area over the 1932–96 period. Temperature records are plotted in their longitudinal (*X*) and latitudinal (*Y*) locations. Isolines represent the factor scores of the first two principal components for mean annual temperature (left box: PC1-temp and right box: PC2-temp), which account for 40.6% and 28.2% of the total variance, respectively. Meteorological stations codes are explained in Table 2.

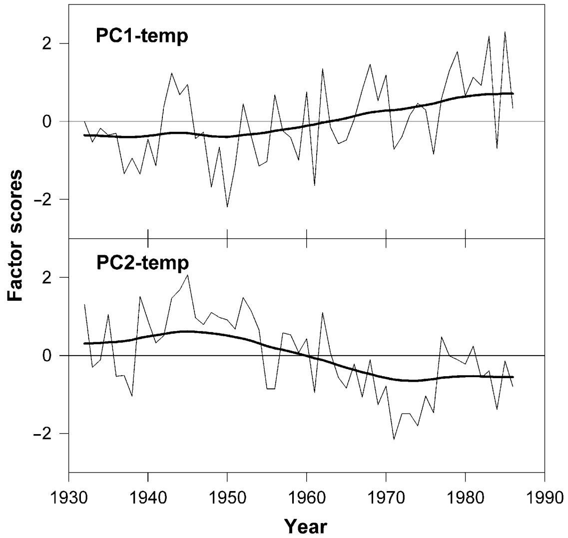

Figure 9 Temporal variations in the factor scores of the first two principal components of mean annual temperature (top: PC1-temp, bottom: PC2-temp) extracted from the nine annual temperature instrumental records for the 1932–96 period. A smoothed line, generated using the filter defined by Essenwanger (1986), is drawn in order to emphasize the low-frequency variations of temperature.

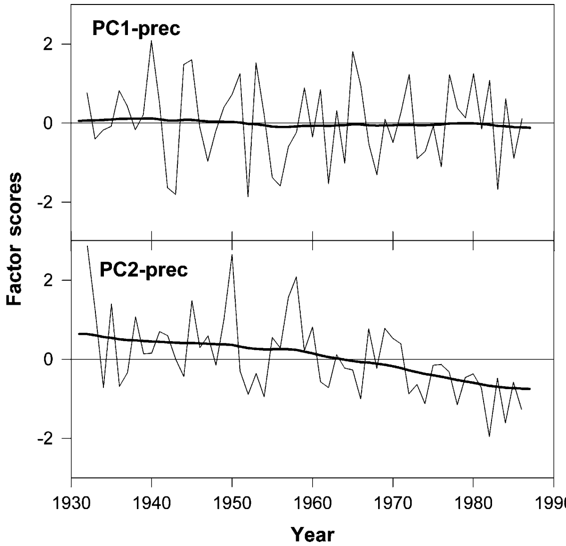

Figure 11 Temporal variations in the factor scores of the first two principal components of annual precipitation (top: PC1-prec, bottom: PC2-prec) extracted from the 11 precipitation instrumental records for the 1932–96 period. A smoothed line, generated using the filter defined by Essenwanger (1986), is drawn in order to emphasize the low-frequency variations of precipitation.

