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ORIGINAL PAPER

Sensitivity of *Nothofagus dombeyi* tree growth to climate changes along a precipitation gradient in northern Patagonia, Argentina

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Abstract

Key message **Recent variations in climate appear to induce similarities in the responses of *N. dombeyi* growth along its entire distribution, supporting global convergence in tree growth responses to climate changes.**

Abstract Understanding forest responses to climate variations is urgently needed for anticipating changes in forest composition and biodiversity. We use twelve tree-ring chronologies from *Nothofagus dombeyi*, the dominant tree at mesic-to-humid sites, to characterize climate–growth relationships along the west-to-east precipitation gradient in Nahuel Huapi National Park, Argentina. A principal components analysis indicates that a large proportion of common variance in tree growth reflects regional-scale influences of climate. Correlation functions between climate and tree-ring indexes show that the critical factor regulating tree growth is spring–summer water deficit induced by above-average temperature and reduced precipitation during the growing season. At high elevations, however, tree growth appears to be less sensitive to water deficit but comparatively more sensitive to warmer conditions. Temporal trends in climate–tree growth relationships supported the occurrence of a dominant large-scale climatic response, but also identify changes in climate–growth relationships over time, primarily at wet and high-elevation sites. These variations in climate–growth relationships are interpreted as a convergence process to similar patterns in tree growth across the entire precipitation gradient, as wet–cool conditions at high-elevation sites turned to be less frequent due to drier and warmer years during the late twentieth century. Sampling along environmental gradients provides a comprehensive view of the potential range of responses of tree growth to climate which is not recorded using traditional dendrochronological sampling at marginal, more climate-sensitive sites. The recent changes in the relationships between climate and growth highlight the vulnerability of *N. dombeyi* to climate changes across its entire range of distribution in Argentina.

Keywords Tree-ring chronology · Climate–growth relationship · Climate variability · Spatial pattern · Temporal tree growth trends

Introduction

At long-term scales, climate and its variability modulate forest composition and distribution. Current climate changes are altering tree growth patterns in response to variations in growing season length, moisture availability, temperature thresholds and related factors. There are large

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uncertainties in the potential changes in tree growth associated with new environmental conditions. Whereas many boreal forests have increased their growth and productivity as a consequence of warmer climates, longer growing seasons, or both (Driscoll et al. 2005; Beck et al. 2011; Fang et al. 2014), forest decline or even widespread mortality, with consequent reduction in carbon sequestration, have been reported worldwide (van Mantgem et al. 2009; Allen et al. 2010; Anderegg et al. 2013; Steinkamp and Hickler 2015).

In this context, dendroclimatology constitutes a useful technique to assess the influence of recent climatic changes on tree growth, allowing a retrospective view of the association between climate and tree growth over the instrumental period (100 years or more). The study of the variations in climate–growth relationships, a common practice in dendroclimatology, proved to be a powerful tool for documenting variations in tree responses to climate changes over time. Studies on the climate–growth relationships at large spatial scales highlight that climate changes induce similarities in tree growth responses at different sites across the species distribution (Huang et al. 2010). For example, in northern Patagonia, Argentina, warmer temperatures have increased the growth rates of *Nothofagus pumilio* at high-elevation sites (Villalba et al. 1997, 2003). In contrast, reduced tree growth of *Austrocedrus chilensis*, *Araucaria araucana*, and *Nothofagus betuloides* trees have been related to a gradual decrease in water availability, reflecting the drying and warming patterns observed at mid latitudes in the Southern Hemisphere (Villalba et al. 2012). Similar patterns were recorded for *Fagus sylvatica*, where warmer growing-season conditions have reduced tree growth at low-elevation or xeric sites by increasing water evapotranspiration in the Mediterranean region (Jump et al. 2006). In consequence, tree stands nearby the margins of the species distribution have been primarily selected for dendroclimatic assessments as their proximity to physiological thresholds imposed by environmental conditions enhance forest responses to climate. However, it is urgently needed to characterize tree growth across the whole range of growing conditions to gain insights on all potential responses to climate variations and their consequences on species rate of growth and distribution.

From a dynamic perspective on climate–tree growth relationships, several studies have addressed significant transient responses between tree growth and climate during recent decades (Wilson et al. 2007; D'Arrigo et al. 2008; Yu et al. 2013; DeSoto et al. 2014). Time dependence of tree growth responses to climate involves shifts in the time along the year in which tree growth is sensitive to climate ["climatic window" *sensu* Fritts (1976)] or significant changes in the strength of the relationships over time. For example, recent studies in coniferous forests at high elevations or high latitudes highlight the reduction of tree growth response to temperature (D'Arrigo et al. 2009). Due to the regional increase in temperature, the growth of these conifers, largely controlled by temperature variations in the past centuries, is no longer limited by thermal conditions but moisture stress or related factors. Observations of the stability in climate–growth relationships are rare in spatially heterogeneous environments or multi-species forests. In the Mediterranean mountain forests, Lebourgeois et al. (2012) recorded no changes in growth sensitivity to recent climate variations at high-elevation sites, but temporal instability in climate–growth relationships for species growing at lower altitudes. Thus, valuable information can be gained from a temporal analysis of climate–tree growth relationships along predefined environmental gradients to improve current models on forest dynamics and carbon sequestration under impending climate change.

Global climate models project substantial changes in climate for most regions in the world during the forthcoming decades, including warmer temperatures and increases in extreme climatic events such as droughts (IPCC 2014). Climate variability have already been documented for Southern Hemisphere (Neukom et al. 2014), and also changes in climate have been documented in Northern Patagonia, Argentina (Villalba et al. 2003; Masiokas et al. 2008), where current climatic conditions have caused tree mortality and decline in the growth of the native conifer *Austrocedrus chilensis* (Villalba and Veblen 1998; Mundo et al. 2010) and the evergreen broadleaf *Nothofagus dombeyi* (Suarez et al. 2004; Suarez and Kitzberger 2010). These changes in tree growth conditions have generated new interest in the study of the climate–growth relationships of native trees and their susceptibility to climate change. Understanding these responses is critical for anticipating changes in forest composition and for establishing appropriate practices for biodiversity conservation and local-scale restoration.

While significant progress has been made on the study of the climatic influence on tree growth, more efforts are needed to provide a broader scale perspective of tree growth responses to climate changes. Thus, broad-scale studies on the influence of climate on tree growth and forest dynamics may aid in understanding how forests will behave in response to scenarios of future climate changes. In this context, we focus on characterizing the climate–growth relationships of *N. dombeyi* along a precipitation gradient in northern Patagonia, where contrasting site conditions should modulate the climatic response patterns. Here, we hypothesized that climate contribution on *N. dombeyi* forests growth is different along the prevailing W–E precipitation gradient of northern Patagonia, Argentina. Thus, we predict that temperature may play an important role in regulating growth at western cool and wet *N. dombeyi* forests, and also at high elevations sites, as found for *N. pumilio* forests (Villalba et al. 1997). In contrast, a synergistic influence (negative to temperature and positive to precipitation) is expected to be significant in forests growing under warmer and drier climates. These forests, located at eastern side of the *N. dobmeyi* distribution, also resulted negatively affected with recent drought (Suarez et al. 2004; Suarez and Kitzberger 2010). In addition, we explore the stability over time of the relationships between climate and tree growth at sites with different environmental conditions. We anticipate that climate–growth relationships in the *Nothofagus* forests are not stable over time, with a non-linear shift in sensitivity due to documented regional changes characterized by prevailing drier climatic conditions. For example, evergreen *N. dombeyi* could take advantage of early growing season warming in humid locations as well as in high-altitude sites, where an earlier onset of snowmelt could lead to increased water availability for growing in recent decades. Finally, a predominance of warmer and drier growing seasons in northern Patagonia, could be related to a lack of correlation between tree growth and climate as a strategy to avoid ecophysiological dysfunctions during stressful periods, similar to other species (Lebourgeois et al. 2012).

