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Relationships between climate variability and radial growth of *Nothofagus pumilio* near altitudinal treeline in the Andes of northern Patagonia, Chile

Claudio Álvarez [a,b,c,*], Thomas T. Veblen [a], Duncan A. Christie [b,c], Álvaro González-Reyes [d]

[a] Biogeography Lab, Department of Geography, University of Colorado, Boulder, USA
[b] Laboratorio de Dendrocronología y Cambio Global, Instituto de Conservación Biodiversidad y Territorio, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, Valdivia, Chile
[c] Center for Climate and Resilience Research (CR)[2], Chile
[d] Departamento de Geología, Universidad de Chile, Facultad de Ciencias Físicas y Matemáticas, Santiago, Chile

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ABSTRACT

Global warming is expected to enhance radial tree growth at alpine treeline sites worldwide. We developed a well-replicated tree-ring chronology from *Nothofagus pumilio* near treeline in a high precipitation climate on Choshuenco Volcano (40°S) in Chile to examine: (a) variation in tree radial growth in relation to interannual climatic variability; and (b) relationships of radial growth to variability in El Niño Southern Oscillation (ENSO) and the Antarctic Oscillation (AAO) at interannual and decadal time scales. A tree-ring chronology based on 99 tree-ring series from 80 *N. pumilio* trees near treeline showed a high series intercorrelation (0.48) indicating a strong common environmental signal. Radial growth is negatively correlated with precipitation in late spring (November–December). Temperature and tree growth are positively correlated during late spring and early summer (November–January). Interannual variability in both seasonal climate and in tree growth is strongly teleconnected to ENSO and AAO variability. Radial growth of *N. pumilio* in this humid high-elevation forest does not show a positive trend over the past half century as predicted from global treeline theory and broadscale warming in the Patagonian-Andean region. Instead, tree growth increased sharply from the 1960s to a peak in the early 1980s but subsequently declined for c. 30 years to its lowest level in >100 years. The shift to higher radial growth after c. 1976 coincides with a shift towards warmer sea surface temperatures in the tropical Pacific which in turn are associated with warmer growing season temperatures. The decline in tree growth since the mid-1990s is coincident with the increasingly positive phase of the AAO and high spring precipitation periods associated with El Niño conditions. The recent shift towards reduced growth of *N. pumilio* at this humid high-elevation site coincident with rising AAO mirrors the reduced tree growth beginning in the 1960s for trees growing in relatively xeric, lower elevation sites throughout the Patagonian-Andean region. The current study indicates that *N. pumilio* growth response in humid high-elevation environments to recent broad-scale warming has been non-linear, and that AAO and ENSO are key climatic forcings of tree growth variability.

1. Introduction

High elevation treelines are believed to be physiologically controlled by low temperatures implying that these ecotones should be highly responsive to global warming (Körner, 1998; Körner and Paulsen, 2004; Hoch and Korner, 2005). Recent research has shown that the *Nothofagus pumilio* treeline in the Patagonian-Andean mid-latitudes of South America is located at an isotherm of 6.6 °C for the growing season which matches the global pattern for most alpine treeline sites (Fajardo and Piper, 2014). For the Patagonian-Andean region centered on 42.5°S latitude, coarse scale (5° latitude) analyses of instrumental climate records indicate an increase of annual and growing season (October–March) mean temperature during 1901–2010 on the order of 1 °C (Veblen et al., 2011; Ji et al., 2014). Furthermore, tree-ring climate reconstructions in the northern Patagonian-Andean region (37°–46°S) show an increase of 0.53 °C

* Corresponding author at: Laboratorio de Dendrocronología y Cambio Global, Instituto de Conservación Biodiversidad y Territorio, Facultad de Ciencias Forestales y Recursos Naturales Universidad Austral de Chile, Valdivia, Chile.
E-mail address: dendro.alvarez@gmail.com (C. Álvarez).

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in mean annual temperature for the 20th century when compared with the mean over the 1640–1899 period (Villalba et al., 2003). Thus, according to conventional explanations of alpine treeline (e.g. Körner, 1998), one would predict increased tree growth near treeline in the Patagonian Andes under recent and continued warming. Although the treeline ecotone is widely considered to be a sensor of climate variability and an excellent environment to test the possible effects of global warming (Körner, 1999; Malanson et al., 2011), relatively few treeline studies have been conducted in the temperate latitudes of the southern hemisphere (Cuevas, 2000; Harsch et al., 2009).

In the Andes of northern Patagonia, large scale tropical and high latitude climate forcings modulate regional climate variability through teleconnections, and consequently should be reflected in tree growth patterns (Villalba, 2007; Villalba et al., 2012). The El Niño-Southern Oscillation (ENSO) and the Antarctic Oscillation (AAO; also known as the Southern Annular Mode, SAM) are the two main large scale climate forcings determining the regional climate of northern Patagonia, operating at different temporal scales and having distinct effects on local temperature and precipitation (Díaz and Markgraf, 2000; Villalba, 2007; Garreaud et al., 2009). These climate forcings influence regional climate variability, and therefore are expected to affect climate-sensitive ecological processes in the temperate forests of the Andes of Northern Patagonia. ENSO is the most widely investigated large scale driver, and is manifested as interannual (2–7 years) variability in sea surface temperatures in the tropical Pacific (Díaz and Markgraf, 2000). In Patagonian-Andean forests, ENSO variability has been shown to significantly affect radial tree growth (Villalba et al., 1997), tree seedling establishment in alpine treeline habitats (Daniels and Veblen, 2004), wildfire activity (Kitzberger and Veblen, 1997; Kitzberger et al., 1997; Veblen et al., 1999; Holz et al., 2012), and tree mortality events in forests and woodlands (Villalba and Veblen, 1998; Suarez et al., 2004).