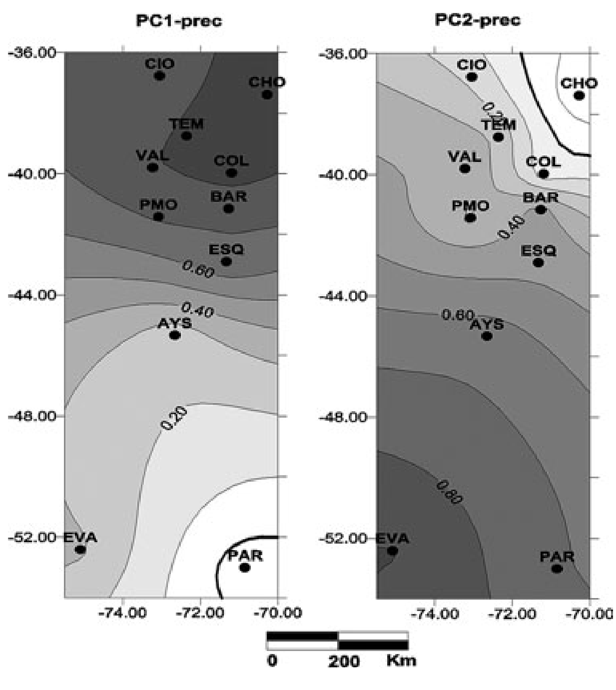

Figure 10 Spatial patterns of annual precipitation variations for the 11 instrumental records in the study area over the 1932–96 period. Precipitation records are plotted in their longitudinal (*X*) and latitudinal (*Y*) locations. Isolines represent the factor scores of the first two principal components for annual precipitation (left : PC1-prec, right: PC2-prec), which account for 53.0% and 14.5% of the total variance, respectively. Meteorological stations codes are explained in Table 2.

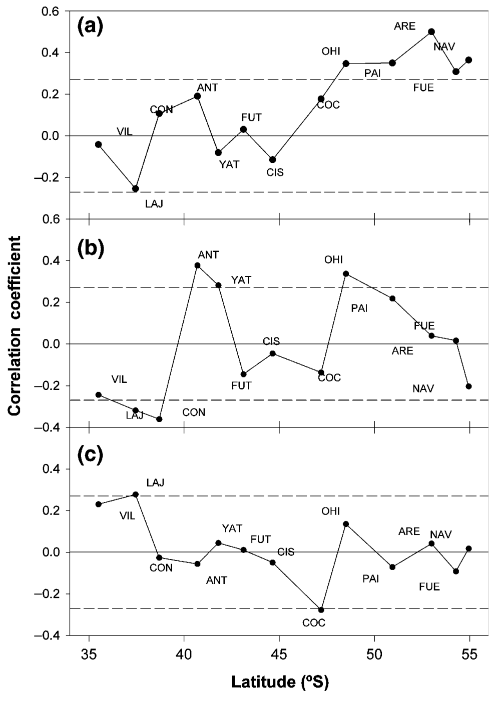

Figure 12 Correlation functions for the 13 regional chronologies for *N. pumilio* (tree-ring indices) with selected climatic variables for the 1932–86 period, plotted in the latitudinal positions of each chronology (° S). The selected climatic variables for each one of the boxes from top to bottom are: (a) PC1-temp; (b) PC2-temp and (c) PC1-prec. Dotted lines indicate the significance level ($P < 0.05$; $r > 0.27$ or $r < 0.27$). Study area codes are explained in Table 1.

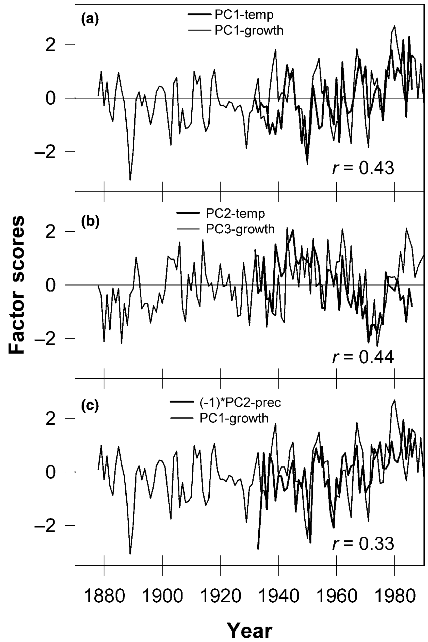

Figure 13 Dominant temporal patterns of tree-growth variation for selected principal components (PCs) extracted from the 13 regional chronologies for the 1878–1996 period, compared with correlated PCs of temperature and precipitation for the 1932–86 period. Boxes from top to bottom show PCs factor scores through time for: (a) PC1-growth and PC1-temp; (b) PC3-growth and PC2-temp; (c) PC1-growth and PC2-prec (inverted). In each box *r* represents the correlation coefficient between the two variables that are plotted for the 1932–86 period, which in each case is statistically significant ($P < 0.05$).