Materials and methods

Study area and sampled sites

The Andes in Patagonia produce a strong rain shadow effect; precipitation decreases from c. 3000 mm year^{-1} on the Andes divide to less than 500 mm year^{-1} over 100 km in W–E direction (Villalba et al. 2003). Regionally, precipitation is seasonal with c. 60 % falling during May through August (austral autumn–winter). Mean annual temperature varies with elevation, latitude and distance to the Pacific Ocean. Maximum temperatures are registered in January and February (austral summer). Along this environmental gradient, the evergreen broadleaf *N. dombeyi* tree occurs in a variety of environments. Near the continental divide in Argentina and on the western slopes of the Andes, rainforests are dominated by tall *N. dombeyi* individuals with dense under stories of bamboos (*Chusquea culeou*). Since the frequency of fires is relatively low in these forests, extensive old-growth *N. dombeyi* reaching maximum longevity (c. 600 years old) occurs. In the rainforests, *N. dombeyi* also form mixed stands with the long-lived conifer *Fitzroya cupressoides* (Mol.) Johnst. Stand-devastating fires frequently affect forests on the mesic eastern Andes slopes with total annual precipitation ranging from 1200 to 1800 mm. In these forests, *N. dombeyi* and the conifer *Austrocedrus chilensis* form even-aged populations. Across this precipitation gradient, *N. dombeyi* ranges from 500 to 1500 m in elevation. At humid sites above c. 1300 m, *N. dombeyi* forms mixed forests with the deciduous *N. pumilio* (Veblen et al. 1996).

Encompassing the altitudinal and precipitation gradients along the distribution of *N. dombeyi*, sampling sites were located along the west-to-east gradient from Cerro Tronador to Lago Guillelmo in Nahuel Huapi National Park (NHNP), Argentina (Fig. 1). Along this environmental gradient, 12 stands were studied (Table 1 for details).

Data collection and chronology development

At each site, dominant trees were sampled in a 1-ha plot. Two cores were obtained from each tree using increment borers. Samples were processed using standard dendrochronological methods (Stokes and Smiley 1968). Dating of tree rings was conducted under a stereo microscope. Since most *N. dombeyi* cores exhibited signature years, visual cross-dating was initially conducted before measuring. Following the Schulman's convention (1956) for the Southern Hemisphere, the date of an annual ring was assigned to the calendar year when growth began. Tree-ring widths were measured under a stereo microscope (50×) using a Velmex measuring bench (0.001 mm resolution).

The quality of the cross-dating was examined using the software COFECHA (Holmes 1983). Standard and residual chronologies were produced by the ARSTAN program (Cook and Krusic 2006). To remove age and other non-climatic trends, each tree-ring width series was standardized using a double detrending. First, tree-ring series were fitted to a deterministic model (negative exponential curve) followed by a cubic-smoothing spline of 67 % of the total length of the series. This double detrending stabilizes the variance in the tree-ring series reducing the larger variability in tree growth during the juvenile phase and amplifying the reduced inter-annual variability in growth associated with tree maturity (Cook and Krusic 2006). Following ARSTAN, mean chronologies were developed using a bi-weighted robust mean estimation and the autocorrelation removed with autoregressive moving average (ARMA) time series models. The confidence and reliability of the chronologies were evaluated by quantifying the degree to which a particular chronology portrays the hypothetically perfect chronology. Values of the Expressed Population Signal (EPS) ≥ 0.85 were used as acceptable statistical quality for the common chronology signal (Wigley et al. 1984).

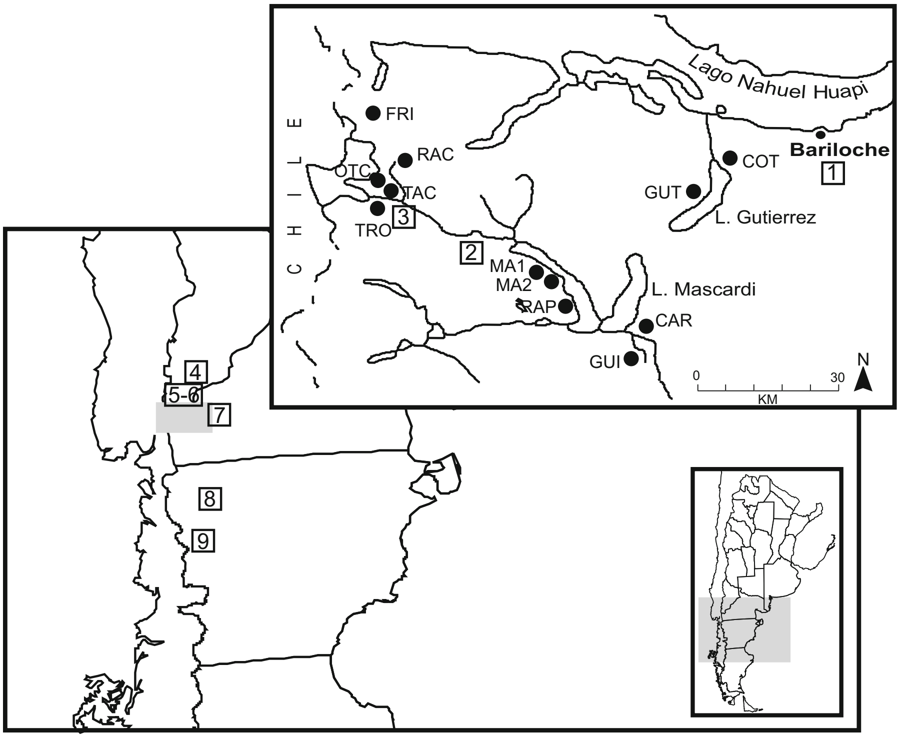

Fig. 1 Location map of the study area showing forest stands sampled in the Nahuel Huapi National Park, Argentina (*filled circle*). Meteorological stations are: 1—Bariloche, 2—Mascardi, 3—Pampa Linda, 4—Huechulafquen, 5—San Martin de los Andes, 6—Chapelco, 7—Traful, 8—Leleque, and 9—Esquel

Table 1 Site description and chronology statistics

Code	Site name	Latitude/longitude	Altitude (m)	Time span ($n \geq 5$)	No. of trees (radii)	Mean sens.	r bar	EPS (>0.85)	Source/collector
TRO	Pampa Linda	41°12′31″/ 71°48′46″	900	1747–2006 (1792)	48 (53)	0.179	0.21	0.75 (1915)	Suarez 2010
FRI	Cno. Frías	41°07′54″/ 71°47′51″	860	1649–2006 (1725)	33 (39)	0.167	0.21	0.85 (1800)	IANIGLA
OTC	Cno. O. Meiling 2	41°11′40″/ 71°47′33″	1491	1587–2007 (1744)	13 (22)	0.224	0.17	0.65 (1890)	This study
TAC	Cno. O. Meiling 1	41°12′20″/ 71°47′3″	1100	1626–2007 (1739)	21 (32)	0.209	0.27	0.70 (1780)	This study
RAC	Río Alerce	41°10′58″/ 71°46′43″	1064	1476–2008 (1627)	17 (31)	0.191	0.24	0.85 (1630)	This study
MA2	Mascardi 2	41°18′31″/ 71°35′20″	897	1844–2001 (1859)	15 (27)	0.195	0.39	0.86 (1880)	IANIGLA
MA1	Mascardi 1	41°18′30″/ 71°35′19″	840	1761–2001 (1789)	22 (40)	0.241	0.19	0.76 (1840)	IANIGLA
RAP	Los Rápidos	41°19′52″/ 71°35′02″	850	1872–2004 (1884)	69 (91)	0.152	0.20	0.93 (1900)	Suarez 2010
CAR	Las Carpitas	41°21′32″/ 71°30′34″	880	1819–2009 (1908)	17 (17)	0.221	0.29	0.70 (1940)	This study
GUI	LagoGuillelmo	41°23′40″/ 71°29′54″	862	1782–2009 (1870)	16 (16)	0.212	0.25	0.60 (1880)	This study
GUT	Lago Gutierrez	41°10′35″/ 71°24′05″	850	1857–2006 (1892)	52 (52)	0.198	0.32	0.74 (1920)	Suarez 2010
COT	V. Los Coihues	41°09′49″/ 71°24′08″	905	1871–2000 (1898)	31 (40)	0.186	0.20	0.88 (1910)	M. L. Suarez