The AAO is the most important extra-tropical climate forcing in the southern hemisphere. It is characterized by departures of opposite sign in atmospheric pressure at sea level over the Antarctic Continent and a circum-global band at 40°–50°S (Thompson et al., 2000; Miller et al., 2006; Garreaud et al., 2009). The persistent positive trend in the AAO since the 1950s has been associated with warmer and drier conditions over the northern Patagonian Andes (Aravena and Luckman, 2009; Garreaud et al., 2009). Interannual variability as well as the post-1950 positive trend in AAO have been shown to affect numerous ecological and hydrological processes in the Patagonian-Andean region, including radial tree growth (Christie et al., 2011; Villalba et al., 2012) and stream discharge in northern Patagonia (Lara et al., 2008; Urrutia et al., 2011; Mundo et al., 2012a), wildfire throughout Patagonia (Veblen et al., 1999; Holz and Veblen, 2011; Mundo et al., 2012b; Holz et al., 2012), rodent population dynamics in northern Patagonia (Murúa et al., 2003), and outbreaks of tree defoliating insects in *Nothofagus* forests in southern Patagonia (Paritsis and Veblen, 2011). However, there are no studies that address the potential effects of AAO variability on radial tree growth of high elevation trees on the humid western side of the Patagonian Andes.

According to conventional treeline control theory, broad-scale climate warming should favor upward advance of treeline and should enhance tree radial growth near altitudinal treeline (Körner, 1998; Körner and Paulsen, 2004; Hoch and Korner, 2005). Thus, in the current research we use dendrochronological methods to examine the potential effects of climate variability on tree growth of *N. pumilio* in a humid high elevation forest near treeline on Choshuenco Volcano (40°S), Chile (Fig. 1). Specific objectives are: (a) to examine the variation in tree radial growth in relation to interannual climate variability and determine relationships to monthly and seasonal temperature and precipitation variables, and (b) to examine possible associations of variability of tree radial growth to variability in ENSO and the AAO at interannual and decadal time scales.

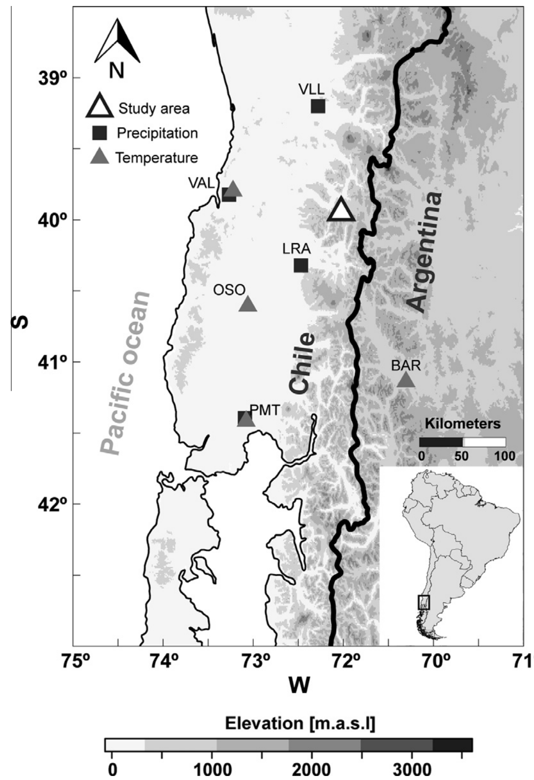

Fig. 1. (A) Location of the Choshuenco Volcano study area and weather stations of temperature and precipitation (for details see Table 1).

2. Material and methods

2.1. Study area

Data collection was conducted in January 2012 on the Chilean side of the Andes on the northwestern flanks of the Choshuenco Volcano at 39°53′S, 72°03′W near altitudinal treeline at elevations between 1350 to 1400 m above sea level (Fig. 1). In this section of the Andes, the summits of the Andean Cordillera generally reach altitudes between 2000 to 2700 m a.s.l. The climate in the study area is oceanic humid temperate with a mild Mediterranean-type influence. Precipitation origin is from the Pacific Ocean and is modulated by the westerly winds (Garreaud et al., 2009). The three nearest climate stations at elevations of 100, 210, and 845 m a.s.l. have mean annual of precipitation from 1946 to 2446 mm and mean annual temperatures ranging from 8.1 to 11.0 °C (Table 1). Precipitation is concentrated in April through August and during those months occurs mostly as snow above of 1000 m a.s.l. (Miller, 1976). Thus, moisture availability is least during the summer months of January through March. Within the century-long rise in growing season temperature since c. 1900 in the northern Patagonian-Andean region (40–45°S/70–75°W) temperatures temporarily cool during the 1960s and rise again after 1976 (Villalba et al., 2003; Veblen et al., 2011). Soils are andisols and have developed from parent material of volcanic ash (Hildebrand-Vogel et al., 1990), which under forests is marked by a black Ah-horizon rich in organic material. Soils are characterized by a high pore volume and high water infiltration rate. This structure results in soils with poor water retention capacity (Hildebrand-Vogel et al., 1990).

Table 1
Characteristics of climate stations used in dendroclimatic analyses.

Station	Parameter	P (mm) or T (°C) mean annual	Latitude (S)	Longitude (W)	Elevation (m)	Record period	Missing data (%)	Source
Villarrica	P	2113	39°12′	72°17′	210	1962–2009	1.36	DGA
Lago Ranco	P	1946	40°19′	72°28′	100	1959–2010	0.31	DGA
Valdivia (UACH)	P	2446	39°48′	72°15′	10	1900–2009	0	DGA
Valdivia (Pichoy)	P	2313	39°37′	72°05′	19	1960–2009	2.23	DMC
Puerto Montt	P	1847	41°25′	73°05′	85	1910–2010	0	DMC
Valdivia-Pichoy	T	11.0	39°37′	72°05′	19	1964–1999	3.15	DMC
Osorno	T	10.5	40°36′	73°03′	65	1961–2000	4.06	DMC
Puerto Montt	T	10.0	41°25′	73°05′	85	1960–2009	0	DMC
Bariloche	T	8.1	41°09′	71°18′	845	1931–2008	6.22	SMN

DGA: Dirección General de Aguas, (Chile); DMC: Dirección Meteorológica de Chile; SMN: Servicio Meteorológico Nacional (Argentina). P = total precipitation and T = mean temperature. UACh = Universidad Austral de Chile.

The study area is located within a National Forest Reserve (Mocho Choshuenco National Reserve) and is characterized by minimal anthropogenic disturbances. There are no roads or signs of past logging, burning or livestock in this environment. The most recent eruptions of the Choshuenco Volcano occurred in 1822 (Caldcleugh, 1836) and 1864 (Vidal Gormaz, 1869) but apparently were small ash eruptions. In comparison with other treeline sites on Volcanoes in southern Chile, there is relatively little area showing evidence of recent (i.e. 20th century) disturbance by volcanic ash falls or lava flow (Veblen et al., 1977). Sites showing obvious signs of recent disturbance (e.g. mudflows, snow avalanches) were avoided in selecting sample sites.

