Climate response and drought resilience of *Nothofagus obliqua* secondary forests across a latitudinal gradient in south-central Chile

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Abstract

The climate response and resilience of tree growth to drought events have been widely reported for Mediterranean and Temperate forests from the Northern Hemisphere. Although a number of studies have evaluated the climate response of tree growth in forests from southern South America, no study so far has assessed this aspect and the growth resilience to droughts on secondary *Nothofagus* forests from this region. This genus comprises commercially important native species that are part of the main productive forests in Chile. In addition, Mediterranean and Temperate forests of Chile are suffering sustained decrease in precipitation and moderate warming concurrently with an unprecedented megadrought that occurs since 2010. This highlights the need of studying the sensitiveness of tree growth from these native productive species to current climate warming in this susceptible area.

[you could improve the first three lines invoking intensifying drought with climate change to justify the study and state what research gap you are addressing…see bold paragraph for nature]

This study evaluated tree-growth patterns, the climate response and drought resilience of nine secondary *Nothofagus obliqua* forests across a latitudinal gradient from Mediterranean to Temperate climate in the Andes of Chile (35.7° to 40.3° S). Moreover, in order to improve our understanding of the spatial variation of productivity patterns, this research assessed trends in the maximum Normalized Difference Vegetation Index (peak in the NDVI from MODIS images) across the gradient for 2001-2018. Tree-growth patterns were highly influenced by stand dynamics, with steep decreasing trends in most of the stands related to a gradual canopy closure. Productivity trends on the other hand, had a flat pattern north of 38°S, but positive trends south of this latitude, which were mostly attributed to

stand development. Tree growth was positively related to precipitation in all the study sites, with annual and summer rainfall being more important in the north (Mediterranean climate) and south (Temperate climate), respectively. Maximum temperature, on the other hand, had a negative effect on growth in most of the studied forests. This implies that projected warmer and drier conditions may have a detrimental effect on *N. obliqua* growth during coming decades. The two northern stands, located at the species dry range edge, were among the most resilient to drought and have not been affected by the current megadrought in the region. Overall climate conditions, however, do not define the tolerance of stands to droughts, probably because local environmental conditions play a key role due to their influence on water availability during drought events. The strong relationship found between tree growth and maximum NDVI in all except one of the study sites is promising for extrapolating interannual variations in productivity at coarser scales. To better inform climate change adaptation of *N. obliqua* forests, future studies should assess the effects of thinning and forest composition on the climate sensitivity and resilience of growth to drought events.

1. Introduction

Forests store more than half of the global carbon (Bonan, 2008), contributing to mitigate the increase of CO_2 concentrations, mainly through the carbon sequestrated in their biomass and soil (Pan et al., 2011). Large net carbon emissions can occur due to fast or massive mortality events, frequently preceded by growth decreases and forest dieback (Breshears and Allen, 2002). The increase in CO_2 atmospheric concentrations during recent decades has stimulated tree growth and forest productivity (Ainsworth and Long, 2005; Camarero et al., 2015; Huang et al., 2017; Martínez-Vilalta et al., 2008; Soule and Knapp, 2006); however, climatic trends and increasingly common large-scale drought extremes, have led to decreases in forest productivity and even to widespread die-off events at regional and global scales (Allen et al., 2010; Allen et al., 2015; Allen et al., 2010; Zhao and Running, 2010). Ongoing changes in climate are affecting the performance and distribution of tree species at an accelerated pace (Parmesan, 2006; Walther et al., 2002), and further reductions in water availability in a warmer climate are expected to decrease tree growth and increase mortality, especially at the equatorial edge of species distribution (Allen et al., 2010; Linares et al., 2011; Sánchez-Salguero et al., 2012; Sarris et al., 2007).

It has been broadly reported how tree growth in the Northern Hemisphere has been responding to changes in climate and droughts (e.g. Pretzsch et al. 2013, Cailleret et al. 2017, Cavin and Jump 2017, Gazol et al. 2017a, Gazol, et al. 2017b, Camarero et al. 2018, Gazol et al. 2018, Serra-Maluquer et al 2019). However, this type of studies is much scarcer in the extra-tropical forest ecosystems of the Southern Hemisphere. In addition, few studies have recently evaluated parameters such as resistance, recovery and resilience of tree growth (Lloret et al., 2011) to drought events in the temperate forests of the Southern

Hemisphere (DeSoto et al., 2020; Fasanella et al., 2020). These three growth traits are essential to assess the stability of forest ecosystems and their adaptation to climate change (Merlin et al., 2015). Resilience to drought events is crucial for long-term tree survival; trees that died during droughts were less resilient in their growth to previous droughts, when compared with surviving trees of the same species at a global scale (DeSoto et al., 2020). Timber species from Europe have shown diverse growth sensitivities to drought events (Kunz et al., 2018), and there is still discussion about the drought susceptibility of some important species in that continent (Bouriaud and Popa, 2009; Cavin et al., 2013; Eilmann et al., 2006). Furthermore, few studies have assessed changes in drought resistance and resilience across a species distribution range (Cavin and Jump, 2017).

In addition to tree-ring analyses, the effects of climate on forests can be quantified at a coarser resolution using satellite imagery, which can provide information on above ground gross primary productivity at stand to regional scales (Gazol et al., 2018). The Normalized Difference Vegetation Index (NDVI) is a proxy of productivity and vegetation activity that has been widely used to assess temporal trends and the impacts of droughts on forests in different regions around the world (Gazol et al., 2018; Klisch and Atzberger, 2016; Vicente-Serrano, 2007). NDVI browning trends were recently reported for sclerophyllous forests in response to protracted drought in Central Chile (Miranda et al., 2020). Studies linking annual tree growth with inter-annual NDVI series (or other productivity satellite products) have generally found a positive relationship between them, though highly variable in strength (Coulthard et al., 2017; Vicente-Serrano et al., 2016, but see Levesque et al., 2019).

Ongoing climate trends across the Mediterranean-Temperate region of southern South America are characterized by a sustained decrease in precipitation and moderate warming (Falvey and Garreaud, 2009; Gonzalez-Reyes and Muñoz, 2013; Lara et al., 2020; Trenberth et al., 2007; Urrutia-Jalabert et al., 2015a). Moreover, the occurrence of extreme and severe droughts in the region has increased since the mid-20^{st} century compared with previous centuries (Christie et al., 2011; Morales et al., 2020). The most severe protracted drought over the last millennium, known as the megadrought, has been taking place in central and south-central Chile (30-38º S) since 2010 (Garreaud et al., 2019). Precipitation deficits during this period have ranged between 25 and 45%, and up to 80% during 2019 in the north part of this area (Barichivich et al., 2020; CR2, 2015; Garreaud et al., 2019; SEGRA, 2020).

Old-growth conifers (e.g. *Austrocedrus chilensis, Araucaria Araucana*) and mature *Nothofagus* trees (e.g. *N. pumilio, N. macrocarpa*) from the Temperate forests of southern South America have shown growth decreases, which are believed to be a consequence of the climate trends during recent decades (Fajardo et al., 2019; Rodríguez-Catón et al., 2015; Urrutia-Jalabert et al., 2015a; Venegas-González et al., 2019a, 2018a; Villalba et al., 2012). Despite these studies, there is still an important knowledge gap regarding the climate response of widespread forest ecosystems in this area, such as the Temperate broadleaved secondary forests. Southern beech (*Nothofagus* spp) forests comprise commercially important species and are one of the main forest resources in Chile, since most of the native forests in the country are dominated by this genus (Ramírez, 1987). *Nothofagus obliqua* (Mirb.) Oerst. is a pioneer deciduous species that can reach ages of 400 years and occurs along a latitudinal gradient (34º 50´- 41 º S) spanning the transition from Mediterranean climate in the north to temperate conditions in the south of its range. Secondary stands of this species are an important productive resource in Chile, but they are also the baseline for the development of diverse and uneven-aged mature forests, which are crucial for the provision of goods and services (Lara et al., 2003).

No study so far has evaluated how *N. obliqua* secondary forests are being affected by climate and how droughts may impact their growth. Given the relatively young age of these forests, we expect that stand dynamics may override any growth trend potentially driven by climate during recent decades. However, we also expect tree growth to be significantly related with climate at an interannual level across the species distribution gradient, and a higher tolerance to drought events towards the north, due to these forests being adapted to drier conditions.

Given this context, we aim to comprehensively analyze tree-growth patterns, tree growth-climate relationships, and growth resilience to droughts in nine *N. obliqua* sites along the Mediterranean-to-Temperate latitudinal gradient in the Andes of Chile. Moreover, in order to go beyond the findings in each particular site and assess any potential change in productivity at a coarser scale across these forests distribution, we aim to analyze NDVI (greening and/or browning) trends and their connections with tree growth and climate during recent decades.

2. Methods

2.1. Study sites

In this study, secondary and even-aged stands with *N. obliqua* adult trees >= 30 cm diameter at breast height (DBH) and without signs of human intervention at least in the last two decades were studied. Nine secondary forests were selected for sampling along a latitudinal transect in the Andes from 35.7º to 40.3º S: Parque Tricahue (TRI) and Melado (MEL) in Maule Region, Rucamanqui (RUC) and Los Prados (LPR) in Bío-Bío Region, Valle Hermoso (VAH) and Namuncai (NAM) in Araucanía Region, and San Pablo de Tregua (SPT), Arquilhue (ARQ) and Riñinahue (RIN) in Los Ríos Region (Figure 1). The elevation of the sampled sites ranged between 156 m a.s.l in RIN (Los Ríos Region) and 1168 m a.s.l in MEL (Maule Region).

Species composition varied from pure *N. obliqua* stands (MEL and RIN) to mixed stands composed by diverse tree species. Thus, LPR had a larger number of *N. nervosa* (deciduous species) than *N. obliqua,* but almost equal basal area of both species. The stand VAH also had *N. nervosa* trees, but a large proportion of the basal area was occupied by the evergreens *N. dombeyi* and *Lomatia hirsuta*. Total basal area generally increased from north to south, and the highest values were found in stands SPT and ARQ in Los Ríos Region (Table 1). All studied stands, except for LPR and VAH, can be classified as pure *N. obliqua* forests, since the species represents more than 70% of the total basal area (Donoso et al., 1993; Gezan et al., 2007). LPR and VAH can be classified as mixed *Nothofagus* forests (Gezan et al., 2007), since basal area covered by both deciduous *Nothofagus* species reached between 62% and 68% of the total (Table 1).