Sites are sorted according to the west-to-east gradient

Meteorological data

Climatic records for Patagonia are scarce and unevenly spatially distributed. Since a single climatic record hardly is representative for the climate along the entire environmental gradient, nine climatic records from weather stations in the northern Patagonian Andes were combined into regional climatic records. The regional precipitation record includes the station of Bariloche (1933–2010), Chapelco (1990–2008), Leleque (1931–2006), Esquel (1916–2010), Huechulafquen (1933–1955), Mascardi (1969–1998), Pampa Linda (1972–1997), San Martin de los Andes (1935–1975), and Traful (1936–1976). Instrumental records for temperature are even scarcer than for precipitation. The regional temperature record includes the records from Bariloche (1931–2010), Esquel (1931–2010), Mascardi (1968–1998) and Pampa Linda (1972–1997). Regional climatic records were estimated by averaging the standard deviations from monthly total precipitation or monthly mean temperature using the routine MET from the DPL program (Holmes 1992).

Tree growth variability and climate–growth patterns

We used principal component analysis (PCA) to identify common patterns of growth variability among the 12 ring-width chronologies over the period 1900–2000. Residual instead of standard chronologies were used because the removal of serial autocorrelation and persistence improves the estimation of the climatic-related growth signal. The broken stick test was performed to determine the significance of the components, and the number of components to be retained for the ordination (Legendre and Legendre 1998). Principal component analysis were inspected with and none rotation. While similar ordination information was obtained after matrix rotation, non-rotation better defined the PC axes and maximizes the spread of the chronology loadings. PCA was calculated from a covariance matrix since the descriptors (tree ring index) were measured in the same units (Legendre and Legendre 1998). To look for the underlying geographical conditions associated with the ordination of the 12 chronologies, first and second principal component loadings were plotted against geographic variables (latitude, longitude and altitude) for each sampled site.

Growth–climate relationships were assessed by comparing site ring-width chronologies with monthly precipitation and temperature from the regional records. Correlation coefficients were computed for a climate-window that extends from April during the current growing season back to September of the previous growing season, encompassing a total period length of 20 months, using the software DENDROCLIM 2002 (Biondi and Waikul 2004). Bootstrapped confidence intervals were calculated to assess the significance of the correlation coefficients. In northern Patagonia, the growing season begins in September/October and ends in March/April of the following year. Correlation functions were examined over the common period between the chronologies and the regional climatic records: 1916–2000 for precipitation and 1931–2000 for temperature. Positive correlation coefficients indicate that above-average values of climate are related to above-average tree growth. Conversely, negative correlation coefficients indicate that above-average values of climate are associated with below-average growth.

Based on the results obtained from the PCA, all series were combined in two subsets of composite chronologies, namely Wet group (OTC, RAC, FRI, TRO, TAC), and Dry group (the rest of chronologies). Following, we compare the growth of two groups with Palmer Drought Severity Index (PDSI; Palmer 1965), sea surface temperature (SSTs) from the Niño 3.4 region (Trenberth and Stepaniak 2001),[1] and geopotential height (850 HPa). The Palmer Drought Severity Index takes into account precipitation, evapotranspiration and soil moisture conditions, all of which are determinants of hydrologic droughts. Recently, Wells et al. (2004) proposed a self-calibrating PDSI (sc_PDSI) by calibrating the PDSI using local conditions, instead of using the (fixed) coefficients used by Palmer (1965) to improve the spatial comparability (Dai 2011). The sc_PDSI showed a better performance than the original PDSI during the twentieth century over North America (van der Schrier et al. 2006). Additionally, Burke et al. (2006) suggested the Penman–Monteith equation (PDSI_pm) to minimize the errors induced by the potential evapotranspiration calculated using the Thornthwaite equation for the PDSI. In consequence, the sc_PDSI_pm monthly series for the study area (1853–2010) was taken from the Dai (2011) 2.5° × 2.5° gridded data set (central point: 38°45′S and 71°15′W) (data downloaded from KNMI Climate Explorer: http://climexp.knmi.nl/select.cgi?id=someone@somewhere&field=sc_pdsi). Pacific SSTs were analyzed as indicator of ENSO, El Niño-Southern Oscillation, a coupled ocean–atmosphere phenomenon rooted in the tropical Pacific, characterized by irregular fluctuations between its warm (El Niño) and cold (La Niña) phases with a periodicity ranging from 2 to 7 years (Diaz and Markgraf 2000). The Annular Mode in the Southern Hemisphere (SAM), also known as the Antarctic Oscillation (AAO), is the dominant pattern of variability in the

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[1] The Niño 3.4 region is the tropical Pacific extending from 5°N to 5°S, and from 170° to 120°W. We used the updated series available from the website of the Global and Climate Dynamics of the National Centre for Atmospheric Research (http://www.cgd.ucar.edu/cas/catalog/climind/TNI_N34/index.html).

tropospheric circulation south of 20°S, and it is characterized by pressure anomalies of one sign centered on the Antarctic and anomalies of opposite sign in the circumhemispheric band at 40–50°S (Thompson and Wallace 2000). During positive phases of the SAM (high pressure on the study area), there is a marked decrease in rainfall in northern and central Patagonia and increased precipitation during negative phases (low pressure on the study area; Aravena and Luckman 2009). In this study, the SAM index (1957–2000) developed by Marshall (2003), based on a selection of pressure station records from mid and high latitudes of the Southern Hemisphere, was utilized in correlation function analyses. The influence of Pacific SST and the geopotential height (850 HPa) on *N. dombeyi* growth was evaluated through spatial correlations between these variables and the wet and dry subsets of composite tree-ring chronologies for the area 20°N–85°S/180°E–0°.[2]

Finally, the large-scale influences of climate on *N. dombeyi* tree growth across the precipitation gradient were inspected by illustrating the occurrence of two severe droughts during the growing seasons of1943 (−0.91 SD precipitation; 1.62 SD temperature) and the spring–summer of 1998 (−1.39 SD spring and −1.33 SD summer precipitation, 1.09 SD spring and 1.70 summer temperature) with two randomly selected years (1964, 1985) with precipitation around the mean and with two years (1941, 1997) with relatively cool–wet growing season.

Temporal stability in climate–growth relationships

Temporal trends in mean sensitivity, and frequency of narrow and wide rings (number of chronologies showing narrow (<1.40 SD) tree-ring indices) along the twentieth century was inspected for the two groups defined by the PCA. Mean sensitivity indexes (ms_x) were computed following Fritts (1976). First, annual sensitivity (s_x) was calculated for each tree-ring series based on the formula $s_x = |I_{t+1}\text{-}I_t|2/(I_{t+1}+I)$, where I_t is the index value for the year t. Then, all s_x series belonging to the same group were averaged.

Temporal trends in correlation coefficients between climate and tree growth were performed with the moving correlation intervals mode in DENDROCLIM 2002. Tree ring chronologies for moving bootstrapped correlation were the groups defined previously. The temporal stability was analyzed on monthly basis for temperature and precipitation separately, and using 35-year moving correlation windows. Thus, a maximum of 42 successive correlation functions were computed for each group on the period 1932–2009 for temperature, and a maximum of 57 successive functions for the period 1916–2009 for precipitation. For all analysis, linear regression and piecewise regression were used to analyze the temporal trend, using segmented package in R (Muggeo 2008).

