

University of São Paulo
"Luiz de Queiroz" College of Agriculture

Tree growth response to climate change in two threatened South American
Biomes: Brazilian Atlantic Forest and Chilean Mediterranean Forest

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Thesis presented to obtain the degree of Doctor in
Sciences. Area: Forest Resources. Option in: Conservation
of Forest Ecosystems

Piracicaba
2017

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**Dados Internacionais de Catalogação na Publicação
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP**

Venegas González, Alejandro Danilo

Tree growth response to climate change in two threatened South American Biomes: Brazilian Atlantic Forest and Chilean Mediterranean Forest / Alejandro Danilo Venegas González. - - Piracicaba, 2017.

92 p.

Tese (Doutorado) - - USP / Escola Superior de Agricultura "Luiz de Queiroz".

1. Dendrocronologia 2. Floresta *hotspot* 3. Mudanças climáticas 4. Secas 5. Densidade da madeira 6. Acumulação de biomassa arborea I. Título

DEDICATION

For my children Taísa and Lautaro, and my beautiful wife that are part of this story.

ACKNOWLEDGMENTS

To my friend and supervisor Mario Tomazello Filho, for believing in this four years, besides trust, guidance, learning and friendship. Also, I am immensely grateful with Fidel Roig and Álvaro Gutiérrez for the opportunity for discussion and learning in my scientific stays in Conicet-Mendoza and Universidad de Chile, respectively.

For funding of different organizations. I was supported by a PhD scholarship from Commission for Scientific and Technological Research of Chile (CONICYT-PAI/INDUSTRIA79090016). This study was funded by the Rufford Small Grants for Nature Conservation (<http://www.rufford.org/>, RSGA application 16502-1) and Coordination for the Improvement of Higher Education Personnel (<http://www.capes.gov.br/>, process: 88887.116430/2016-00).

For scientific comments, I am grateful of Karen Peña, Claudio Lisi, Alci Albiero Junior, Claudio Anholetto Junior, Jose Luis Marcelo Peña, Duncan Christie, and Martin Hadad.

For help of the fieldwork, I thank you immensely for all your help of Pablo Fresia, Alci Albiero Junior, Claudio Anholetto Junior, Jose Luis Marcelo Peña and my father Alejandro.

For my lab friends, I thank you immensely for all your generosity and your friendship of Mariana Pires Franco, Luciana Souza, Angel Ferreira, Alci Albiero Junior, Claudio Anholetto Junior, Luiz Santini Junior, Ricardo Ortega, Bruno Gomes, Matheus Chagas and Jose Luis Marcelo Peña.

For the authorization of the fieldwork and support in the logistics, In Chile: (i) Chilean National Forest Corporation (CONAF, <http://www.conaf.cl/>), especially Christian Díaz (National Park “La Campana”) and Julio Vergara (National Reserve ‘Robleria del Cobre de Loncha’); (ii) Nature sanctuary ‘Altos Cantillana’ (<http://www.altosdecantillana.com/>), especially Fernanda Romero; (iii) director of the community ‘Capilla de Caleu’ in charge of Nature sanctuary ‘Cerro El Roble’; (iv) Francisco Muller by supported in Nature sanctuary “Alto Huemul”. In Brazil: Instituto Florestal - Governo do Estado de São Paulo, Ricardo Romero, and all the friends who helped out at the state park ‘Serra do Mar’ and ‘Carlos Botelho’;

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RESUMO

Resposta do crescimento das árvores às mudanças climáticas em dois biomas sul-americanos ameaçados: Mata Atlântica Brasileira e Floresta Mediterrânea Chilena

Os biomas classificados como Mata Atlântica Brasileira (MAB) e da Floresta Mediterrânea Chilena (FMC) têm sido afetados pela pressão antrópica que tem causado uma diminuição considerável de sua superfície florestal. No entanto são ricas em biodiversidade e providenciam muitos serviços ecossistêmicos, pelo que foram classificadas como *hotspot* (florestas em risco). Portanto, é fundamental estudar a dinâmica natural e a resposta climática das árvores dessas florestas para incluir em projetos de conservação. Para atingir esses objetivos, a literatura científica reporta que os anéis de crescimento das árvores são os únicos indicadores ecológicos com resolução anual que podem ser eficientes e de elevada precisão para obter essas informações. Neste contexto, o projeto de pesquisa tem como objetivo geral a análise retrospectivo de crescimento radial de espécies florestais em diferentes comunidades vegetacionais da MAB e FMC em resposta às mudanças climáticas. Para atingir esse objetivo foram elaboradas quatro perguntas-chave: 1) Que variável explica melhor a variabilidade do crescimento radial a diferentes escalas espaciais e temporais? 2) Qual é a resiliência em crescimento das árvores às mudanças climáticas recentes? 3) Há alguma população mais vulnerável respeito às mudanças climáticas esperadas?. Foram coletadas amostras de lenho, através de método não destrutivo, de cinco sítios (sete populações) de *Cedrela odorata* e *C. fissilis* na MAB no estado de São Paulo em Brasil, e cinco sítios (10 populações) de *Nothofagus macrocarpa* na FMC na região central do Chile, para aplicação de técnicas dendrocronológicas. Para responder essas questões foram desenvolvidos quatro capítulos. O capítulo I busca analisar a resiliência em crescimento radial às mudanças na variabilidade climática regional e secas, em escala temporal e espacial, em florestas remanescentes da região biogeográfica Serra do Mar da Mata Atlântica, usando as espécies bioindicadoras *Cedrela fissilis* and *C. odorata*. Os resultados mostram que o crescimento radial dos sítios mais úmidos (chuvas no inverno superam os 240 mm) dependem das condições hídricas da estação seca, enquanto que a população mais alta é mais sensível à condição hídrica favorável do verão, qual seria explicado porque essa população recebeu uma menor temperatura respeito às outras populações de cedrela estudadas. No capítulo II analisou-se como a variabilidade climática recente estaria afetando o crescimento radial in *N. macrocarpa* populations. Observa-se que todas as populações estão estreitamente ligadas às precipitações de Maio-Novembro (fim de outono/fim de primavera) e temperatura média de Outubro-Dezembro (mediados de primavera/inícios do verão). Especificamente, há uma tendência negativa significativa no crescimento radial apartir de 1980 que esta associada a uma variação do clima regional. No capítulo III, continuo-se explorando as respostas do crescimento radial ao clima nas populações da FMC com objetivo de encontrar diferenças biogeográficas. Neste sentido, foi avaliado se essa diminuição significativa de crescimento é diferenciada entre populações e classes de idade, e analisar se o efeito positivo da fertilização de CO₂ compensa a diminuição da precipitação e aumento da temperatura nas últimas décadas no crescimento de árvores velhos, maduros e jovens. Os resultados mostram uma tendência negativa significativa em todas as classes apartir do ano 2000, qual estaria associada a diminuição da precipitação em todas as populações enquanto a temperatura teve mais associada às populações do sul. Não foi encontrado um efeito positivo do aumento de CO₂. Finalmente, o capítulo IV integrou os resultados dos dois biomas comparando as projeções de biomassa arborea sob dois cenários climáticos do projeto CMIP5 (leve e severo), com objetivo de conhecer quais populações são mais vulneráveis ao aumento da temperatura previsto para o ano 2100, usando crescimento radial, densidade de madeira e equações alométricas. Os resultados mostram que a população com maior influência urbana e a mais seca são as mais vulneráveis ao aumento exacerbado de temperatura nas regiões de MAB and FMC, respectivamente. O presente estudo permitiu-nos apresentar uma visão da adaptação às mudanças climáticas recentes e projetadas de dois biomas *hotspot*. Embora sejam diferentes em estrutura-biodiversidade-clima estão em risco. Assim, podemos entender a vulnerabilidade de florestas neotropicais ao aquecimento global, embora estejam em áreas protegidas, não garante sua persistência.

Palavras-chave: Dendrocronologia; Florestas *hotspot*; Mudanças climática; Secas; Densidade da madeira; Acumulação de biomassa arborea

ABSTRACT

Tree growth response to climate change in two threatened South American Biomes: Brazilian Atlantic Forest and Chilean Mediterranean Forest

Biomes classified as Brazilian Atlantic Forest (BAF) and the Chilean Mediterranean forest (CMF) have been affected by anthropic pressure that has caused a considerable decrease of their forest surface. However, they are rich in biodiversity and they provide many ecosystem services and were, therefore, classified as 'hotspots' (forests in risk). Therefore, it is essential to study the natural dynamics and the climatic response of the trees of these forests to include conservation projects and strategic measures. To achieve these objectives, the scientific literature reports that tree growth rings are the only ecological indicators with annual resolution that can be efficient and highly accurate to obtain this information. In this context, the research project has as main objective the retrospective analysis of radial growth of forest species in different vegetation communities of BAF and CMF in response to climatic changes. To achieve this goal, four key questions were elaborated: 1) Which variable explains better the variability of radial growth at different spatial and temporal scales? 2) What is the growth resilience to recent climate changes? 3) Is there some more vulnerable population to expected climatic changes? A total of five sites (seven populations) of *Cedrela odorata* and *C. fissilis* in BAF from the State of São Paulo in Brazil, and five sites (10 populations) of *Nothofagus macrocarpa* (FMC) from the central region of Chile were sampled, using a non-destructive method. Four chapters were developed to answer these questions. Chapter I seeks to analyze the resilience in radial growth to changes in regional climate variability and droughts, in temporal and spatial scale, on Atlantic forest remnant forests of biogeographic region Serra do Mar. Results show that radial growth in wet sites (winter rains exceed 240 mm) depend on the moisture conditions in dry season, while the higher population is more sensitive to the favorable summer water condition, which would be explained because this population received a lower temperature than the other *Cedrela spp.* populations studied. Chapter II analyzed how recent climatic variability affected the radial growth in *N. macrocarpa* populations. It is observed that all the populations are closely linked to the precipitations of May-November (end of autumn/end of spring) and average temperature of October-December (mid-spring/early summer). In Chapter III, we continued exploring the growth responses to climate in the FMC populations in order to find biogeographic differences. In this sense, we evaluated if this significant decrease in tree growth is differentiated between populations and age classes, and determine if the positive effect of CO₂ fertilization compensates the precipitation decrease and temperature increase in the last decades in the growth of older, maturer and younger trees. Results show a significant negative trend in all classes from the year 2000, which would be associated to a decrease in precipitation in all populations while temperature was more associated with the northern and southern populations (distribution limit). We did not find a positive effect of rising CO₂. Finally, chapter IV integrated the results of the two biomes comparing the projections of aboveground trees biomass under two climatic scenarios of CMIP5 project (light and severe), in order to know which populations are more vulnerable to rising temperature forecasted by year 2100, using ring width data, wood density and allometric equations. This study will provide an overview of adaptation to recent and projected climatic changes of two hotspot neotropical biomes. Although they are different in structure-biodiversity-climate are in risk. Thus, we can understand the vulnerability of threatened forests in South America to global warming that, although they are in protected areas, does not guarantee their persistence.