Stand density varied across the latitudinal gradient. The two densest stands were RUC and LPR from Bio Bio Region (1100 and 990 trees/ha, respectively), and the sparsest ones were MEL from Maule and VAH from Araucanía (390 and 470 trees/ha, respectively, Table 1).

Climate in the study area ranged from Mediterranean in the north with a marked dry period in spring-summer to Temperate with some Mediterranean influence in the south (Figure

S1). Annual precipitation in the northernmost sites was almost as high as in the southernmost sites (Table 1), but differences were mostly given by the amount of precipitation especially falling during spring-summer (20% in the north and 38% in the south) and the summer season (4.5% in the north and 17% in the south, Table 1). Total precipitation in each study site was obtained from the closest meteorological station considering the period 1995-2015 (Figure 1, Table 1, Centro de Ciencia del Clima y la Resiliencia 2017).

Table 1. Location and stand characteristics of the studied forests across the gradient. Annual precipitation close to each study site and percentages of it falling during spring-summer and summer are also shown. Features of each tree-ring chronology are shown at the bottom of the Table. Parque Tricahue (TRI), Melado (MEL), Rucamanqui (RUC), Los Prados (LPR), Valle Hermoso (VAH), Namuncai (NAM), San Pablo de Tregua (SPT), Arquilhue (ARQ), Riñinahue (RIN).

Sites	**TRI**	**MEL**	**RUC**	**LPR**	**VAH**	**NAM**	**SPT**	**ARQ**	**RIN**
Southern latitude (°)	35.7	35.9	37.2	37.5	38.3	39.2	39.6	40.2	40.3
Western longitude (°)	71.1	70.9	71.7	71.6	71.9	71.8	72.1	72.1	72.2
Altitude (m)	954	1168	987	668	696	630	671	455	156
Stand density (N/ha)	760	390	1100	990	470	650	910	690	730
N. obliqua density (N/ha) and % of the stand[a]	320 42%	390 100%	730 66%	350 35%	180 38%	520 80%	540 59%	480 70%	730 100%
Stand basal area (m^2) and % that is *N. obliqua*[a]	35.2 73%	36.8 100%	41.1 85%	57.2 68%	45.4 62%	52.5 96%	73.6 85%	71.8 82%	60.5 100%
QMD[b] (cm)	24.3	34.7	21.8	27.1	35.1	32.1	32.1	36.4	32.5
N. obliqua QMD (cm)	31.9	34.7	24.7	37.7	44.7	35.1	38.5	39.5	32.5
AP (mm)[c]	2056	1932	1781	1998	1366	2682	2532	2595	2595
SpP(mm)[d]	20%	20%	28%	30%	35%	33%	33%	37.8%	37.8%
SuP(mm)[e]	4.5%	4.7%	8.7%	9.8%	13.5%	14%	13.5%	17%	17%

Chronology Length (years)	158	177	62	84	97	72	62	72	51
Rbar[f]	0.45	0.31	0.47	0.31	0.31	0.32	0.34	0.27	0.24
EPS[f]	0.95	0.87	0.97	0.93	0.91	0.95	0.88	0.91	0.91
MS[f]	0.31	0.37	0.22	0.21	0.23	0.19	0.15	0.18	0.15

[a] In the case of LPR and VAH the *Nothofagus* density and basal area also include both *N. obliqua* and *N. nervosa.* [b] QMD: Quadratic mean diameter. [c] AP: Annual precipitation. [d] SpP: Spring precipitation (September-March). [e] SuP: Summer precipitation (December-March). [f] Rbar is the mean correlation coefficient for all possible pairs of tree-ring series calculated for a specific interval of time. For the Maule longer chronologies we used a 50-year window and 25-year overlap and for all the other chronologies, we used a 25-year window with a 12,5-year overlap (Briffa, 1995). EPS is the mean Expressed Population Signal and values above 0.85 are indicative of a strong common growth signal (Briffa, 1995). MS or mean sensitivity is a measure of the interannual ring-width variability in each chronology (Fritts, 1976).

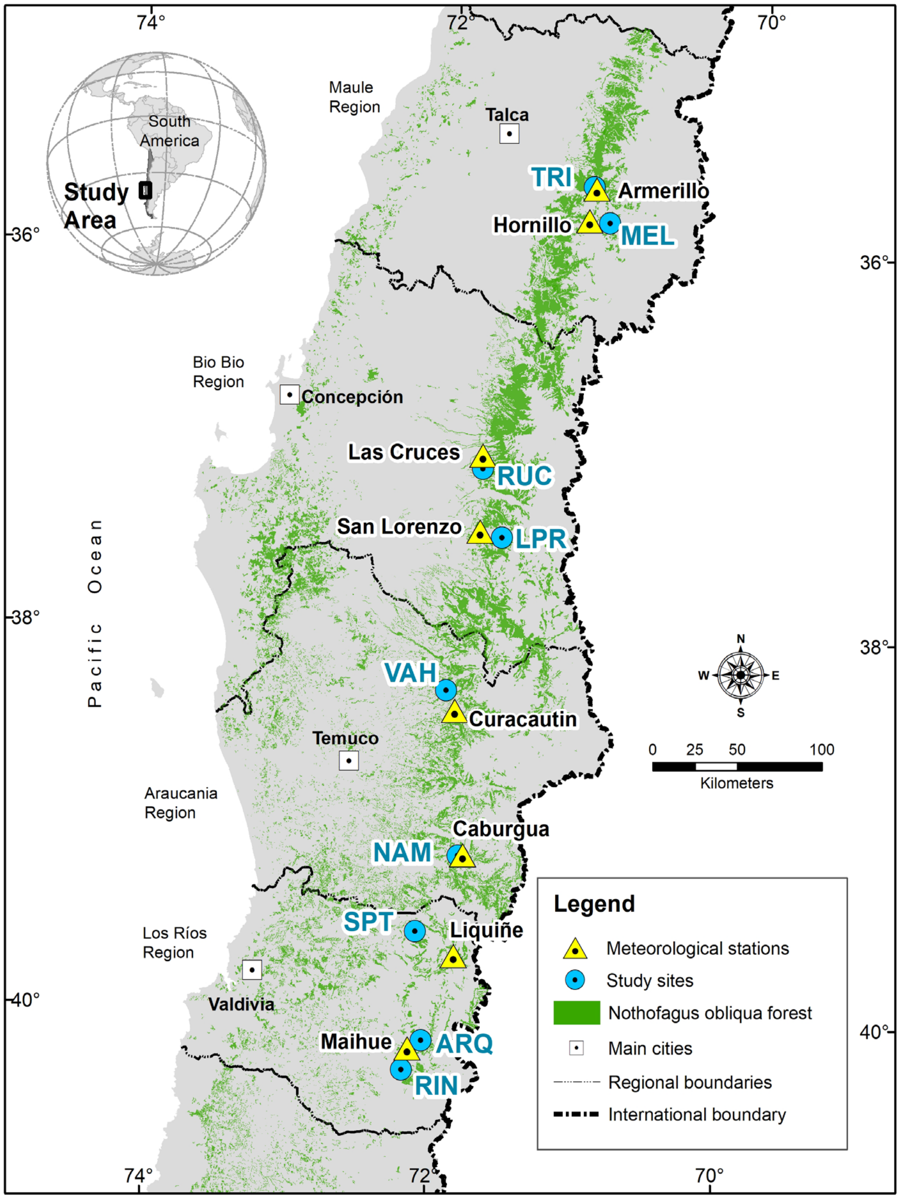


Figure 1. Map showing the geographical distribution of *Nothofagus obliqua* forests in Chile, the location of the nine study sites and their nearest meteorological stations. See Table 1 for site abbreviations.

2.2. Sampling and tree cores processing

A 1000 m^2 plot was installed in each site where the DBH of all individuals larger than 10 cm diameter was measured. We sampled 25 dominant trees, which were double cored at approximately 1.3 m above ground level with a 5 mm diameter increment borer. Cores were mounted, sanded and tree-ring series were visually dated using a binocular microscope. The Schulman convention, which assigns to each ring the date of the year in which tree growth started, was used for dating purposes (Schulmann, 1956). Tree-ring widths were measured under magnification to 0.001mm precision with a measuring device (Velmex Inc., Bloomfield NY, USA) interfaced with a computer, and cross-dating quality was verified and improved using the computer program COFECHA (Holmes, 1983).

2.3. Tree-growth patterns assessment and tree-ring width chronologies development

Raw ring-width series (mean of two series per tree when available) were used to calculate the basal area increment (BAI) of each stand, using the following formula:

$$BAI_t = \pi\,(SR_t^2 - SR_{t-1}{}^2)$$

Where SR is the stem radius and t is the year of tree ring formation.

Mean BAI chronology illustrates the development history of each stand, compensates the age-size effect related to the geometry of the stems, and preserves low-frequency variability at the same time (Biondi, 1999).

In order to better assess growth patterns and know if the stands were affected by disturbances that caused abrupt growth releases, the radial-growth averaging technique (Nowacki and Abrams, 1997) was used. The package TRADER was used for this purpose (Altman et al., 2014), considering as a release a growth increment of at least 50% when five years pre- and post-disturbance were compared. When the events around a specific year affected at least 30% of the number of sampled trees in a stand, the release event was considered as significant and the specific year in which the disturbance event occurred was calculated as the weighted mean of contiguous years, considering the number of trees with releases per year. Years with release events were plotted on top of the BAI calculated for each site.

In order to minimize the variability that is not related to climate (e.g., tree age, stand development, demographic changes), raw tree-ring width measurements of each series were standardized with a negative exponential curve or a regression line using the ARSTAN44xp program (Cook and Krusic, 2005). Moreover, a Principal Component Analysis (PCA, Cooley and Lohnes 1971) with a varimax normalized rotation, was run for the standardized chronologies during the common period, in order know if there exist a common growth pattern among stands across the studied latitudinal gradient.

2.4. Extraction of NDVI data and productivity trends

The 16-day Terra MODIS NDVI (Normalized Difference Vegetation Index, MOD13Q1) was obtained from AppEEARS Team (2020) for the entire latitudinal range where *N. obliqua* is the dominant species of the secondary forests across the Andes (CONAF, 1999). These images have a 250 m resolution and are available since 2000 (Didan, 2015). A spatial mask was created to select only pixels representing secondary forests with *N. obliqua* as a dominant species based on the official national inventory of native forest cover derived from aerial photographs and satellite imagery between 1994 and 1997 (CONAF, 1999). A second mask was subsequently applied to retain 250 m pixels with more than 90% of coverage by broadleaved secondary forests based on a land cover product derived from Landsat 8 imagery for 2014 at a spatial resolution of 30 m (Zhao et al., 2016). This double masking was necessary to ensure that the selected pixels represent stands dominated by *N. obliqua*, with a minimum of influence from other land cover types. The Timesat software (Jönsson and

Eklundh, 2004) was used to smooth the data and obtain phenological parameters. The peak of the growing season was estimated as the maximum NDVI value of the smoothed time series recorded during the period between green-up and brown-down, usually occurring between September and March (Jönsson and Eklundh, 2004). The temporal trend in peak NDVI along the study area was obtained for the period 2001-2018. A Generalized Additive Model (GAM) using latitude as the predictor was used to characterize the overall zonal pattern of mean and trend of peak NDVI (predictands) along the latitudinal gradient (Curtis and Simpson, 2014).