The species studied is *N. pumilio* which is a deciduous tree that can reach 30 m in height and up to 1.7 m of diameter, and can attain ages up to 400 years (Donoso, 1974; Rebertus and Veblen, 1993; Villalba et al., 2003). *N. pumilio* has an extensive latitudinal distribution along the Chilean and Argentinean Andes between 35° and 55°S (Donoso, 1993; Veblen et al., 1996), and from sea level to altitudinal treeline (Veblen et al., 1996; Lara et al., 2005). Along its extensive geographic distribution *N. pumilio* forms pure stands or is associated with other tree species such as *Araucaria araucana*, *Nothofagus antarctica*, *Nothofagus dombeyi* and *Nothofagus betuloides* among others (Veblen et al., 1996).

In the study area the upper forest limit is located between 1320 and 1500 m a.s.l., and is formed by pure old *N. pumilio* forests abutting alpine shrublands (Hildebrand-Vogel et al., 1990). From the lowest to the highest elevation the following structural types are present in the last 40 m of upper limit forest. Old pure forest of *N. pumilio* with erect trees from 20 to 25 m tall occur at the lower elevations. The most common shrub species found in the understory of old forest are *Drymys winteri*, *Maytenus disticha*, *Maytenus magellanica* and *Gaultheria phillyreifolia.* Immediately above the upper limit of old *N. pumilio* forest is a patchy belt of variable width of younger *N. pumilio* forest that appeared to have developed following avalanches or other types of snow-related disturbances. This belt was typically 8–16 m broad with small trees of 8–10 m of height, saplings and seedlings. Finally, upslope above the young forests there is a dense shrubland of 1.5–2 m in height and variable width from 5 m to more than 30 m approximately, composed mainly of *Embothrium coccineum* and *Berberis* spp.

2.2. Field sampling

Tree cores were collected from *N. pumilio* in old forest (i.e. stands not showing signs of coarse-scale disturbance within the past 100 years) located at the upper limit of tall forest in 24 belt transects. Belt transects were 20 m × 5 m in size and oriented upslope. For each tree in a belt transect, tree diameter at breast height (DBH) was measured. For this purpose, trees were defined as individuals >5 cm DBH. A range of 3–5 trees per 10 cm DBH class per transect were selected to core, and one or two cores per tree at 1.3 m height were extracted using increment borers. Trees selected for dendroclimatic analyses corresponded to trees of DBH > 25 cm with a dominant position in the canopy and healthy status.

2.3. Climate data and analyses of teleconnections with climate forcings

Nine climate stations closest to the sample site and with the longest and most complete records extending from 1900 to 2010 were used for analyses of tree growth response to individual climate records. Screening of station records resulted in the elimination of some records (e.g. temperature or precipitation) due either to missing records or trends in the data not observed in close by stations. Preliminary analyses yielded similar climate-growth results using individual stations which justified averaging them into a composite record for common periods beginning in 1954 and 1957 for precipitation and temperature, respectively (Table 1). Eight weather stations are located in Chile and one was located just east of the Andes in Argentina. Precipitation data are from the weather stations of Villarrica, Lago Ranco, Valdivia (Isla Teja), Valdivia (Pichoy) and Puerto Montt (Tepual). Weather stations used for records of temperature were Valdivia (Pichoy), Osorno, Puerto Montt (Tepual) and Bariloche (Table 1). Records selected had very few months of missing data, but in cases where data were missing the long-term average value was substituted.

Each record was normalized so that monthly standard deviations of temperature and precipitation could be averaged to create regional monthly records of precipitation and temperature departures. These composite regional records of temperature and precipitation departures were correlated at a monthly time-scale with the indices of the Southern Annular Mode and ENSO described below. In order to remove serial autocorrelation in the time series, datasets of temperature, precipitation and indices of climate forcings were prewhitened with an autoregressive model using the AR function in the R-project program (R Development Core Team, 2013). Prewhitening removes the persistence in a time series so that the residual may be more suitable for studying the influence of climate on tree growth.

2.4. Tree-ring chronology development

Standard dendrochronological procedures were used to develop chronologies of tree-ring width variations (Fritts, 1976; Cook et al., 1990). Tree cores were mounted, sanded using sandpaper of increasingly finer grain, and dated following the techniques outlined in Stokes and 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 calendar year in which tree growth started (i.e. November). Tree-ring widths were measured under a microscope to the nearest 0.01 mm, and the computer program COFECHA (Holmes, 1983) was used to quantitatively detect measurement and possible crossdating errors. After ring-width series were crossdated each series was standardized with a negative exponential curve or linear regression, and then averaged with a biweight robust mean to produce a standard tree-ring chronology for the study area utilizing the ARSTAN program (Fritts, 1976; Cook and Holmes, 1984; Cook et al., 1990). This standardization procedure of the ring-width series is intended to remove the effects of decreasing ring width due to tree age, disturbances and competition while also preserving the variance of low frequency variability in the series (Fritts, 1976). This process detrends the ring-width series, reduces the variance among cores, and transforms ring widths into dimensionless index values.

2.5. Analysis of relationships of tree growth to climate variability

We utilize correlation function analysis to examine the relationships between monthly climate variables and the tree-ring chronology. The R program package bootRes was applied which uses bootstrap resampling to obtain robust estimates of the significance of correlation coefficients (Zang and Biondi, 2013). This method consists of correlating the interannual variations in the standardized ring widths with monthly variations in climatic data. Because radial growth often shows a significant relationship with climate conditions one year prior to the formation of an annual ring (Fritts, 1976), correlation analyses were performed for a 22 month period from June of the previous growing season through March of the current growing season.