Keywords: Dendrochronology; Hotspot forest; Climate change; Droughts; Wood density; Trees biomass accumulation

1 INTRODUCTION

Greenhouse gases (GHG) are related to global warming, and the increase in their concentration is a widely discussed topic of great relevance in the scientific, political, economic and social level due to the damaging consequences to the planet. Although historically the increases of GHG has been natural, an exponential increase has been observed related to the industrial revolution from the mid-nineteenth century, mainly due to the intensive use of fossil fuels (Fig. 1a) (Forster et al. 2007). On the other hand, deforestation and degradation of forest ecosystems in recent decades has also caused a significant increase in the amount of atmospheric CO₂ concentrations in different regions of the world (Shine et al. 2005). Those increases GHG have caused a generalized global warming, mainly from mid-1970s in Southern Hemisphere (Fig. 1b) (Jones and Moberg 2003). It is expected that those temperature trends will be intensified at the end of 21st century (Pachauri et al. 2014)

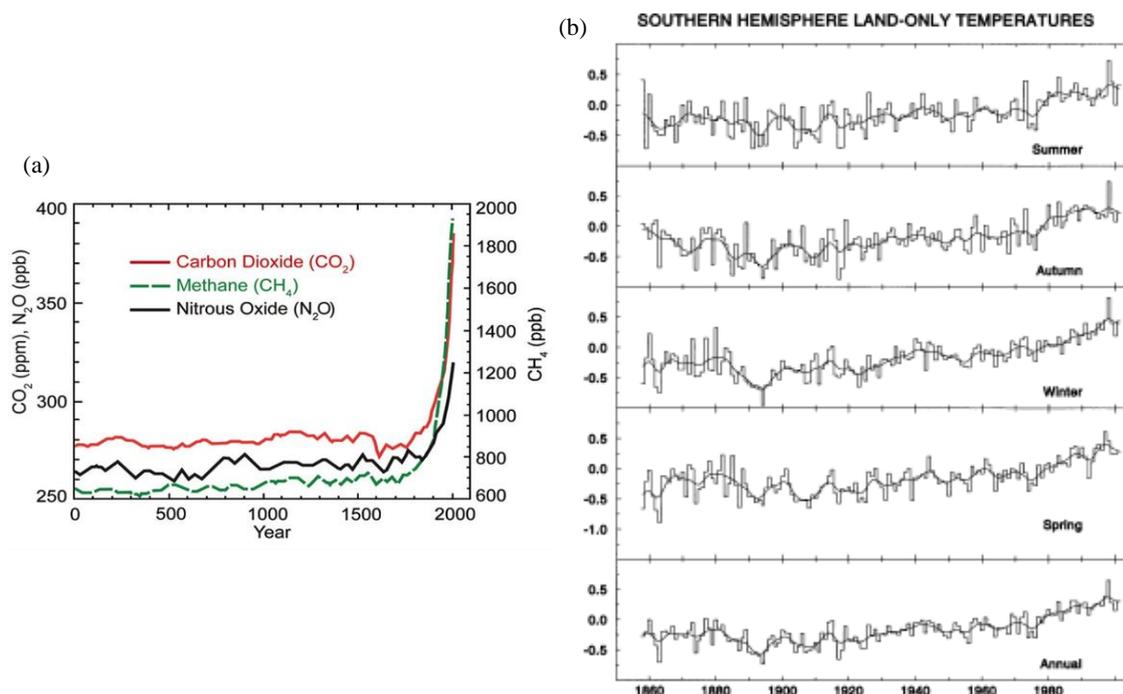


Figure 1. (a) Evolution of carbon dioxide, methane, and nitrous oxide in last 2000 years. It is marked increased of present-day atmospheric levels over pre-industrial level. Figure source: Forster et al (2007). (b) Seasonal and annual time series (1858–2001) for the Southern Hemisphere. Figure source: Jones and Moberg (2003)

Among the most threatened forest ecosystems in South America are the Brazilian Atlantic Forest of Brazil (BAF) and the Chilean Mediterranean forest (CMF). BAF is a plant formation present in a large part of the Brazilian coastal region, but mainly due to the urban occupation and the exploitation of its wood resources, it currently occupies from 11.4% to 16% of the original Atlantic forest cover (Ribeiro et al., 2009). CMF has a similar history to the one of MAB, since it is located in cities with the largest population and industries of Chile. In addition, it presents a great pressure for the substitution by forest plantations and by agricultural crops, representing a rate of loss of 1.7%, so that in 70 years this ecosystem could disappear (Schulz et al. 2010). However, in both biomes the best preserved forest remnants are found in protected areas, whether public or private, such as ‘Serra do Mar’ in BAF and Mediterranean deciduous forest in CMF.

Studies on forest dynamics become important in threatened biomes due to they allow us to know how has been the natural growth variability of forests and how they would react to possible environmental changes. In this sense, the dendrochronology (study of annual rings in trees) allows us to evaluate the forest growth and their association with the climate at different spatial and temporal scales (Fritts 1976). A major advantage of dendroecological studies is the analysis of tree growth rate over time, compared to studies of permanent plots that have averaged 20 years (Rutishauser et al. 2015). It is considered that the climate is the one that best explains the trees growth at cell level (vascular cambium), which can be extrapolated for forest stands (Gea-Izquierdo et al. 2013; Pompa-García et al. 2017). The vascular cambium is the lateral meristem responsible for diametric growth (secondary growth) in trees, which is activated by macro- and microclimatic factors present at the site where trees are growing, forming wood with distinct anatomical features (Callado et al. 2013). The seasonal variation in these factors over a year is responsible for the annual tree ring formation in trees (Fritts 1976). Thus, characterizing annual forest growth patterns along climatic gradients has a great potential to project the vulnerability of tree populations to climate warming (Sanchez-Salguero et al. 2016).

Therefore, it is fundamental to study the growth dynamics and climatic response of trees in Brazilian Atlantic Forest of Brazil and Chilean Mediterranean forest, which will be useful for projects of conservation, restoration or climatic change mitigation. The present research focuses on the information provided by the dendrochronological data in two South American threatened biomes, aiming understand their growth resilience to recent and expected climate changes. The main objective of the study is to perform a retrospective analysis of radial growth of forest species in different vegetation communities of BAF and CMF in response to climatic changes. We used forest species with dendrochronological potential, such *Cedrela fissilis* and *C. odorata* in BAF, and *N. macrocarpa* in CMF. To achieve this goal, four key questions were elaborated: 1) Which climatic variable explains better the variability of radial growth at different spatial and temporal scales? 2) What is the growth resilience to recent climate changes? 3) Is there some more vulnerable population to expected climatic changes? Four chapters were developed to answer these questions.

- 1) **Cedrela spp. growth response to drought and climate change varies across enviromental gradient in an Atlantic forest.** This chapter seek to analyze the resilience in radial growth to changes in regional climate variability and droughts on Atlantic forest remnant forests of biogeographic region Serra do Mar
- 2) **Recent radial growth decline in response to increased drought conditions in the northernmost *nothofagus* populations from South America.** Here, we analyzed how recent climatic variability affected the radial growth in *N. macrocarpa* populations.
- 3) **Worrying growth response to climate change in Chilean Mediterranean forest: evidence from younger, maturer and older trees *Nothofagus macrocarpa*.** In this chapter, we continued exploring the growth responses to climate in the *Nothofagus macrocarpa* populations in order to find biogeographic differences.
- 4) **Reduction of aboveground trees biomass of two threatened biomes of South America due to climate change.** Final chapter integrated the results of the two biomes comparing the projections of aboveground trees biomass under two climatic scenarios of CMIP5 project (light and severe), in order to know which populations are more vulnerable to rising temperature forecasted by year 2100, using ring width data, wood density and allometric equations.

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2 *CEDRELA SPP.* GROWTH RESPONSE TO DROUGHT AND CLIMATE CHANGE VARIES ACROSS ENVIRONMENTAL GRADIENT IN A ATLANTIC FOREST

Abstract

Severe droughts caused by climate change have recently reduced biomass in neotropical forests, including the Atlantic forest hotspot from Southeastern Brazil, being São Paulo one of the most affected states. However, in this state is the remnant forests in better state of conservation located in the biogeographic subregion ‘*Serra do Mar*’ (AFSM). This study aims to analyze the resilience in radial growth to changes in regional climate variability and droughts, in temporal and spatial scale, on remnant forests of AFSM, using the bioindicator species *Cedrela fissilis* and *C. odorata*. We selected five populations of *Cedrela spp* from AFSM (22°-24°S) for a dendroecological analysis. We used correlation and regression analysis to explore the relationship between tree growth and climate variability, using regional data from CRU dataset of precipitation, temperature and Standardized Precipitation-Evapotranspiration Index. The results indicate that trees depend on the dry season water conditions in the areas with the highest rainfall in winter (dry season). While populations with lower summer temperatures (hot and rainy season), it is the humidity favorable condition of this season that plays a determining factor in the tree growth dynamics. We found that the highest population is more vulnerability to global warming and driest population is more sensitivity to droughts. Therefore, there are AFSM regions more vulnerable than others to climate change and increase of drought events, which should be considered in future conservation studies in the coastal region of Sao Paulo.

Keywords: Tropical dendroecology; Biogeography; Serra do Mar, Secondary forest

2.1 Introduction

The Atlantic forest is one of the largest areas of tropical ecosystem and biodiversity in the world, which is present in much of the Brazilian coastal region, and also covering parts of the north Argentina and eastern Paraguay (Rodrigues et al. 2009). Although it is an ecosystem that occurs in almost all the Brazilian coast, it is one of the most threatened biomes of South America due to the devastation that suffered by occupation (pastures, crops and higher urban centers) and intensive exploration of its resources (mainly timber resources) (Dean 1996). Currently the Atlantic forest is highly fragmented and limited to small portions, ranging from 11.4% to 16% of the original Atlantic forest cover (Ribeiro et al., 2009). For this reason and due to its high biodiversity, it was declared as a Biosphere Reserve by UNESCO and National Patrimony, and has received the status of conservation hotspot (Myers et al. 2000).

The Atlantic forest from coastal areas correspond to about 60% of this biome in Southeastern Brazil (Rodrigues et al. 2009). São Paulo is one of the states with the greatest fragmentation and deforestation of this biome, which is concentrated almost exclusively in the coastal region (commonly called “Serra do Mar”) (Colombo and July 2010). This biogeographic subregion has an environmental and altitudinal gradient ranging from 0 to 2000 meters, where it is changing floristic composition and structure of the tree community (Lacerda 2001)

The forest ecosystem from Serra do Mar represents the best-preserved Atlantic forest patch, which holds 36.5% of its original vegetation (Rodrigues et al. 2009), including some *Cedrela spp.* populations. *Cedrela odorata* L. and *Cedrela fissilis* Vell., due their status of vulnerability, were defined as target species in the red book of the Brazilian flora (Martinelli and Moraes 2013), as a consequence of large explorations in Atlantic forest in the center-south of Brazil (Dean 1996). Both species have similar morphology, wood anatomy, phenology, and autoecology (Tomazello Filho et al. 2000; Muellner et al. 2010).

