Influence of droughts on *Nothofagus pumilio* forest decline across northern Patagonia, Argentina

MILAGROS RODRÍGUEZ-CATÓN,† RICARDO VILLALBA, MARIANO MORALES, AND ANA SRUR

Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA–CONICET), Mendoza 5500 Argentina

Abstract. Understanding the influence of climatic variations on forest decline is a major challenge for scientists investigating global changes. Although reductions in tree growth have previously been associated with forest decline, comprehensive efforts to understand these relationships are rare. Based on ring-width variations, we determine the influence of climatic fluctuations on the onset and temporal evolution of *Nothofagus pumilio* forest decline in the Patagonian Andes. Basal area increment (BAI) data from 294 *Nothofagus* trees at 11 stands in a 500-km latitudinal transect along the forest–steppe ecotone were used to identify the dominant patterns of regional growth. Three *Regional dominant patterns*, showing common variations in BAI, were derived. Two BAI patterns show high rates of growth from early to mid-20th century, followed by sustained negative trends over the last 3–6 decades, whereas the third pattern is characterized by a positive trend since the 1960s. Tipping points in growth trends of the first two patterns are associated with two extreme dry–warm climate events in spring–summer of 1942–1943/1943–1944/1944–1945 and 1978–1979. Both severe droughts were preceded by up to 10 yr of wet periods that promoted above-average tree growth. We concluded that severe droughts occurring after wet periods trigger the decline of large, dominant *N. pumilio* trees with high rates of growth. The coincidence between major changes in regional growth with two of the most severe droughts in the instrumental records shows that climatic variations over northern Patagonia synchronize the beginning of forest decline at a regional scale. As these dry–mesic *N. pumilio* sites will face more severe droughts in the 21st century, as suggested by future climate scenarios, the areas affected by forest decline would increase substantially.

Key words: basal area increments; crown dieback; extreme climatic events; growth decline; plant–climate interactions; tree size.

Received 8 September 2015; revised 7 March 2016; accepted 23 March 2016. Corresponding Editor: C. Kwit.
† **E-mail:** mrodriguez@mendoza-conicet.gob.ar

INTRODUCTION

Climate fluctuations affect the dynamics, composition, and distribution of forest ecosystems (Walther et al. 2002). In recent decades, numerous reports around the world have associated forest decline and massive mortality with global climate changes (e.g. LeBlanc and Foster 1992, Allen et al. 2010, Carnicer et al. 2011, Zhou et al. 2014). Extreme climatic events have been postulated to act as triggers of forest decline in stands predisposed to be affected by physiological imbalances related to tree ages, stand history, or site characteristics (Manion 1981). Once the decline begins, other contributing factors such as insects and diseases promote or accelerate the loss of forest health leading to the death of previously stressed trees (Gaylord et al. 2013). The multiple interactions between affected trees and environmental factors make the comprehensive understanding of forest dieback and mortality extremely difficult (Franklin et al. 1987, Manion

and Lachance 1992, McDowell et al. 2008). However, the identification of the major causes of forest decline and its probable relationship with future, predicted climate changes is critical for implementing present forest management and long-term conservation practices.

To date, most studies have focused on the effect of climate variations on mortality events (van Mantgem et al. 2009, McDowell et al. 2010, Michaelian et al. 2011, Anderegg et al. 2013 and references therein). However, the role of climate as a trigger of forest decline has been comparatively poorly addressed (Leaphart and Stage 1971, Di Filippo et al. 2010, Liu et al. 2013). In our contribution, the terms "forest decline" and "forest dieback" do not necessarily involve or imply tree death, but refer to the premature processes such as crown defoliation and/or growth reduction that ultimately could lead to tree mortality.

Studies documenting the relationships between droughts and episodes of forest decline or mortality have largely been conducted in Northern Hemisphere forests (van Mantgem et al. 2009, Allen et al. 2010, Williams et al. 2013), but similar studies in the Southern Hemisphere are scarce. Extreme climatic events such as severe droughts, intense precipitation, or a combination of both were proposed as triggers of *Nothofagus* forest dieback in New Zealand (Grant 1984, Ogden et al. 1993). More recently, extreme drought events in the Patagonian Andes have induced extensive episodes of tree mortality in both *Austrocedrus chilensis* and *Nothofagus dombeyi* forests (Villalba and Veblen 1998, Suarez et al. 2004). Mundo et al. (2010) also documented a strong relationship between growth reductions in *A. chilensis* and water deficit in northern Patagonia. Following extreme drought events, the growth of decline-affected *A. chilensis* trees was consistently lower than in healthy trees.

Drought influences on forest dynamics are more evident in areas with limited water supply (Chang et al. 2014). For instance, interannual variations in soil moisture modulate the rates of tree growth, tree establishment, and tree mortality in the dry forest–steppe ecotone in northern Patagonia (Villalba and Veblen 1997, 1998, Mundo et al. 2010, Suarez and Kitzberger 2010). Given the strong precipitation gradient imposed by the Cordillera de los Andes, it is expected that decreasing water availability concurrent with higher summer temperatures would accentuate the water deficit in the most easterly *Nothofagus pumilio* forests. Toward the eastern edge of its distribution, *N. pumilio* radial growth is positively related to rainfall and negatively to temperature (Schmelter 2000). Consistently, field observations record a larger percentage of partial crown mortality in the dry *Nothofagus* forests near the eastern limits of its distribution (Veblen et al. 1996).

Dendrochronology is a useful tool to evaluate the role of climate events as a driving force of forest decline (Jump et al. 2006, Sánchez-Salguero et al. 2012). In this study, we determine the influence of climate on the decline of *N. pumilio* forests on the eastern border of its distribution in northern Patagonia. We use a combination of dendrochronological methods and instrumental data to link extreme climatic events with past changes in tree growth associated with forest decline. We postulate that the onset of long-sustained periods of *N. pumilio* growth reduction at the regional scale was induced by adverse climate events such as droughts. While other studies in northern Patagonia have associated mortality of *A. chilensis* and *N. dombeyi* with droughts (Villalba and Veblen 1998, Suarez et al. 2004), this is the first attempt to determine the relationship between extreme climatic events and *N. pumilio* forest decline in the Patagonian Andes.

MATERIALS AND METHODS

Study sites

The study sites are located along a 500-km transect on the eastern boundary of *Nothofagus pumilio* distribution in northern Patagonia, Argentina, between 38° and 43° S (Fig. 1). Most selected plots were located in pure *N. pumilio* stands near the eastern limit of the species distribution between 1000 and 1500 m of elevation. In this area, summers are mild and relatively dry, whereas winters are cold and wet (Fig. 2, Villalba et al. 2003). At these latitudes, there is a strong precipitation gradient from west to east due to the rain-shadow effect of the Andes. Therefore, trees located near the eastern boundary of *N. pumilio* distribution are more frequently affected by water stress than those located to the west. The steppe boundary at approximately
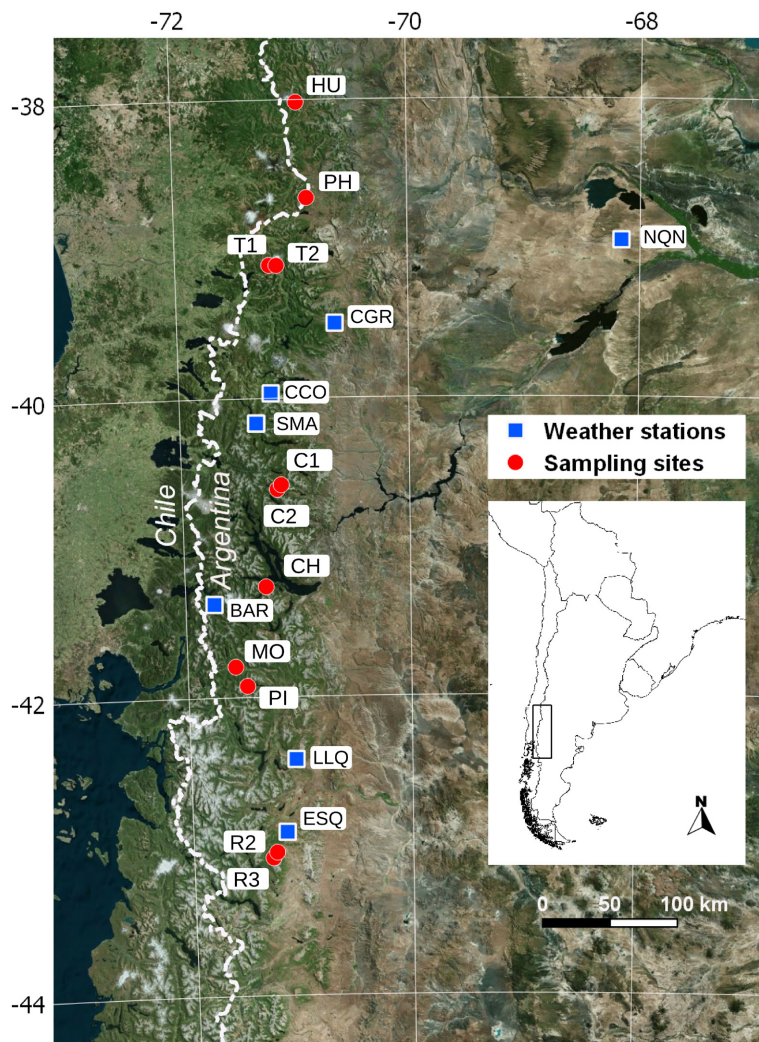
Fig. 1.   Geographical locations of selected sites and meteorological stations used for assessing the influence of climate on radial growth variations of *Nothofagus pumilio* in northern Patagonia (for codes of weather stations, see Table 1, and for codes of sampling sites, see Appendix S1: Table S1).