2.6. Analyses of relationships between climate forcings and tree growth

To evaluate relationships between tree growth and large-scale climate forcings, we utilized correlation functions between the *N. pumilio* tree-ring chronology and prewhitened monthly indices of ENSO and the AAO. The indices of ENSO and AAO utilized were the Multivariate ENSO Index (MEI) and the AAO-NCEP index, respectively. The MEI is based on six variables recorded over the eastern tropical Pacific including Sea Surface Temperature (SST), air surface temperature, Sea Level Pressure (SLP), zonal and meridional components of the surface wind, and total cloudiness fraction of the sky (Wolter and Timlin, 2011, http://www.esrl.noaa.gov/psd/enso/mei/). Positive (negative) values of MEI indicate warm (cold) phases of ENSO (i.e. El Niño (La Niña)-like conditions). The AAO index is calculated from SLP anomalies south of 20°S (Thompson et al., 2000; NOAA www.cpc.noaa.gov/). In addition to annual correlations with monthly indices, moving windows of 10 and 15 years were used to examine decadal-scale relationships between the tree-ring chronology and the MEI and AAO for the tree growing season months (October–March).

To determine the main oscillatory modes and cycles of *N. pumilio* growth we employed the Multi-Taper Method (MTM) (Mann and Lees, 1996), and we performed a Continuous Wavelet Transform analysis (WT) to expand the tree-ring chronology into time–frequency space and localize intermittent periodicities in the record (Torrence and Compo, 1998). Finally, to evaluate causal relationships in the time–frequency space between the *N. pumilio* growth and climate forcings at a century scale, we conducted Cross Wavelet Transform (XWT) analysis (Grinsted et al., 2004) between the *N. pumilio* chronology and the most recent ENSO and AAO reconstructions. For this purpose we used the tree-ring ENSO and AAO reconstructions recently developed by Li et al. (2013) and Villalba et al. (2012), respectively. Cross Wavelet Transform analysis shows the common power and relative phase between time-series in the time–frequency space, to determine whether they present a consistent phase relationship, and consequently whether they are physically related (Jevrejeva et al., 2003). Monte Carlo methods were used to assess the statistical significance against autocorrelation persistence (Grinsted et al., 2004).

3. Results

3.1. Teleconnections of local climate variability to climate forcings

Regional temperature (based on the composite record of the Valdivia, Osorno, Bariloche and Puerto Montt weather stations) tends to be positively correlated with MEI during the summer season and is statistically significant in March ($r = 0.36$; $p < 0.05$; Fig. 2A). Thus, El Niño-like conditions (warm tropical sea surface temperatures) are associated with warmer summers. Regional precipitation (based on the composite record of the Villarrica, Valdivia, Lago Ranco and Puerto Montt weather stations) is positively correlated with the MEI index in spring (October and November; $r = 0.39$ and $r = 0.35$ respectively; $p < 0.05$) but is negatively correlated with MEI in summer (January and February; $r = -0.35$ and $r = -0.27$ respectively; $p < 0.05$) (Fig. 2A). Thus, El Niño-like conditions are associated with wetter springs and drier summers.

Negative correlations between the AAO and regional precipitation occur during spring (September through December) and again during late summer (February–March) and early fall (April–May; Fig. 2B). Thus, positive AAO is associated with reduced precipitation over most of the year, and particularly in late spring (December). Regional temperature and AAO are negatively correlated in August of the current growing season ($r = -0.33$ $p < 0.01$; Fig. 2B) but tend to be positively correlated during spring–summer (October, December and February; Fig. 2B). Thus, positive AAO is associated with warmer–drier springs (October and December) implying earlier snowmelt, and with warmer–drier summers (February).

3.2. Tree-ring width chronology and climate influence on tree-growth

The resulting chronology of 99 tree-ring series from 80 trees covered the time period from 1768 to 2010 (Fig. 3). The mean series intercorrelation of 0.48 indicates a highly similar pattern of annual variability in tree-growth across the site sampled which covered a narrow elevation range from 1326 to 1484 m. Sample depth (i.e. number of tree-ring series included) exceeds 10 tree-ring series after ca. 1830 and exceeds 40 after c. 1877.

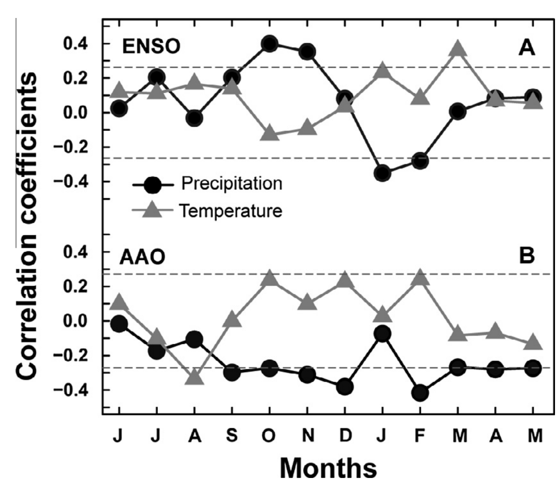

Fig. 2. Correlation coefficients of monthly temperature (1957–2010) and precipitation (1954–2009) with monthly values of MEI (ENSO index) (A) and AAO (B) from 1954 to 2010. All correlations were calculated using pre-whitened values from autoregressive models of the temperature and precipitation variables, MEI and AAO. Black lines indicate precipitation and grey lines indicate temperature. Dotted horizontal lines indicate confidence intervals and statistical significance ($p < 0.05$).

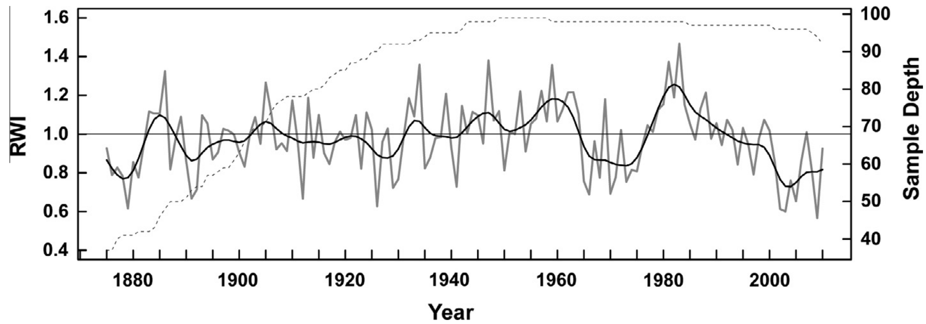

Fig. 3. Tree-ring width annual indices (RWI; gray trace) and sample depth of the standard chronology of *N. pumilio* in old forests near altitudinal treeline on the Choshuenco Volcano. The chronology starts at 1875 when at least 40 tree-ring series are included. Dotted line indicates sample depth per year (number of tree-ring series). Ten years smoothing cubic spline (black line) was designed to emphasize the decadal scale variations of the tree-ring chronology.