In order to find out how NDVI actually relates with tree growth in the area, the array of the closest 3x3 pixels centered on every study site was averaged. Correlations were calculated between the standard version of tree-ring chronologies and the maximum NDVI value calculated for every study site during the common period 2001-2017. For these analyses, Schulman years were correlated with the corresponding growing season and previous growing season peak NDVI.

2.5. Climate and drought data

Climate variables used to correlate with tree growth included precipitation and maximum temperatures. Data from stations in each region were obtained from Explorador Climático (Centro de Ciencia del Clima y la Resiliencia, 2017) and mean regional standardized departures were calculated in reference to a certain period in each region (Z scores). The length of precipitation records decreased from north to south, so the common reference period was 1970-2000 in all regions, except for Los Ríos Region where the reference period was set to 1985-2010. The reference period for maximum temperature records was 1985-2010 in all regions. In the case of Araucanía Region, there was only one long-term temperature record, and this was used in the subsequent analyses (no departures were calculated in this region). Trends in climate records were calculated using linear regressions and the Mann-Kendall non-parametric test when data is not normality distributed. Annual precipitation had negative trends across the gradient, with significant trends present from Maule to Araucanía Regions (Figure 2). Maximum summer temperatures showed significant positive trends across all the studied regions (Figure 2). This means that at least since the 1960 climate has been drying and warming across south-central Chile.

The self-calibrating Palmer Drought Severity Index (scPDSI; Wells et al., 2004, van der Schrier et al., 2013, Barichivich et al., 2020) was computed for each region using regional mean precipitation from the available stations, monthly potential evapotranspiration from the CRUTS v. 4.04 dataset (Harris et al., 2020), and soil water holding capacity from the Food and Agriculture Organization digital soil map of the world (FAO, 2003). The PDSI integrates soil water availability throughout the year and it has been demonstrated to correlate strongly with tree growth in South America (Christie et al., 2011; Morales et al., 2020).

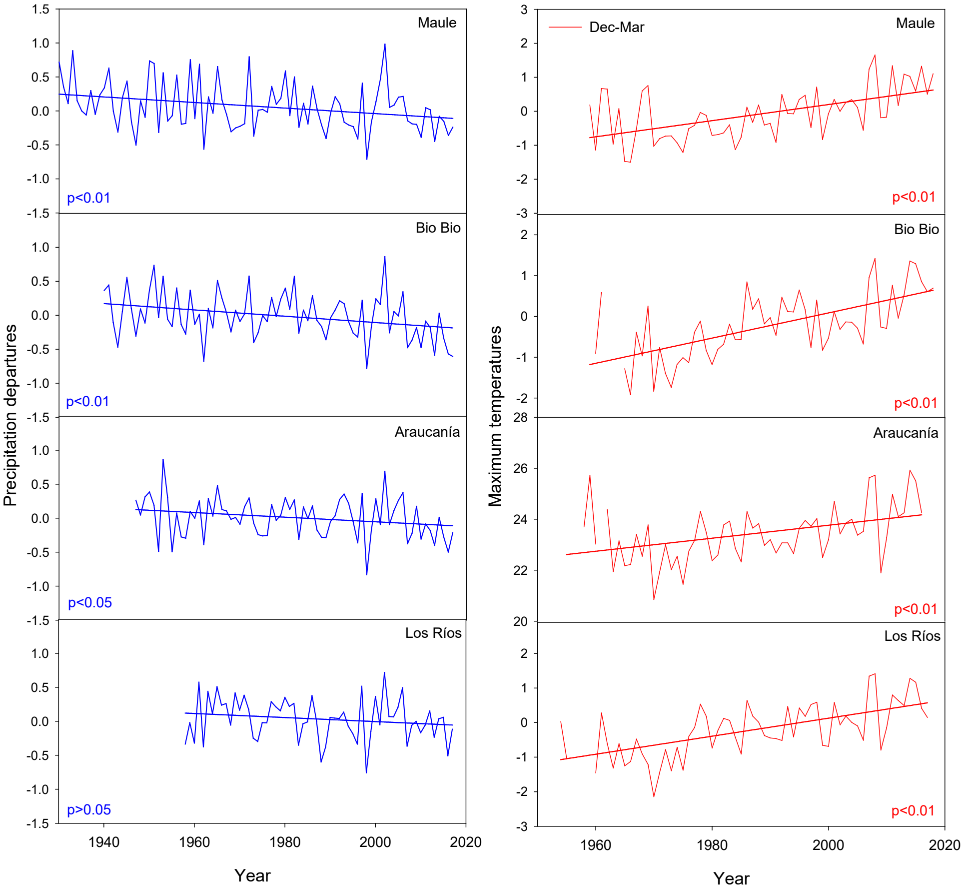


Figure 2. Left panel: Annual precipitation departures for each region across the study gradient. Right panel: Summer maximum temperature departures (or maximum temperatures in the case of Araucanía) for each region across the study gradient. p values denote the statistical significance of linear trends.

2.6. Tree growth-climate relationships

Bootstrapped correlations were calculated between the standard version of tree-ring chronologies and monthly climate variables (from January of the previous summer to March of the current one), including means (maximum temperature) and sums (precipitation) for previous and current summer months (i.e. December-March, December-February), as well as current spring-summer months (i.e. September-March). Correlations were calculated using the cor and boot functions from the Stats and Boot R packages, respectively (R Development Core, 2014), and coefficients significant at the 95% confidence level were considered.

2.7. Resilience to drought events

Droughts were determined using the scPDSI. The annual mean scPDSI was considered for the Maule Region and the September-March (spring-summer) scPDSI was considered for all the other regions. Indices lower than -2 were considered as droughts (moderate to extreme droughts according to Palmer, 1965). Moreover, and to be more secure about the definition of droughts, we only considered scPDSI droughts that were also recorded by the corresponding three-months Standardized Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano et al., 2010).

Indices for tree-growth resistance (Rt), recovery (Rc) and resilience (Rs) in relation to drought occurrence were calculated using the standardized chronologies following the approach of Lloret et al. (2011). The standardized chronologies were chosen, because they do not show any strong temporal trend like the raw and BAI chronologies (Kunz et al., 2018; Merlin et al., 2015). The resilience indices can be regarded as indicators of a species ´capability to tolerate stress (Pimm, 1984). These three indices were calculated using growth during the drought, pre-drought and post-drought periods as follows: Rt = drought/pre-drought; Rc= post-drought/drought; Rs=post-drought/pre-drought (Lloret et al., 2011). It is important to mention that the multi-year drought since 2010, referred as the megadrought, could not be considered for this analysis, because this long-term event is not over yet. Pre-drought and post-drought periods were calculated as the mean of growth three years before and three years after the drought, respectively (Merlin et al., 2015; Pretzsch et al., 2013). Five years were also considered, providing similar results to the three-years period. However, three years were finally chosen to avoid considering a higher number of post-drought years occurring during the megadrought period. This, primarily as part of the well-known drought that occurred in 2008. Moreover, in cases when pre-drought years were well below the mean standardized growth, the pre-drought period was calculated using the three-year period immediately before (see issues with the reference period mentioned by Schwarz et al. (2020).

The further the Rt values falls below 1, the lower the resistance. Rc >1 indicates growth recovery compared with the value reached during the drought year and Rs >1 indicates full recovery or growth increase after the drought. The opposite holds true if values are <1, indicating low resilience. The average across all drought years per site was used to calculate Resistance, Recovery and Resilience (Gazol et al., 2017a). Differences in the indices among sites were assessed using the Kruskal-Wallis Test. Furthermore, to have an integrated interpretation of these Indices and get a better ranking of the different sites´ drought tolerance, we used the framework proposed by Schwarz et al. (2020), that compares the observed relationship between recovery and resistance with the hypothetical one that represents full resilience (resilience = 1) at any given value of resistance:

Recovery = 1/ Resistance

Finally, to investigate the effects of recent climate trends and the megadrought occurring in Central Chile on tree growth, we analyzed the basal area increment trends of the two northernmost and older sites using a linear regression. These only two sites were analyzed to avoid any potential tree density effect present in the other younger sites. BAI trends since 1970 and BAI values during the megadrought period were compared with values pre-megadrought.

3. Results

3.1. Growth patterns across the gradient

N. obliqua growth rates were lower and trees were much older in the two northern sites (TRI and MEL) than in the others, despite the size of sampled trees being similar (Figures 3 and S2). Most of the stands had trees between ~50 and 80 years old, while trees were ~160 and ~180 years old in TRI and MEL, respectively. Tree growth rates were particularly high up to the first 20 years and steeply decreased afterwards in all the stands, except in TRI and MEL (Figure S2). Tree growth rates and BAI reached the highest values in the southernmost site RIN, which was also the youngest stand (~ 50 years, Figures 3 and S2). The differentiation in radial growth rates among sites was more conspicuous until 1980 (between ~1 mm and 7 mm). Thereafter, differences narrowed down and growth rates across the different sites ranged between ~0.5 and < 4 mm/year (1980-2000, Figure S2). Moreover, after 2010 radial growth ranged between 0.5 and 2 mm in the different stands (Figure S2).

Regarding the occurrence of disturbances, TRI and MEL stands presented almost synchronic events occurring in 1925-1926 and 1962-1963, which caused growth releases in at least 40% of the trees (Figure 3). In the case of NAM, there was an event close to the stand establishment in 1954 that caused a release in more than 38% of the trees (Figure 3). The same was also observed for RIN around 1976 (Figure 3). In the case of ARQ, more than 45% of the trees showed a release around 1999. No disturbances that caused significant growth releases according to the applied criteria occurred in RUC, LPR, VAH and SPT.