Results

Tree-ring width chronologies

Coincident with a higher frequency of disturbances, mainly fires, in the mesic and dry sites (Kitzberger and Veblen 1999), the *N. dombeyi* chronologies from the eastern stands are shorter. The longest chronologies are from stands located in humid and high-elevation environments (Table 1 and Supplementary Appendix). Presently, the longest *N. dombeyi* record already developed is from the Río Alerce (RAC) stand, encompassing a period of 532 years (Table 1 and Supplementary Appendix). The new chronologies show high signal-to-noise ratio reflecting a high percentage of common variance between cores at single stands. The mean sensitivity varies from 0.15 to 0.24 between sites, suggesting relatively low to middle inter-annual ring-width variability (Table 1). The mean r-bar ranges from 0.17 to 0.35. The chronology reliability (EPS) resulted acceptable in most study sites after about 1900, the period concurrent with the largest number of series in all sites (Table 1).

The common variance

The principal component analysis from the 12 residual chronologies shows that the first two significant eigenvectors, accounting for a cumulatively 57.5 % of the total variance, contribute with 44.8 and 12.7 % of the total variance, respectively. The relatively high percentage of common variance associated with the first principal component indicates a large proportion of common inter-annual variations in tree growth along the environmental gradient and reflects the influence of regional climate on *N. dombeyi* radial growth. All sites show positive loadings on PC1, but tree-ring chronologies from upper-elevation sites (TAC and OTC) shows the lowest loadings values, separating the group from the rest of the chronologies. The distribution of sites along a diagonal on the PCA plot suggests that both components partially contributes to the characterization of dry–wet spatial growth pattern, showing that tree-ring chronologies toward the eastern sector of the gradient (MA1, MA2, RAP, GUT, GUI, CAR, COT) share larger common variance (Fig. 2). The comparison of the PC chronology loadings with geographic variables reveals that the PC1 and more clearly PC2 separates the drier (positive loadings) from the wetter (negative loadings, Fig. 3) sites

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[2] These spatial correlation analyses were performed through the National Oceanic and Atmospheric Administration website (http://www.esrl.noaa.gov/psd/data/correlation/).

located east and west of ~71.7°W, respectively. In addition, upper-elevation sites also have negative factor loadings in the second component.

Climate–growth patterns

The climate–tree growth relationships for *N. dombeyi* vary between sites across the precipitation gradient (Fig. 4). The dominant pattern is characterized by positive associations with precipitation and negative with temperature during the current growing season. Some departures from this general pattern reflect differences in local conditions along the precipitation gradient. Relationships between precipitation and tree growth are stronger at eastern than western sites and at lower- than higher-elevation stands (Fig. 4). At the westernmost-located (wetter) sites, these relationships encompass most months during the current growing season, but also some months in the previous growing season. The negative relationship between temperature and *N. dombeyi* growth is more pronounced during the growing season. In addition, the length in months of the negative significant period increases with increasing distance from the Andes (drier sites, Fig. 4). The influence of temperature on tree growth during the previous growing season becomes more important towards the western, humid sites. Relationships between precipitation and temperature in winter and tree growth were more notable in wet and high-elevation sites. Positive correlations between growth and winter temperature were recorded at site OTC, whereas sites FRI and RAC show positive and negative correlations with winter precipitation and winter temperature, respectively, possibly associated with earlier snowmelt at lower elevations.

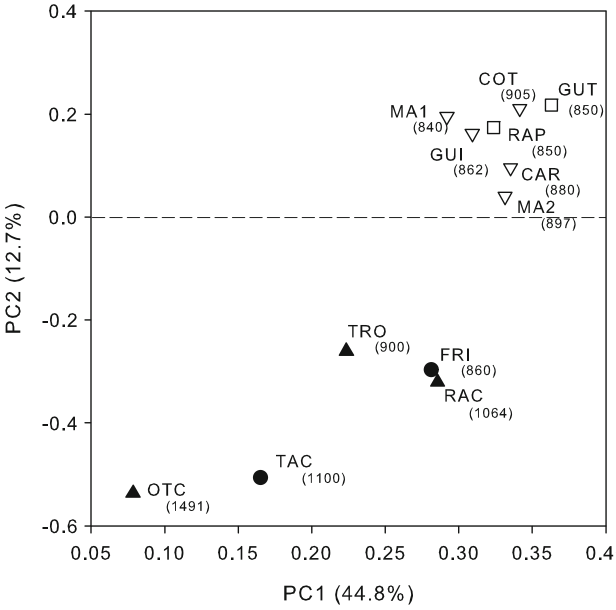
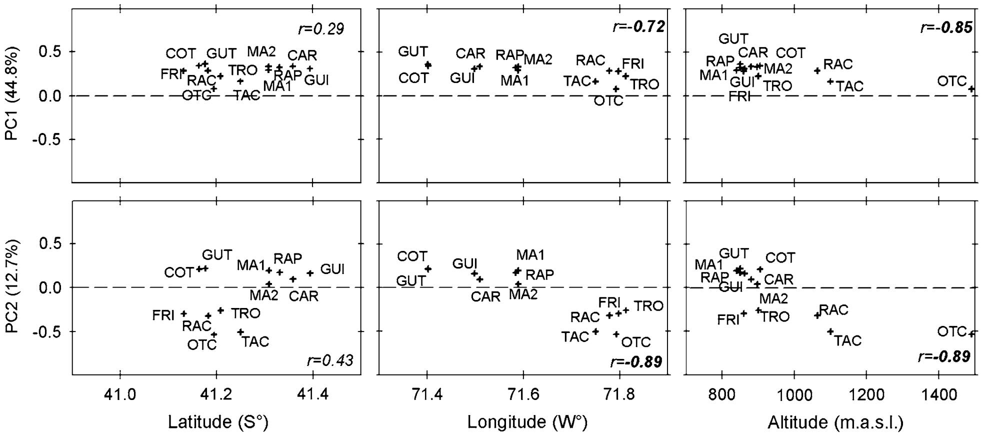


Fig. 2 Scatter plots of relative positions of *N. dombeyi* residual chronology according to their axis loadings defined by the first and second principal components (PC). The analyzed period is 1900–2000 for residual chronologies. *Symbols* indicate mean annual precipitation [(Barros et al. 1983): (*filled triangle*) 3000 mm/year, (*filled circle*) 2500 mm/year, (*empty square*) 1800 mm/year, (*diamond*) 1600 mm/year, (*inverted empty triangle*) 1400 mm/year. *Empty symbols* highlight the driest and eastern sites along the gradient. Data of meter above sea level of each site is indicated in *brackets*

Comparisons between the *N. dombeyi* growth (wet and dry groups) and PDSI showed a strong positive correlation during spring and summer during the current growing season for dry group (Fig. 5). In contrast, wet group showed only significant correlation with PDSI for few months (September, December and March). Consistent with the PDSI relationships previously described, the strongest negative associations between *N. dombeyi* tree-ring growth and SAM index were recorded from December to February during current growing season for the dry group of chronologies (Fig. 5). In terms of spatial correlation and coinciding with previous results, regional *N. dombeyi* growth at the regional level, but mainly in the drier sites, is favored by relatively low geopotential heights over the study area at the current summer (Fig. 6). No significant pattern was found between both groups of

Fig. 3 Scatter plot of PC loadings in relation to latitude (*left*) longitude (*center*) and elevation (*right*)