Radial tree growth is negatively correlated with late spring precipitation (November and December; $r = -0.40$ and -0.33 $p < 0.05$, respectively; Fig. 4A). Thus, above average November–December and April precipitation reduces radial tree growth during the current growing season. Temperature and tree growth are positively correlated during early summer of the current growing season (November $r = 0.24$ $p < 0.05$, December $r = 0.39$ $p < 0.01$ and January $r = 0.24$ $p < 0.05$) (Fig. 4B). Thus, there is a consistent association of above average growth with warmer and drier spring to early summers and early falls. Late spring- early summer precipitation (November–December) and tree-ring width indices tend to track each other closely but are inversely related ($r = -0.53$; $p < 0.05$; Fig. 5B).

Tree growth is positively correlated with late spring and early summer temperature (November through January; $r = 0.42$; $p < 0.05$; Fig. 5C). The synchrony of the temperature curve with tree growth is greatest from the 1970s to the mid-1990s. However, after the mid-1990s tree growth declines while November through January temperature remains relatively steady (Fig. 5).

3.3. Climate forcings and tree growth relationships

Monthly MEI of the previous growing season tends to be positively correlated with tree-ring growth, and MEI in March is significantly correlated with tree growth ($r = 0.28$, $p < 0.05$; Fig. 6). Thus, El Niño-like warm conditions in the eastern tropical Pacific are followed a year later by above average tree growth. This is consistent with the association of El Niño-like conditions with warmer and drier summers (Fig. 2A) and the positive correlation of warmer and drier late springs–summers with tree growth. Tree growth tends to be positively correlated with AAO index during spring (October through December) of the current growing season (Fig. 6). The association of enhanced tree radial growth with positive AAO is strongest in late spring to early summer when the correlation reaches statistical significance for November ($r = 0.32$, $p < 0.05$; Fig. 6).

The relationships between tree growth and climate forcing (ENSO and AAO) seem to be non-stationary. Over the period from 1950 to 2010, the correlation of tree growth with MEI for the months of October through March at a time scale of 10–15 years shifts from positive to negative (Fig. 7A). From a peak positive correlation in the 1970s it declines to a consistently negative correlation after c. 1980 (Fig. 7A). Conversely, the correlation between the

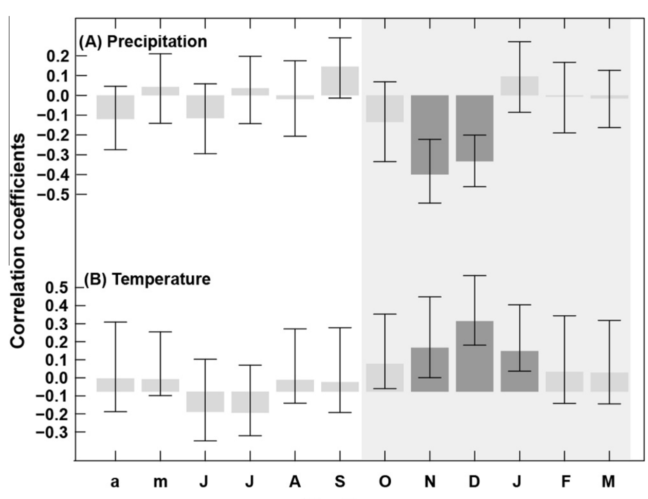

Fig. 4. Correlation coefficients between monthly precipitation (A) and mean monthly temperature (B) from the composite regional climate record, and annual tree-ring indices from the standard chronology of *N. pumilio* for 1954–2009 and 1957–2010, respectively. Weather stations used are given in Table 1. The shaded area represents current growing season (October through March). The darker bars indicate a correlation coefficient significant at $p < 0.05$; the vertical lines represent 95% confidence intervals.

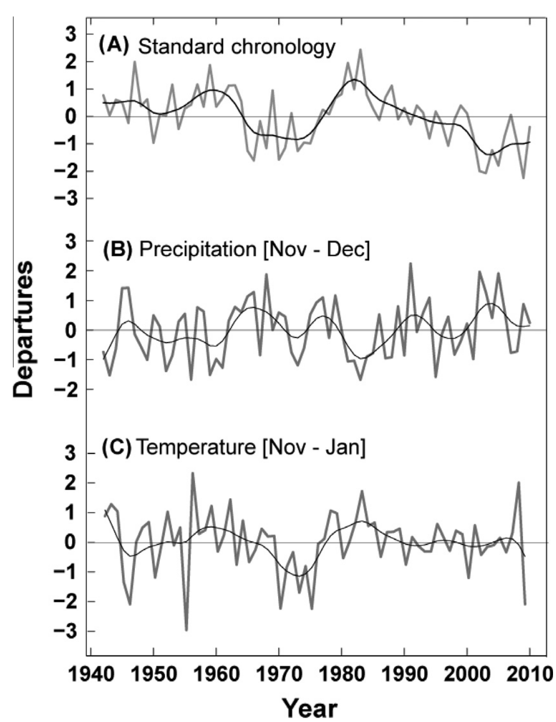

Fig. 5. (A) Tree-ring index (standard chronology) of *Nothofagus pumilio*. (B) November and December total precipitation. (C) Mean temperature of December through January. The black continuous lines are 10-year smoothing splines.