The PCA analysis of the tree-ring width chronologies over the common period 1967-2017 showed that 57% of the total variance of growth across the climate gradient was explained by the first component and only 13% by the second component (Figure S3). All but two sites had the highest loadings in the first component, suggesting a common regional signal in tree growth variability across most of the climate gradient. The two northernmost sites TRI and MEL had the highest loading (>0.8) in the second component (Figure S3), indicating that this pattern of inter-annual growth variability represents northern *N. obliqua* forests. These two northern chronologies also had the highest mean sensitivity (Table 1), reflecting a more variable radial growth and higher interannual variability associated to environmental conditions (Fritts, 1976). The overall mean sensitivity generally decreased from north to south in the gradient (Table 1).

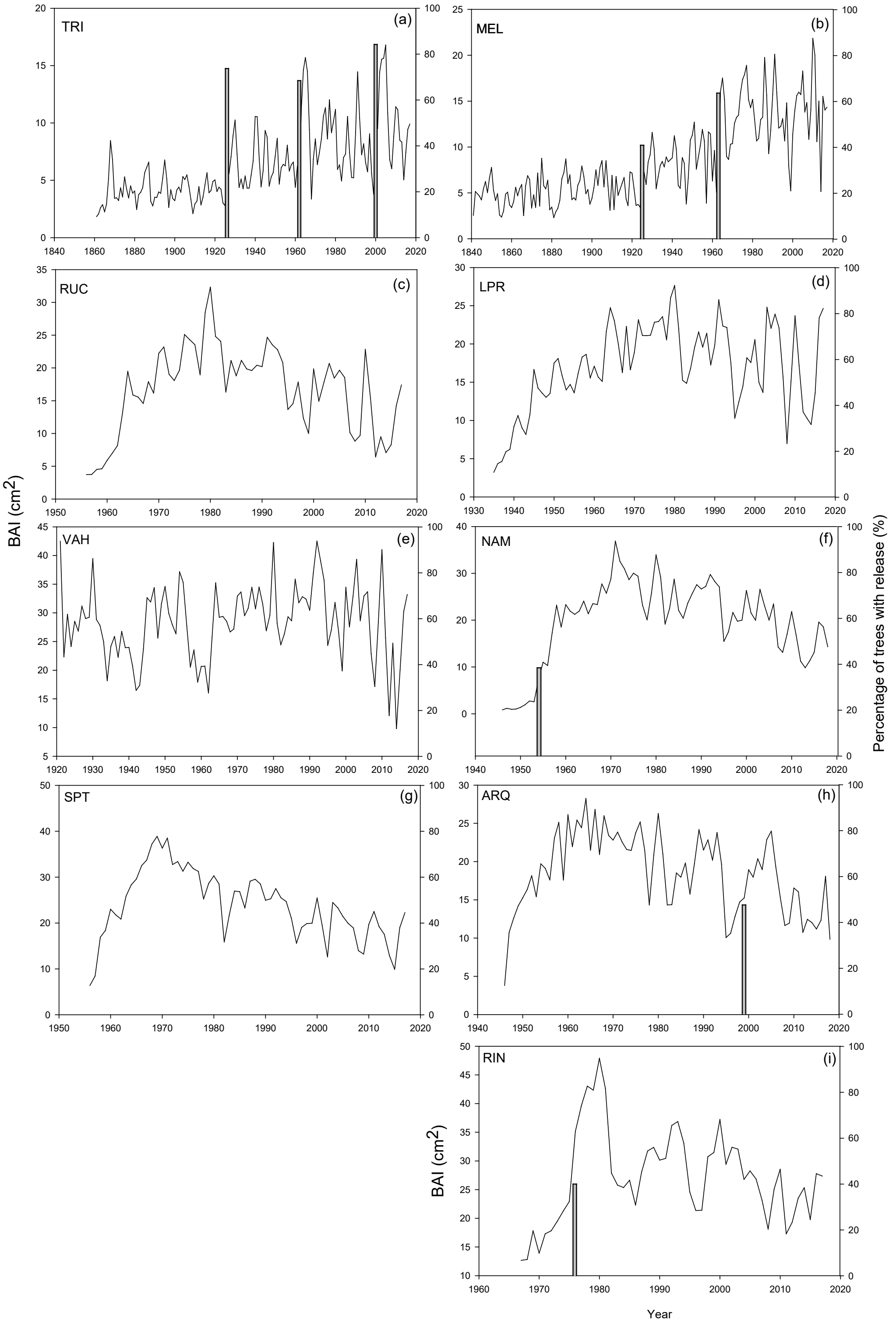


Figure 3. Mean annual basal area increment (BAI) recorded in each stand from north to south (top to bottom). Grey bars show the years with growth releases that affected more than 30% of the trees sampled in each stand (see Methods). See Table 1 for site abbreviations.

3.2. Productivity trends across the gradient

Peak NDVI of secondary *N. obliqua* forests fluctuated around 0.88 across most of south-central Chile, but north of 37°S it steadily decreased to around 0.82, suggesting that productivity levels were similar over most of the region and declined only in the north under drier conditions and lower stand densities (Figure 4). The mean pattern of zonally-averaged long-term trends in peak NDVI across the gradient fluctuated around zero in the northern region between 36-38°S, indicating that productivity has not changed over the period 2001-2018. In contrast, dominantly positive trends indicated that productivity increased towards the temperate region and also in the northern end of the climate gradient (Figure 4).

A general significant association was found between the inter-annual variation in tree growth and the maximum annual NDVI (peak NDVI) at each site. Eight of the nine stands showed a significant correlation between them (Figure 5). In the case of NAM and ARQ the best correlation was found between growth and the peak NDVI of the previous growing season (Figure 5).

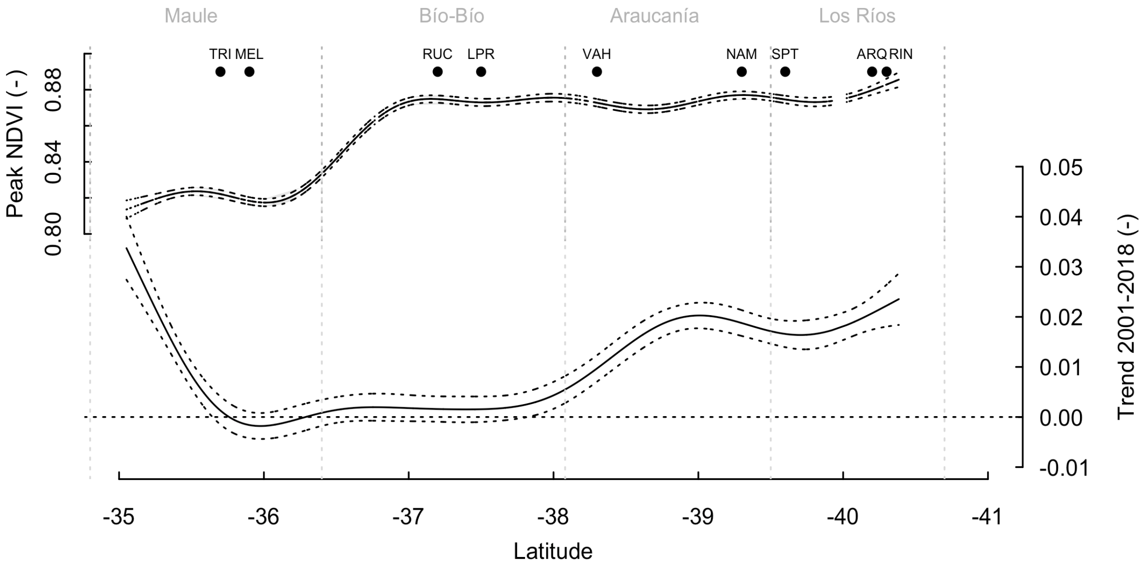


Figure 4. Latitudinal profiles of mean peak NDVI of *N. obliqua* secondary forests and its temporal trend over the period 2001-2018 in the study region. For each latitude, all MODIS pixels dominated by *N. obliqua* were averaged across longitudes (i.e., zonal mean) and then the linear trend was calculated. A GAM smoothing was used to model the change in mean peak NDVI and trend as a function of latitude. The dotted lines represent the 90% confidence intervals of the fit. The location of each study site is indicated at the top. See Table 1 for site abbreviations.