700 m elevation has annual precipitation of 800 mm, mainly in winter (Fig. 2). In northern Patagonia, December, January, and February are the driest and warmest months of the year (Fig. 2).

Basal area increment chronologies

Rodríguez-Catón et al. (2015) have previously described the dominant patterns of *N. pumilio* radial growth based on 294 trees from 11 stands in northern Patagonia showing external symptoms of forest decline. Principal components analysis (PCA) was used to identify the dominant trends of growth at each stand. PCA was applied to both ring-width index (RW) and raw basal area increment (BAI) series using a common period of ≥50 yr that allowed including as many trees as possible per plot. At most stands, the first two or three Principal Components (PCs) accounted for at least 45% of the total variance in RWs or BAIs. Rather than using the original PC scores, individual tree series of RWs and BAIs were grouped according to their similarities with the PCs ($r \geq 0.45$), and subsequently averaged to develop the dominant patterns of growth for RW and
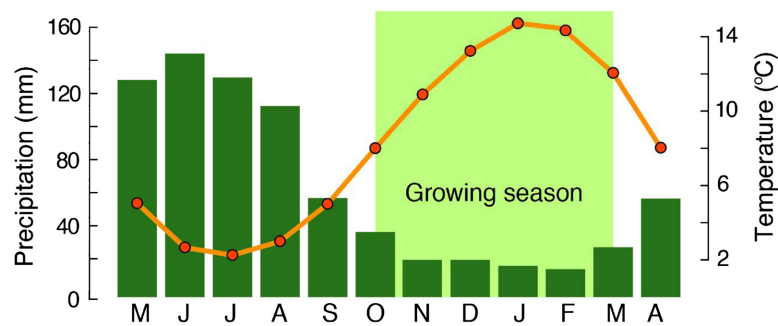
Fig. 2. Monthly total precipitation (bars) and mean temperature (dots) for Bariloche (700 m; period 1951–2009), northern Patagonia. Total annual precipitation and mean annual temperature at Bariloche are 803 mm and 8.1°C, respectively. The drought period for the region (November–March) coincides with the growing season of *Nothofagus pumilio.* A climate diagram figure following the method of Walter and Lieth (1960) was added as supplementary information to shed light on the drought period for northern Patagonia (Appendix S1: Fig. S1).

BAI at stand level. Thus, the new resulting growth patterns covered a larger period (more than 50 yr used to estimate the PCs), from 1880 to the sampling year, providing an extended perspective of long-term changes in tree growth. Each dominant pattern represented the common growth pattern from a subset of trees at the stand. Following Rodríguez-Catón et al. (2015), these dominant patterns of tree growth from the 11 stands were identified as *Local growth patterns* (see Appendix S1: Fig. S2 for *Local BAI growth patterns*). In a second step, the *Local growth patterns* from the 11 stands were correlated between them to identify common patterns at regional level. Those *Local growth patterns* exhibiting similar trends (mean intercorrelations $r \geq 0.3$, $P < 0.05$) were subsequently grouped to obtain the *Regional dominant patterns of tree growth*. Based on ring widths and BAIs, two and three Regional dominant patterns of *N. pumilio* tree growth, respectively, were identified by Rodríguez-Catón et al. (2015). As BAI measures are arguably better estimates of forest decline than ring widths (Johnson and Abrams 2009, Rodríguez-Catón et al. 2015), the BAI series composing each of the dominant patterns were used in this contribution. The three BAI chronologies were developed by averaging the raw BAIs from all trees within each pattern. In addition, we obtained residual chronologies for each growth pattern. Residual chronologies were developed by standardizing the BAIs using a horizontal line equal to the

series mean followed by autoregressive time series modeling (Cook 1985). This procedure eliminates the long-term trends in tree rings to provide a better representation of the high-frequency variations in tree growth. Chronologies were developed using the R package dplR (Bunn 2008, Bunn et al. 2012, R Core Team 2014). The quality of the chronologies was assessed by calculating the Rbar and Expressed Population Signal (EPS) statistics on 50-yr length windows lagged 25-yr between consecutive segments. Rbar is the mean correlation coefficient resulting from comparison of all 50-yr segments between series in a chronology (Briffa 1995). The EPS measures the total signal existing in the chronology in relation to an infinitely replicated chronology (Wigley et al. 1984). EPS values close to or greater than 0.85 indicate that the number of samples that integrates the chronology in a particular year contains a significant amount of the theoretical signal in an infinitely replicated chronology.

To evaluate the relationships between variations in tree growth and crown dieback, crown health conditions for each individual tree were grouped into one of four categories, namely class 1 (<25% of the crown dead), class 2 (25–50% dead), class 3 (50–75% dead), and class 4 (>75% dead). Diameter at breast height (DBH) was also recorded for each sampled tree. Significant differences in crown mortality and DBH between growth patterns were tested using Mann–Whitney rank test (Field 2009).

Table 1. Geographical locations and details of the selected meteorological stations used in this study.

Met. station	Code	Latitude S	Longitude W	Elevation (m)	Data	Period	Sources
Neuquén Aero	NQN	38°34'12"	68°04'48"	271	Temp	1957–2009	SMN
Ea. Campo Grande	CGR	39°30'00"	70°38'00"	960	Prec	1947–1998	CENPAT
Ea. Collun-co	CCO	39°58'00"	71°12'00"	875	Prec and Temp	1914–1998	SMN
S. Martín de los Andes	SMA	40°10'00"	71°20'00"	426	Prec	1936–1975	SMN
R. Manso-Los Alerces	RMA	41°22'25"	71°44'45"	770	Prec and Temp	1954–2012	SRH
S. Carlos de Bariloche	BAR	41°05'24"	71°06'00"	700	Prec and Temp	1951–2009	SMN
Leleque	LLQ	42°25'12"	71°03'00"	699	Pre	1921–1988	CENPAT
Esquel	ESQ	42°54'24"	71°08'48"	797	Prec and Temp	1901–2011	SMN

Notes: Data abbreviations are as follows: Temp, temperature; Prec, precipitation. Sources: SMN, Servicio Meteorológico Nacional; CENPAT: Centro Nacional Patagónico; SRH, Subsecretaria de Recursos Hídricos de la Nación.

Climatic records

Climatic records were obtained from eight meteorological stations along the north–south transect (Fig. 1, Table 1). Monthly total precipitation and mean temperature records from each station were normalized using the common intervals 1951–1975 and 1949–1989, respectively. The regional means were obtained by averaging the standard deviations from seven precipitation and five temperature records. Using standard deviations, each station contributes similarly to the regional mean, irrespective of the absolute values of precipitation and/or temperature related to each station (Villalba et al. 1997).