Temperature control in *N. pumilio* tree growth in the southern portion of the gradient (48°30′–55° S, Fig. 12a) is consistent with the positive correlation between the growth of *N. pumilio* from individual sites in southern Chilean Patagonia (51–55° S) and summer temperature (December–January) reported by Aravena *et al.* (2002). A positive correlation between temperature and *N. pumilio* radial growth at tree line stands with erect trees and in krummholz stands has also been described for sites located in northern Patagonia, both at the western and eastern slopes of the Andes at 40–41° S (Villalba *et al.*, 1997; Daniels & Veblen, 2004). The precipitation control in tree growth found for the northern portion (Fig. 13c) is consistent with the positive correlation between *N. pumilio* growth and the late-spring and early summer precipitation from individual sites located between 35°36′ and 37°34′ S (Lara *et al.*, 2001). A negative correlation between tree growth and spring temperature, probably due to an increase in evapotranspiration and decrease in water availability under a summer-dry Mediterranean-type climate was also described for this northern portion of *N. pumilio* range (Lara *et al.*, 2001).

The negative significant ($P < 0.05$) correlation of tree growth and precipitation found for Cochrane (Fig. 12c) has also been reported for other *N. pumilio* chronologies located in northern Argentinean Patagonia, as well as in the central Andes and southern Patagonia in Chile (Villalba *et al.*, 1997; Lara *et al.*, 2001; Aravena *et al.*, 2002). This negative correlation of tree growth with precipitation has been interpreted as a result of the cooling effect of cloud cover, a shorter growing season due to a prolonged snow cover, and occasional foliage damage by late-season wet snowstorms at tree line environments (Alberdi *et al.*, 1985; Lara *et al.*, 2001).

The high correlation of tree growth and precipitation in the northern portion of the latitudinal gradient with a Mediterranean-type climate allowed the reconstruction of summer precipitation from *N. pumilio* tree rings in the central Andes of Chile (36–39° S) for the 1837–1996 period (Lara *et al.*, 2001). Conversely, in southern Chilean Patagonia (51–55° S) the high correlation of tree growth with temperature was the basis for the reconstruction of minimum annual temperatures for the 1829–1996 period (Aravena *et al.*, 2002).

The interaction of temperature and precipitation has also been described as a controlling factor for both tree growth and seedling establishment at *N. pumilio* tree lines in the northern Chilean and Argentinean Patagonia at 41° S (Daniels & Veblen, 2004). The important contrasts between the relatively wetter western Andean slopes in Chile compared with the relatively drier eastern slopes in Argentina introduce marked differences in the patterns of seedling establishment, although they are separated by only 150 km (Daniels & Veblen, 2003, 2004).

Growth–climate temporal relationships

For the common interval 1932–86, there is a significant correlation ($r = 0.43$; $P < 0.05$) between the dominant patterns of annual temperature (PC1-temp) and tree growth (PC1-growth), both characterized by increasing trends since 1950 (Fig. 13a). The increase in the annual values of *N. pumilio* tree growth since 1950 may be associated with a rise in temperature, reflected by an increase in PC1-temp in this period (Fig. 13a). Increased *N. pumilio* tree growth since the 1950s and 1960s, as a response to a rise in mean annual temperature (51–55° S), has also been described by Boninsegna *et al.* (1989) in the Argentinean portion of Tierra del Fuego and by Aravena *et al.* (2002) for southern Chilean Patagonia. A steady increasing trend of mean annual temperatures from instrumental records for southern Patagonia in Chile and Argentina since 1932 has been reported (Rosenblüth *et al.*, 1997; Villalba *et al.*, 2003).

Tree-ring chronologies from *N. pumilio* at tree line and high elevation sites in Argentina and Chile have been recently used to reconstruct mean annual temperature departures for northern and southern Patagonia since 1640 (Villalba *et al.*, 2003). These reconstructions are based on composite tree-ring chronologies, using standardization methods that retain as much low-frequency variance as possible. These records indicate that temperatures in the twentieth century have been anomalously high in the context of the past 360 years. This warming trend is also evident from glacier records and intensifies at higher southern latitudes, particularly during the most recent decades (Luckman & Villalba, 2001; Villalba *et al.*, 2003).