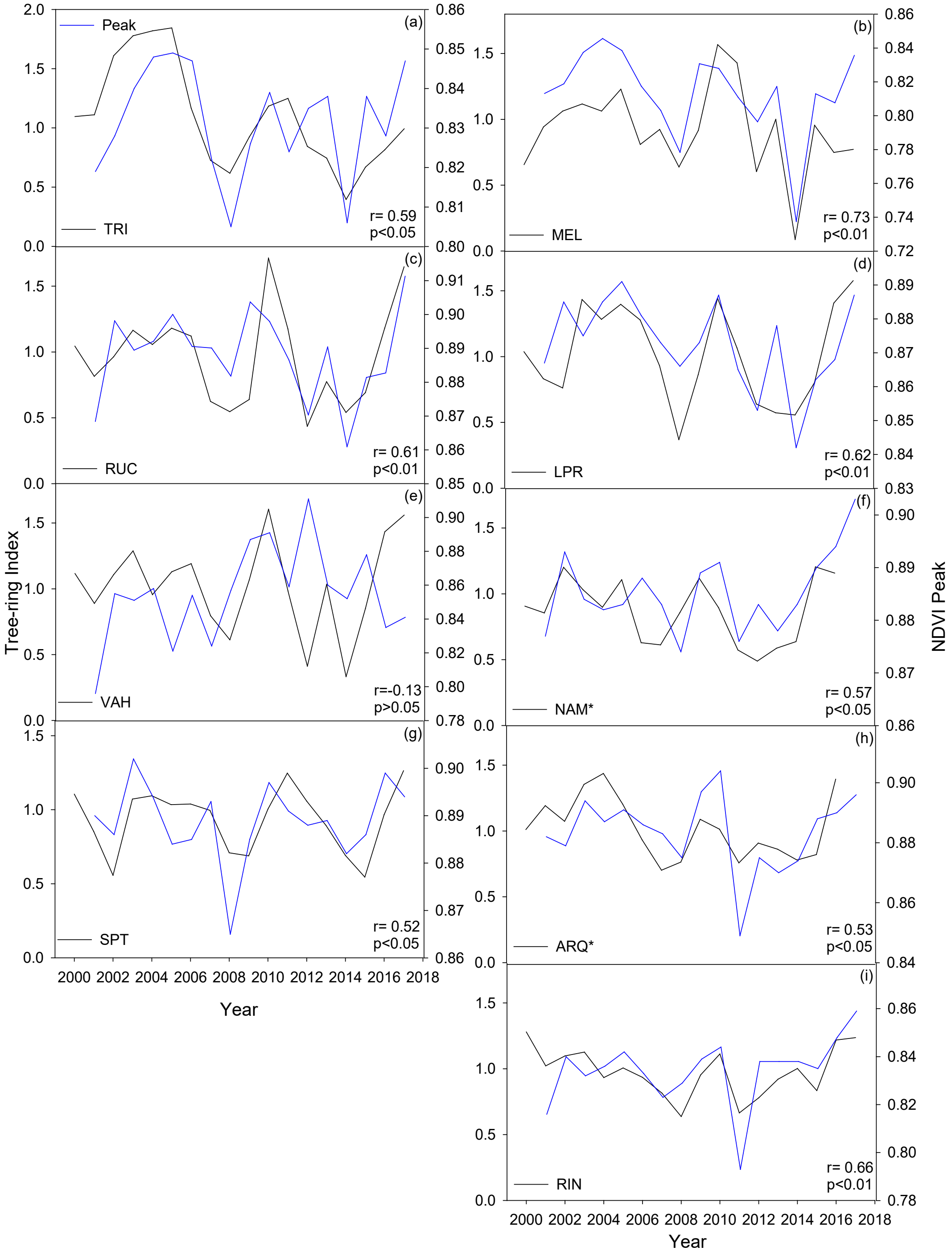


Figure 5. Comparison between tree-ring standardized chronologies in each of the study sites (black) and the peak growing season NDVI of the nearest MODIS pixels (blue) for the period 2001-2017. There are no significant trends in these records in any of the sites. Correlation coefficients and their significance are shown at the bottom right of each plot. Asterisks in f and h indicate that the relationship shown was with the NDVI of the previous growing season. See Table 1 for site abbreviations.

3.3. Relationships of annual tree growth with climate

Monthly and seasonal correlations of tree-ring chronologies with precipitation and maximum temperature are shown in Figures S4 and S5, respectively. The highest correlations found in each site are summarized in Table 2, and Figures 6 and 7 for precipitation and maximum temperatures, respectively. Correlations between growth and precipitation were positive and significant in all the sites ($p < 0.05$), and the strongest relations were found with annual rainfall in the northernmost sites, TRI and MEL. To the south of Maule Region, the highest correlations with rainfall were found considering the growing season period and correlations with summer precipitation were the highest in the southernmost sites (SPT and ARQ, Table 2). Significant and negative correlations with maximum temperatures were found in all study sites except for RUC and RIN, and they were in most of cases lower than correlations with precipitation. VAH and NAM (Araucanía Sites) were exceptions to this pattern.

Table 2. Most significant correlations ($p<0.05$) found between tree-ring standardized chronologies and regional climate variables. The periods for the calculation of correlations were the following for precipitation: TRI and MEL: 1930-2017, RUC: 1956-2017, LPR: 1941-2017, VAH: 1948-2017, NAM: 1948-2017, SPT and ARQ: 1959-2017, RIN: 1967-2017; and for Maximum temperature: TRI and MEL: 1959-2017, RUC and LPR: 1960-2017, VAH and NAM:1958-2017, SPT and ARQ: 1955-2017 and RIN: 1967-2017. See Table 1 for site abbreviations.

	TRI	**MEL**	**RUC**	**LPR**	**VAH**	**NAM**	**SPT**	**ARQ**	**RIN**
Precipitation									
Annual	0.49	0.44							
September-March			0.43		0.42	0.28			0.34
December-March							0.40	0.37	
December-February				0.32					
Maximum Temperatures									
December-March				-0.3				-0.31	
December-February	-0.32				-0.48				
December						-0.37			
March							-0.39		
Previous December-March		-0.43							

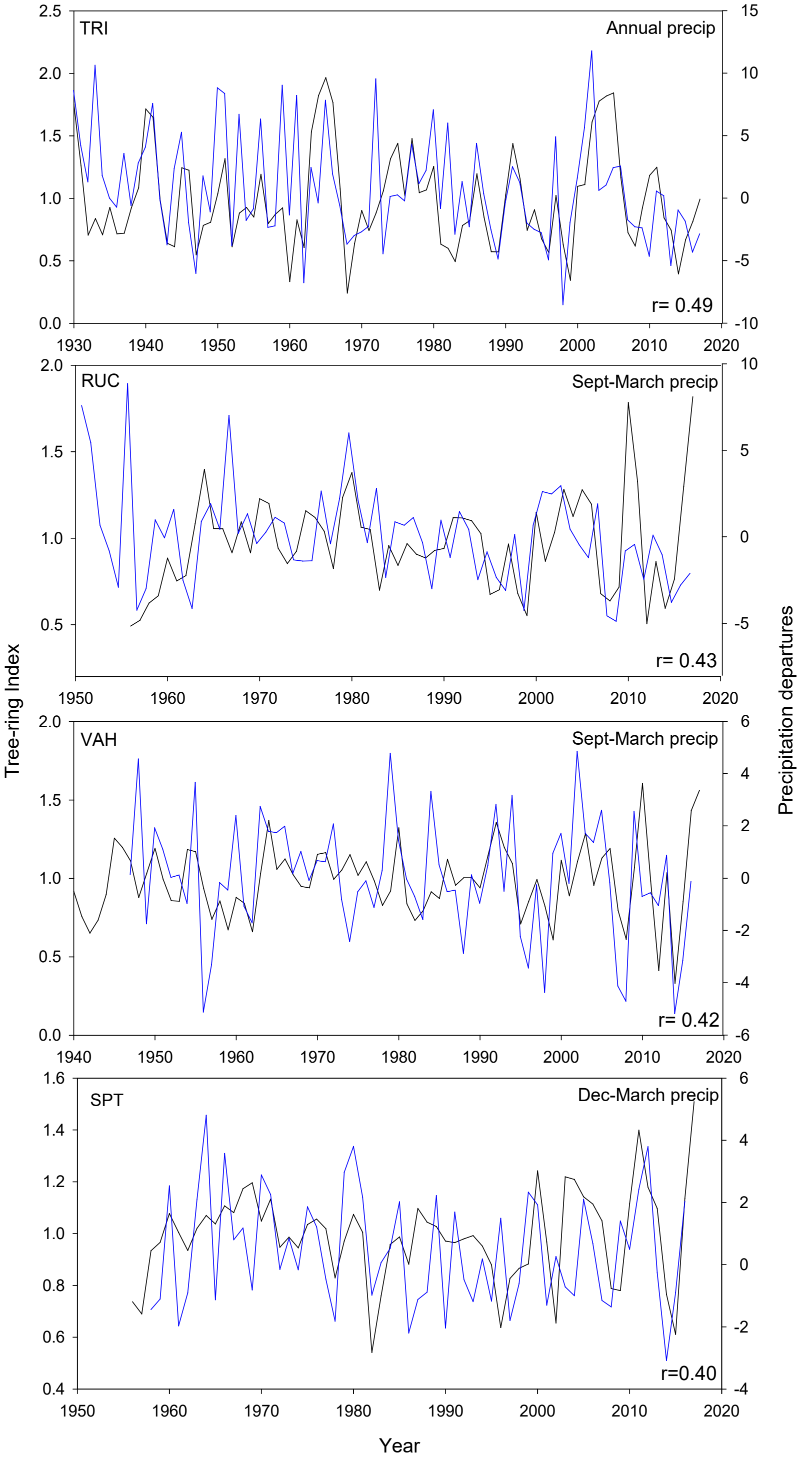


Figure 6. The strongest correlations between tree-ring standardized chronologies (black) and seasonal precipitation departures (blue) found in each region. The overlapping period varies according to the length of both records in each case (see Methods section). The significant

correlation coefficient (r, p<0.05) is shown at the bottom right side of each plot. See Table 1 for site abbreviations.

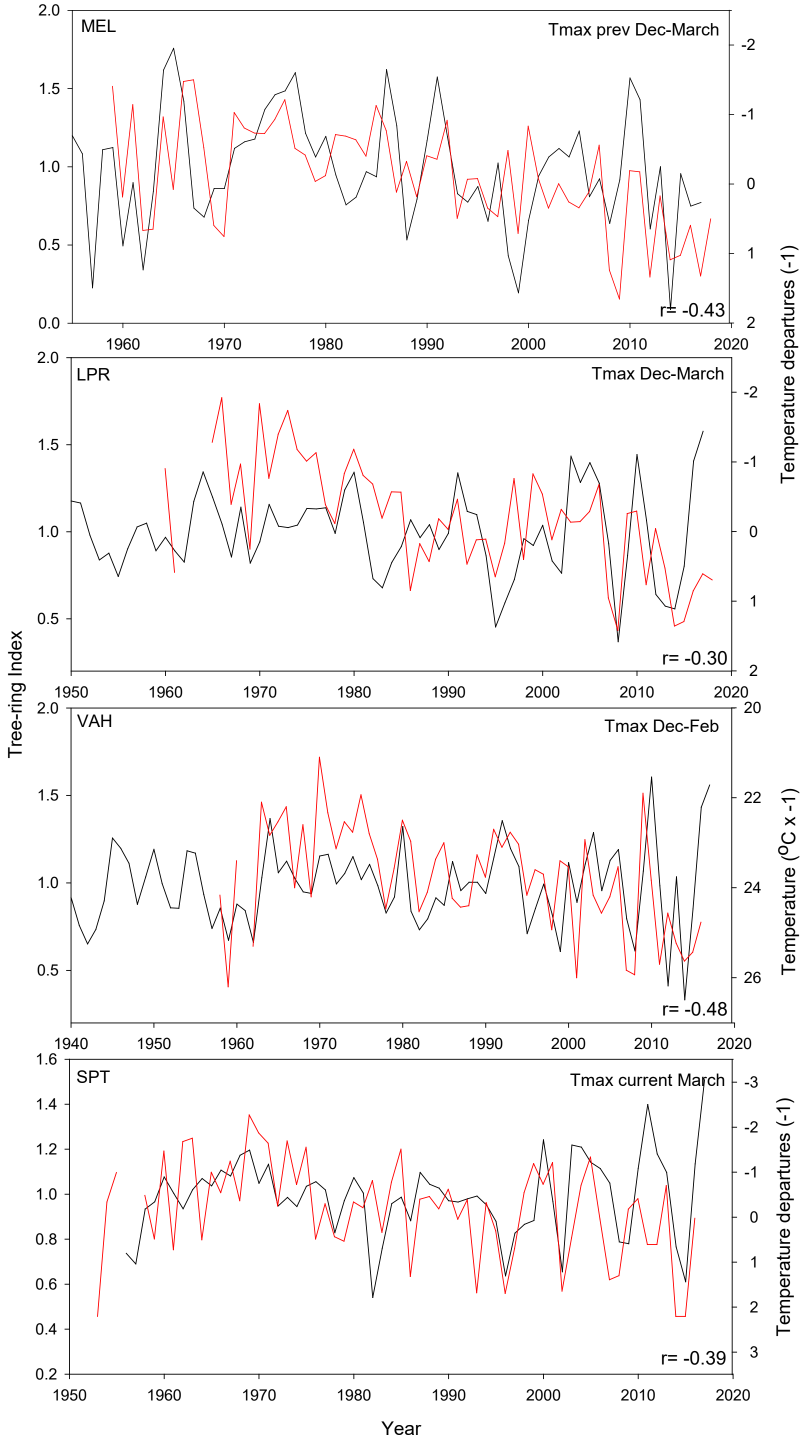


Figure 7. The strongest correlations between tree-ring standardized chronologies (black) and seasonal maximum temperatures (red) found in each region. For MEL, maximum temperatures are from the previous summer season. The overlapping period varies according to the length of both