Climate–growth relationships

The annual BAI values of the three residual *N. pumilio* chronologies were compared with regional precipitation and temperature records using bootstrap correlation functions to establish the climate–growth relationships (Blasing et al. 1984). Monthly values from July of the previous year to April of the current year of growth (22 months) were included in the analysis. The relationships were documented over the common period 1914–2008. The R package bootRes was used for calculating the correlation functions (Zang and Biondi 2013, R Core Team 2014).

Climate–growth relationships were also evaluated through the recognition of characteristic, very narrow rings (pointer years). In our study, the pointer years are those in which 50% or more of all series in each BAI chronology showed a decrease of at least 15% in tree growth compared to the previous year. This procedure was conducted with the *pointer* function of dplR package (Bunn et al. 2012). The relationship between

pointer years and regional precipitation and temperature variations was examined using superposed epoch analysis (SEA) for the period 1914–2008. For the pointer years, we determined the climate conditions of the driest and warmest months (December and January, Fig. 1). For each event, a 5-yr window was examined which includes the 2 yr before and 2 yr following the pointer year. Based on 1000 Monte Carlo simulations of the observed temperature and precipitation variations, program Event provides the confidence intervals to determine the statistical significance of the mean climatic anomalies (Mooney and Duval 1993, Holmes and Swetnam 1994). Precipitation or temperature deviations larger than those expected by chance lie outside the 95% ($P < 0.05$) confidence intervals and are considered statistically significant climatic anomalies.

Abrupt changes in BAI

The most significant change in BAIs in each of the three chronologies over the period 1914–2008 was determined using piecewise linear regression (Venables and Ripley 2002). This technique detects the break point that maximizes the differences in regression trends before and after a selected point. After iteratively adjusting regression lines to all two consecutive segments of variable length in the time series, the most significant break point corresponds to the year showing the minimum mean squared error (Crawley 2007).

Following the break point determination, climate–growth relationships were assessed for 20-yr periods before and after the break point years to detect possible changes in growth

Table 2. Statistics from the *Nothofagus pumilio* basal area increment chronologies associated with the three dominant patterns of growth (R1, R2, and R3) at the regional scale.

Metric	R1	R2	R3
No. of trees	90	96	108
Entire length	1716–2008	1677–2008	1668–2008
EPS > 0.85	1895–2008	1830–2008	1895–2008
Mean Rbar	0.296	0.232	0.440

Note: Mean Rbar was estimated over the chronology periods with >10 tree-ring series.

response to climate after major changes in growth trends. The relationships between tree growth and a moisture index were estimated using Pearson correlation coefficients over the 20-yr interval before and after the break points. The moisture index was estimated by subtracting the standard deviations of spring–summer (November–March) precipitation from those of temperature over the same season (Villalba and Veblen 1998).

RESULTS

Regional BAI chronologies

Statistics for the raw BAI chronologies R1, R2, and R3 are shown in Table 2. The number

of trees composing the chronologies (*N*) varies between 90 and 108, and the periods covered by the chronologies vary between 293 (1716–2008) and 341 yr (1668–2008), but are best replicated since AD 1895 (R1), 1830 (R2), and 1895 (R3). Rbar and EPS values indicate that these BAI chronologies have an important common signal from the middle (R2) and the end (R1 and R3) of the 19th century (Table 2). Therefore, the three chronologies have the strong common signal needed to assess climate–growth relationships from the end of 19th century to the present.

The temporal development of the three regional patterns of growth is shown in Fig. 3, based on raw BAIs (upper) and residual indices (bottom). While the long-term variability in tree growth is observed in the raw BAI chronologies, the residual chronologies highlight the interannual variability in regional growth. Raw BAI chronologies R1 and R2 showed sustained reductions in BAI from the decades of 1940 (R1) and 1970 (R2) to the present. In contrast, the pattern R3 showed a positive trend in growth starting in the 1960s (Rodríguez-Catón et al. 2015).

The trees included in patterns R1 and R2 show persistent negative trends in growth and have both larger percentages of crown mortality and
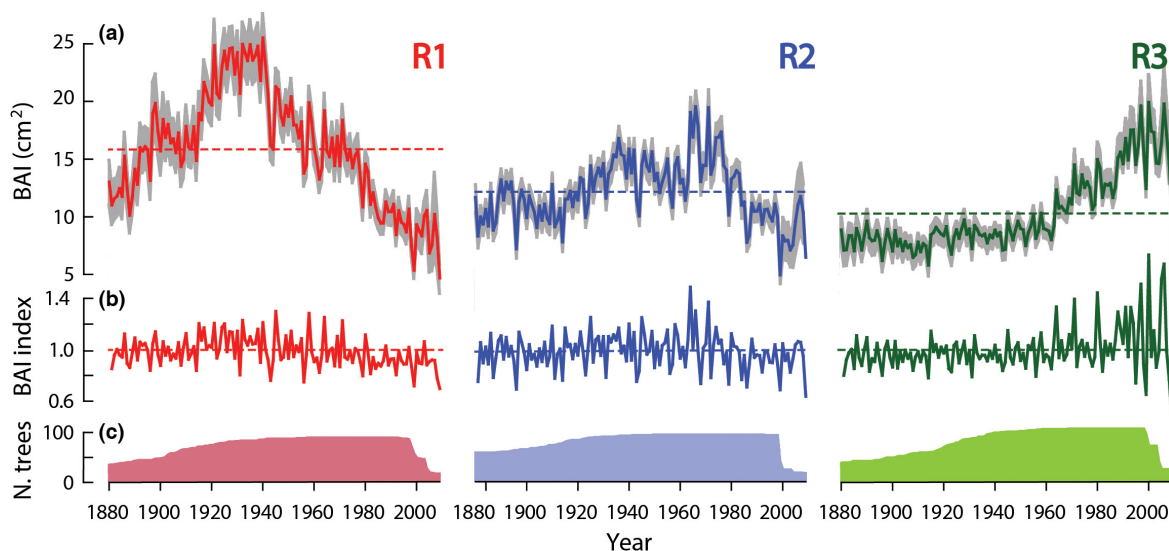

Fig. 3. Dominant patterns of basal area increments (BAIs; R1, R2, R3) according to (a) raw and (b) residual chronologies. (c) Sample depth for each chronology. Shaded areas in (a) represent ±1 SE of BAI raw measurements.
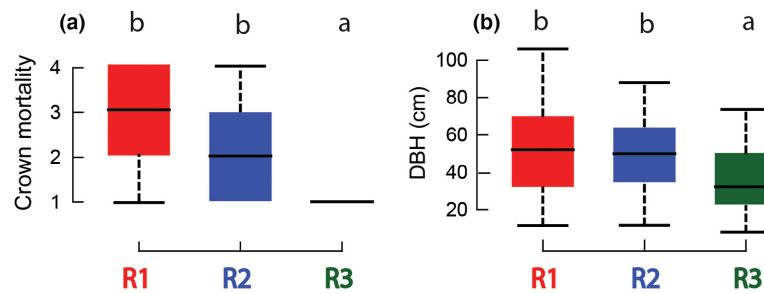
Fig. 4.   Crown mortality classes (a) and DBH (b) for the three dominant growth patterns of *Nothofagus pumilio* in northern Patagonia. Different letters indicate significant differences between growth patterns at $P < 0.05$ according to Mann–Whitney rank test.

larger diameters than the trees included in the pattern R3 (Fig. 4). Although the mean crown mortality rate is higher in pattern R1 than in R2, the difference is not statistically significant. A similar pattern is recorded in relation to differences in stem diameter, with R1 and R2 having larger diameters than R3 but there is no significant difference between R1 and R2 (Fig. 4).

Relationship between tree growth and climate

Correlation functions showed mostly positive and negative relationships between BAI, summer precipitation, and summer temperature, respectively (Fig. 5). Fig. 5a shows positive relationships between rainfall and growth in December and January of the current growing season. The residual chronologies are significantly related to precipitation during late summer–autumn during the previous growing season. Negative relationships between temperature and tree growth in R1 and R2 chronologies were recorded during the growing season, particularly from December to March (Fig. 5b). In addition, spring–autumn temperatures during the previous year are also negatively related to tree growth in the patterns R1 and R2. In contrast to R1 and R2, R3 shows weaker negative correlations with temperature during the previous growing season.