It has been observed an increase of global warming at 0.07°C per decade since 1900 (Jones and Moberg 2003); trend that will be intensified during the 21st century according to models predicts of Intergovernmental Panel on Climate Change (Pachauri et al. 2014). We hold the relevance of increasing our knowledge of how tree growth in

the Atlantic forests reacts to the current climate conditions and future scenarios. As expected, more frequent of warm nights and extreme precipitation events will occur in Southeastern Brazil (Marengo et al. 2009), compromising plant diversity and sustainability of the Atlantic forest (Colombo and Joly 2010).

The analysis of forest growth in environmental gradients is relevant to understand autoecology and plasticity of organisms to variations in environmental conditions. Since precipitation and temperature may vary along gradients, that change is finally reflected in the growth of trees, giving opportunity to identify the influence of stress factors on extremes of a gradient (e.g. Camarero & Gutiérrez 2004, Lara et al. 2005). Therefore, environmental gradients can serve as potential natural laboratories to infer forest responses to global warming and climate change (Jump et al. 2009). However, the climatic response and drought sensitivity of *Cedrela spp* tree populations along climatic gradients has not yet been explored, a situation that must be overcome if we try to predict what the situation of these forests will be in the face of future intensification of climate change conditions. Previous dendrochronological studies in *Cedrela fissilis* and *Cedrela odorata* from tropical and subtropical regions showed that radial growth variability is more sensitive to rainfall amount at the end of the previous growing season (Worbes 1999; Dunisch et al. 2003; Brienen and Zuidema 2005; Dünisch 2005). However, none of these studies considered a dendroecological vision under a biogeographic approach. In the subtropical forests of Serra do mar, moreover, the role of rainfall in annual xylem development of *Cedrela spp* is poorly known, particularly when intense droughts occur.

To partially solve the uncertainty of how droughts and long-term precipitation changes impacts on the growth of Atlantic forests remnants, we must explore at what level the climate affects the radial growth variability at different spatial and temporal scales along a climatic gradient. Based on the principles that tree-ring can respond with differential intensity to climate variability (Fritts 1976; Schweingruber 1996) across environmental gradients (Jump et al. 2009), we first hypothesized that this phenomenon is related to the forests of *Cedrela* in existing gradients of the SE of Brazil. Considering the divergences proven by different patterns of drought-growth responses in others neotropical species, mainly in long-term sensitivity (Mendivelso et al. 2014), we hypothesized that drought severity periods affect the radial growth, inclusive the next years post-drought period. Observing the ecological evidences of negative impacts by recent climate change on forest ecosystems in the world (Walther et al. 2002; Bonan 2008), and the negative relationship between temperature and elevation (Jump et al. 2009), we hypothesized a negative growth resilience to rising temperature, mainly in highest altitudes populations.

2.2 Materials and Methods

2.2.1 Study sites and selected species

Five study sites, with populations of *Cedrela odorata* and *C. fissilis*, were selected in the Atlantic forest hotspot from Southeastern Brazil, São Paulo state. These sites are located in the center of the biogeographic subregion of the Atlantic forest, the so called Serra do Mar (AFSM), and all cases are represented by a secondary forest phytophysognomy (Fig. 1). The study was conducted at the following sites (from North to South): Campos de Jordão (State Park - CJ), São Sebastião (State Park - SS), Juquitiba (private forest - JU), Carlos Botelho (State Park - CB), and Bom Sucesso de Itararé (private forest - BS) (Table 1). In this last site, we sampled three populations. All sites According to Köppen's classification, is climatically characterized as Cf (humid subtropical) with a hot/rainy summer (December to February) and a cold/dry winter (June to August). However, there is no a notorious dry

season, since in winter fall $>65 \pm 14$ mm per month (Alvares et al. 2013). However, in some sites there are months (June, July, August) with approx. 50 mm, so is enough rainfall to induce tree growth stop (Worbes 1995).

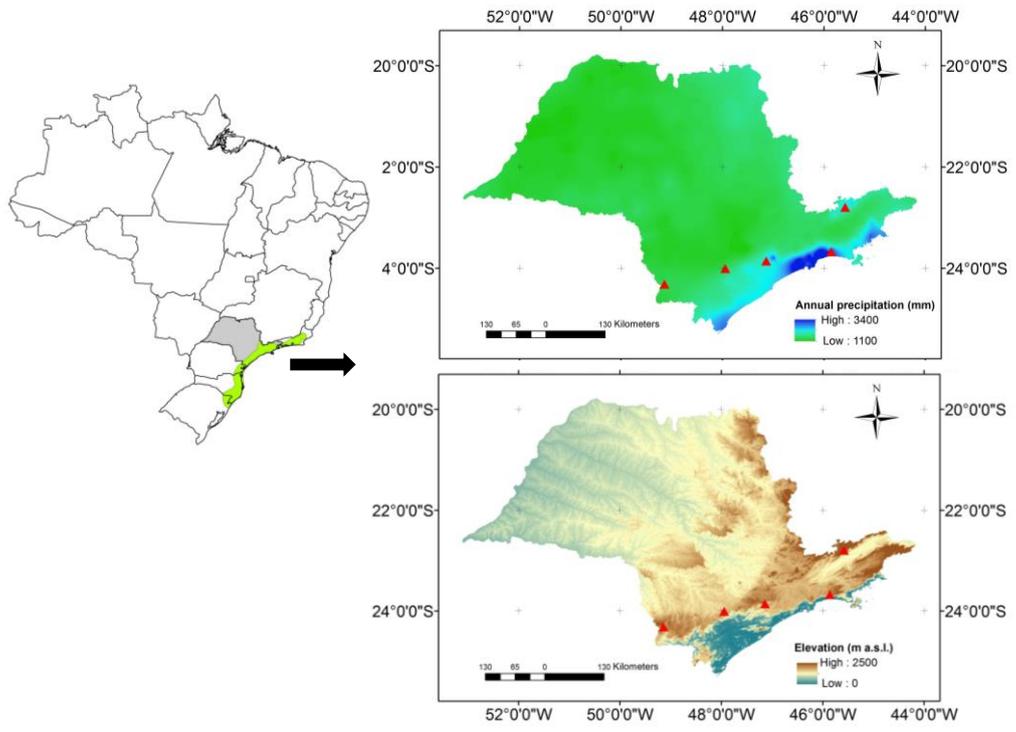


Figure 1 - Location of *Cedrela* spp. populations (red triangles) in São Paulo State, Brasil (from east to west: CJ, SS, JU, CB, BS). São Paulo state is showed in gray in left map, while that AFSM distribution is showed in green (figure adapted from Ribeiro et al. [2009]).

Table 1 - Characteristics of studied sites and descriptive statistics of the chronologies (see Methodology for site code definitions)

Site (code)	Species	Alt ^a	T ^b	P ^c	Trees ^d	TS ^e	RW \pm SD ^f	MS ^g	Rbt ^h	ARI ⁱ
CJ	<i>C. fissilis</i>	1,600	17.3	1,700	12/10	1900-2005	2.07 \pm 1.40a	0.51	0.47	0.43
SS	<i>C. odorata</i>	50	20.3	2,050	20/18	1960-2014	4.05 \pm 1.40d	0.47	0.47	0.48
JU	<i>C. fissilis</i>	680	19.4	1,600	26/23	1955-2015	2.35 \pm 1.56b	0.52	0.48	0.49
CB	<i>C. odorata</i>	750	21.2	1,690	28/20	1949-2014	2.16 \pm 1.62b	0.54	0.40	0.49
BS1	<i>C. odorata</i>	900	19.2	1,490	20/17	1935-2005	2.40 \pm 1.77b	0.60	0.57	0.44
BS2	<i>C. odorata</i>	900	19.2	1,490	10/10	1936-2003	3.25 \pm 2.30c	0.62	0.64	0.40
BS3	<i>C. odorata</i>	900	19.2	1,490	6/4	1932-2005	3.59 \pm 2.12c	0.48	0.33	0.54
Regional BS ^k	<i>C. odorata</i>	900	19.2	1,490	35/27	1927-2005	2.65 \pm 1.93c	0.60	0.57	0.42

^a Site altitude (m a.s.l.); ^b Annual mean temperature ($^{\circ}$ C); ^c Annual accumulated precipitation (mm); ^d Numbers of trees sampled (trees used for the chronology), Chronology time span considering at least three trees; ^e Mean ring width \pm standard deviation (mm), different letters indicate significant difference according Kruskal-Wallis test ($P < 0.05$); ^f Mean sensitivity of tree-ring series; ^g Mean correlation coefficient between all the tree-ring series; ^h First-order autocorrelation of tree-ring series; ⁱ Regional chronology from Bom Sucesso Itaré

The vegetation of the Atlantic forest from Serra do Mar is defined as Ombrophilous Dense Forest, with 150-170 plant species per hectare (Dos Santos et al. 1998; Guilherme et al. 2004). Whose height of tree canopy may reach up to 50 m, and its dense understory is composed of ferns, shrubs, palm, vines, and epiphytes (bromeliads and

orchids) (IBGE 2004). A relevant ecological feature of the forest structure resides in their ombrophilous characteristic. This dense cover structure is related to the highest thermo-pluviometric indexes that characterize the coastal region, where precipitation is roughly distributed throughout the year, only decreasing in the winter months where lower temperatures can favor lower evapotranspiratory rates (Veloso et al. 1991). The occurrence of complex and non-linear gradients suggests the importance of several other abiotic features in the spatial distribution and abundance of arboreal species in the Atlantic Ombrophilous Dense Forest in the state of São Paulo (Scudeller et al. 2001).

Cedrela odorata and *C. fissilis* (Meliaceae), commonly called cedro, are neotropical species composed of large trees reaching up to 40 m. Those species are deciduous, heliophytes, and selective hygrophytes, which are founded both in primary and secondary forests (Muellner et al. 2010). In the Atlantic forest from Serra do Mar, *Cedrela odorata* and *C. fissilis* are rare species that behave as a late secondary (shadow tolerant) stage. They are highly dependent of light resource, depending on gap formations to develop (Santos and Takaki 2005). The tree-rings of *Cedrela spp.* are well distinct and demarcated by a thin marginal parenchyma row and the vessel arrangement as a semi-porous, with notoriously large vessels in the earlywood (Tomazello Filho et al. 2000). The cambium activity alternates between an active period coinciding with the rainy season and tree leaf-out, and a dormant period which coincides with the dry season when trees loss their leaves (Marcati et al. 2006). Overall, active growth season of *Cedrela spp* trees from AFSM occur from November to May (spring to fall) (Andreacci et al. 2017).

