Contents lists available at ScienceDirect



Forest Ecology and Management



journal homepage: www.elsevier.com/locate/foreco

Recent radial growth decline in response to increased drought conditions in the northernmost *Nothofagus* populations from South America



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ARTICLE INFO

Keywords: Chilean Mediterranean-type forest Dendroecology Forest decline Global warming Precipitation decrease ENSO

ABSTRACT

An emerging phenomenon of forest decline in Mediterranean-type ecosystems has been detected in response to climate change during the last century. It is expected that the Mediterranean regions will likely experience drought events during this century with consequences for biodiversity maintenance. Although the Chilean Mediterranean-type forests are among the most threatened forest ecosystems in South America, their responses to recent increased drought events due to global warming are poorly documented. In the same region, the endangered and endemic forests of Nothofagus macrocarpa (Nothofagaceae) are found on mountain peaks. It is unclear how N. macrocarpa forests are responding to increased drought conditions occurring in the area over the last few decades. Here, we analyzed how recent climatic variability has affected the growth of N. macrocarpa. We selected five sites along the whole geographic distribution of N. macrocarpa forests in central Chile (32.5-34.5°S) to develop tree-ring chronologies. Climate-growth relationships were analyzed through correlations with local (precipitation, temperature and drought index) and large-scale climate data (ENSO index and Antarctic Oscillation). N. macrocarpa growth was positively influenced by May to November precipitation (austral winterspring seasons) and negatively influenced by temperature from October to December (austral spring/earlysummer seasons). Using a piecewise regression analysis, we identified a significant decrease in growth from 1980 onwards that resembled a precipitation decline and temperature increase in central Chile during the same time period. Tree-ring chronologies were positively correlated to the ENSO index and negatively correlated to the Antarctic Oscillation index during the current growing season, and more strongly from 1980 onwards. Based on our results, we conclude that increased drought conditions have produced a decline in radial growth of N. macrocarpa forests in the last decades. We propose that increased drought conditions predicted for this century in this region will exacerbate this declining N. macrocarpa growth trend with unknown consequences for the survival of these endemic and endangered forest ecosystems.

1. Introduction

Mediterranean-type forests are generally characterized by dry summers, and represent biodiversity hotspots because they are found in the most populated areas of the world, and maintain high and endemic species richness (Myers et al., 2000). It is expected that the Mediterranean region will likely experience the greatest proportional change in biodiversity on terrestrial ecosystems because of the substantial influence of different drivers, mainly climate change (Sala et al., 2000). An emerging global pattern of tree mortality has been detected in different Mediterranean forests in response to droughts during the last century (Allen et al., 2010). For example, droughts in the Mediterranean Basin have intensified at the end of the 20th century compared to their natural variability over the last 900 years (Cook et al., 2016; Gea-Izquierdo and Cañellas, 2014; Sarris et al., 2011). In Mediterranean ecosystems of central Chile, the severity of recent drought events has been cataloged as unprecedented climatic events for the last century in the context of the previous six centuries (Christie et al., 2011). Therefore, a better understanding of Mediterranean forests responses to increased drought conditions is increasingly needed.

The Mediterranean forests of central Chile (MFCC) are within the most threatened ecosystems in South America (32°-35°S; Myers et al., 2000; Schulz et al., 2010; Hernández et al., 2016). The MFCC provide multiple ecosystem services for the most populated area of Chile, and

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https://doi.org/10.1016/j.foreco.2017.11.006

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Received 17 August 2017; Received in revised form 30 October 2017; Accepted 2 November 2017 0378-1127/@2017 Elsevier B.V. All rights reserved.

play an important role in adaptation and mitigation of climate change effects (Donoso and Otero, 2005; Schiappacasse et al., 2012). However, the geographical distribution of MFCC has considerably diminished at a rate of 1.7% per year since 1975 due to urban pressure, commercial forest and crop plantations, wildfire, and unsustainable logging (Donoso, 1982; Miranda et al., 2016; Schulz et al., 2010).

Some of the most vulnerable Mediterranean forests of central Chile are those dominated by Nothofagus macrocarpa (DC.) Vásquez and Rodr (Nothofagaceae). This tree species is endemic to central Chile, represents the northernmost distribution of Nothofagus in America (Amigo and Rodriguez-Guitian, 2011), and conforms a remnant of relict forests from the last glacial period (Villagrán, 1995). The N. macrocarpa forests are fragmented in isolated populations found on the mountain peaks of central Chile (Gajardo, 2001). N. macrocarpa form distinct and annual growth rings (Donoso et al., 2010) making it feasible to study its growth sensitivity to climatic variability. The distribution of N. macrocarpa covers approximately the latitudinal distribution of MFCC (Amigo and Rodriguez-Guitian, 2011), allowing for the understanding of regional climatic factors that may affect tree growth along the MFCC geographical distribution. The same region is currently affected by drought conditions lasting > 5 years and unprecedented heat during summer (i.e. -21% rainfall, leading to marked decline in water reservoirs and an extended forest fire season; Boisier et al., 2016). These increased drought conditions (i.e. precipitation decrease and temperature increase) are an unprecedented climatic trend from 1850 (Le Quesne et al., 2009).