Pointer years, showing at least 50% of trees in the three regional raw chronologies with year-to-year decreases equal or larger than 15% in radial growth, were identified for the years 1914, 1931, 1943, 1956, 1972, 1979, 1986, 1992, 1998, and 1999. During these years, significant below-average rainfalls were registered for the period December–January (Fig. 6). In contrast, temperatures in December–January were significantly warmer

than those expected by chance during the period 1914–2008. Although some differences were recorded between patterns, the general picture is similar when SEA was conducted for each of the three tree-growth patterns (Appendix S1: Fig. S3). Therefore, low rates of growth (pointer years) are coincident with dry and warm spring–summer periods.

Abrupt changes in BAI and the influence of climate

Piecewise linear regressions indicate that the most important changes in growth trends occurred in 1942 (pattern R1) and 1978 (pattern R2). A remarkable positive trend in R1 from the early 20th century until 1942 contrasts sharply with the persistent negative trend from 1942 to the present (Fig. 7a). A similar change in trend, although less remarkable, was observed in 1978 for pattern R2. In contrast to R1 and R2, the growth pattern R3 changed to a more positive trend in 1964 and continues to the present with greater variability in recent years (Fig. 7a).

The most significant shift in pattern R1, from a persistent positive to a pervasive negative trend, was concurrent with extreme dry–warm spring–summers in 1942–1943, 1943–1944, and 1944–1945 (hereinafter 1942–1944) in northern Patagonia (Fig. 7c, Table 3). The relatively long period with cool and humid summers from 1932 to 1941 (Fig. 7c) was abruptly interrupted by the driest summer of the instrumental period (1914–2008) during December 1942 and January 1943 (December–January 1942, Table 3). The extreme climate conditions in summer of 1942 were followed by two warm summers, listed as the second (1943) and fourth (1944) warmest summers in the
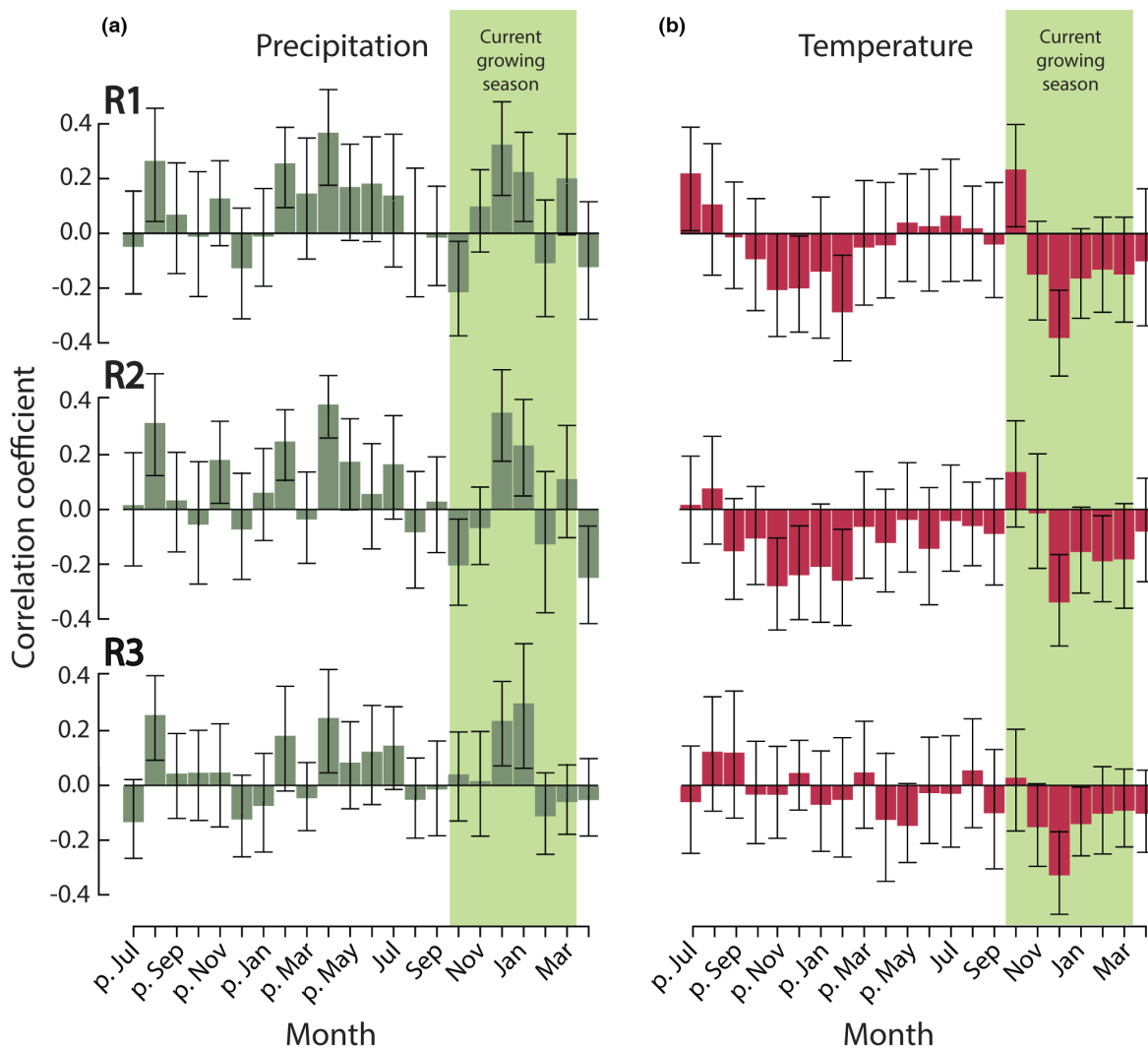
Fig. 5. Correlation functions between the three regional patterns of growth, monthly precipitation (a), and temperature (b) over the period 1914–2008. Monthly climate data extend from July of the previous year (p) to April at the end of the current growing season. Pearson correlation coefficients (vertical bars) and their confidence intervals of 95% (vertical lines) are shown.

climate records (Table 3). In addition, December 1944 was the driest in the entire record (Table 3) and intensified the water deficit at regional scale. Consistent with these observations, the moisture index recorded the longest lasting negative event over the 20th century (Fig. 7c).

Although the trees included in pattern R2 also show a reduction in the positive trend in BAI after the 1942–1944 drought, they maintained a relatively stable growth rate during the following two decades. R2 trees reached their highest rates of growth at the stand level during the

1960s and 1970s, a period with relatively moist–cool spring–summer conditions in northern Patagonia (Fig. 7, Appendix S1: Fig. S2). This positive trend in growth was abruptly interrupted in 1978 and replaced by a steady negative growth trend. The spring–summer of 1978–1979 (hereinafter 1978) was the driest of the previous 36 yr and the sixth driest in the entire instrumental record (Table 3). Reduced summer precipitation was concurrent with warm temperatures (the seventh warmest December–January summer in Table 3). However, the shift to a more positive growth
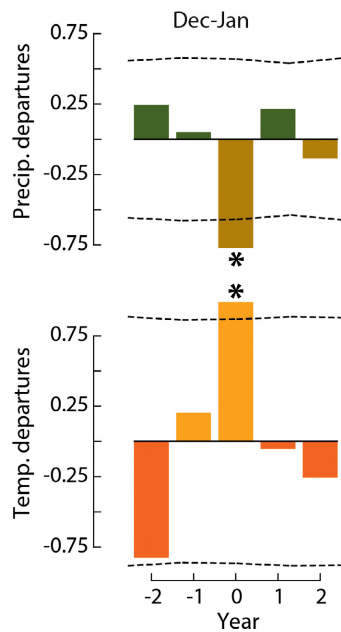
Fig. 6. Superposed epoch analysis comparing December–January precipitation and temperature in the study area during pointer years (based on 10 events over the 1914–2008 period). The *x*-axis represents a window of 5 yr (2 yr before to 2 yr following the pointer year). Solid lines represent the 95% confidence limits based on 1000 Monte Carlo simulations. Bars capped with an asterisk are statistically different (*P* < 0.05). The different colors of the bars indicate positive or negative figures.

trend in the pattern R3 around 1964 is not clearly related to an extreme weather event (Fig. 7).