2.2.2 Sampling design

At each site, 12-36 trees per site along one transect were randomly selected to include individuals of different age and size, totaling 122 trees. Two-three cores per tree were sampled. The samplings were made on different dates. CJ and BS were sampled in November 2006, JU and SS were sampled in March-April 2016, and CB was sampled in November 2015. We sampled others five sites from AFSM, but we decided to exclude these in the comparisons since they were collections of less than 10 trees per site. It should be noted that *Cedrela* is considered a rare species (Muellner et al. 2010) occurring in species-rich forests such as the AFSM (Dos Santos et al. 1998; Guilherme et al. 2004). This this situation and its history of forest use make difficult to find optimal populations for dendroecological studies. Previous dendrochronological reports with *Cedrela spp* have been based on the use of cross-sections of logs, taking advantage of adjacent logging concessions (e.g. Dunisch et al. 2003, Brienens & Zuidema 2005) The use of discs can allow a more easy identification of the growth rings and an the possibility of integrating a greater number of measured radii, avoiding local distortions in the width of the rings. However, national laws do not currently allow timber exploration in AFSM, forcing the use of pressler increment borers in obtaining wood samples. Wood cores were glued into wooden holders, and the cross-sections were polished with a sandpaper gradient, varying between 80 and 800 grains mm⁻² until the anatomical features related to the ring boundaries were clearly identified (Stokes 1996).

2.2.3 Building tree-rings chronologies

Polished wood cross-sections were scanned at 2400-dpi resolution with a reference scale, and tree-ring widths were measured using the ImageJ software (Rasband 1997). The cross-dating quality was checked with the software COFECHA (Holmes 1986), which calculates correlation coefficients between individual tree-ring series as a way to identify absent or false rings. This software identify tree-growth patterns that can be synchronized between

the samples of the same tree and between trees, allowing the building of a master series of tree-rings width dated in the exact year of their formation (Grissino-Mayer 2001).

To built population chronologies, we first removed the long-term growth trends potentially related to non-climatic fluctuations (tree ontogeny and forest natural dynamics) by a cubic spline with a 50 % frequency response cutoff equal to 67 % of the series length of ring-width measurements, preserving high-frequency climatic information, and then obtaining ring-width indices. We used the residual chronologies since the temporal autocorrelation related to the previous year growth was removed. This procedure was performed using the ARSTAN program (Holmes et al. 1986b). The chronologies were characterized using the classic statistic parameters in dendrochronology (Fritts 1976), i.e., average and standard deviation of tree ring width, series mean sensitivity (MS), series intercorrelation (Rbt), First-order autocorrelation of tree-ring series (AR1) and expressed population signal (EPS) of residual chronologies. EPS represents the chronology that has been infinitely replicated and is sensitive to both variations in the series intercorrelation and sample size, being used ≥ 0.85 threshold for non-tropical tree species (Wigley et al. 1984), but we employed a 0.80 threshold that is accepted in tropical species (Mendivelso et al. 2014).

2.2.4 Climate data

There are few climate records in the AFSM region of São Paulo state. Therefore, and centered on the study sites, we obtained monthly climate data (mean temperature and accumulated precipitation) for the 0.5 x 0.5 grid from the Climate Research Unit dataset, University of East Anglia, version 4.00, using the KNMI-Climate explorer webpage <http://climexp.knmi.nl/>. The gridded areas used for comparison with our tree-ring sites are: CJ (22.5–23.0S, 45.5–46.0W), SS (23.5–24.0S, 45.5–46.0W), JU (23.5–24.0S, 47.0–47.5W), CB (24.0–24.5S, 47.5–48.0W), and BS (24.0–24.5S, 48.5–49.0W).

To analyze the relationship between growth and drought stress, we used monthly values of the Standardized Precipitation-Evapotranspiration Index (SPEI) calculated at 1, 3, and 6 month scales (Vicente-Serrano et al. 2010). The SPEI considers the effect of temperatures on the evapotranspiration rate with negative and positive SPEI values reflecting dry and wet conditions, respectively. The SPEI was calculated for the same 0.5 x 0.5 grid per site, and it was obtained from KNMI-Climate explorer webpage.

2.2.5 Statistical analyses

To evaluate the effect of mean temperature and accumulated precipitation on the residual chronology obtained for each site, we used a multiple regression analysis. This method detected which seasonal climatic variables are specifically related to the ring width variability. Year seasons are fall: March to May, winter: June to July, spring: September to November, and summer: December to March. Predictor variables were selected by stepwise iterative construction of the regression model, allowing to an automatic selection of independent variables already included in the model and rejection of any variable that does not produce a *T-student* significant at the 0.90 level (Di Rienzo et al. 2001). We used the Variation Inflation Factor (VIF) to evaluate the multicollinearity that exists between the predictor variables, with VIF values close to 1, indicating a low or null multicollinearity whereas VIF values >10 indicates a certain collinearity between predictors (O'brien 2007). We calculated the regression models and the VIF with the Infostat software (Di Rienzo et al. 2001). We evaluated the effect of SPEI (1, 3, 6 months) on the ring-width index obtained for each site using a correlation function analysis. Correlations were performed for the period between January of the previous growth year to May of the current growth year, since a tree ring formation in the Southern

Hemisphere is considered to be influenced by climate conditions that occur in shared summer months for two consecutive years. For this reason we followed Schulmann's convention to establish the calendar year of a tree ring for the Southern Hemisphere (Schulmann 1956). We used package `bootRes` to dendroclimatic analysis (Zang and Biondi 2013) in R (R core Team 2017), and significance was assumed at $P = 0.05$. We use 54 years of analyzed period to avoid possible bias in this analysis (CJ and BS for the period 1951-2005; SS, JU, and CB for the period 1960-2014).

To analyze the growth resilience to drought periods, we built a regional SPEI chronology (calculated 1-months) for the area 22.5–24.5S, 45.5–49.0W, using the same database mentioned before. We applied a spline-10 year to identify at least 10 years continuous of SPEI data below the mean of the regional SPEI chronology. Later, we compared the mean growth per trees (average of tree-ring series) before, during and after drought period through a Kruskal-Wallis non-parametric H-test (95% confidence level). To avoid potential problems with ontogenetic trends, the first ten years of growth were excluded from analysis.

To evaluate the influence of regional warming on tree rings, we performed a piecewise regression analysis of mean temperature at each chronology site. This approach allows to observe significant changes in temporal trends showing the break year. Piecewise regression models were made using the `segmented` package (Muggeo 2008) in R (R core Team 2017). Subsequently, linear regression analyses were performed between ring width and most significant seasonal mean temperature resulted from multiple regression analysis.

2.3 Results

2.3.1 Spatial patterns of climate variation

The region where we conducted this study show a mean annual rainfall is 1700 ± 210 mm and the mean annual temperature is 19.5 ± 1.5 °C with the hottest and coldest months with 22.4 ± 1.2 °C (February) and 15.4 ± 1.2 °C (July), respectively. However, the five sampled locations are included in both an altitudinal and latitudinal climate gradient, as seen in Fig. 1. CJ and BS have the lowest mean temperature and lowest accumulated rainfall, respectively, while SS and CB are the rainiest and hottest sites, respectively (Table 1). The higher correlation was founded between altitudinal gradient and mean temperature ($R^2 = 0.58$ and $r = -0.76$), indicating a temperature decrease by elevation of *Cedrela spp* populations (Fig. 2a). The slope of this linear regression shows an average decrease (from lowest to highest altitude) in elevation of 290 m per Celsius degree (°C). As defined in this study the CJ is the highest and coldest population, SS is the lowest and rainiest population, CB is the hottest population, and BS is driest and southern population. JU shows an intermediate behavior.

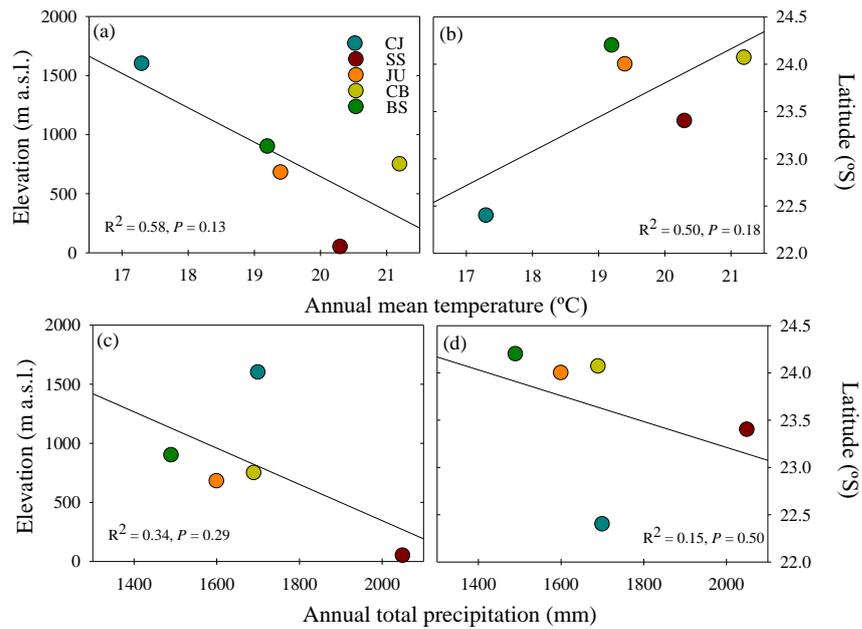


Figure 2 - Relationship between (a,b) annual mean temperature (°C) and (c,d) annual total precipitation (mm), with altitude (m a.s.l.) and latitude (°S) for the five study areas.

2.3.2 Chronology characteristics and growth-climate relationship

Table 1 shows a summary of the statistics considered to evaluate the quality of the obtained *Cedrela spp.* chronologies. The average tree-ring width of all trees was 2.6 ± 1.5 mm, being the highest and lowest values found in SS and CJ, respectively. All five chronologies show a high (>0.47) mean sensitivity (MS), corresponding the highest values to the southern stands (CB and BS). Overall, intercorrelation between series (Rbt) was high in all sites ($r > 0.47$), except in CB where Rbt was 0.40 but equally significant ($p < 0.01$). BS3 population showed lowest values of Rbt and MS from Bom Sucesso de Itararé site, so this was not considered in the BS regional chronology.