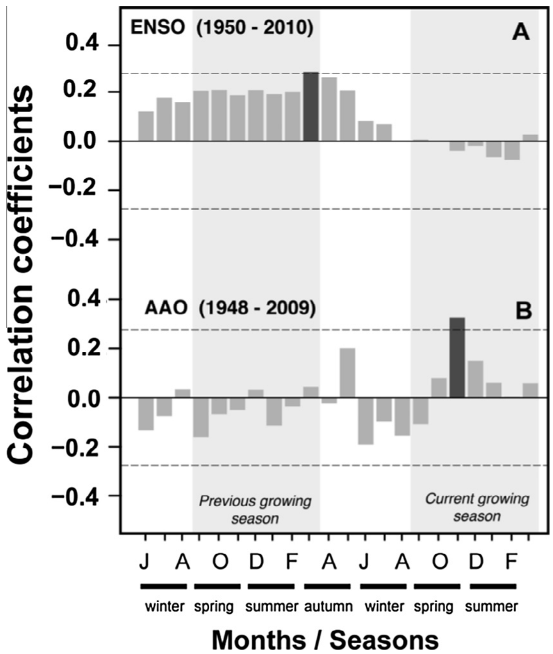

Fig. 6. Correlation coefficients between monthly indices of MEI (A), and AAO (B) and annual departures (standard deviations) of ring-width indices from the standard chronology of *Nothofagus pumilio* for the periods 1950–2010 and 1948–2009, respectively. Analyses were performed for 22 month periods including the current and previous growing seasons. The darker bars indicate a correlation coefficient significant at $P < 0.05$ and dashed horizontal lines represent the 95% confidence intervals.

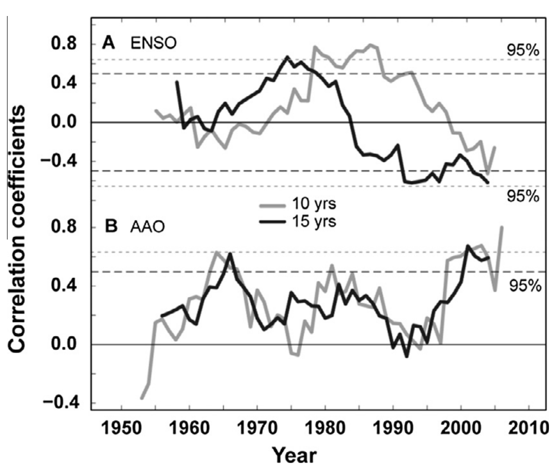

Fig. 7. Running correlations of the standard chronology of *N. pumilio* with MEI index from ENSO (A) and AAO-NCEP index (B) for growing season (October through March). The moving windows are 10 and 15 years. Horizontal dashed and dotted lines indicate 95% confidence intervals for the 10 and 15 years moving windows respectively.

standard chronology and AAO during the growing season (October–March) remains positive from the 1950s onwards and with periods of statistical significance (Fig. 7B).

The results of the Multi Taper Method spectral analysis of the tree-ring chronology show that tree-growth exhibits significant oscillatory modes both at sub-decadal (2.5, 2.7 and 5.1 years) and multi-decadal frequencies (27.7 years; Fig. 8A). However, the continuous Wavelet Transform spectral analysis demonstrates that these spectral modes are intermittent and non-stationary, with tree-growth exhibiting high spectral power in the high-frequency domain (<7 years) before the 1970s and in the low-frequency domain with multi-decadal periodicities before 1900 and after 1940 (Fig. 8B). With respect to the Cross Wavelet Transform spectral analysis between the *N. pumilio* tree-ring chronology and the large-scale climate forcings, the results show that tree growth has an intermittent physical association with the ENSO and AAO reconstructions at a sub-decadal scale during the period from 1880 to 2005 (Fig. 8C and D). Moreover, the tree-ring chronology shows a constant association with the AAO reconstruction in the low-frequency domain since 1940 (Fig. 8D). These results imply an intermittent physical association between tree growth and ENSO and AAO at an interannual scale and also between tree growth and AAO at a low frequency scale since the middle of the 20th century.

4. Discussion

4.1. Tree-ring chronology and decadal scale trends in the growth of N. pumilio

The tree-ring chronology developed from 99 ring-width series from 80 trees provided a suitable record of *N. pumilio* tree growth to examine the climatic influences on tree growth variability during the last century in this humid high-elevation forest in the Patagonian Andes. Specifically, this well-replicated chronology included 40 tree-ring samples since 1877 and more than 90 samples after the year 1940. The mean series intercorrelation of 0.48 is high in comparison with previous dendrochronological research on this species (e.g. 0.13–0.39 for 8 chronologies in Lara et al., 2001). The high series intercorrelation indicates that the trees growing near the altitudinal forest limit on the Choshuenco Volcano have a high common climate signal in their radial growth.

The *N. pumilio* tree-ring chronology shows two strong declines since the second half of the 20th century, a sharp and short-lived decline between 1960 and 1970 which is coincident with a well-known decadal scale cooling in northern Patagonia, and a second long-lasting decline after the early 1980s (Fig. 3). A sharp increase in tree growth from 1976 to the early 1980s was coincident with increases in November–January temperature (Fig. 5C). The association of above average tree growth with warmer temperatures from 1976 to the early 1980s was also found for *N. pumilio* at sites near treeline on Mont Tronador at 41°S on the eastern leeward side of the Andes (Villalba et al., 1997). Trends in the growth of *N. pumilio* in high-elevation forests on Mont Tronador and in the current study on Choshuenco Volcano are highly similar over the 1950 to 1990 period when the Tronador record ends (Villalba et al., 1997).

The steep reduction in *N. pumilio* growth on Choshuenco Volcano after the early 1980s (Fig. 3) is similar to declines reported for tree species growing in relatively xeric lower elevation habitats at numerous sites across the Patagonian-Andean region and attributed to a drying hydroclimate linked to the unprecedented upward trend in the AAO (Villalba et al., 2012). Growth reductions since the early 1980s are reported for *Austrocedrus chilensis* and *A. araucana* on both the Chilean and Argentine side of the Andes at latitudes 32° to 43°S (Christie et al., 2011; Mundo et al., 2012a; Villalba et al., 2012). Reduced growth with warming in these less humid habitats is expected, but the Choshuenco study site is a cool high elevation site with a high annual precipitation estimated from a short-lived weather record from a nearby treeline site to be at least 4000 mm (Veblen et al., 1977). Further consideration of the influences of seasonal precipitation and temperature on the growth of *N. pumilio* below helps to explain this apparent paradox.