A comparative examination of 20-yr periods before and after the drought events triggering the trend changes in BAIs reveals some interesting points. In both R1 and R2 patterns, the growth decline was preceded by several consecutive years with above-average moisture conditions (Fig. 8). During this period with favorable climate conditions for growth, the trees in R1 and R2 recorded the highest rates of growth over the 20th century (Figs. 3 and 7). Both wet periods were abruptly terminated by a single or two consecutive summers with extremely low rainfall and warm temperatures (Fig. 8). Although the climate returns to the long-term conditions 2 or 3 yr after the droughts, trees in the R1 and R2 groups were not able to recover the growth rates experienced prior to the extreme event. It is also interesting to note that following the onset of growth declines, dry

summers were more frequent in the period 1979–1998 (Fig. 8c) than during 1943–1962 (Fig. 8a), consistent with a more pronounced reduction in tree growth after the droughts for pattern R2 (Fig. 8d) than for R1 (Fig. 8b).

Additionally, variations in BAI from trees included in the R1 pattern were more sensitive to year-to-year variations in climate during the period preceding (*r* = 0.59, *P* < 0.05) than following (*r* = 0.29, n.s.) the onset of the long-term reduction in tree growth (Fig. 8). Similarly, BAI variations in the R2 pattern were strongly modulated by climate between 1959 and 1978 (20 yr before the decline; *r* = 0.48, *P* < 0.05) concurrent with the highest rates of radial growth (Fig. 7). After the change in growth trend, the relationships between variations in climate and BAIs in R2 are significantly weaker (*r* = −0.17, n.s., Fig. 8).

DISCUSSION

In this study, we evaluated the magnitude and duration of climatic events triggering *Nothofagus pumilio* forest decline. In northern Patagonia, extreme drought events preceded by relatively wet–cool intervals precipitated the onset of long-term negative trends in *Nothofagus* tree growth. To our knowledge, this is the first study that shows that the combination of two climatic events triggers forest decline rather than the occurrence of unrelated wet and dry isolated periods. We found that interannual variations in tree growth at our sampling sites are largely modulated by water deficit during late spring–summer season (Figs. 5 and 6), consistent with studies of the response of *N. pumilio* radial growth to climate in relatively dry sites of the Patagonian Andes (Schmelter 2000, Lara et al. 2001). Abundant precipitation in December–January favors tree growth for all trees included in the three dominant patterns of growth. In contrast, above-average temperatures in summer increase evapotranspiration reducing the soil water available for growth.

Long-term negative trends in tree growth, starting in the mid-1940s (R1) and late 1970s (R2), characterize two of the three dominant regional patterns of growth. The years 1942 (R1) and 1978 (R2) represent major break points separating increasing from declining growth trends in these patterns. Climatic conditions during the spring–summers of 1942–1944 and 1978
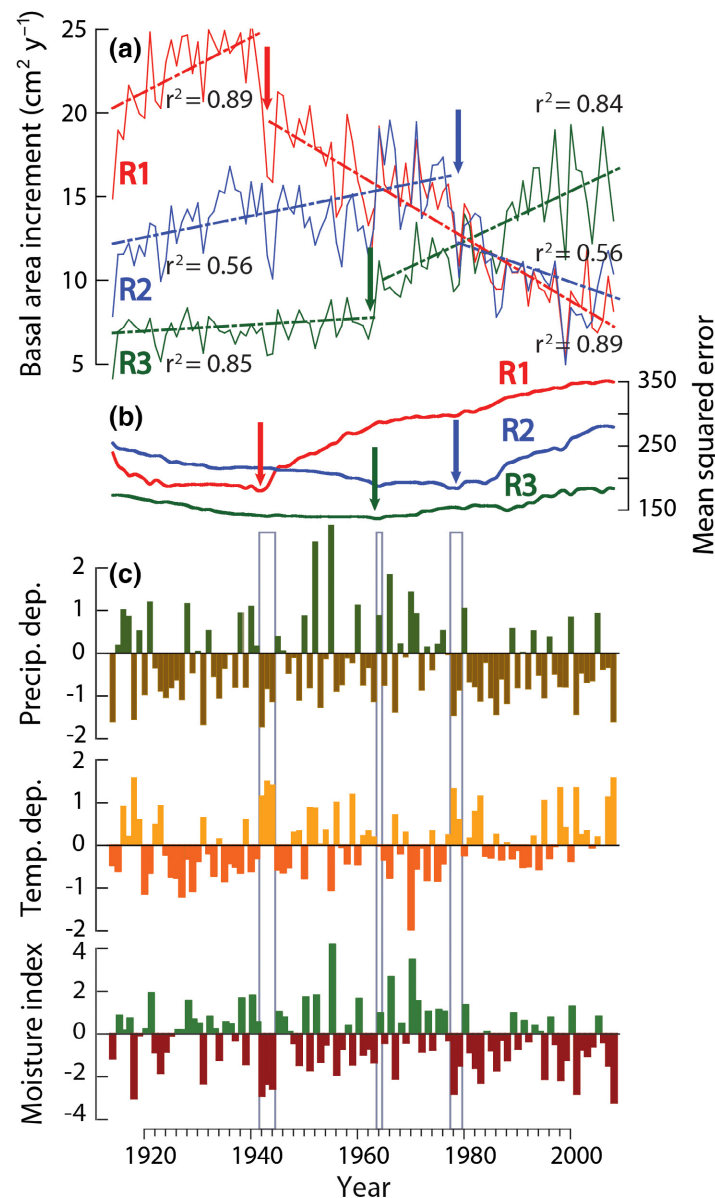
Fig. 7. The most significant break points during the last 100 yr recorded in regional patterns of tree growth in *Nothofagus pumilio* forests with manifest external decline in northern Patagonia. Regional growth patterns (a), mean square error (MSE) for iterative regression models (b), and climate variable departures (c). Break points (arrows), related to minimum MSE values, were determined by piecewise regression models. The total variance (r^2) explained by the linear regressions is indicated before and after the break points (a). All regressions are statistically significant ($P < 0.001$). Barplots represent precipitation, temperature, and moisture index departures for December–January. Climatic conditions associated with break points are highlighted with vertical bars. The different colors of the bars indicate positive or negative figures.

were extremely dry at the onset of these long-term changes in tree growth (Fig. 7, Table 3). The coincidence between these significant changes in regional growth patterns with two of the most severe droughts in the instrumental record shows that climate plays a major role inducing the onset of tree growth decline. Similar relationships between droughts and growth

Table 3. Regional ranking of the driest and warmest summers over the 1914–2008 period (94 yr).

Rank	Driest precipitation		Warmest temperature	
	Dec	Dec–Jan	Dec	Dec–Jan
1	**1944**	**1942**	1995	2008
2	1939	1931	**1943**	**1943**
3	1931	2008	1952	1918
4	1924	1914	1939	**1944**
5	1932	1918	1956	1998
6	**1942**	**1978**	2008	2001
7	2001	1986	1918	**1978**

Notes: Ranking is based on December (Dec) and December and January (Dec–Jan) departures. Years concurrent with the largest shifts in regional growth trends are indicated in bold.

decline have been documented in southeastern Spain where reduced water availability during the period of active cambial activity, and consequently of wood formation, was identified as the major triggering of Scots pine decline. The decline was characterized by a rapid reduction in radial growth and widespread defoliation in Scots pine (Sánchez-Salguero et al. 2012).