Tree-ring chronologies obtained from lower altitude stands (SS and JU) covered a shorter time period compared to stands at higher altitudes (CJ, CB and BS) (Fig. 3). All chronologies have EPS values below to a referenced threshold (0.80) in early chronology periods, mainly due to the low number of series included in this period. However, four chronologies (CJ, JU, CB, BS) seem to show a temporal stability, good quality and a strong common signal for all the chronologies during the past 50 years, approximately, with EPS values above the threshold after 1960. *Growth-climate spatial relationships*

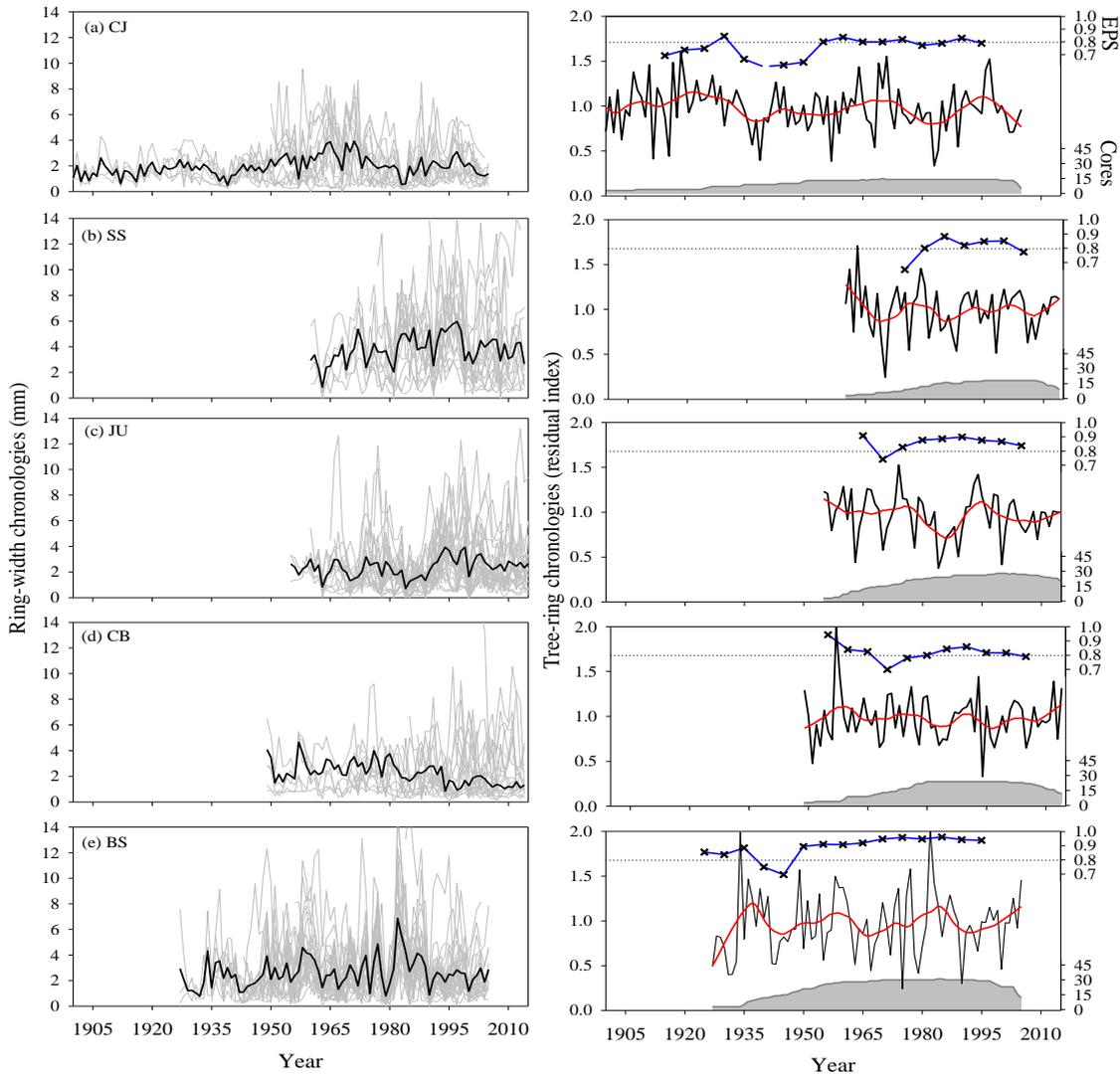


Figure 3 - Ring-width and tree-ring residual chronologies of five studied sites. Left column indicates measurements of raw ring-width data in mm (gray lines are series and black line is the average). Right column represent the residual chronologies (black line) with spline of 15 years (red line). EPS statistic (blue line) computed in 20-year windows with an overlap of 15 years, with 0.80 threshold (dotted line). Numbers of cores sampled for each year is indicated by gray area. (a) Campos de Jordão (CJ), (b) São Sebastião (SS), (c) Juquitibá (JU), (d) Carlos Botelho (CB), (e) Bom Sucesso Itararé (BS).

Multiple linear regression analysis showed a different relationship between tree radial growth and precipitation and temperature (Table 2). Precipitation from March to May before the growing season is positively associated with tree-ring chronologies of SS, JU and BS. In contrast, there is a strong positive correlation between rainfall of the rainy season (December to March) and tree growth of highest population (CJ) during the current growing season, with $p < 0.01$. Also, we found a negative association of winter precipitation with Juquitibá chronology (JU, $p < 0.05$). Overall, temperature was the second predictor variable in all sites. Ring-width chronologies of CJ, JU, CB, and BS were negatively correlated with mean temperature of winter, fall, summer and spring, respectively ($p < 0.10$). However, we found a positive relationship between summer temperature and winter temperature in SS ($p < 0.05$) and BS ($p < 0.01$) populations, respectively.

Table 2 - Results of the multiple regression analysis for the studied *Cedrela spp* populations. Tree-ring chronologies at each population were compared against seasonal climatic variables (accumulated precipitation and mean temperature). Seasons are fall: March to May, winter: June to July, spring: September to November, summer: December to March (fall and winter is previous growing season and spring and summer is current growing season). Predictor variables were selected by stepwise selection. See site acronyms in Table 1. Retained variable at the 0.10 significance level. Significance level at *0.10, **0.05 and *** 0.01.

Site	Months	Parameter Estimate \pm SE	Intercept \pm SE	<i>t-value</i>	Mean square error	Variation inflation factor	R ²
CJ	P DJF	0.0017 \pm 0.0006	1.33 \pm 0.58	2.683***	0.057	1.01	0.15
	T JJA	-0.0917 \pm 0.0408		-1.718*		1.00	
SS	P MAM	0.0010 \pm 0.0006	-0.96 \pm 0.81	1.780*	0.050	1.05	0.14
	T DJF	0.0779 \pm 0.0365		2.136**		1.05	
JU	P MAM	0.0014 \pm 0.0008	2.20 \pm 0.86	1.832*	0.056	1.02	0.16
	P JJA	-0.0025 \pm 0.0011		-2.276**		1.02	
	T SON	-0.0997 \pm 0.0591		-1.812*		1.00	
CB	T MAM	0.0964 \pm 0.0410	0.73 \pm 1.03	2.352**	0.045	1.28	0.10
	T DJF	-0.0985 \pm 0.0445		-1.765*		1.29	
BS	P MAM	0.0010 \pm 0.0004	0.40 \pm 0.97	4.340**	0.097	1.55	0.20
	T JJA	0.1500 \pm 0.0601		2.725***		1.06	
	T MAM	-0.1106 \pm 0.0590		-1.880*		1.13	

2.3.3 Growth–drought spatial relationships

The correlation between the index SPEI and our tree-ring residual chronologies of studied is showed in Fig. 4. This analysis improved of interpretation of the relationship between tree growth and precipitation and temperature, since we analyzed the tolerance of *Cedrela spp* tree-ring chronologies to drought stress at scale of 1, 3, and 6 months. Larger variability in growth-drought relationship was found at scale 1-month, since the chronologies were sensitivity to SPEI-1 in different months (CJ: February+1 $r = 0.31$; SS: September $r = 0.33$; CB: July $r = 0.25$, all with $p < 0.05$; and JU: October $r = 0.44$, with $p < 0.01$). In contrast, legged SPEI at 3-and-6-month showed higher significant correlation than lag SPEI at 1-month. Populations from CJ, SS and BS are most sensitivity at 3-month scale in the same month of SPEI 1 ($r \geq 0.35$, $p < 0.01$). In the highest population (CJ), strong SPEI-growth correlations were for the time scale of 6-month in March+1 ($r = 0.31$, $p < 0.05$), while the lowest population (SS) showed always positive correlation values before and during the growing season, with strong correlations in September and October ($r \geq 0.39$, $p < 0.01$). In southern populations (CB and BS), these significant correlations were observed before the growing season starts (fall, winter, and begin spring), indicating that favorable moisture conditions of previous year influences positively the growth responses at the following year.

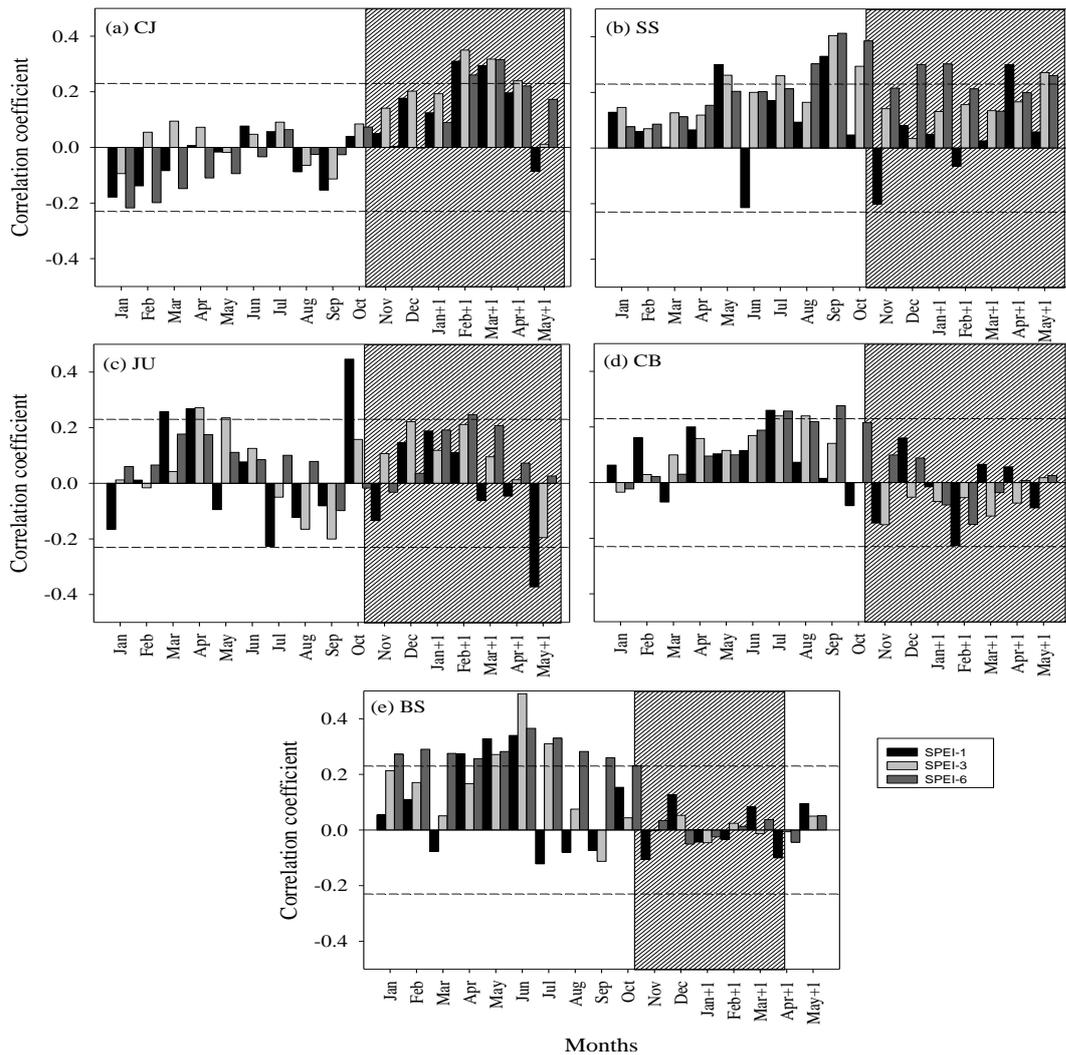


Figure 4 - SPEI-growth Relationship between residual chronologies of studied *Cedrela spp.* populations and SPEI drought index (calculated at 1-3- 6 month scales) during 55 years of common period. (a) Campos de Jordão (CJ), (B) São Sebastião (SS), (c) Juquitibá (JU), (d) Carlos Botelho (CB), (e) Bom Sucesso Itararé (BS). The common period for CJ and BS were 1951-2005; while that for SS, JU and CB were 1960-2014. Dashed horizontal lines indicate statistical significance at the 95% confidence level. Shaded areas indicate current growth season. (+) and (-) months refer to the calendar year.