4.2. Influences of climate variables on tree growth

The correlation analyses yielded a coherent pattern of how regional monthly temperature and precipitation influence the radial

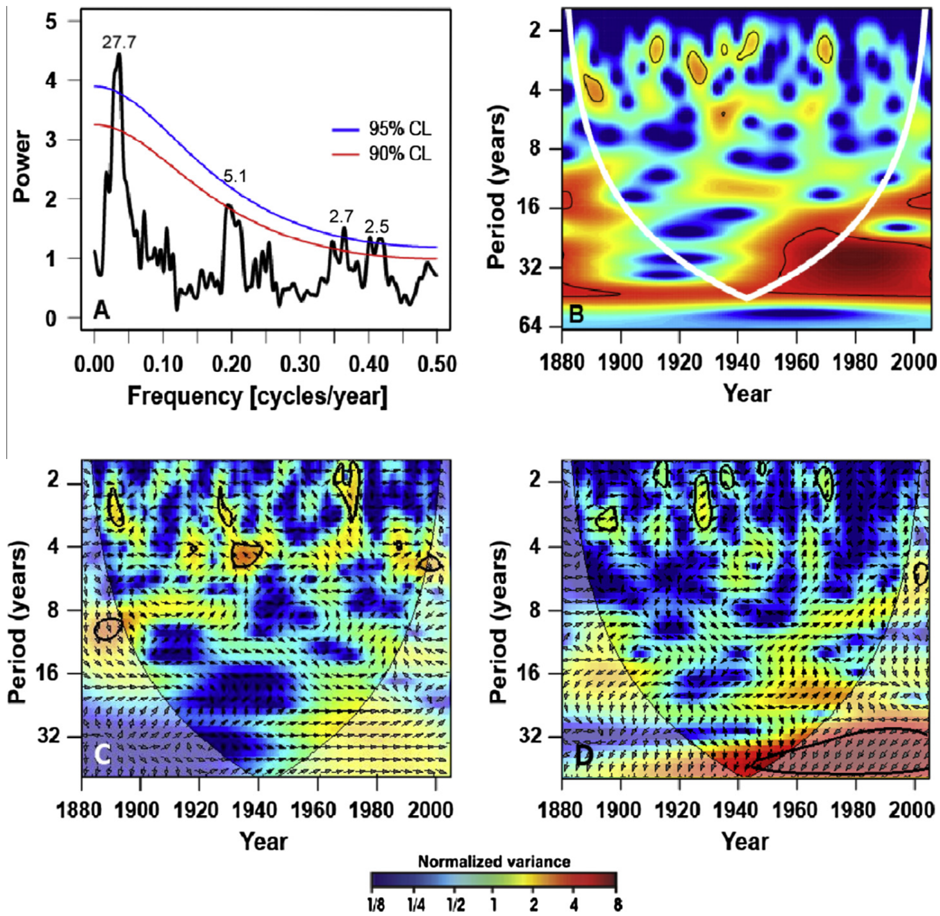

Fig. 8. (A) Multi Taper spectral Method (MTM) of *Nothofagus pumilio* growth (standard chronology); the continuous red (blue) line indicates 90% (95%) confidence limit. (B) Continuous Wavelet Transform (WT) for detection of spatial and temporal cycles in the *N. pumilio* standard chronology. (C) Crosswavelet analysis (XWT) between the *N. pumilio* standard chronology and ENSO index reconstructed (Li et al., 2013) for the period 1880–2005. (D) Crosswavelet analysis (XWT) between the *N. pumilio* standard chronology and AAO index reconstructed (Villalba et al., 2012) for the period 1880–2005. Red tone indicates higher power spectrum, black thick contours denote 95% significance level using a red noise background, and the white line delimits the cone of influence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

growth of *N. pumilio*. Nevertheless, an important caveat in interpreting the results derives from the fact that all the weather stations are located at low elevation. Overall, above average tree growth for *N. pumilio* at altitudinal treeline is associated with below average precipitation in late spring (November–December; Fig. 4A). During those months most of the precipitation at the elevation of the study site would be in the form of snow. Previous research based on snow cover data in similar environments in Patagonia concluded that spring snow persistence depends primarily on November precipitation and temperature which positively and negatively correlate with snow persistence, respectively (Villalba et al., 1997). Higher temperatures in December favor liquid precipitation and melting of snow. The combination of reduced November precipitation with higher temperatures (Fig. 4B) implies that earlier snowmelt accounts for the observed increase in tree growth from c. 1976 to the mid-1980s at Choshuenco Volcano. These results are consistent with similar findings at other *N. pumilio* sites near treeline on the eastern (leeward) and western (windward) sides of the Andes at Tronador and Conguillío (41°11′S and 38°37′S, respectively; Villalba et al., 1997; Lara et al., 2001) indicating that at sites with deep snow accumulation, *N. pumilio* growth is strongly controlled by snow cover duration into late spring-early summer.

The generally positive and negative associations of *N. pumilio* growth with seasonal temperature and precipitation, respectively, help to explain the decadal-scale trends in the *N. pumilio* growth on Choshuenco Volcano. The above average tree growth between 1976 and 1986 closely tracks rising summer temperature (November–January), and also coincides with reduced November–December precipitation (Fig. 5). Following the peak in November through January temperature during the 1980s, tree growth initiates a long-lasting decline. Tree growth is reduced to below the long-term average immediately following 1990, a year characterized by the wettest spring and fall in the record which was also cool implying exceptionally late and early snowfalls (Fig. 5B and C). Tree growth well below the long-term average after c. 2000 coincides with slightly above average November–January temperatures, a more significantly warmed growing season (October–March), and a sharp upward shift in annual temperature (Fig. 5C, Supplemental Fig. 1). Despite the increase in growing season temperatures since the mid-1960s in both the composite regional temperature record of the current study and the broad-scale gridded data for 40–45°S/70–75°W (Masiokas et al., 2008; Veblen et al., 2011; Ji et al., 2014), *N. pumilio* growth on Choshuenco Volcano has declined from a peak in the early 1980s.