A notable outcome from this study is related to the climatic conditions prior to the beginning of the declining trend in growth. The 1942–1944 and 1978 extreme droughts occurred after several years of relatively cool and wet conditions in northern Patagonia (Fig. 8). Changes in *N. pumilio* growth trends were not associated with other regional drought events of similar magnitude in the instrumental records. Therefore, the beginning of a persistent period of decline in radial growth depends on the occurrence of a humid–cool period favorable for tree growth, abruptly interrupted by a severe drought and not simply an abrupt drought event. It is the combination of these two climatic events that triggers *Nothofagus* forest decline. Those trees affected by the summer droughts of 1942–1944 and 1978 have not recovered the rates of growth recorded before the onset of the decline. After an apparent slowdown in the
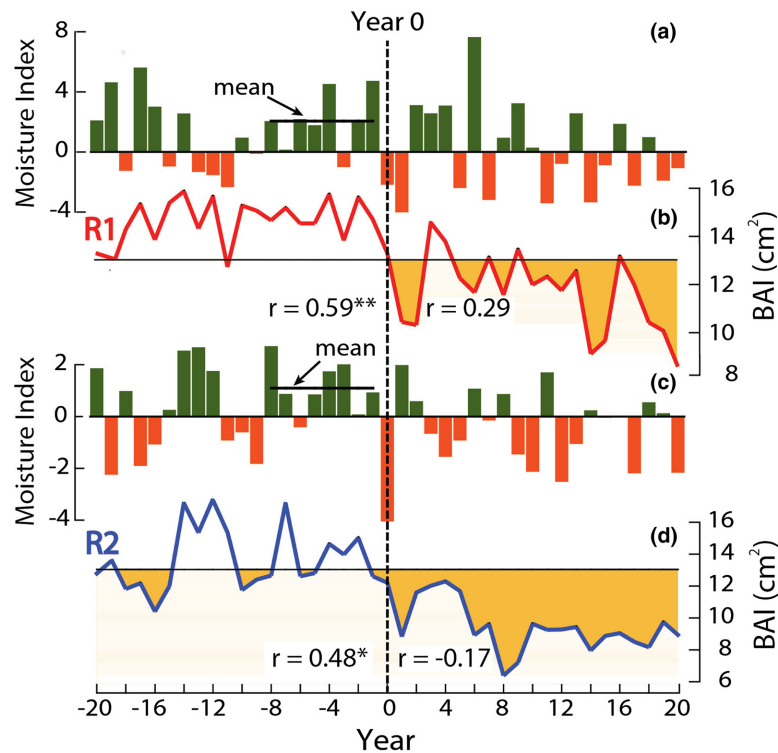

Fig. 8. Comparison of growth patterns and moisture index for 20-yr periods before and after the beginning of growth decline. Moisture index (a) and growth pattern R1 (b) for the period 1922–1962. Moisture index (c) and growth pattern R2 (d) for the period 1958–1998. The Pearson correlation coefficients (*r*) between the growth patterns and moisture index are indicated for each 20-yr window. Asterisks indicate 0.01 (**) and 0.05 (*) significances.

declining trend of pattern R1, the growth decline accelerated in 1978, concurrent with the onset of the declining growth trend in pattern R2. The pronounced dry conditions prevailing in the last two decades of the 20th century have intensified the decrease in growth for pattern R1 (Appendix S1: Fig. S5). Indeed, the trees included in the R1 and R2 patterns showed the lowest rates of BAI during the past two decades (Fig. 3a).

The absence of long-term monitoring records of forest health in northern Patagonia prevents a direct validation of our major findings. However, photographic pairs from the *N. pumilio* forests at Paso Córdova (PC; Fig. 1, Appendix S1: Table S1) allow comparison of the health of the affected forest (Fig. 9). The comparison shows that forests were healthier in 1937 and have a significant increase in partial crown mortality in recent decades. Although continuous monitoring of forests is the best tool to identify the onset of forest decline accurately, these old photographs provide a clear indication that prior to the droughts of 1942–1944, forests in Paso Cordova were healthier than today.

In the mesic-to-dry *Nothofagus* forests, we noted that the above-mentioned differences in long-term trends of radial growth between trees are related to external health conditions and tree size. The R1 and R2 trees that show long-term negative trends in BAI during the recent decades exhibit significantly higher crown mortality than R3 trees (Fig. 4). The close association between patterns of tree growth and crown dieback recorded in our study is consistent with previous work in other species and further supports the use of long-term negative trends in radial growth as a major indicator of forest decline. In southern Quebec, Duchesne et al. (2003) found that the BAI of *Acer saccharum* (Marsh.) trees with decline symptoms was significantly lower than that of healthy trees.

Considering that DBHs and growth rates could be taken as rough indicators of tree canopy status (Rathgeber et al. 2011), our measurements point out the dominance of trees in patterns R1 and R2 with respect to trees in pattern R3. In addition, based on DBH reconstructions, we observed that these differences in DBH were similar at times of abrupt changes in growth (see Appendix S1: Fig. S4). Although no statistically significant differences in DBHs were recorded between trees in patterns R1 and R2, trees from R1 were larger in DBHs than

trees in R2 during the 1942–1944 drought, supporting a dominant canopy position for trees in R1.

Canopy trees, recording the highest rates of growth in response to a prior period of favorable environmental conditions, were the most affected by the dry–warm climate from 1942 to 1944. In consequence, our results point out that there can be different responses of *Nothofagus* trees in the same stand to unfavorable weather events. Large trees with the highest rates of growth are the most susceptible to abrupt unfavorable climate events. As larger crowns involve greater water demand, those branches that fail to meet the water requirements of their foliage are the most likely to die, starting the tree dieback process. In addition, higher respiration rates of large trees under warmer conditions may also contribute to increase the susceptibility of canopy trees to adverse climatic events. These results are in line with studies suggesting that dominant, large trees are most at risk of suffering drought-driven growth decline (Piovesan et al. 2008, McDowell and Allen 2015). Therefore, the probability that a *Nothofagus* tree will be affected by an extreme climatic event appears to be related to its size and current rate of growth. In addition, our observations are consistent with the concept of "decline disease stabilizing selection" which states that dominant trees are most likely to be affected by mortality to genetically stabilize the forest (Manion 2003). According to Manion (2003), short-term environmental disturbances, such as droughts, affect highly competitive dominant trees but facilitate stress-tolerant trees to attain the upper canopy and, in consequence, breeding positions in the population.