The difference in SPEI-growth relationship between the highest population (CJ) to others sites seems to be associated to climatic gradient of winter and summer (Fig. 5). CJ population receives less rainfall during end-fall/beginning-winter (May to July), which would negatively influence the tree-ring sensitivity to July SPEI 3-month and September SPEI 6-month (Fig. 5a,c). Moreover, highest site with lower summer temperatures showed significant correlations between ring the width chronology and February SPEI 3-month and SPEI 6-month during the growing current season (Fig. 6 a,c).

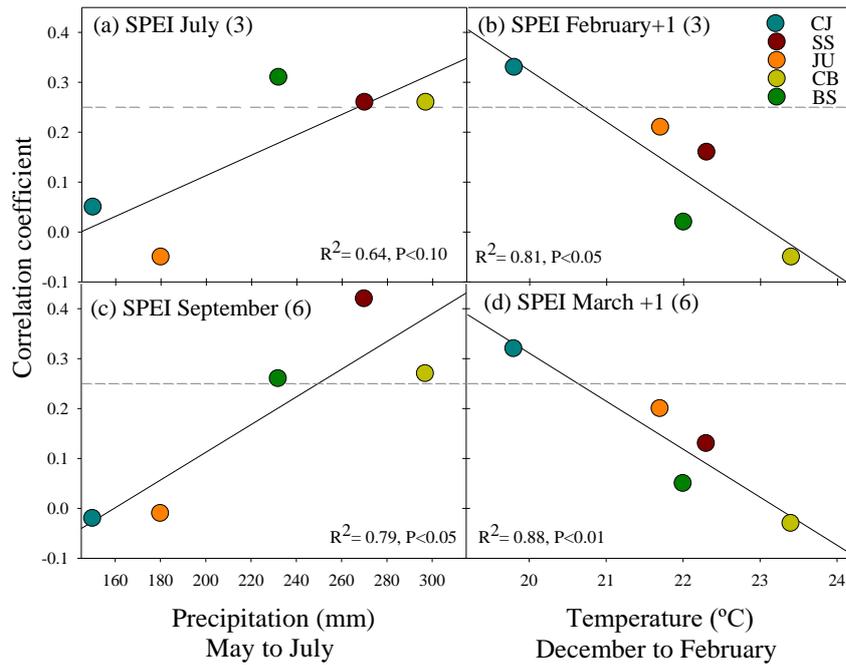


Figure 5 - Highest correlations between tree-ring chronologies and SPEI drought index (calculated at different month scales) against the climatic gradient of studied populations (accumulated precipitation of May to July, and mean temperature of December to February). (a) July SPEI at 3-month scale, (b) February+1 SPEI at 3-month scale, (c) September SPEI at 6-month scale, (d) March SPEI at 6-month scale.

2.3.4 Effect of drought periods on tree-ring width

The chronology of SPEI calculated at 1-month scale with spline of 10 years shows two drought periods after 1950: (i) 1961-1970 and (ii) 1985-1994 (Fig. 6a). For the first drought period, we observed significant results only in the southern population (BS), with lower tree-ring width values than previous wet period (1951-1960) ($H = 6.87$, $p = 0.032$) (Fig. 6b). In the second drought period, both BS and CB population showed lower growth during and post-drought period (Fig. 6c). Now, we observed lower tree-ring width values during and post-drought period in BS (BS: $H = 19.83$, $p < 0.001$; CB: $H = 9.43$, $p = 0.009$).

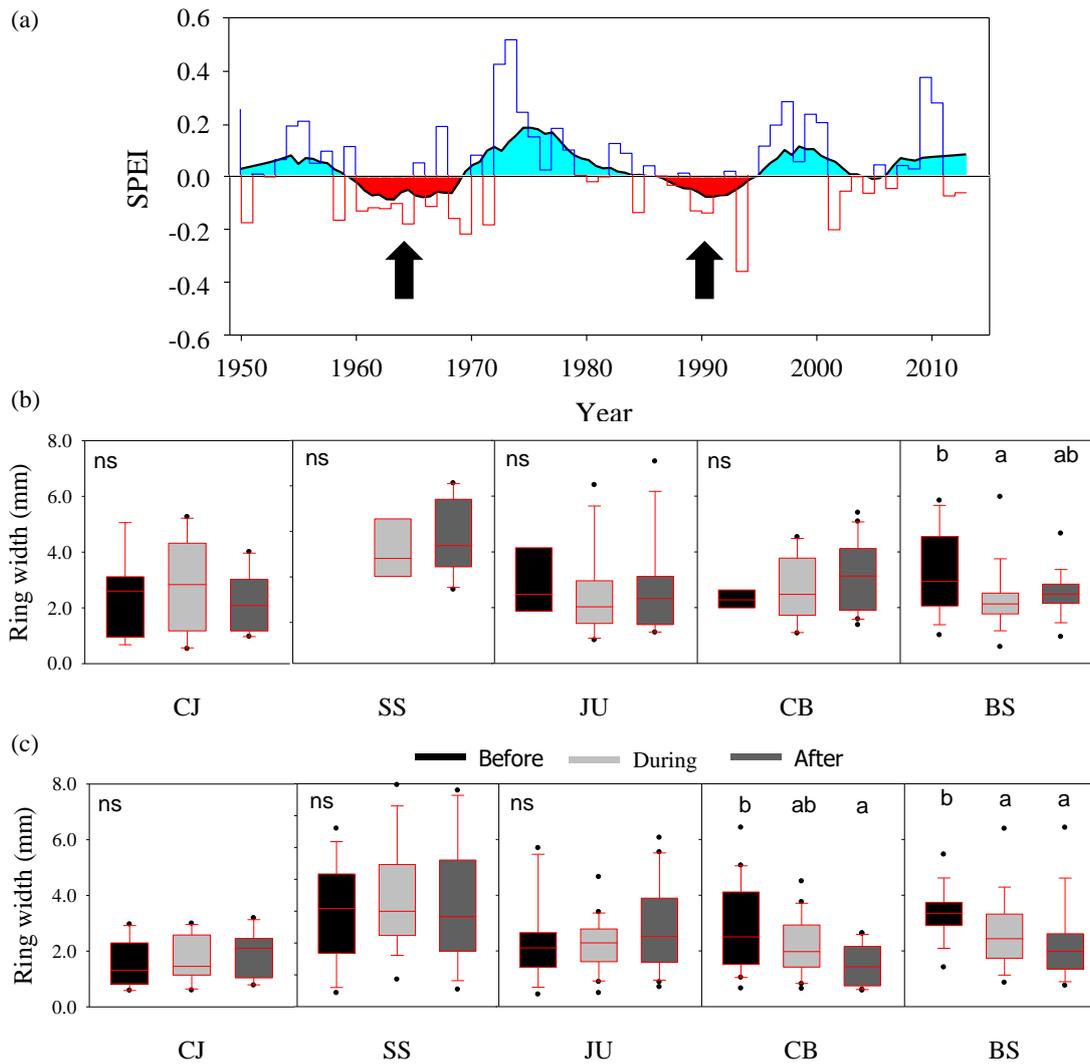


Figure 6 - (a) Chronology of SPEI calculated at 1-month scale. Spline with a periodicity of 10 years shows the wet and dry periods. Arrows indicate two drought periods after 1950: (i) 1960-1970 and (ii) 1985-1994, but to analyze the same number of years we consider the first drought from 1961 to 1970. (b) and (c) Box plots show the comparison of tree-ring widths before, during and after of first and second drought period, respectively. Different letters indicate if there are significant differences ($P < 0.05$, ns = non-significant results) and the horizontal lines of each box indicate the medians.

2.3.5 Effect of temperature trends on chronologies

We observed a significant increase in annual mean temperature since 1990 in all studied sites of *Cedrela spp* populations (Fig. 7a). These significant trends in winter (June to August) caused a decrease in tree-ring growth at the highest population (CJ) ($r = -0.56$, $p < 0.05$) (Fig. 7b). However, this rising temperature in winter had a positive effect on tree-ring growth of the southern tree population (BS) ($r = 0.63$, $p < 0.05$) (Fig. 7f). SS and CB do not show significant results (Fig. 7c, e). We do not observe significant trends in precipitation (results not shown).

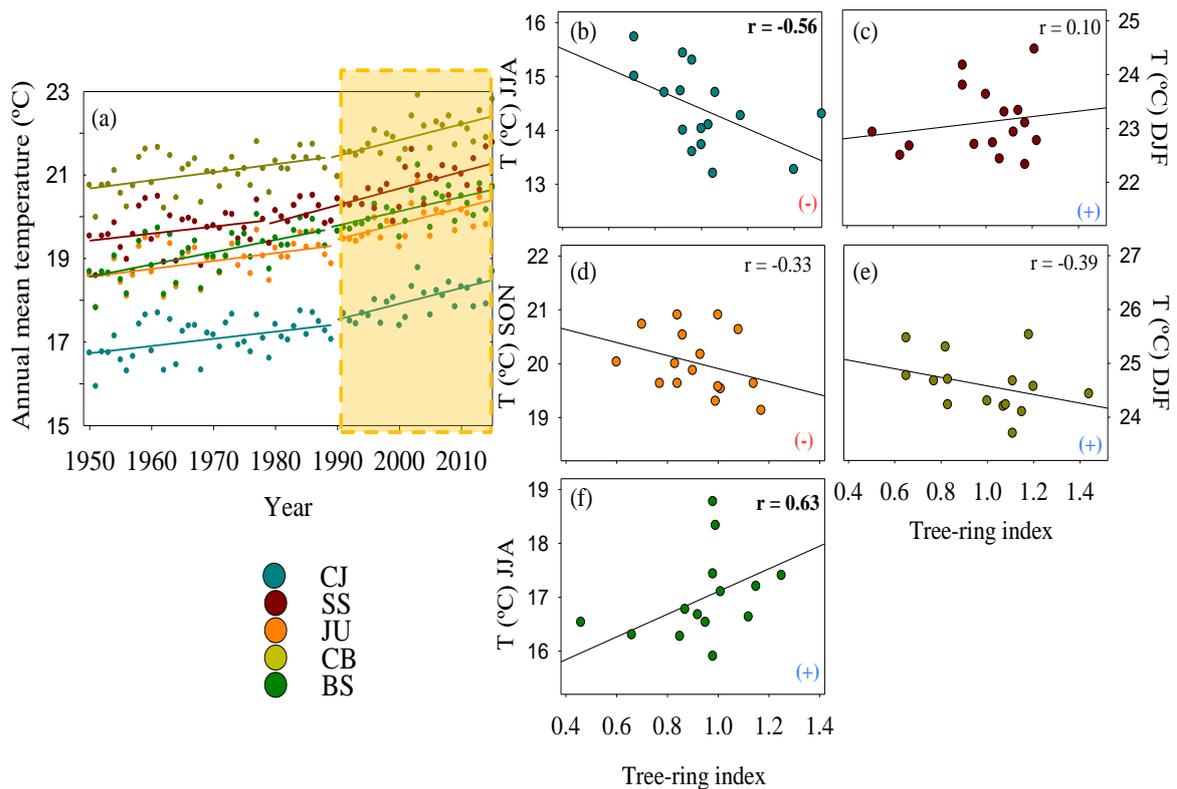


Figure 7 - (a) Temperature trends in the five sites for the period 1950-2014. Piecewise regression model identified different break years ($p < 0.01$) in all sites (CJ: 1990, SS: 1979, JU: 1989, CB: 1990 and BS: 1989). Orange rectangle represent the common period of significant increase in temperature in all sites (1990-2014). (b) to (f) shows the relationship between tree-rings residual chronology and most significant mean seasonal temperature of multiple regression analysis (see table 2), during the common period (1990-2005). Positive (+) and negative (-) trends since 1990 are indicated in each figure according residual chronologies (see Fig. 3). In bold significant correlations at 95% confidence level.