4.3. Relationships between local climate, climate forcings, and tree growth

The positive correlation of MEI with tree-ring indices indicates that El Niño-like conditions in the tropical Pacific (i.e. warmer SSTs) are followed the next year by above average tree growth of *N. pumilio* (Fig. 6A). Our analyses through the year 2010 as well as previous studies document that the warm phase of ENSO is associated with warmer and drier summers in the study region (Fig. 2A; Daniels and Veblen, 2000; Montecinos and Aceituno, 2003). These teleconnected summer weather conditions are favorable to radial growth of *N. pumilio* at the Choshuenco Volcano study site (Fig. 4A). Analogously, positive anomalies of AAO during spring are linked to enhanced tree growth through a reduction in precipitation (Figs. 2B and 6B). Positive values of AAO imply a poleward shift of westerly storm tracks resulting in reduced precipitation at the latitude of Choshuenco Volcano. A recent tree-ring based AAO reconstruction shows that the present positive trend in the AAO index has reach unprecedented values in comparison with the last 600 years (Villalba et al., 2012), and according to climate models this trend will continue during the next 100 years with the subsequent effects of drier and warmer conditions in our study area (Miller et al., 2006).

According to correlation functions, positive interannual departures of both MEI and AAO should enhance tree growth due to their effects of elevated growing season temperatures and reduced spring precipitation, respectively (Figs. 3 and 6). Indeed, the steep increase in tree growth in c. 1976–1986 appears to primarily reflect effects of warmer tropical SSTs (positive MEI) on regional temperature (Fig. 5C, Supplemental Fig. 1) which has been documented to influence the growth of *N. pumilio* over a broad area in the Patagonian-Andean region (Villalba et al., 2003; Daniels and Veblen, 2004). However, both the AAO and Pacific tropical SSTs (correlated with MEI) continue to rise during the post-1976 period (Abram et al., 2014), yet tree growth declines sharply after c. 1980 (Fig. 5A). At a decadal time scale the correlations of tree-ring indices with MEI shifts from a positive correlation in the 1970s to a negative correlation after the early 1980s (Fig. 7A). The decline in tree growth since the mid-1990s exhibits a nonlinear departure from summer temperature potentially as a result of short-lived above average values in spring precipitation centered in the years 1992 and 2001 (Fig. 5B), or an exceeded threshold of moisture deficit in middle or late summer (Fig. 5). The mechanistic causes of the recent growth decline should be further investigated with different approaches including physiological measurements.

The results of the spectral analysis demonstrate that *N. pumilio* growth contains oscillatory modes at interannual to secular scales related to ENSO and AAO. The results of Multi-Taper Method and Wavelet Transform analyses of the chronology show that tree growth variability occurs at wave forms of high and low frequency over the 1880–2005 periods with sub- and multi-decadal cycles (Fig. 8A and B). Cross-wavelet Transform analyses between tree growth and large-scale forcing reconstructions show that although the tree-ring chronology shows associations with both forcings at a sub-decadal scale, the association is stronger with ENSO at cycles of 3 to 7 years over the entire period (Fig. 8C and D). In addition, cross-wavelet analyses show either in-phase or anti-phase behavior between the ENSO index and *N. pumilio.* For example, an anti-phase behavior exists from 1930 to 1940, a period in phase from the late 1960s to mid-1970s and again an anti-phase period from 1980 to c. 2000 (Fig. 8C) as indicated by the vector directions (Grinsted et al., 2004). These results are consistent with our findings of a shift from a positive to negative association between ENSO and tree growth (Fig. 7A). Moreover, since the 1940s to present the tree-ring chronology exhibits at the low-frequency scale common oscillation modes only with the AAO, demonstrating that during the last 135 years tree-growth has occurred at least partially associated with both climatic forcings.

The reduction in the growth of *N. pumilio* at this humid high-elevation site evident since the mid-1990s is coincident with the shift towards reduced tree growth observed since the 1960s for *Araucaria* and *Austrocedrus* at more xeric sites in Patagonia attributed to rising AAO (Villalba et al., 2012). It is also coincident with a higher frequency occurrence of El Niño-like conditions during the last decade (Li et al., 2013) associated with an increase in spring precipitation which decreases tree growth on the Choshuenco Volcano. Given the predicted regional climatic scenarios for this century of a continued positive phase of the AAO (Miller et al., 2006), an increase in the interannual variability of ENSO (Guilyardi et al., 2009), and warmer and drier climatic conditions (Fyfe and Saenko, 2006), it is likely that *N. pumilio* growth at this humid high elevation site on the Choshuenco Volcano will not increase linearly in association with continued regional warming. Instead, the growth of *N. pumilio* is likely to continue to decline. In contrast to the expectation of enhanced tree growth for a high precipitation site near altitudinal treeline due to broad-scale warming (Körner, 1998; Körner and Paulsen, 2004; Hoch and Korner, 2005) our results show a steep decline in tree growth over the past 30 years.

5. Conclusions

Radial growth of *N. pumilio* in a humid high-elevation forest near altitudinal treeline on Choshuenco Volcano failed to show an upward trend over the past half century as predicted from global treeline theory and broadscale warming in the Patagonian-Andean region. Instead, tree growth increased sharply from the 1960s to a peak in the early 1980s but subsequently has declined for c. 30 years to its lowest level in >100 years. Above average radial growth is most strongly associated with warmer spring-early summers and reduced spring precipitation. This pattern of tree-growth response to interannual climate variability is consistent with other studies of *N. pumilio* in high-elevations habitats of deep snow accumulation where excessive duration of snow persistence is correlated with reduced radial growth.

At a decadal time scale, the shift to higher radial growth of *N. pumilio* on Choshuenco Volcano in c. 1977 to the mid-1980s coincides with a shift towards warmer SSTs in the tropical Pacific (reflected by higher MEI) which in turn are associated with warmer growing season temperatures. During the decline in tree growth since the mid-1990s, summer AAO has been in an increasingly positive phase thus depressing precipitation in most months. Higher Pacific tropical SSTs during this period exacerbate warmer and drier conditions during the summer months but increase spring precipitation which in turn is negatively associated with *N. pumilio* tree growth. The present tree-ring record demonstrates that the relationships between *N. pumilio* growth and climate during the last 20 years appears to be more complex than the previous period, and that the periodicities of tree growth during the last 125 years are partially associated with the AAO and ENSO variability. The recent shift towards reduced tree growth of *N. pumilio* at this humid high-elevation site coincident with rising AAO mirrors the earlier tree growth reduction beginning in the 1960s broadly documented for trees growing in less humid sites in the Patagonia-Andean region. Overall, the current study indicates that the response of tree growth in humid high-elevation environments in northern Patagonia to broad-scale warming can be non-linear.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.01.018.

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