In contrast to the declining R1 and R2 patterns during the past decades, a sustained growth increase is recorded in R3 pattern trees from 1964 to the present. The occurrence of a relatively wet and cold period from 1963 to 1977 has possibly favored the steady increase in the growth of trees with the R3 pattern. However, the positive tree-growth trend has continued during the last decades, concurrent with dry and warm conditions in northern Patagonia. We postulate that R3 trees have been favored by the gradual release of resources, particularly light and water, due to the progressive dieback of individuals with R1 and R2 patterns (Appendix S1: Fig. S1). If the positive trend in radial growth recorded in R3 trees continues, resulting in the development of large trees with fast
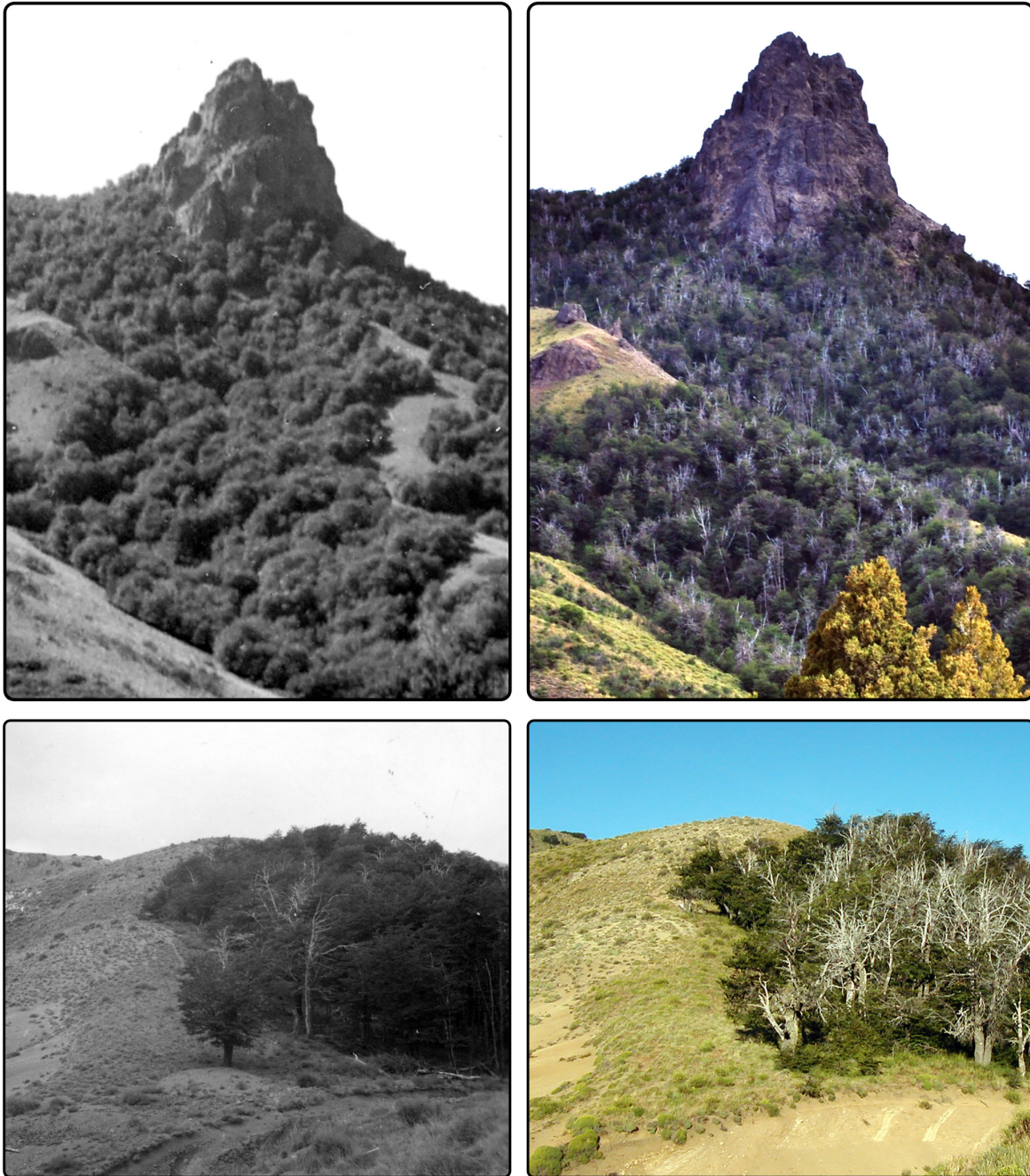
Fig. 9. Old photographs taken by Erik Kalela, a prestigious Finnish forester who visited Patagonia in 1937 (Kalela 1941), compared with recent photographs from presently affected *Nothofagus pumilio* forests at our sampling sites located in Paso del Córdova (40°35' S, 71°08' W). Left: *N. pumilio* forest located in Paso Córdova prior to the dry events between 1942 and 1944 (no dieback). Right: The same forest of *N. pumilio* today (with dieback; up 2011 and bottom 2004).

rates of growth, these trees will be more vulnerable to future droughts, similar to those recorded in the declining R1 and R2 trees. These results are valuable to assess the susceptibility of trees to climatic impacts. Thus, early warning indicators of forest decline in *N. pumilio*, such as tree size and fast growth rates, should be taken into account to predict future events of drought induced biomass mortality (Lenton 2011, Camarero et al. 2015).

Meso- to macroscale climatic variations over northern Patagonia synchronize the onset of forest decline episodes at the regional scale. Large similarities in growth patterns from 11 stands of *N. pumilio* distributed across a 500-km transect in the Patagonian Andes indicate that large-scale climatic events are the main trigger of long-term persistent negative trends in tree growth related to forest decline in the region. Auclair et al. (1996) have associated episodes of massive crown mortality of mature trees in the United States with root injuries due to freezing events during winters of reduced snow cover followed by droughts. Consistent with our results, the authors propose that the combination of these climatic events synchronizes regional episodes of forest dieback. They were able to connect these extensive episodes of forest dieback with hemispheric-to-global climate forcing, by examining indices combining the mean Northern Hemisphere temperature and the Southern Oscillation. In northern Patagonia, the occurrence of extensive *N. pumilio* dieback is consistent with regional-scale climate events previously described in relation to episodic mortality of *Austrocedrus chilensis* during the 20th century (Villalba and Veblen 1998).

The relationships between climate and tree growth before and after the onset of the decline reveal a loss of radial growth sensitivity to climatic variations following the dry event. Similar losses in tree sensitivity to climate following forest decline have been reported for several North American species (Youngblut and Luckman 2013). Indeed, Johnson et al. (1988) postulated that the weaker response of tree growth to climate after extreme climate events is another manifestation of forest decline. Although the causes associated with the loss of sensitivity to climate are unknown, our results provide a warning against using *N. pumilio* trees affected by decline in climate reconstructions (Wilmking et al. 2004, Andreu et al. 2007, Büntgen et al. 2010).

General circulation model simulations of future climate scenarios predict a gradual increase in temperature, a pronounced decrease in rainfall, and a large recurrence of extreme weather events for northern Patagonia (Vera et al. 2006, Blázquez 2012, IPCC, 2013). According to these model simulations, most sites in northern Patagonia will become drier during the next decades. As the risk of partial or total crown mortality increases with water deficit due to carbon stock depletion (McDowell et al. 2008, Adams et al. 2009, McDowell 2010), the *N. pumilio* forests presently located in the relatively mesic sites will become more susceptible to extensive decline, similar to that recorded in the easternmost drier environments. Possible consequences of forest decline and mortality are the alteration of regional carbon balance and a reduction of the potential of Andean forest to mitigate the effect of climatic changes (Huang et al. 2010). Long-term monitoring of the *N. pumilio* forest decline is currently needed to establish their precise relationships with environmental changes at intra- to interannual scales. A thorough understanding of this complex and dynamic phenomenon necessitates comprehensive studies including the identification of predisposing, triggering, and contributing factors to forest decline. This information will lead to a better ability to predict future health conditions of the austral forests.

LITERATURE CITED

Adams, H. D., M. Guardiola-Claramonte, G. A. Barron-Gafford, J. C. Villegas, D. D. Breshears, C. B. Zou, P. Troch, and T. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality

portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences USA 106:7063–7066.

Allen, C. D., A. K. Macalady, H. Chenchouni, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change 3:30–36.

Andreu, L., E. Gutiérrez, M. Macias, M. Ribas, O. Bosch, and J. J. Camarero. 2007. Climate increases regional tree-growth variability in Iberian pine forests. Global Change Biology 13:804–815.

Auclair, A. N. D., J. T. Lill, and C. Revenga. 1996. The role of climate variability and global warming in the dieback of Northern Hardwoods. Water Air and Soil Pollution 91:163–186.

Blasing, T. J., A. M. Solomon, and D. N. Duvick. 1984. Response function revisited. TreeRing Bulletin 44:1–15.

Blázquez, J., M. N. Nuñez, and S. Kusunoki. 2012. Climate projections and uncertainties over South America from MRI/JMA global model experiments. Atmospheric and Climate Sciences 2:381–400.

Briffa, K. R. 1995. Interpreting high-resolution proxy climate data—the example of dendroclimatology. Pages 77–94 in H. Von Storch and A. Navarra, editors. Analysis of climate variability, applications of statistical techniques. Springer, Berlin, Germany.

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26:115–124.

Bunn, A. G., M. Korpela, F. Biondi, P. Merian, F. Qeadan, and C. Zang. 2012. dplR: dendrochronology program library in R. R package version 1.5.5. https://cran.r-project.org/web/packages/dplR/index.html

Büntgen, U., D. Frank, V. Trouet, and J. Esper. 2010. Diverse climate sensitivity of Mediterranean tree-ring width and density. Trees 24:261–273.

Camarero, J. J., A. Gazol, G. Sangüesa-Barreda, J. Oliva, and S. M. Vicente-Serrano. 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. Journal of Ecology 103:44–57.

Carnicer, J., M. Coll, M. Ninyerola, X. Pons, G. Sánchez, and J. Peñuelas. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences USA 108:1474–1478.

Chang, K. H., D. T. Price, J. M. Chen, W. A. Kurz, C. Boisvenue, E. H. Hogg, T. A. Black, A. Gonsamo, C. Wu, and R. Hember. 2014. Simulating impacts of water stress on woody biomass in the southern boreal region of western Canada using a dynamic vegetation model. Agricultural and Forest Meteorology 198–199:142–154.