Despite the warming trend during the twentieth century, and its effects on increased tree growth, available studies for the Chilean portion of Tierra del Fuego indicate that this warming trend has not resulted in the establishment of *N. pumilio* seedlings above the present tree line. Tree lines in this area have remained relatively static in the last 160 years (Cuevas, 2002). Similar stability has been reported for *N. menziesii* tree lines in north Westland, South Island, New Zealand (42° S, Cullen *et al.*, 2001). This stability contrasts with the general patterns described for North America and Europe, where an upward movement of tree line associated with a warming trend has been described for the twentieth century or the last decades (Innes, 1991; Kullman, 1991).

The cooling trend shown by PC2-temp since the mid-1940s to mid-1970s, is reflected in PC3-growth variations. Indeed both patterns are significantly correlated ($r = 0.44$; $P < 0.05$; Fig. 13b). This cooling period was followed by a pronounced increase in temperature in 1976 and a slight decrease in annual values thereafter (Fig. 13b). The cooling trend for the period 1950–75 has been reported from instrumental records (Rosenblüth *et al.*, 1997; Daniels & Veblen, 2000; Villalba *et al.*, 2003). It has also been documented from temperature reconstructions from *Fitzroya cupressoides* tree rings (Lara & Villalba, 1993). More recently, a *Nothofogus pumilio* composite regional temperature reconstruction for northern Patagonia has also shown this 1950–75 cooling trend within a long-term trend towards increased temperatures between 1850 and 1989 (Villalba *et al.*, 2003). Similarly, prevailing cool–wet conditions during 1957–76 in northern Patagonia, and low temperatures during the growing season limited radial growth at krummholz stands studied between 40 and 41° S in Chile and Argentina (Daniels & Veblen, 2004).

The 1950–75 period already described is followed by a pronounced increase in 1976 scores for PC2-temp and PC3-growth, and slightly decreasing values thereafter (Fig. 13b). This pattern is consistent with the increase in mean annual temperatures after 1976 dominated by summer warming (Villalba *et al.*, 2003). This warming has been reported as a prominent and widely distributed pattern recorded in instrumental records throughout northern and southern Patagonia in Chile and in Argentina (Villalba *et al.*, 2003). As a response to this increase in summer temperatures, a clear increase in *N. pumilio* growth has been described for sites located in northern Argentinean Patagonia (Villalba *et al.*, 1997, 2003). Increased radial growth of krummholz has also been described for sites located in Chile and Argentina at 40–41° S (Daniels & Veblen, 2004).

In addition to temperature as the main climatic factor controlling *N. pumilio* growth, PC2-prec shows a negative significant correlation with PC1-growth ($r = -0.33$; $P < 0.05$; Fig. 13c). In Fig. 13c, PC2-prec has been inverted to show the correlation and synchronous variation with PC1-growth more clearly. Therefore, the dominant pattern of PC2-prec is actually a decreasing trend for the 1932–86 period, while PC1-growth increases. These temporal patterns are highly determined by the instrumental records and regional chronologies located in the southernmost portion of the latitudinal gradient (53–55° S), as shown by the high factor scores of PC2-prec and PC1-growth in this region (Figs 6 & 10). A significant negative correlation between precipitation and *N. pumilio* tree growth has been described as a dominant pattern in southern Patagonia, especially for those sites located in the southernmost portion in Navarino at 55° S (Aravena *et al.*, 2002). As discussed earlier, this negative correlation may be explained as the result of reduced temperatures and other sources of stress associated with rain and snow precipitation, which reduce tree growth (Alberdi *et al.*, 1985; Lara *et al.*, 2001). The negative correlation between precipitation and temperature is demonstrated by the negative correlation between PC2-prec and PC1-temp ($r = -0.26$, non-significant $P < 0.05$, not shown), both with high factor scores in the southern portion of the gradient.