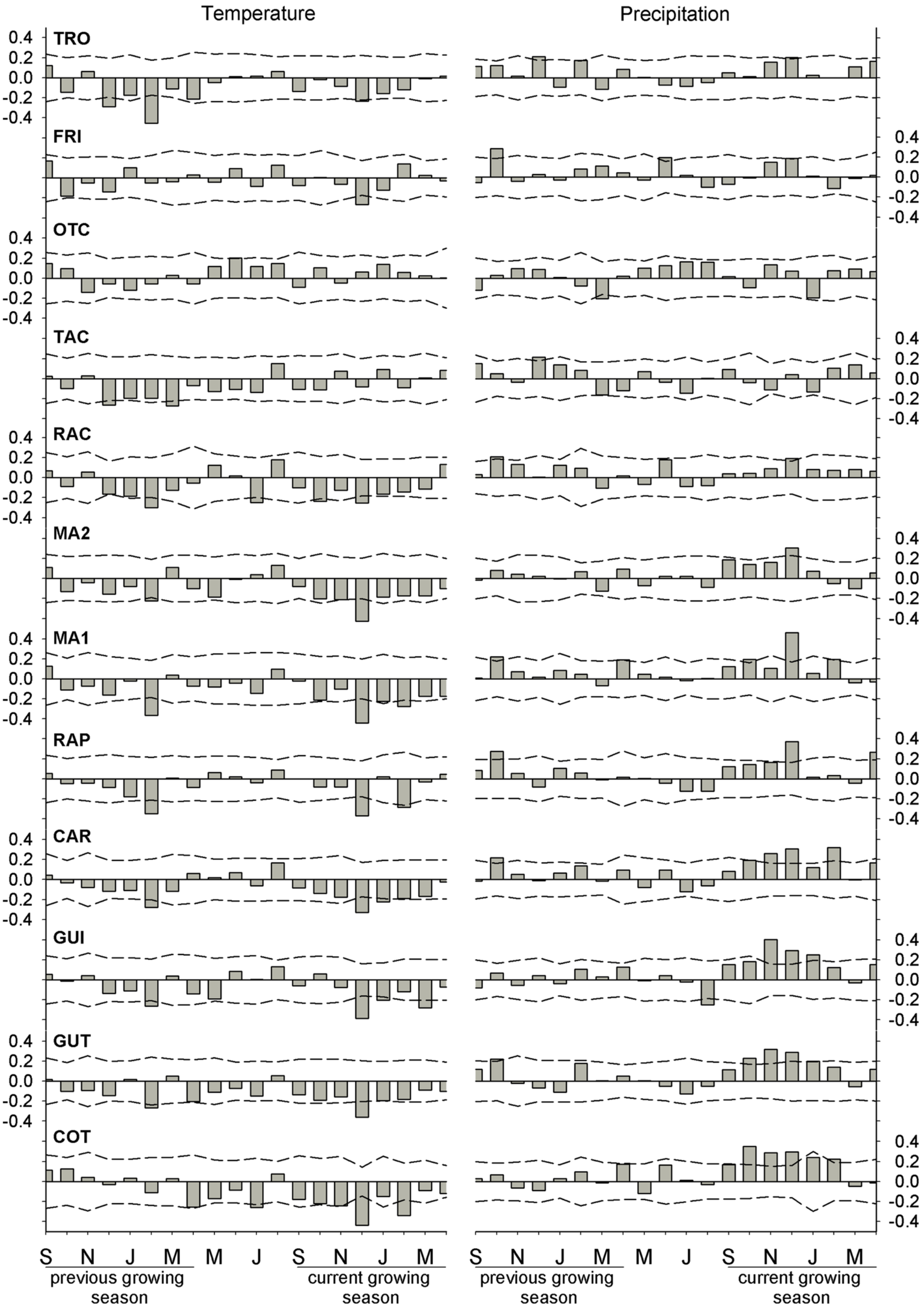


Fig. 4 Correlation functions based on tree-ring residual chronologies and monthly climate data. Climate data consisted of standard deviations from mean monthly temperature (1931–2010) and total monthly precipitation (1916–2010) of the regional climatic record. The time span encompassed 20 months prior to the end of the current growing season. *Dashed lines* indicate significant bootstrapped correlation coefficients

chronologies and SST temperatures, indicating no clear influence of ENSO in *N. dombeyi* growth.

The large-scale influence of climate on *N. dombeyi* tree growth (negative influence of temperature and positive influences of precipitation on growth during October–February) across the precipitation gradient is clearly illustrated during the occurrence of two severe droughts along the growing seasons of 1943 and 1998. We compared the droughts during the summer of 1943, and the spring–summer of 1998 with two randomly selected years (1964, 1985) with precipitation around the mean and with two years (1941, 1997) with relatively cool–wet growing season. Tree-ring widths were narrow in all stands during the severe droughts, including the wettest stands in Tronador (TRO) and Río Alerce (RAC), but effects of these events were more pronounced at the drier locations highlighting the influence of droughts along the transect (Fig. 7). Above-mean temperature and reduced precipitation during

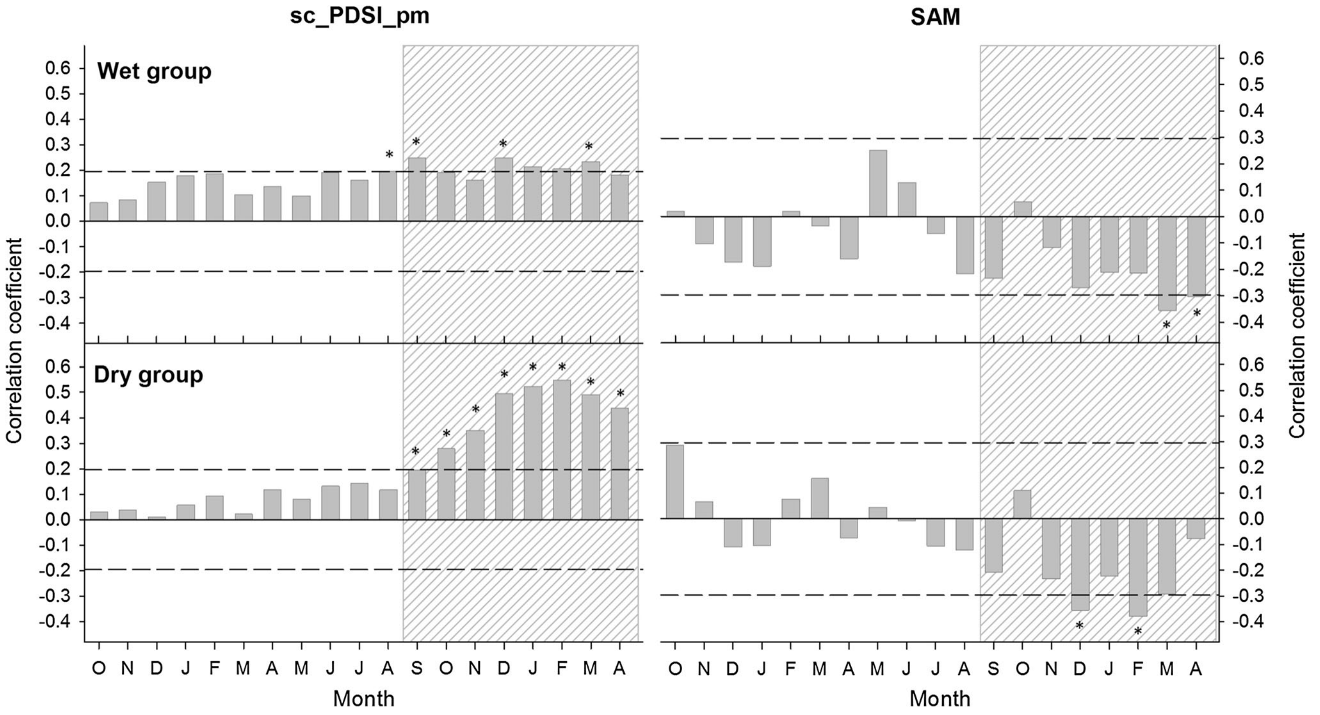


Fig. 5 Correlation coefficients between the PC1 amplitudes for the wet (*upper panels*) and dry (*lower panels*) groups of chronologies, and monthly sc_PDSI_pm for the interval 1900–2000 (*left panels*) and monthly SAM for the interval 1957–2000 (*right panels*). In both *panels*, the *shaded areas* represent the current growing season (October–April) and the *dashed lines* the 95 % confidence limits ($r = \pm 0.196$; $P < 0.05$ for PDSI and $r = \pm 0.297$; $P < 0.05$ for SAM)