2.4 Discussion

We analyzed the impact of local climate variability and drought episodes over the growth resilience of *Cedrela* forests from the Atlantic forest biome distributed along the region of Sierra do Mar (AFSM) in Brazil. To our knowledge, this is the first study conducted in the region which addresses a biogeographical approach to understand the radial growth variability linked to a climatic gradient influenced by altitude and latitude. The severity of a summer drought occurred during 2014 and 2015 in Sao Paulo state (Coelho et al. 2016) and the global increase of air temperature in the tropics (Jones et al. 2007), justify studies in threatened tropical forests such as the AFSM. Moreover, and in frame of deforestation contributing in global climate change process, the biomass resilience of Neotropical secondary forests play an important role in carbon storage, having a net carbon uptake 11 times the uptake rate of old-growth forests (Poorter et al. 2016).

Overall, tree-ring chronologies of *Cedrela* from AFSM shows high inter-series correlations (r mean = 0.48), and mean expressed population signal > 0.85 , statistical elements that indicate a good performance of our tree ring chronologies for dendroclimatic studies (Wigley et al. 1984). These correlation between trees were higher than any other attained in prior studies with *Cedrela* $r < 0.28$ (Dunisch et al. 2003; Paredes-Villanueva et al. 2016), but lower than observed by Brienen and Zuidema (2005) with $r = 0.57$, so series intercorrelation in *Cedrela* chronologies has great variability and depends on the number of samples used for its building. CB population had the lowest

intercorrelation series, a fact that be the reason of the weaker climatic (mainly precipitation) signal contained in this chronology (Table 2). Mean sensitivity was >0.30 in all chronologies, showing that trees react to the environment through their annual growth variability (Grissino-Mayer 2001). The high values of first-order autocorrelation of tree-ring series justify use residual chronologies (Cook et al. 1990).

2.4.1 Hypothesis 1: Growth–climate relationship vs. climatic gradient

We found that tree-ring variability of remnant *Cedrela* forests from AFSM depend on favorable humidity conditions in different months; therefore, any change in precipitation – which is directly related to soil water – and temperature – which controls evapotranspiration rates – would specifically affect the growth performance at each population. Four populations (SS, JU, CB and BS) showed sensitivity to favorable moisture conditions during fall and winter months before the growing season (Table 2, Fig. 4), coinciding with others studies in the Neotropics (Dunisch et al. 2003; Brienen and Zuidema 2005). This interrelation seem to be associated with the influences of water supply on food reserves, which are mobilized at the beginning of the next growth period when soil moisture is essential for physiological functions of activation of meristematic tissues (Dunisch et al. 2003). However, Brienen and Zuidema (2005) indicate that is needed to clarify this relationship with detailed physiological studies. In contrast to these results, highest and coldest populations (CJ) did not show significant influence of rainfall over xylem production at the times of the prior growing season, which seem to be linked to rainfall contributions from May to July (Fig. 5a,c). In addition, this population is subjected to the lowest mean temperature recorded in the regional gradient (Fig. 3), indicating a broad mechanisms of adaptation or species plasticity of *Cedrela* forests to different environmental conditions, affecting phenology at cambium and leaf fall behavior.

At site CJ we found an interesting relationship in its radial growth sensitivity to summer rainfall during current growing season (Table 2), where maximum cambial activity occurs during the rainy season. This pattern has also been identified in other Brazilian tropical trees such as *Svietenia macrophylla* (Dunisch et al. 2003), *Amburana cearensis*, *Tachigali vasquezii* (Brienen and Zuidema 2005), *Tectona grandis* (Venegas-González et al. 2016), and *Hymenaea courbaril* (Locosselli et al. 2013). Paredes-Villanueva et al. (2016) found a similar growth sensitivity to precipitation during the rainy season in three *Cedrela spp* populations (*Cedrela odorata*, *C. fissilis* and *C. angustifolia*), indicating that radial growth is determined by the availability of water supply during the current growing season. In the case of the CJ site, this association may be explained because this site is at the highest altitudinal position, where lower temperatures during summer (Fig. 5b,d) would avoid an exacerbated evapotranspiration maintaining a higher water availability than in the other analyzed sites.

2.4.2 Hypothesis 2: Growth–drought relationship vs. climatic gradient

Tree-ring sensitivity to SPEI drought index in different months confirm the tree growth dependence to favorable soil moisture conditions, being vital for highest population (CJ) during growing season and before growing season for the others populations (SPEI 1 and 3-month). In contrast, SPEI 6-month showed, beside the said results (such we said above the highest site is favored by a lower mean temperature in summer), that the lowest and rainiest site (SS) had positive correlations with December and January, demonstrating that this site is also favored by water surplus during the beginning of the growing season. Site SS has high precipitation during December and January, so this condition can exercise greater control over evapotranspiration than other three populations (JU, CB, BS). We observed that this population had the higher mean ring width values that would be explained by a larger rainfall amount ($>2,000$ mm annual). Other biogeographic studies showed that wet sites correspond to higher tree-ring

widths in different forests (e.g. Camarero et al. 2013; Lyu et al. 2017). Our results confirm the SPEI-growth relationship founded by a global study showing that wet forest respond to drought events during short periods of time, i.e. three to six-months (Vicente-Serrano et al. 2013).

We observed that a drought lasting for 10 years have strong negative effect on tree growth of southern population (BS), which is located in the driest site. Then, we can infer that those populations are most sensitive to drought, with lower growth resilience during a post-drought period (Fig. 6c). Therefore, we can speculate that these populations in the gradient could be the most vulnerable to extreme drought episodes, risk that has been indicated at the global level (Allen et al. 2015). Tropical trees respond to drought altering their phenology by regulating their leafless times, improving the uptake water from deep soils sources, and increasing their resistance to cavitation or enhance water storage in the stem and branches (Markesteijn et al. 2011). However, a leaf fall reaction to dry conditions would reduce transpiration rates, affecting tree growth processes (Wright and Cornejo 1990), being embolisms the extreme functional risk which can be caused by a severe drought (Choat et al. 2012).

2.4.3 Hypothesis 3: Growth–global warming relationship vs. climatic gradient

A recent temperature increase, as corroborated in this study, would have incidence in the AFSM vegetation dynamics (Fig. 7a), which are directly proportional to the temperature per season. However, we observed a negative trend in tree growth for the last decades that would be related to rising winter temperature only in CJ (highest population) (Fig. 7b). This relationship might be explained by an increase of soil water deficit coupled with rising temperatures during the dry season, a fact that would affect the cambial activity some months later (i.e. more evapotranspiration). Also, it is important to remember that the highest population receives the least amount of rainfall during winter (Figs. 5a and 1S). Temperature directly affects fundamental physiological processes, such as photosynthesis and evapotranspiration. Therefore, any significant increase affects forests dynamics and global carbon cycle (Malhi et al. 2002). Paredes-Villanueva et al. (2016) also found negative correlations between *Cedrela spp.* tree rings and dry season temperature, a fact that is associated with water deficit. Prior temperature values to cambium activity start leads to greater hydrological deficit that reduces the water availability during the growth period in tropical tree species (López and Villalba 2011).

However, we observed a positive trend linked to winter temperature in the southern site (Fig. 7f) and a positive correlation between tree growth and summer temperature in rainiest site (Table 3). This can be explained by the fact that warmer temperatures provoke more transpiration than must be compensated by rehydration of the plant through an efficient xylem hydraulic system of xylem in deciduous tropical trees (Venegas-González et al. 2015). Therefore, we can think that this regional rise in temperature has affected particularly the trees growing at highest site (~1.500 m a.s.l), where both water availability and soil fertility seems to impact on tree growth and species distribution (Oliveira-Filho et al. 1998; Toledo et al. 2011). Overall, the highest site has shallow soil and lower fertility than the others study sites (Modenesi-Gauttieri and Hiruma 2004), so a temperature change may have implications in water and nutrient availability of soils, affecting the tree growth of remnants forest.

2.5 Conclusion

We concluded that growth-climate relationship of *Cedrela* forests varies across an environmental gradient in the Atlantic hotspot forest of the biogeographic subregion Serra do Mar. We propose that the highest population is more vulnerability to global warming and driest population is more sensitivity to droughts. The recent drought in the region (2014 to 2015), caused strong incidences in water shortage that have affected human population and local

economies (Coelho et al. 2016; Nobre et al. 2016). We believe that dry decades in the future would be greatly affecting the driest populations. To our knowledge, the present study is the first to report about tree rings and SPEI index calculated at different time-scales in Atlantic Forest; therefore, we verified the importance of include SPEI-growth relationship in tropical dendroecological studies, allowing to know how trees react to drought both at long and short-time scales. On the other hand, our results partially verify the worse effect of climate change on growth dynamic of species in endemic biotas of Neotropical forests in highest regions (i.e. montane forest) (Pounds et al. 1999; Moritz and Agudo 2013). Therefore, we consider that growth forest from highest site in AFSM is highly threatened by global warming and they would need urgent conservation strategies to mitigate climatic change. We think that it is necessary to continue increasing tree-rings chronologies of *Cedrela spp* in whole Atlantic forest (taking advantage of great climate sensitivity and wide geographic distribution), and include permanent plot data, which will give us a more detailed vision on which areas is most vulnerable to climate change in the entire biome.

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3 RECENT RADIAL GROWTH DECLINE IN RESPONSE TO INCREASED DROUGHT CONDITIONS IN THE NORTHERNMOST *NOTHOFAGUS* POPULATIONS FROM SOUTH AMERICA

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 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 winter-spring seasons) and negatively influenced by temperature from October to December (austral spring/early-summer 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 decline growth trend of *N. macrocarpa* with consequences for the survival of these endemic and endangered forest ecosystems that need further research.