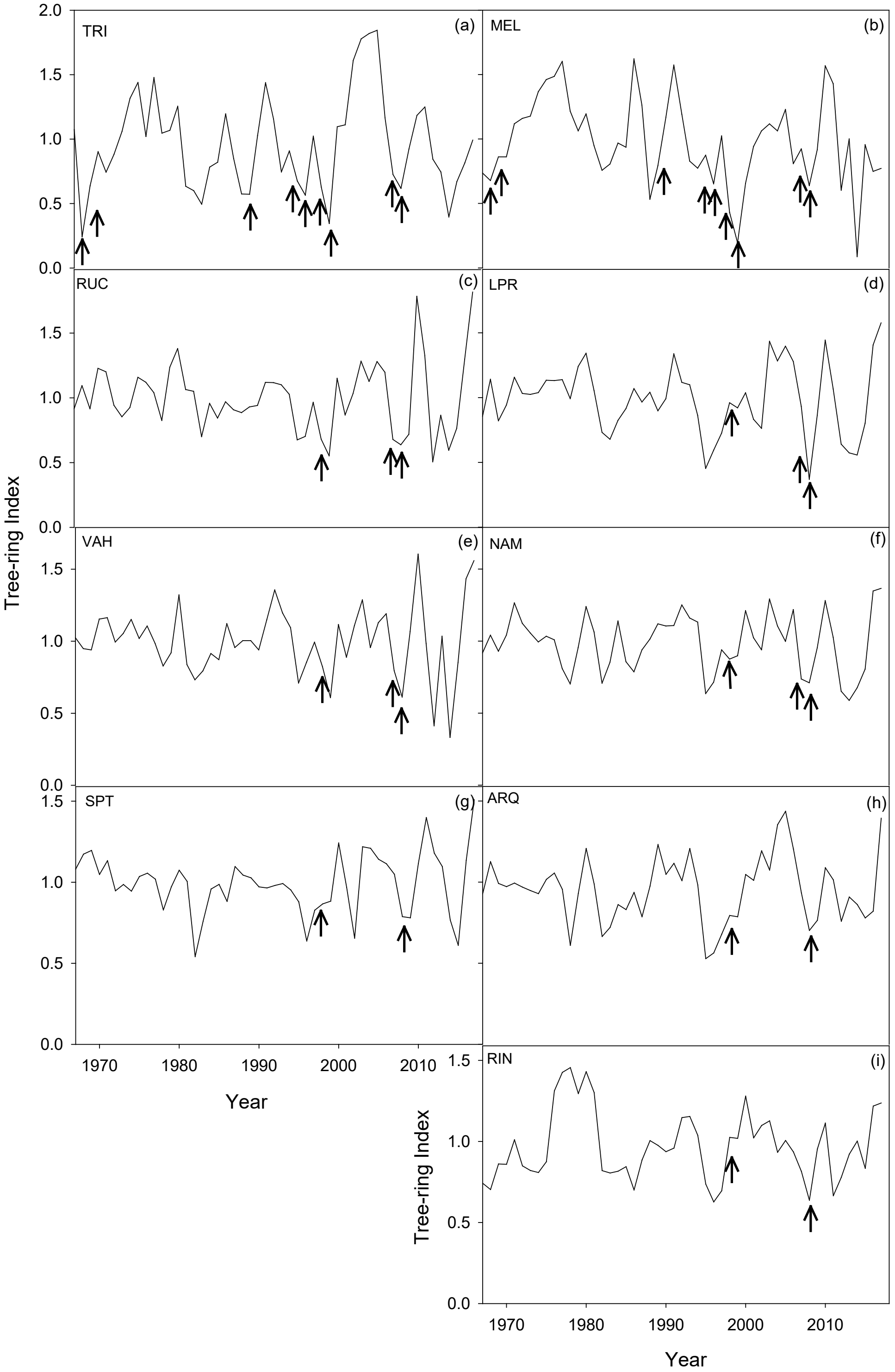
records in each case. The correlation coefficient (r, $p<0.05$) is shown at the bottom right side of each plot. See Table 1 for site abbreviations.

3.4. Tree-growth resilience to droughts

Droughts defined through the PDSI were more recurrent in the Mediterranean Maule Region, where nine events were identified since 1967, compared to the temperate sites which had only two to three drought years (Table 3, Figure 8). Common drought years across the latitudinal gradient were the ones occurring in 1998 and 2008.

Table 3. Droughts according to the annual PDSI for the Maule Region and September-March PDSI for the other regions. Only years also reported by the corresponding three-months SPEI were considered as droughts.

Region	**Droughts**
Maule	1968, 1969, 1989, 1995, 1996, 1998,1999, 2007, 2008
Bío Bío	1998 2007, 2008
Araucanía	1998, 2007, 2008
Los Ríos	1998, 2008



TRI
(a)
MEL
(b)
RUC
(c)
LPR
(d)
VAH
(e)
NAM
(f)
SPT
(g)
ARQ
(h)
RIN
(i)
Tree-ring Index
Year
0.0
0.5
1.0
1.5
2.0
1970
1980
1990
2000
2010

Figure 8. Tree-ring standardized chronologies for the common period 1967-2017 in the stands arranged from north to south (top to bottom). Arrows show the years reported as droughts according to PDSI and SPEI (see methods section). See Table 1 for site abbreviations.

Resistance of growth to drought was higher in the southernmost site RIN, indicating that trees in this site did not decrease their growth as much during a drought event (Figures 9a and S6a). The opposite was true for the northernmost site TRI, whose trees declined their growth considerably during droughts (Figure 9a and S6a). The stand with the greatest growth recovery after drought was TRI, followed by MEL and RUC, and the ones with the lowest recovery were the southernmost ARQ and RIN (Figure 9b and S6b). Finally, the most resilient sites included the northernmost sites TRI and MEL, as well as the southern site SPT, and the site with the lowest resilience was ARQ (Figure 9c and S6c). Except for certain variability, there was an overall trend for increasing resistance and decreasing recovery from north (Mediterranean climate) to south (Temperate climate) across the latitudinal gradient (Figure S6).

Following the same approach used to calculate the Resilience Indices, Figure S7 shows a simpler interpretation of tree-growth before, during and after droughts across the latitudinal gradient. The largest growth reduction of more than 40% with reference to the pre-drought period was observed in the northern sites (Maule Region, Figure S7). This reduction decreased to around 30% in the middle of the gradient (Bío Bío and Araucanía Regions) and to a bit more than 20% in Los Ríos Region (Figure S7). The complete recovery of growth occurred the second year after the drought event in all sites and was maintained for a little longer and at higher values in the Maule sites than in the rest of the regions.

According to the approach presented by Schwarz et al., (2020) to get a more integrated interpretation of the Resilience Indices, Figure 10 shows the observed Recovery-Resistance relationship in each site in reference to a line of full resilience. This figure indicates that TRI is the site that at low values of resistance (< 0.6) can reach the highest values of recovery, much higher than the line of full resilience. MEL, LPR, SPT and RIN, are also above the line of full resilience, indicating a higher recovery at any given value of resistance (above 0.7). Sites that do not reach the line of full resilience, but are close are RUC, VAH and ARQ.

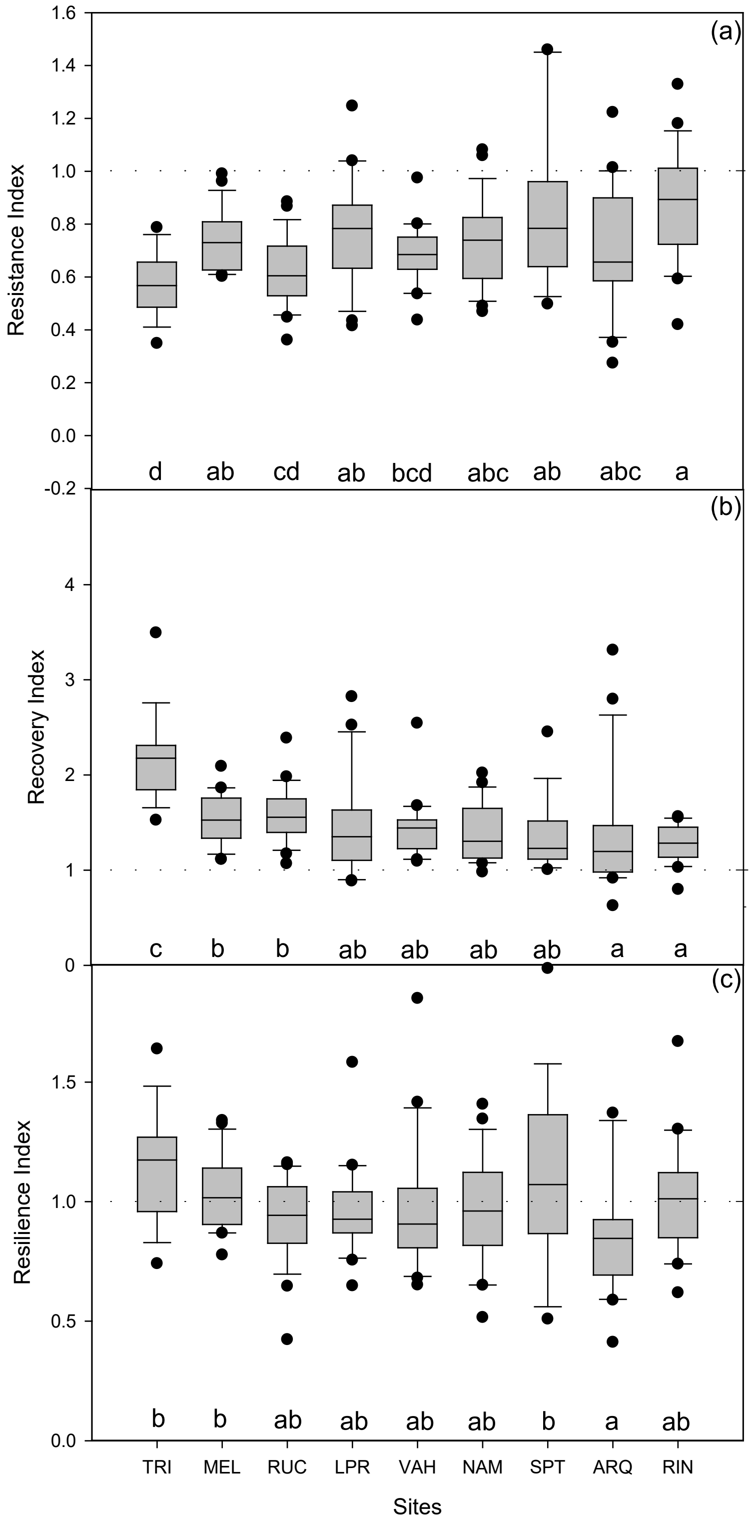


Figure 9. Variation in resistance, recovery, and resilience parameters of *N. obliqua* along the climate gradient. a) Resistance Index, b) Recovery Index and c) Resilience Index for all the studied