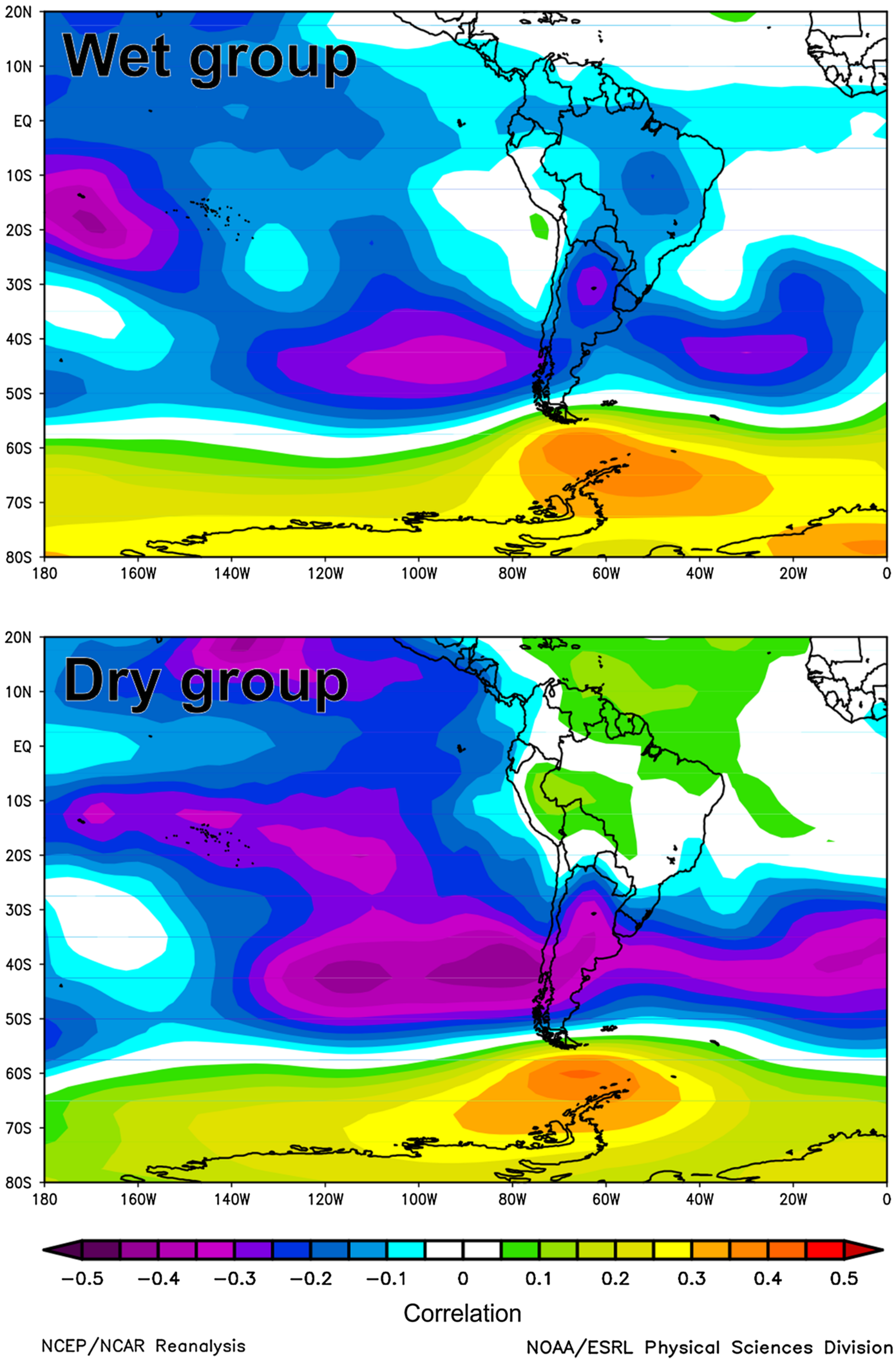
the growing season negatively affected tree growth even at places where water is supposed not to be limiting for growing. On the other hand, during cool and wet growing seasons, lower tree-ring indexes are more frequent at stands located in the westernmost locations (Fig. 7).

Stability in climate–tree growth relationships

The variability within chronologies changed between dry and wet group and toward the mid of the twentieth century. For wet group, the mean sensitivity (ms_x) showed a sustained increasing trend since the mid-1940s, coincident with an increase in regional drought in northern Patagonia (Table 2; Villalba et al. 2003; Masiokas et al. 2008). In contrast, the mean sensitivity showed a decrease since the mid-1950s for the dry group (Table 2). Consistent with ms_x, the proportion of narrow rings in wet group increases along the twentieth century (significant fitted linear regression, Table 2) with break point coincident with the change in mean sensitivity (1940s), while frequency of wide rings decreased at the same period of time. The frequency of narrow rings in dry group steadily increased during the twentieth century, but kept stable since 1950s; while frequency of wide rings decreased at the same period of time.

Correlation analysis using 35-year moving windows supported the occurrence of a dominant climatic response along the gradient during most of the twentieth century, but also identified changes in climate–growth relationships over time providing a dynamic perspective in the response of tree growth to climate variations. Those changes were marked in both groups and could be interpreted as a trend to increased similarity in climate–tree growth toward the mid-to-end part of the twentieth century between dry and wet chronologies (Fig. 8). In particular, changes in climate–growth responses were detected during spring (Sep to Nov) and summer (Dec and Feb), whereas the relationships during the rest of the months remained stable. The influence of temperature on tree growth varied over time during October, November and February for the dry group. While the negative influence during October increased in strength since the end of 1960s, the relationship between growth and temperature during November and February showed a weak association since early 1960s and mid 1970s, respectively (Fig. 8). For the wet chronologies, weaknesses in climate–growth relationship were detected for November (since 1965) and February (since 1970; Fig. 8). In a similar way, changes in precipitation–growth relationships were detected almost for the same months. For dry chronologies, the inspection of the relationship between

Fig. 6 Spatial correlation patterns during the interval 1949–2000 between the PC1 amplitudes for the wet (*upper panel*) and dry (*lower panel*) groups of chronologies and 850 HPa geopotential height during the current December–March interval. Analyses were performed through the National Oceanic and Atmospheric Administration website (http://www.esrl.noaa.gov/psd/data/correlation/)



precipitation and tree growth showed the most notable change during October, November and February months. In this case, while the positive relationship during October slightly decreased since 1950s, the decrease in trend resulted more notable during November and February since that time. For chronologies in the wet group, changes in climate–growth relationship involve a declining trend in the positive relationship with September precipitation since 1955, and a possible change to a significant negative relationship with February precipitation since 1965 (Fig. 8). In addition, the slight negative relationship with January precipitation seemed to disappear since the mid of 1960s. Finally, both groups showed a positive trend in the relationship between December precipitation and tree growth along the twentieth century, but while the relationship resulted positive and significant during the whole period for dry chronologies, the relationship has become significant since mid-1960s for the wet group.