CONCLUSIONS

In this paper we provide a comprehensive description of the dominant spatial and temporal patterns of *N. pumilio* radial growth and how these patterns relate to temperature and precipitation instrumental records along a latitudinal gradient. We analyse *N. pumilio* dominant growth patterns from a network of 13 regional composite chronologies developed from 48 tree line and high-elevation sites, covering the entire latitudinal range of the species in the Chilean Andes along 2200 km, from 35°40′ to 55° S.

The wide range of environments in which *N. pumilio* grows at tree line in the Chilean Andes is represented by the decrease of tree line from 1600 to 400 m a.s.l. over its latitudinal range at an average rate of 60 m per degree of latitude (111 km), as mean annual temperature decreases southwards. Other studies indicate that elevation of *N. pumilio* tree line is higher in the eastern Andean slopes in Argentina compared with the western slopes in Chile, partially due to a more continental climate (Daniels & Veblen, 2004).

The spatial relationships between *N. pumilio* tree growth and climate show important variations in the relative importance of temperature and precipitation as environmental controls of *N. pumilio* radial growth. Tree growth at the northernmost portion of the gradient shows a positive correlation with precipitation and negative correlation with temperature, under a Mediterranean-type climate where water availability is a major limiting factor. Conversely, tree growth is positively correlated with mean annual temperature in the southern portion of the gradient, under a cooler climate with little seasonality in precipitation. If the overall latitudinal gradient is analysed, temperature has a spatially larger control of *N. pumilio* growth than precipitation, as indicated by a significant ($P < 0.05$) positive or negative correlations of tree growth with the PCs of temperatures for nine of the 13 regional chronologies (69.2% of the total), whereas precipitation is significantly correlated with only two chronologies (15.4% of the total).

Temporal patterns of *N. pumilio* tree growth indicate an increasing trend with above the mean values after 1963, with high loadings in the southern part of the gradient. This trend may be explained by a well-documented increase in temperature in southern Patagonia (Boninsegna *et al.*, 1989; Rosenblüth *et al.*, 1997; Aravena *et al.*, 2002; Villalba *et al.*, 2003). Another dominant pattern throughout the region is the decrease in temperatures (PC2-temp) and tree growth (PC3-growth) from the mid-1940s to the mid-1970s followed by a prominent increase in 1976. A third dominant temporal pattern is a decrease in precipitation (PC-2) throughout the 1932–86 period. This trend is dominated by the southernmost instrumental records and is inversely correlated with PC1-growth, which is experiencing an increasing trend since 1963.

Ongoing and future research focused on the analysis and integration of *N. pumilio* tree-ring records along west–east and altitudinal transects, as well as on the spatial and temporal patterns of temperature and precipitation records and growth–climate relationships, covering the Chilean and Argentinean Andes will improve the knowledge of long-term climate fluctuations during the past three to four centuries. This research will provide a better understanding of global climatic change at a wide range of spatial and temporal scales.

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BIOSKETCHES

Antonio Lara is Professor at Instituto de Silvicultura, Universidad Austral de Chile, Valdivia, Chile. His areas of research include forest dynamics, disturbance regimes, dendrochronology, climate reconstruction, as well as silviculture, and conservation of native forests.

Ricardo Villalba is Research Scientist at the Department of Dendrochronology and Environmental History, IANIGLA, Mendoza, Argentina. His areas of research include climate and glacier history across Patagonia, impact of climate on forest dynamics, and long-term changes in South American ecosystems in relation to global change.

Alexia Wolodarsky-Franke is an ecologist whose main research interests are dendrochronology, global change, fire dynamics and conservation of native forests.

Juan Carlos Aravena is a botanist, presently a doctoral student at the University of Western Ontario, Canada. His main research interests are dendrochronology, ecology and dynamics of native forests, global change and Quaternary studies.

Brian Luckman is Professor of the Department of Geography, University of Western Ontario, London, Canada. His main research interests are geomorphology, palaeoenvironmental reconstruction and dendrochronology, with an emphasis on alpine environments.

Emilio Cuq is a technician at the Tree-Ring Laboratory at Universidad Austral de Chile, developing tree-ring chronologies and other aspects for dendrochronological research.

Editor: Philip Stott