The inter-annual climate variability in central Chile is influenced by two outstanding modes of global climatic variability, as represented by El Niño-Southern Oscillation (ENSO) and the Antarctic Oscillation (AAO) (Christie et al., 2011). ENSO is a phenomenon characterized by unusual change of the sea surface temperature (SST) in the equatorial central/eastern Pacific Ocean that is warmed (cooled) during El Niño (La Niña) events (Trenberth, 1997). AAO (also referred as the Southern Annular Mode) is a non-seasonal atmospheric circulation variation that occurs south of the 20°S, and is characterized by pressure anomalies of one sign centered in the Antarctic and anomalies of the opposite sign on a circumglobal band at about 40-50°S (Thompson and Wallace, 2000). Both atmospheric circulation patterns have a strong influence on precipitation and temperature in central Chile (Montecinos and Aceituno, 2003; Garreaud et al., 2009), and are indirectly affecting tree growth because of their effect on local climate variability (e.g. Álvarez et al., 2015; Villalba et al., 2012).

In this study, we analyzed the interaction between climate variability and radial growth along the whole distribution of *N. macrocarpa* in South America for the last 150 years. To the best of our knowledge, the growth response of the endemic *N. macrocarpa* forests to recent climatic trends has not been documented. Such an evaluation is critical to understand the dynamics of these Mediterranean forest ecosystems in response to climate change (Gazol et al., 2017). Specifically, we assessed (i) which climate variables best explain the radial growth variability of *N. macrocarpa* at different spatial and temporal scales, (ii) how global climatic oscillations (AAO and ENSO) affect radial growth? and (iii) whether there is a distinguishable growth trend of *N. macrocarpa* in response to recent climate change in central Chile.

2. Material and methods

2.1. Study sites

We selected five sites along the remnant geographic distribution of *N. macrocarpa* forests from Mediterranean-type forests of central Chile (MFCC) (32°57-34°52′S, Fig. 1a, Table 1). In this region shrubland and thorns steppes cover most of the lower hillslopes and piedmont, while creeks and mountain tops are dominated by open forests of evergreen and sclerophyllous tree species. *N. macrocarpa* forests are located at the highest elevations of mountains (between 1000–1800 m a.s.l.) and

represent isolated populations throughout its distribution area (Fig. 1b, Donoso, 1982; Gajardo, 2001). The *N. macrocarpa* patches are scattered in the most industrial and densely human populated area of the MFCC, from where wood has historically been exploited (Gajardo, 2001; Schulz et al., 2010). Therefore, forest patches are mainly young secondary forests with the exception of the old-growth *N. macrocarpa* forests at Alto Huemul and Alto Cantillana sites. There are no studies of cambial activity in this species, but it is expected that the growing season occurs from September to March as suggested by the presence of green foliage during the year (observations *in situ*).

The climate where the MFCC are distributed is Mediterranean, with a dry period of 5–7 months and a total annual precipitation between 300 and 600 mm, and a mean annual temperature between 11 and 13.5 °C modified by latitude and elevation (see also Supporting Information, Fig. S1; Luebert and Pliscoff, 2006). The total annual precipitation has a year-to-year variation in response to climatic oscillation such as El Niño Southern Oscillation (ENSO) and the Antartic Oscillation (AOO) (Garreaud et al. 2009). Forest in the Andes Mountain develop on soils originated from volcanic or granitic rocks and from glacial sediments (Villagrán, 1995). Along the Coastal range, soils are formed from granitic rocks and are poorly developed, usually from residuals on rocky outcrops (Donoso, 1982).

2.2. Tree sampling and ring-width chronologies

At each site, we sampled two or three populations, with the exception of Robleria del Cobre de Loncha where one population was sampled (Table 1). All populations were sampled in April-May 2015, so the last ring formed is from 2014 according to Schulmann's convention for the Southern Hemisphere (i.e. biological year does not coincide with calendar year, (Schulmann, 1956). At each population, we cored around 15 trees in an area of 0.5-1 ha of forest. We randomly selected trees in order to sample different stem sizes, thus avoiding bias in the selection of individuals, and including young and adult trees (Nehrbass-Ahles et al., 2014). We obtained two to three cores per tree at 1.3 m stem height using increment borers. We processed cores using standard dendrochronological methods (Stokes and Smiley, 1996). We examined cores under a stereomicroscope (×10 magnification) and identified the boundary of each tree ring. N. macrocarpa has diffuseporous wood, thus we recognized tree-ring boundaries by the presence of a thin layer of thick-walled fibers at the latewood (Fig. 1c). We measured tree-ring widths using a scanned image of each core at 2400dpi resolution with a reference scale (ImageJ software, Rasband, 1997).

We used the software COFECHA to statistically validate the crossdating and measurement quality of each core, and to find potential errors during the dating stage (Holmes et al., 1986). We constructed a chronology for each site by pooling all tree ring series of their populations, using the ARSTAN software. ARSTAN removes the biological age trend of individual tree series and any other stand-dynamics trends (Cook, 1985). For this procedure, we used a cubic spline with a 50% frequency response cutoff equal to 67% of the series length, thus isolating the high frequency variability. We used the residual chronology for the analyses in order to remove its temporal autocorrelation (Cook et al., 1990).

We characterized site chronologies using ring widths average and standard deviation, mean sensitivity (MS), series intercorrelation (SI), Running Bar (RBar), first-order autocorrelation (AR1) and expressed population signal (EPS) (Fritts, 1976). MS represents the mean percentage change of year-to-year growth variability. SI is the mean value of all possible correlations between individual series. RBar describes the mean correlation coefficient for all possible pairings of ring-width series over a common time. AR1 is a measure of the association between treering growths in two consecutive years (Holmes et al., 1986). EPS measures the strength of the common signal in a chronology over time and verifies the hypothetically perfect chronology, with a theoretical threshold ≥ 0.85 (Wigley et al., 1984). MS, SI and AR1 were calculated

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