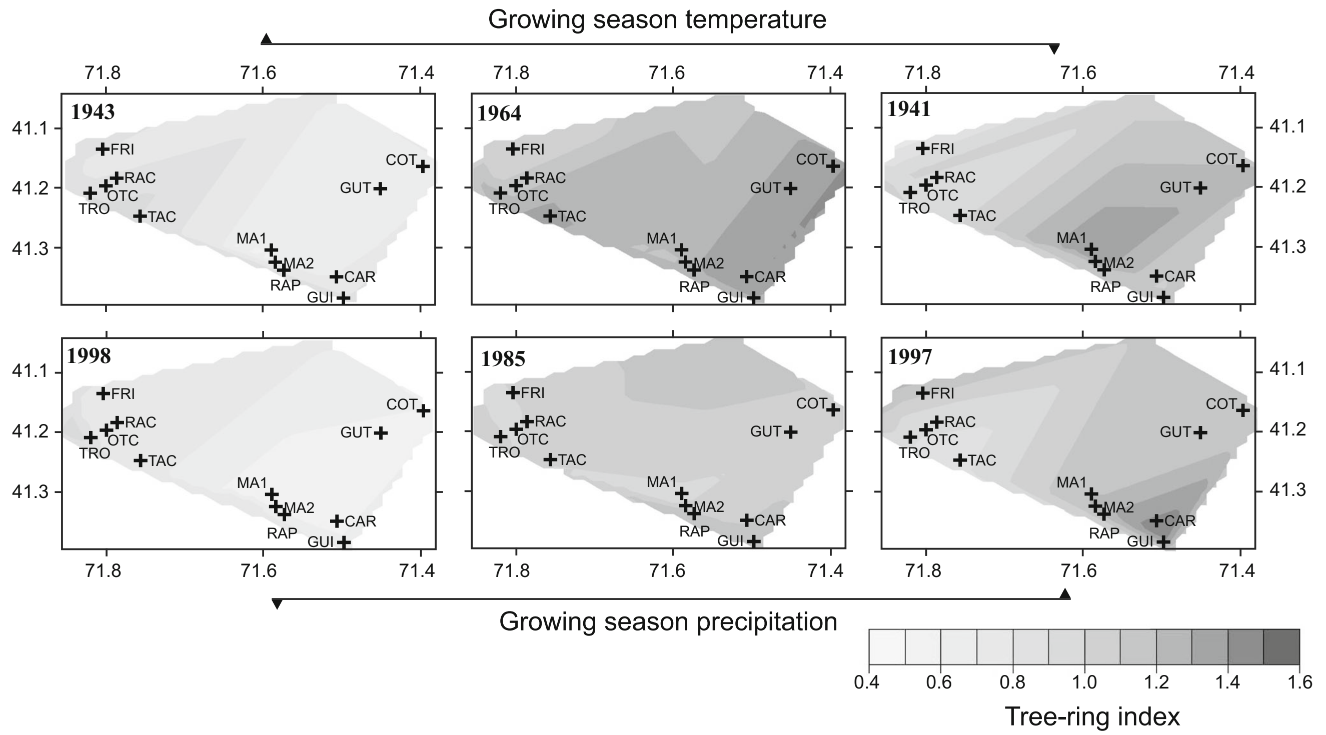


Fig. 7 Spatial patterns of tree-ring index (residual chronology) for particular years. The two droughts (1943 and 1998) highlight the strong influence of dry conditions along the precipitation transect, the 2 years showing the less common pattern of a different climatic response in high humid sites during humid or cold growing seasons (1941 and 1997), the years 1964 and 1985 correspond to climatic average years

Table 2 Piecewise regression of mean sensitivity, and narrow and wide rings (relative frequency of chronologies showing narrow/wide (<1.40 SD) tree-ring indices)

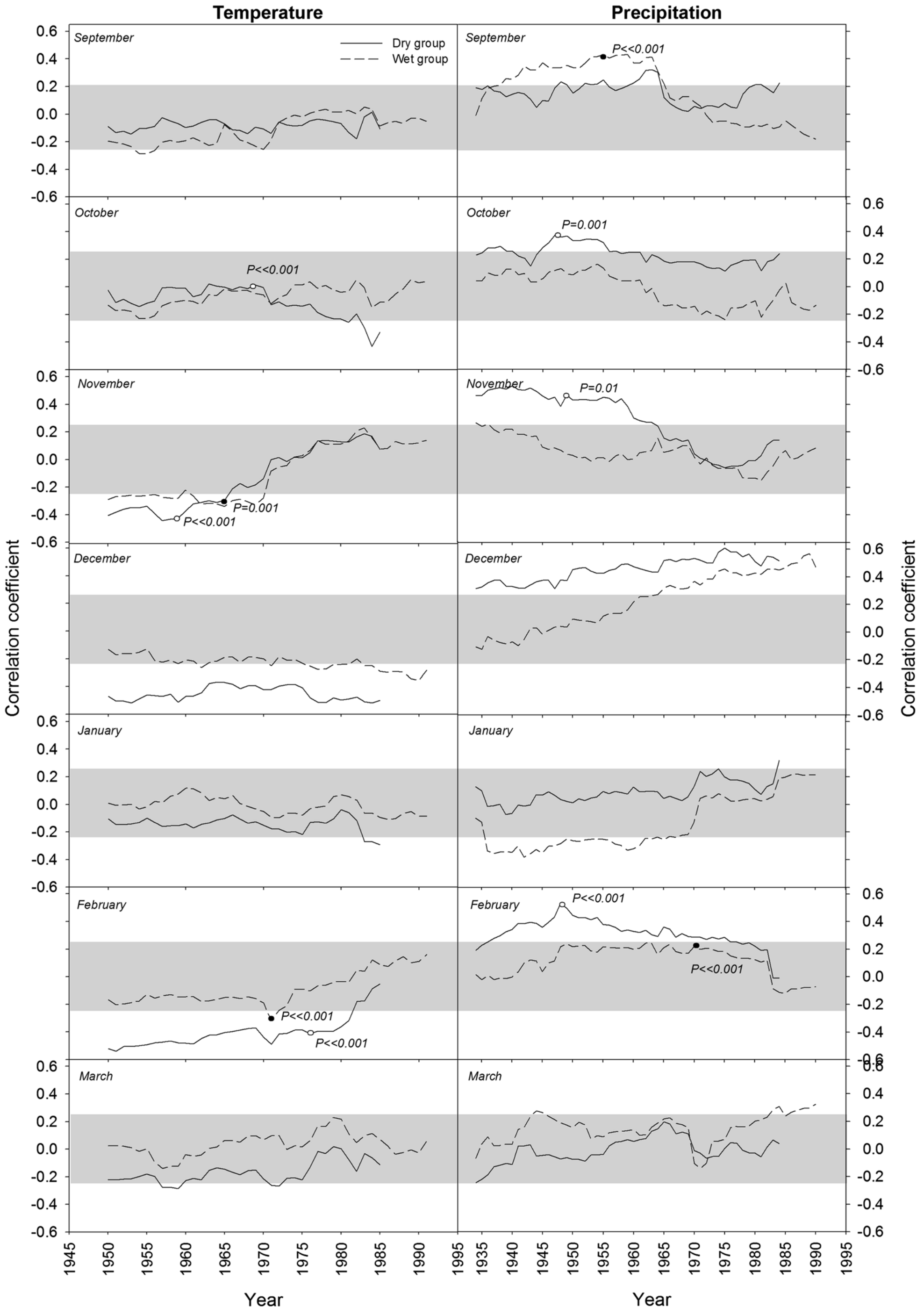
Variable	Linear trend (slope 1)	Break point (mid year)	Linear trend (slope 2)	*P*
Mean sensitivity				
Wet group	$y = -0.00038 \times \text{time} + 0.21$	1940	$y = 0.00086 \times \text{time} + 0.21$	$\ll 0.001$
Dry group	$y = -0.00092 \times \text{time} + 0.24$	1950	$y = -0.000093 \times \text{time} + 0.24$	$\ll 0.001$
Narrow rings				
Wet group	$y = -0.23 \times \text{time} + 7.07$	1942	$y = 0.31 \times \text{time} + 7.07$	$\ll 0.001$
Dry group	$y = 0.28 \times \text{time} + 11.5$	1950	$y = 0.01 \times \text{time} + 11.5$	0.01
Wide rings				
Wet group	$y = 0.69 \times \text{time} + 13.3$	1942	$y = -0.79 \times \text{time} + 13.3$	$\ll 0.001$
Dry group	$y = 0.60 \times \text{time} + 13.2$	1950	$y = -0.15 \times \text{time} + 13.2$	$\ll 0.001$

P values correspond to significance of break point selected in piecewise regression

Discussion

This study provides a regional perspective on the relationship between climate and radial growth of *N. dombeyi* along environmental gradients. Distinct environmental conditions between sites induce differences in the relationships between climate and tree growth. In our study, variations in the relationships between climate and *N. dombeyi* tree growth were evaluated at several sites along a strong precipitation gradient ranging from xeric, low-elevation (i.e., CAR) to wet (i.e., RAC) and high-elevation (i.e., OTC and TAC) sites. However, all chronologies show a strong regional common signal supported by the high amount of total common variance explained by PC1 (44.8 %), with only OTC and TAC showing slightly deviating from the main group on PC1. These results suggest common climate forcing of tree growth across the environmental gradient as recorded for *Araucaria araucana* in Northern Patagonia (Mundo et al. 2012). Although climate influences on tree growth vary

Fig. 8 Moving correlation coefficients estimated by the comparison of *N. dombeyi* tree-ring index and regional records of precipitation and temperature. Moving correlation functions were calculated for 35-year periods. The *gray areas* indicate significant bootstrapped correlation coefficients. The years correspond to the mid year of each interval. *Empty* (dry group) and *fill* (wet group) *circles* indicate significant breakpoint in the broken-line relationship



according to the local limiting factors operating at each site, the dominant factor regulating *N. dombeyi* growth along the gradients is the spring–summer water deficit induced by above-average temperatures and reduced precipitation during the current growing season (Figs. 4, 5).Correlation functions indicate that the water deficit in spring–summer is the common environmental forcing influencing tree growth across the study area. However, tree growth at high-elevation stands are less sensitive to growing season droughts but comparatively affected in large degree by warm conditions.