Cook, E. R. 1985. A time series analysis approach to tree ring standardization. Aslib Proceedings. Dissertation. University of Arizona, Tucson, Arizona, USA.

Crawley, M. J. 2007. The R book. John Wiley and Sons, Chichester, UK.

Di Filippo, A., A. Alessandrini, F. Biondi, S. Blasi, L. Portoghesi, and G. Piovesan. 2010. Climate change and oak growth decline: dendroecology and stand productivity of a Turkey oak (Quercus cerris L.) old stored coppice in Central Italy. Annals of Forest Science 67:706.

Duchesne, L., R. Ouimet, and C. Morneau. 2003. Assessment of sugar maple health based on basal area growth pattern. Canadian Journal of Forest Research 33:2074–2080.

Field, A. 2009. Discovering statistics using SPSS. Third edition. Sage, London, UK.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. BioScience 37:550–556.

Gaylord, M. L., T. E. Kolb, W. T. Pockman, J. A. Plaut, E. A. Yepez, A. K. Macalady, R. E. Pangle, and N. G. McDowell. 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. New Phytologist 198:567–578.

Grant, P. J. 1984. Drought effect on high-altitude forests, Ruahine Range, North Island, New Zealand. New Zealand Journal of Botany 22:15–27.

Holmes, R. L., and T. Swetnam. 1994. Program EVENT users manual: superposed epoch analysis in fire history studies. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA.

Huang, C., G. P. Asner, N. N. Barger, J. C. Neff, and M. L. Floyd. 2010. Regional aboveground live carbon losses due to drought-induced tree dieback in piñon–juniper ecosystems. Remote Sensing of Environment 114:1471–1479.

IPCC. 2013. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Johnson, S. E., and M. D. Abrams. 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. Tree Physiology 29:1317–1328.

Johnson, A. H., E. R. Cook, and T. G. Siccama. 1988. Climate and red spruce growth and decline in the northern Appalachians. Proceedings of the National Academy of Sciences USA 85:5369–5373.

Jump, A. S., J. H. Hunt, and J. Peñuelas. 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Global Change Biology 12:2163–2174.

Kalela, E. 1941. Über die holzarten und die durch die klimatischen Verhältnisse verursachten Holzartenwechsel in den Wäldern Ostpatagoniens. Annales Academiae Scientiarum Fennicae, Ser. A., IV. Biologica, 2, Helsinki. Annales Academiae Scientiarum Fennicae, Helsinki, Finland.

Lara, A., J. C. Aravena, R. Villalba, A. Wolodarsky-Franke, B. Luckman, and R. Wilson. 2001. Dendroclimatology of high-elevation *Nothofagus pumilio* forests at their northern distribution limit in the central Andes of Chile. Canadian Journal of Forest Research 31:925–936.

Leaphart, C. D., and A. R. Stage. 1971. A factor in the origin of the pole blight disease of *Pinus monticola* Dougl. Ecology 52:229–239.

LeBlanc, D., and J. Foster. 1992. Predicting effects of global warming on growth and mortality of upland oak species in the Midwestern United States: a physiologically based dendroecological approach. Canadian Journal of Forest Research 22:1739–1752.

Lenton, T. M. 2011. Early warning of climate tipping points. Nature Climate Change 1:201–209.

Liu, H., et al. 2013. Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. Global Change Biology 19:2500–2510.

Manion, P. D. 1981. Tree disease concepts. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Manion, P. D. 2003. Evolution of concepts in forest pathology. Phytopathology 93:1052–1055.

Manion, P. D., and D. Lachance. 1992. Forest decline concepts. APS Press, St. Paul, Minnesota, USA.

McDowell, N. G., C. D. Allen, and L. Marshall. 2010. Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. Global Change Biology 16:399–415.

McDowell, N. G., and C. D. Allen. 2015. Darcy's law predicts widespread forest mortality under climate warming. Nature Climate Change 20:12–20.

McDowell, N. G., W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams, and E. A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytologist 178:719–739.

Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology 17:2084–2094.

Mooney, C., and R. Duval. 1993. Bootstrapping: a non-parametric approach to statistical inference. Sage, Newbury Park, California, USA.

Mundo, I. A., V. A. El Mujtar, M. H. Perdomo, L. A. Gallo, R. Villalba, and M. D. Barrera. 2010. *Austrocedrus chilensis* growth decline in relation to drought events in northern Patagonia, Argentina. Trees 24:561–570.

Ogden, J., C. H. Lusk, and M. Steel. 1993. Episodic mortality, forest decline and diversity in a dynamics landscape: Tongariro National Park, New Zealand. Pages 261–274 *in* R. F. Huettl and D. Mueller-Dombois, editors. Forest decline in the Atlantic and Pacific regions. Springer-Verlag, Berlin, Germany.

Piovesan, G., F. Biondi, A. Di Filippo, A. Alessandrini, and M. Maugeri. 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Global Change Biology 14:1–17.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://cran.r-project.org

Rathgeber, C. K., S. Rossi, and J. D. Bontemps. 2011. Cambial activity related to tree size in a mature silver-fir plantation. Annals of Botany 108:429–438.

Rodríguez-Catón, M., R. Villalba, A. M. Srur, and B. Luckman. 2015. Long-term trends in radial growth associated with *Nothofagus pumilio* forest decline in Patagonia: integrating local- into regional-scale patterns. Forest Ecology and Management 339:44–56.

Sánchez-Salguero, R., R. M. Navarro-Cerrillo, J. J. Camarero, and Á. Fernández-Cancio. 2012. Selective drought-induced decline of pine species in southeastern Spain. Climatic Change 113:767–785.

Schmelter, A. 2000. Climatic response and growth-trends of *Nothofagus pumilio* along altitudinal gradients from arid to humid sites in northern Patagonia—a progress report. Pages 193–215 *in* F. Roig, editor. Dendrocronología en América Latina. EDIUNC, Mendoza, Argentina.

Suarez, M. L., L. Ghermandi, and T. Kitzberger. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus*—site, climatic sensitivity and growth trends. Journal of Ecology 92:954–966.

Suarez, M., and T. Kitzberger. 2010. Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. Journal of Ecology 98:1023–1034.

van Mantgem, P. J., et al. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524.

Veblen, T., R. S. Hill, and J. Read. 1996. The ecology and biogeography of *Nothofagus* forests. Yale University Press, New Haven, Connecticut, USA.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York, New York, USA.

Vera, C., G. Silvestri, B. Liebmann, and P. González. 2006. Climate change scenarios for seasonal

precipitation in South America from IPCC-AR4 models. Geophysical Research Letters 33:L13707.

Villalba, R., J. A. Boninsegna, T. T. Veblen, A. Schmelter, and S. Rubulis. 1997. Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. Climate Change 36:425–454.

Villalba, R., A. Lara, M. Masiokas, S. Delgado, J. C. Aravena, F. A. Roig, A. Schmelter, A. Wolodarsky, and A. Ripalta. 2003. Large-scale temperature changes across the southern Andes: 20th-century variations in the context of the past 400 years. Climatic Change 59:177–232.

Villalba, R., and T. T. Veblen. 1997. Spatial and temporal variation in *Austrocedrus* growth along the forest—steppe ecotone in northern Patagonia. Canadian Journal of Forest Research 597:580–597.

Villalba, R., and T. T. Veblen. 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. Ecology 79:2624–2640.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Walter, H., and L. Helmut. 1960. Klimadiagramm-Weltatlas. Jena: G. Fischer.

Wigley, T. M. L., K. R. Briffa, and P. D. Jones. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydro-meteorology. Journal of Climate and Applied Meteorology 23:201–213.

Williams, A. P., C. D. Allen, A. K. Macalady, et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Wilmking, M., G. Juday, V. Barber, and H. Zald. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biology 10:1–13.

Youngblut, D. K., and B. H. Luckman. 2013. Evaluating the temperature sensitivity of radial growth patterns from whitebark pine in the western Canadian Cordillera. Dendrochronologia 31:16–28.

Zang, C., and F. Biondi. 2013. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. Dendrochronologia 31:68–74.

Zhou, L., et al. 2014. Widespread decline of Congo rainforest greenness in the past decade. Nature 508:86–90.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1390/supinfo