stands. Different letters indicate significant differences, according to the Kruskal-Wallis Test. Sites are arranged from north to south (left to right). See Table 1 for site abbreviations.

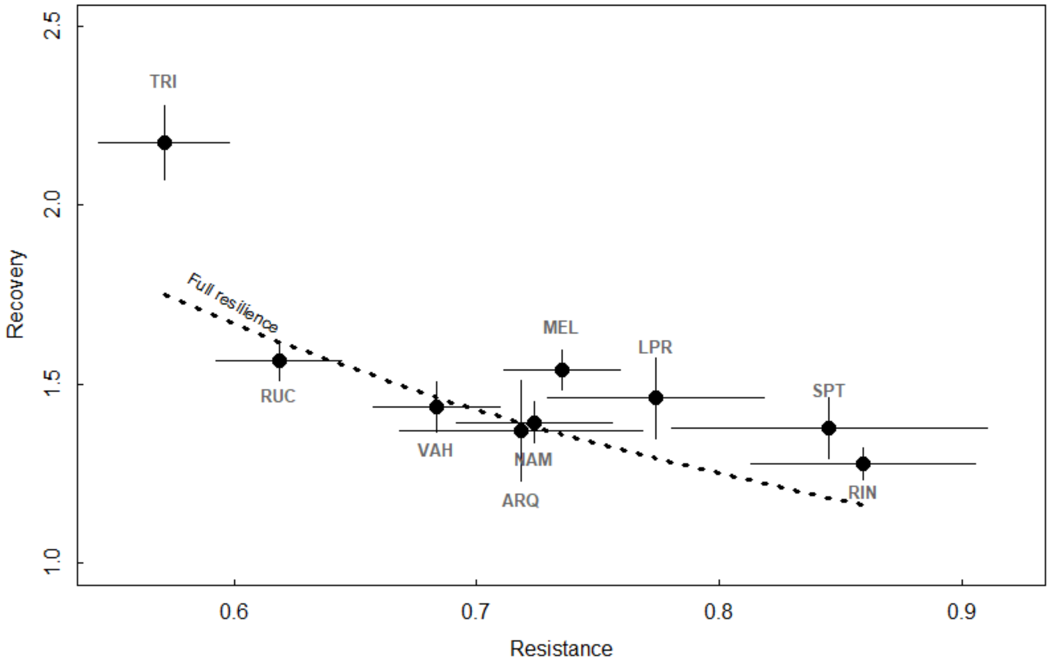


Figure 10. Comparison of the relationship between observed values of mean resistance and recovery in each of the nine sites and the hypothetical function that represents the line of full resilience (Resilience=1) at any value of resistance. The standard errors of resistance and resilience are indicated for each site.

Regarding the effects of precipitation and temperature trends during recent decades on tree growth in the northern sites TRI and MEL, no significant BAI trends were found since 1970 (Figure 11). Moreover, considering the long-lasting megadrought period (2010-2017), there was no unprecedented BAI reduction since basal area increment values were similar to those found in the mid-late 1990s (Figure 11).

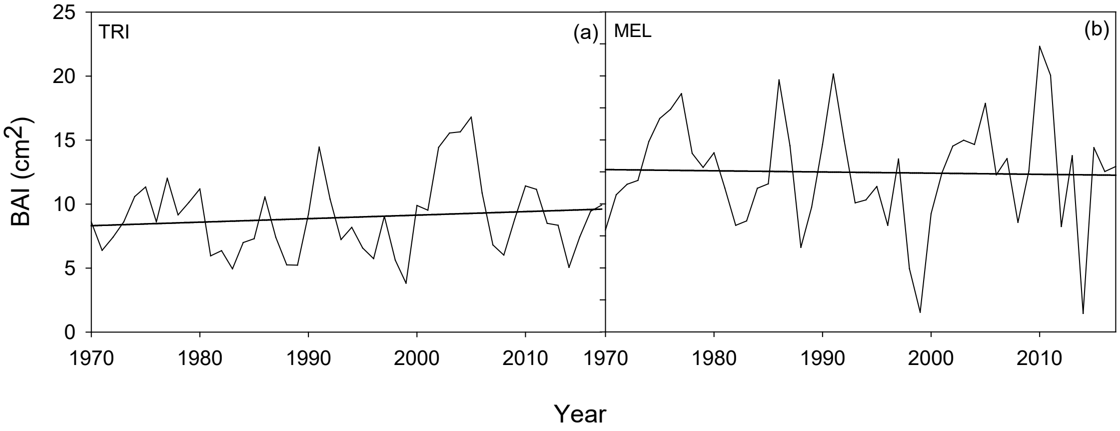


Figure 11. Basal area increment (BAI) for TRI (a) and MEL (b) stands during the 1970-2017 period. No significant linear trends are shown.

4. Discussion

4.1. Tree growth patterns and productivity trends across the gradient

Tree growth rate was low in the two northernmost sites from Maule Region, and it did not substantially decrease during the first decades of the stand development, compared with the other sites. This agrees with earlier findings showing that stand growth in the region does not have a defined age for the growth maximum, being this around 10-30 years old (Donoso et al., 1993). By contrast, stands south of Maule showed a much higher juvenile growth rate and this steeply decreased especially after the first two decades. Radial growth rates of trees in these stands when they were around 60 to 70 years old were similar to the growth rates of trees from the two northern sites along their complete lifespan.

Five of the nine stands presented distinguishable sudden growth releases attributable to disturbance events that occurred during their development history. These events probably corresponded to thinning, which usually occurs in these forests due to the high quality of their wood and good accessibility (Echeverría and Lara, 2004). The northern stands were affected by almost synchronic disturbance events, one around 1925-1926. It is not possible to discard that this release could be related to one of the driest years on record (1924) in Central Chile in the last millennia (Le Quesne et al. 2006), since droughts may cause tree death, gap formation in the forest canopy and consequently growth releases (Rubio-Cuadrado et al., 2018). None of the other release events recorded in the different sites could be related to drought´s occurrence. Tree density in MEL was the lowest, and besides growth releases, there were various stumps in the site, so past logging could be the explanation of the low density in this stand. Tree density was also low in VAH; however, there were just few stumps and no signs of synchronous release events that affected at least 30% of the trees in this site.

Inter-annual growth variability in these secondary forests had a strong regional signal across most of the climate gradient, but the northern region differed, as shown by the principal component analysis. An earlier study of growth patterns of *N. pumilio* at the treeline (36º to 39º S) also found a similar result for the northern populations from Maule region (Lara et al., 2001). These results are probably a consequence of the Mediterranean climate in the northern area of the central Andes of Chile, while at the south of 37º S climate becomes more temperate and wetter (Luebert and Pliscoff, 2006). On the other hand, the mean sensitivity of tree-ring chronologies was the highest in the drier Mediterranean part of the transect, pattern that was also observed in an aridity gradient of *Araucaria Araucana* forests (Muñoz et al., 2014), but not in a large latitudinal gradient of *N. pumilio* forests (Lara et al., 2005).

Climate trends indicated that warmer and drier conditions are becoming increasingly dominant in south-central Chile. Despite this, and as it was expected, it was not possible to identify trends in the tree-ring records potentially driven by climate, given the strong influence of forest dynamics (i.e., decreasing growth trends associated to the gradual closing of the canopy) on the largely young stands that constitute the secondary *Nothofagus* forests of Chile. Trends in peak NDVI showed no change in productivity for the *Nothofagus* stands north of 38ºS, and an increasing trend south of this latitude and in the northern end in the last two decades. The latter should be interpreted with caution because it could be an artifact caused by very few *N. obliqua* pixels available north of 35.5°S and the intense land use change in this region. Increases in productivity at a global level have been mainly attributed to a CO_2 fertilization effect (Zhu et al., 2016), which cannot be discarded for stands south of 38º S. However, given the sustained positive trend of peak NDVI south of this latitude and the rising basal areas from north to south, the observed greening is probably attributable to changes in stand development. It has been reported that increases in leaf size, number of leaves, stand density, as well as woody regrowth are important drivers of increases in productivity (Buitenwerf et al., 2018; Chen et al., 2019). Thus, climate change may have little effect on the reported greening of forests in these temperate sites, especially because current warmer and drier conditions cannot lead to this pattern.

The strong correlation found between tree growth and peak NDVI indicates that NDVI might be a good proxy for productivity in these secondary forests at larger spatial scales, contributing to fill out the research gap reported for studies at a higher resolution and in different environments (Gazol et al., 2018). Significant relationships could be partly explained, because dry years may cause early leaf shedding in the species (Martinez, 2000; Veblen et al., 1996), condition that affects current NDVI and tree growth in the current and following growing season. The relationship did not hold equally for all the sites though, which could be potentially due to the varying proportion of *Nothofagus* deciduous species in the stands (the lowest relationship was reported for VAH, the site with the lowest basal area of *N. obliqua* and a large proportion of evergreen species). Caution should be exerted then, when extrapolating and interpreting productivity values from NDVI records and tree-ring series in mixed stands.