It is well known that dry conditions, commonly promoted by shallow soils, north to west-facing slopes, and relatively open canopy surroundings, increase soil water deficits inducing positive responses of tree growth to wet years (Villalba et al. 1998; Martínez-Vilalta et al. 2008;

Huang et al. 2010; Candel-Pérez et al. 2012). In this study, we recorded unfavorable conditions for tree growth at the driest eastern-located stands (Suarez et al. 2004). Above-average temperatures and low precipitations in February (the driest month of the year) deplete soil water inducing lower rates of tree growth than in mesic sites (e.g. GUT, MA1 and MA2, Fig. 4). Since stem growth constitutes a low priority in the photosynthate allocation for trees, the abundance of narrow or absent tree rings in the eastern-located, low-holding water capacity sites, is consistent with the large environmental stresses (Fritts 1976; Case and Peterson 2007). The observation that *N. dombeyi* growth at eastern locations is highly controlled by spring–summer moisture availability in the current growing season is also supported by the strong positive correlation between tree growth and PDSI and negative correlation with SAM over the same period (better growth during wet years). The PDSI index includes information on precipitation, temperature, evapotranspiration and soil moisture, representing a better indicator of drought conditions that limit *Nothofagus* growth at dry locations.

The growth of *N. dombeyi* appears to be also sensitive to factors limiting the formation of metabolic reserves in previous years, a common feature in many species worldwide (Huang et al. 2010; Chen et al. 2011; Bošel'a et al. 2014). The positive correlation between growth and previous summer precipitation could be related to the accumulation of reserves rather than to a direct effect of changes in soil water balance operating in the following growing season. Moister conditions, possibly in combination with moderate temperatures, reduce water stress, increase photosynthesis rates and facilitate carbohydrate storage to be used during the following growing season.

While climate conditions during the growing season modulate *N. dombeyi* growth at most sites along the gradient, the documented rise in temperature during the dormant season in northern Patagonia do not appear to be associated with any change in the rate of growth at the western, high-elevation sites. Dendroclimatic studies have demonstrated significant positive correlations between winter temperatures and radial growth for both evergreen and deciduous species at high-elevation sites (Villalba et al. 1997; Pederson et al. 2004; Lebourgeois et al. 2010). An earlier cambial reactivation, lower rate of root mortality, lower frost damages, and shorter periods of snow persistence has been invoked to explain this positive relationship. Positive influences of warmer winter (Jun–Aug) temperatures on *N. dombeyi* growth were only recorded at the most temperature-limited site close to 1500 m (OTC; Fig. 4). For *N. dombeyi*, warmer winters, possibly mediated by shorter periods of snow persistence, seem to improve radial growth at the highest elevation sites of its distribution.

Finally, the absence of stronger relationships between radial growth and growing season temperature at high- vs. low/mid-elevation stands is not consistent with most climate–growth relationship observed at high-elevation environments (Villalba et al. 1997; Case and Peterson 2007; Goldblum 2010; Yu et al. 2013). Whereas tree growth from stands at high altitudes generally shows positive relationships with growing season temperatures, this relationship for *N. dombeyi* is much weaker than those recorded for other species. For instance, high-elevation Douglas-fir stands show above-average radial growth during years with above-mean temperatures, whereas below-mean temperatures limit tree growth (Case and Peterson 2007). In the southern Andes, tree-ring records of *N. pumilio* along elevation gradients in Mount Tronador, Patagonia, display similar relationships with temperature (Villalba et al. 1997). At high-elevation sites (1700 m), tree growth is positively correlated with temperature, but strongly negative with precipitation, reflecting the cooling effect of clouds and/or wet snowstorms on growth during the growing period (Alberdi 1995). In contrast to *N. pumilio, N. dombeyi* is not present at the upper treeline in the Andes. It is likely that in addition to temperature, other environmental factors regulate the growth of *N. dombeyi* at its upper limit of distribution.

Stability in climate–tree growth relationships

In northern Patagonia, instrumental temperate records show that most of the warming during the twentieth century was related to a marked increase in temperature starting in 1977 (Villalba et al. 2003). For the last decades, droughts in northern Patagonia have become more frequent (Masiokas et al. 2008). In particular, the 1998–99 strong La Niña event in the tropical Pacific led to a severe drought in northern Patagonia, the strongest dry period in the context of the climatic variability over the last four centuries (Lara et al. 2008). This extreme drought was related to a widespread mortality event of *N. dombeyi* trees (Suarez and Kitzberger 2010). As drier conditions during the growing season are detrimental for the growth of *N. dombeyi* at most sites across its distribution in Argentina, we hypothesized an increase in the sensitivity of *N. dombeyi* to climate during the late twentieth century, even at the high-elevations sites.

Recently, it has been documented that climatic changes during the last decades may lead to temporal instability in climate–growth relationships (Tardif et al. 2003; Zhang et al. 2009; Lebourgeois et al. 2012; Yu et al. 2013; DeSoto et al. 2014). At wet sites near Mount Tronador, northern Patagonia, variations of the climate influences on tree growth (particularly during Nov and Feb) suggest that new limiting factors for tree growth have recently been operating at these sites. Warmer temperatures and lower rainfalls in the growing season during the past 3–4 decades may have enhanced soil water deficits that ultimately reduced growth even at the relatively humid sites. Conversely, the weakness of the relationships between climate and tree growth during summer (Feb) in most dry sites suggests a shortening of the period favorable for tree growth. Similar to Lebourgeois et al. (2012) findings, temperature sensitivity of tree growth at low-elevation sites increase until a physiological threshold is reached; afterwards tree growth is not connected to temperature. Considering the intense water deficits recorded in Patagonia over the last decades, some physiological processes in *N. dombeyi* trees could be limited during warmer and drier summers. In addition, our results show a reinforcement of the positive influence of late spring/early summer (Dec) precipitation on tree growth during the most recent decades. In comparison to climatic conditions prevailing during the first half of the twentieth century, recent warmer conditions in Patagonia might have induced an earlier onset of the growing season increasing the role of spring climate on determining tree growth.

In addition to the reported changes in the climate–tree growth relationship, we note an increase in the similarity of the tree growth response to climate during the last decades of the twentieth century. Changes in climate conditions affecting the onset or end of the growing season are modifying the climate–growth relationships. Whereas the influence of late summer climate on tree growth has decreased in recent decades, the influences of spring climate have increased. Therefore, the regional increase in aridity at the end of twentieth century might have favored the convergence to similar patterns in tree growth across the precipitation gradient in northern Patagonia. Since the negative influence of temperature during the summer months has also been recorded at humid and high-altitude sites in recent decades, our results indicate an increase in the vulnerability of *N. dombeyi* to droughts across its entire range of distribution east of the Andes. This findings support insights on a global convergence in the vulnerability of forests to droughts along its entire range, where forest decline and mortality are not only restricted to worsening environments predominant at drier regions (Choat et al. 2012).

Author contribution statement First author contributed to the original idea, sampling design, field sampling, chronologies building and analysis, and manuscript writing. Second and third authors contributed to field sampling, analysis and manuscript writing, and the fourth author contributed with MA1 and MA2 tree-ring chronologies.

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

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