4.2. How climate relates with tree growth in *N. obliqua* forests

Correlations between tree growth and climate demonstrated that precipitation was the main driver of *N. obliqua´s* growth across the latitudinal gradient. A dependency of growth on rainfall has been reported for diverse broadleaved species in Europe, with increasing influence during recent decades (Čater and Levanič, 2015; García-Suárez et al., 2009; Rozas et al., 2015; Rozas and Olano, 2017). Generally, correlations between rainfall and radial growth were stronger towards the drier edge of the distribution range, a pattern that was also found in studies at transitional areas between Mediterranean and Temperate climates (De Luis et al., 2013; Rozas et al., 2011). Correlations between growth and precipitation were higher with annual rainfall in the north, with growing season precipitation in the middle of the gradient and with summer rainfall towards the south. This may be explained by the Mediterranean-Temperate climate transition across the gradient, where summers become shorter, rainier and more important for tree-growth when moving to the south. A positive significant relationship between precipitation and growth was previously observed for the related species *N. macrocarpa* (32.5º-34.5º S), where winter-spring precipitation was the most important factor controlling growth (Venegas-González *et al* 2018b, 2018a). Moreover, *N. pumilio* growth in the treeline was also reported to be significantly related with annual precipitation at their northernmost distribution (Lara et al., 2005).

Correlations of growth with maximum temperature were negative in some of the sites, indicating a detrimental effect of warmer summer conditions on the growth of *N. obliqua*. Negative effects of spring-early summer temperatures on tree growth have been reported for *N. macrocarpa* (Venegas-González *et al* 2018a, 2018b), and of spring and annual temperatures for *N. pumilio* at the northern edge of their distribution (Lara *et al* 2001, 2005). Moreover, negative relationships with temperature were recently reported for *N. pumilio* tree growth at its lower elevation margin in northern Patagonia (Serrano-León and Christie, 2020). Higher maximum temperatures may increase the vapor pressure deficit in the atmosphere, increase evapotranspiration rates and reduce water availability for the plants (Lara et al., 2001; Urrutia-Jalabert et al., 2015b). Particularly high negative correlations between tree growth and maximum temperature were found in MEL and VAH. VAH was the closest site to the Central Depression where warmer conditions predominate, and annual precipitation recorded in the area was the lowest, so that might explain the strong negative effect of summer temperature on tree growth. It is interesting to note the case of MEL, where maximum temperatures from the previous growing season had the strongest negative effect on tree growth. This may be the result of warm temperatures that cause higher respiration rates and consequently reduce the starch reserves for growth during the following season (Deslauriers et al., 2014).

The overall negative effect of dry and usually hot summers on *N. obliqua´s* tree growth may also be partly caused by the early leaf shedding that affect the species under these conditions (Martinez, 2000; Veblen et al., 1996). Given the warmer and drier conditions projected for south-central Chile (Fuenzalida et al., 2007), it can be expected that climate change will negatively affect the radial growth of *N. obliqua*.

4.3. Tree-growth resilience to droughts

Results from this study suggest that the impacts of droughts on *N. obliqua* productivity vary across the climate gradient, supporting previous findings from other Mediterranean-to-Temperate transitional areas (Sánchez-Salguero et al., 2018; Zang et al., 2014). According to the resilience analyses, tree growth in the southernmost population from Los Ríos Region (RIN), showed the highest resistance to drought, following high inter-site variability, but a general trend towards increasing drought resistance to the south. Thus, the greatest reductions in growth during droughts were found at the northernmost site TRI. This pattern was also found in other studies in Europe (De Luis et al., 2013; Gazol et al., 2017b; Sánchez-Salguero et al., 2018; Zang et al., 2014); however, it is in contrast, to what was found for *Fagus sylvatica -Quercus petraea* forests in southwest Germany, where a higher resistance was found at drought-prone sites (Kunz et al., 2018).

Recovery indices indicated that trees from all stands may recover growth rates after drought occurrence. Moreover, growth recovery was greater in the northern Mediterranean sites than in the south. This is in line with what has been reported in other places in the world, where growth of populations from drier areas showed lower resistance to drought and higher recovery capacity after drought, compared with populations from wetter sites (Gazol et al., 2017b; Sánchez-Salguero et al., 2018; Zang et al., 2014). This result implies a trade-off between resistance and recovery in the response of *N. obliqua* to drought along its distribution range. Such response has been confirmed for several studies that has used this approach (Schwarz et al., 2020) and may be modulated by the variation in mean climate conditions across the latitudinal gradient (Sánchez-Salguero et al., 2018).

The most resilient to drought trees grew in north (drier) stands and also included one stand from the south (SPT), which was located in a deep soil and close to a stream. All the other sites, except ARQ, were not significantly different from these three stands, although they overall had a resilience <1 (except LPR). Interestingly, ARQ, a stand located in the southernmost and wettest region, had the lowest resilience probably because this site was located on a North aspect (drier aspect in the southern hemisphere) at 31° of slope, and showed a moderate attack of the wood-boring beetle *Holopterus chilensis*. This indicates that regional climate conditions in the study sites did not define the resilience of trees to drought events. Local environmental conditions (e.g. slope, aspect, soil texture and depth) are probably quite important, since they might significantly alter water availability during drought events (Gazol and Camarero 2012, Sánchez-Salguero *et al* 2018). Furthermore, when using the integrated interpretation to better define the tolerance of the different stands to droughts (Schwarz et al., 2020), we confirmed that the northern stands, as well as SPT, were within the ones with the best tolerance to drought, because trees could reach higher values of recovery at any given value of resistance compared to the hypothetical relationship (Schwarz et al., 2020). The southernmost site RIN and LPR, a stand located in the middle of the gradient, were also well above the line of full resilience. The stands that were below this line, although very close, were VAH, ARQ, as well as RUC, a very dense stand located in the middle of the gradient. The fact that all the stands were not far from the line of full resilience indicates that they have not been that strongly impacted by droughts so far. Future studies should characterize local environmental and soil conditions in each site to account for the effects of local climate and soil water retention capability on tree responses to drought (Sánchez-Salguero and Camarero, 2020).

Northern stands did not show any significant decreasing growth decline during recent decades. This is somewhat surprising, since other tree species growing in south-central Chile have mainly shown decreasing trends associated to changing climatic conditions (Venegas-González et al., 2019a, 2018a; Villalba et al., 2012). Studies across the whole range of *N. macrocarpa* in central Chile found a growth decline since the 1980´s that resembles the prevailing drying and warming trends in the area (Venegas-González et al., 2019b, 2018a). This trend, however, was not found in young trees of the species (< 80 years old) growing at the highest elevations of its distribution (Venegas-González et al., 2019b). This response of young trees at cooler high elevations was attributed to a possible CO_2 fertilization effect, which would have counteracted the negative effect of climate change on tree growth in recent decades (Venegas-González et al., 2019b). In this study we mainly assessed the effects of climate on tree growth, but since tree responses to a changing climate also depend on the increasing levels of CO_2 in the atmosphere, it is essential to evaluate if these forests are responding to it. CO_2 has increased from 321.4 to 402.5 ppm in the 1967-2017 period (25%, Tans and Keeling, 2020) and intrinsic water use efficiency (iWUE) in tree rings during this period has been reported to increase between 18 and 33% in diverse broadleaved and coniferous species from southern Chile (Camarero, 2020; Camarero and Fajardo, 2017; Peña, 2015; Urrutia-Jalabert et al., 2015a). Given this context, and despite the rate of iWUE increases is slowing down globally (Adams et al., 2020), isotope analyses are being carried out to examine potential changes in water use efficiency in some of the studied populations during recent decades.

The lack of recent growth decline in *N. obliqua* at its northern distribution area, together with the high resilience to drought events and the non-unprecedented growth reduction rates during the megadrought period (at least until 2017), suggest that the species is being able to tolerate the current drier and warmer conditions in this area. These results are in line with what was reported for *Fagus sylvatica* L. at the dry edge of its distribution range in Europe*,* where a high tolerance to drought and almost no-evidence of a growth decline was observed (Cavin and Jump, 2017). In addition, other studies have found that growth sensitivity to drought was lower in Mediterranean than mesic tree populations (Babst et al., 2013; Weber et al., 2013). Our results support that, although low water availability is expected to reduce growth and increase mortality at the dry end of the range of forest species (Allen et al., 2010; Linares et al., 2011; Sánchez-Salguero et al., 2012; Sarris et al., 2007), range-edge contraction is not universal and tree responses to drought may depend on the adaptive plasticity of tree species modulated by local environmental constraints (Cavin and Jump, 2017; Rozas et al., 2020; Zas et al., 2020). Finally, tree competition and high stand density can be the main drivers of growth decline in some forests (e.g. mixed Fagaceae forest, Rubio-Cuadrado et al., 2020). Therefore, forest management and particularly thinning, have been reported to enhance forest resilience to drought events due to a reduction of inter-tree competition intensity (D'Amato et al., 2013; Giuggiola et al., 2013). Moreover, it has been reported that temperate tree species can be facilitated and have a greater resilience to drought when growing in mixed forests coexisting with other species (Pretzsch et al., 2013). To better inform climate change adaptation measures in Chile, future studies should address the effects of thinning and forest composition on the climate sensitivity and resilience of *N. obliqua* to drought events.

5. Conclusions

Although tree-growth trends during recent decades showed to be independent of climate trends in the studied forests, we found that warm and dry conditions are detrimental for the growth of *N. obliqua* and may affect future growth patterns across the studied latitudinal gradient in Chile. We found contrasting patterns in drought´s resistance and recovery across the gradient, which could suggest diverse strategies to face these events under different environmental conditions. Stands from Temperate areas had a higher growth but were less able to recover after droughts than trees under Mediterranean conditions. Resilience to drought events was the highest in the Mediterranean area and in a stand growing under good site conditions in the south. On top of this, the integrated framework to define the tolerance of stands to drought events confirmed this finding, and two more sites (RIN and LPR) were found to be tolerant to droughts. These evidences suggest that tolerance to droughts would be modulated by site conditions in this species, with northern/drier populations showing a particularly high tolerance to droughts. Although assessed drought events do not strongly impacted the growth of *N. obliqua* so far, future studies should assess the impact of the long-term megadrought that is occurring in Chile and particularly of the severely dry conditions of 2019 on tree growth. This would allow us to have a better understanding of the resilience of these forests to climate change (Anderegg et al., 2015; Gazol et al., 2017b). Finally, further studies should address the hydraulic vulnerability of the species to drought events, in order to go beyond what tree growth can reveal.

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