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

3.1 Introduction

Mediterranean-type forests are generally characterized by dry summers and rainy winters, and represent hot spots of biodiversity because they are found in the most populated areas of the world, and maintain high and endemic species richness (Myers et al. 2000). However, by year 2100, it is expected that the Mediterranean region likely will experience the greatest proportional change in biodiversity because of the substantial influence of different drivers, where climate change being one of the main (Sala et al. 2000). In this sense, an emerging global pattern of tree mortality has been detected in different parts of the world in response to climate change and droughts during the last century (Allen et al. 2010), including Mediterranean-type climate regions (Allen et al. 2015). A recent increase in droughts in the Mediterranean Basin has been found compared to its natural variability over the last 900 years, which have intensified at the end of the 20th century (Sarris et al. 2011; Gea-Izquierdo and Cañellas 2014; Cook et al. 2016). In Mediterranean-type ecosystem of central Chile, the severity of recent drought events in the 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-type forest responses to increased drought conditions is increasingly needed.

The Mediterranean-type 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 thus 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; Schulz et al. 2010; Miranda et al. 2016).

Some of the most vulnerable Mediterranean-type forests of central Chile are those dominated by *Nothofagus macrocarpa* (DC.) Vásquez & Rodr (Nothofagaceae). This tree species is endemic to central Chile, represents the northernmost distribution of *Nothofagus* in America (Amigo and Rodríguez-Guitián 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 Rodríguez-Guitián 2011), allowing for the understanding of regional climatic factors that may affect tree growth along 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 & Wallace, 2000). Both atmospheric circulation patterns have a strong influence on precipitation and temperature in central Chile (Montecinos & Aceituno, 2003; Garreaud et al., 2009), and are indirectly affecting tree growth through their effect on local climate (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 have not been documented. Such an evaluation is critical in understanding the dynamics of these Mediterranean-type ecosystems in response to climate change and droughts (Gazol et al. 2017a). 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?.

3.2 Materials and Methods

3.2.1 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 area and densely human populated from 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 growing season occur from September to March due to the presence of green foliage (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. The total annual precipitation has a year-to-year variation in response to climatic oscillation such as El Niño Southern Oscillation (ENSO) and the Antarctic Oscillation (AOO) (Garreaud et al. 2009). Along the Andean range soils are developed 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 residual on rocky outcrops (Donoso, 1982).

3.2.2 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 2014, according Schulmann's convention for the Southern Hemisphere that indicate biological year \neq calendar year (Schulmann 1956). We sampled an area of 0.5 – 1 ha by population, where an average of 15 trees were cored. We randomly selected trees in order to sample different stem sizes, avoid bias on the selection of individuals, and include 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 ($\times 10$ magnification) and identified the boundary of each tree ring. *N. macrocarpa* has diffuse-porous 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 2,400-dpi resolution with a reference scale (ImageJ software, Rasband, 1997).

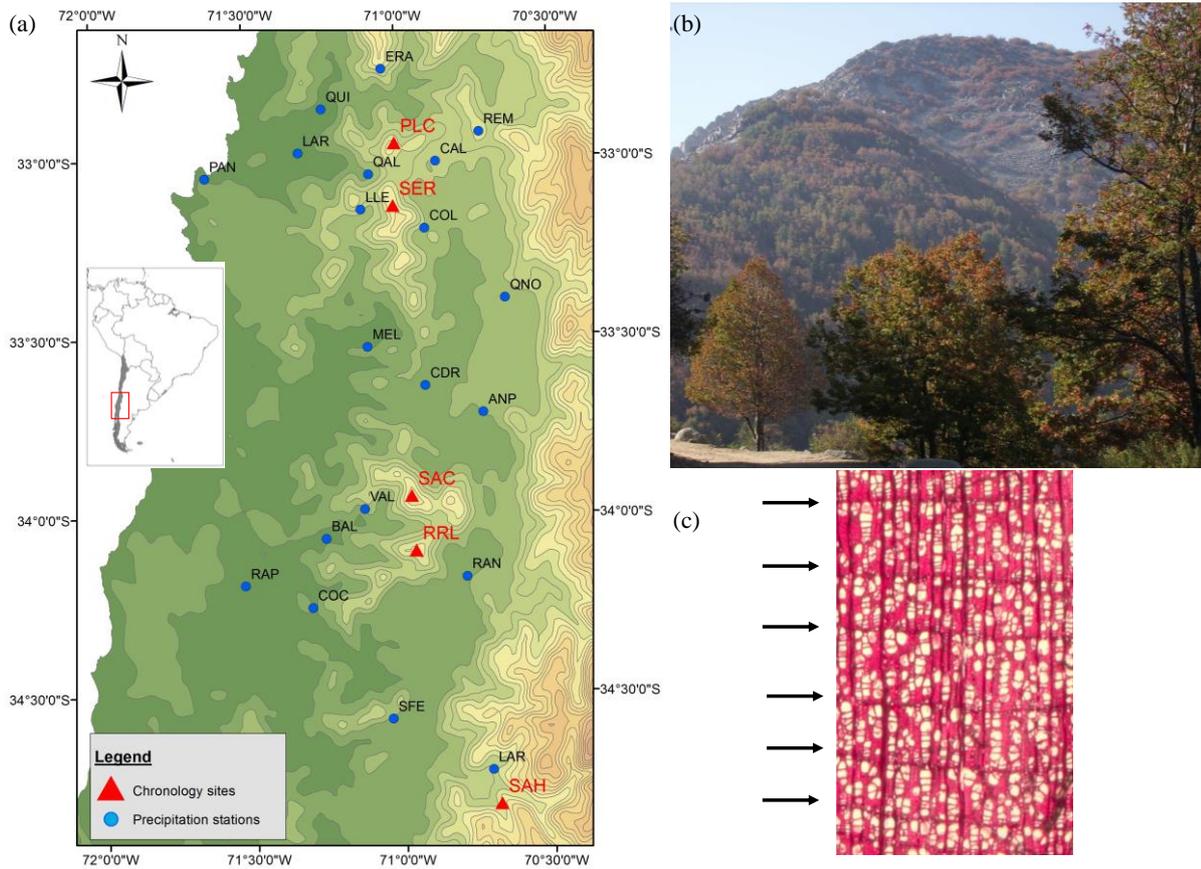


Figure 1 - (a) Study population locations (red triangles) and precipitation stations (blue circles) in central Chile (see Table 1 for site acronyms). Contour lines show elevation each 250 m a.s.l. and the shape of the terrain (b) *N. macrocarpa* forest at El Roble site. (c) Anatomical structure of annual tree rings of *N. macrocarpa*.

We used the software COFECHA to statistically validate the cross-dating and measurement quality of each core, and to find potential errors during the dating stage (Holmes et al. 1986b). To increase the number of trees per site, we grouped the populations of same site due to they had a common climate sensitivity and good inter-correlation. We constructed a chronology of 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 tree-ring 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 on tree-ring width series, while RBar and EPS are based on residual series.

Regional chronology was calculated as the robust biweighted mean of all available tree ring indices in a given year. Also, we used a principal component analysis (PCA) to identify the common patterns of growth variability among the site chronologies. The first principal component (PC1) is commonly used to analyze the tree-ring sensitivity to climate based on mean residual series, which estimates the common variability in growth among all sites, explaining the larger percentage of the climate-related variance (e.g. Lara *et al.*, 2005). Piecewise regression models of tree-ring width were used to analyze the significant change in temporal trends using years as the independent variable. For this, we used the *segmented* package (Muggeo 2008) in R (R core Team 2017). This analysis detects the most significant break years between two adjusting regression lines before and after of a selected year.

3.2.3 Climate data

To analyze the effect of local climate variability on tree growth, we used monthly climatic data of total precipitation and mean temperature. We obtained instrumental weather records from 20 meteorological stations that were closer to study sites (<http://explorador.cr2.cl/>) (Table 1, Fig. 1a). For precipitation, we used a composite record resulting from the average of two to six nearest stations to each site chronology, being the common period 1943-2014 (Table 1). However, those stations had a lot of missing temperature data, so we used gridded datasets of reconstructed temperature from CRU TS3.24 produced by the Climate Research Unit (Royal Netherlands Meteorological Institute, <https://climexp.knmi.nl/>), with 0.5° spatial resolution for the period 1901-2014 (Table 1). Although these grids cover a larger area (12,500 km² approximately), the temperature at 0.5°x0.5° is proportional (not equal) in whole area, which would not modify the dendroclimatic analysis. To analyze the climate–growth relationship at regional level, we estimated regional climatic anomalies (period 1930-2014) by averaging the standard deviations from monthly precipitation or monthly mean temperature using the software MET from the DPL program (Holmes 1992).

To study the relationship between water deficit and tree growth, we used the drought index Standardized Precipitation–Evapotranspiration Index (SPEI, 0.5° spatial resolution for the period 1901-2014), which is based on a combination of precipitation and temperature (effect on evapotranspiration rate) from the same spatial dense dataset of CRU (Vicente-Serrano *et al.* 2010). SPEI data was extracted by web KNMI Climate Explorer (<https://climexp.knmi.nl/>). This index has the advantage to combine a multiscalar character for drought assessment through a basic water balance calculation, and has been widely used in recent dendrochronological studies to drought-growth relationship due to higher correlation than other drought indices, such as the Palmer Drought Severity Index (Camarero *et al.* 2013; Labuhn *et al.* 2016).

Table 1 - Sites used for constructing tree-ring chronologies and meteorological stations used in this study

Site (Code)	Max time period	Latitude (S)	Longitude (W)	Elevation (m a.s.l.)
La Campana (PLC)	1904-2014	32°57.7'	71°07.5'	1,280
El Roble (SER)	1845-2014	33°00.5'	71°01.5'	1,600
Altos Cantillana (SAC)	1789-2014	33°55.1'	70°58.5'	1,800
Robleria del Cobre de Loncha (RRL)	1858-2014	34°07.6'	70°57.9'	1,090
Alto Huemul (SAH)	1767-2014	34°51.9'	70°40.2'	1,550
Precipitation data obtained from Centro de Ciencia del Clima y la Resiliencia (CR ² Explorador Climatico)				
Estero Rabuco ¹ (ERA)	1965-2014	32°50.8'	71°07.4'	300
Quillota ¹ (QUI)	1978-2014	32°53.7'	71°12.5'	130
Los Aromos ¹ (LAR)	1974-2014	32°57.4'	71°20.7'	100
Punta Angeles ¹ (PAN)	1899-2014	33°01.0'	71°38.0'	41
Caleu ^{1,2} (CAL)	1957-2014	33°00.3'	70°59.6'	1,120
Rungue Embalse ^{1,2} (REM)	1943-2014	33°01.1'	70°54.5'	700
Quebrada Alvarado ² (QAL)	1990-2014	33°03.0'	71°06.0'	290
Colliguay ² (COL)	1950-2014	33°10.1'	71°08.8'	490
Lliu-Lliu Embalse ² (LLE)	1978-2014	33°05.9'	71°12.8'	260
Quinta Normal ^{2,3} (QNO)	1899-2014	33°26.7'	70°40.9'	527
Melipilla ³ (MEL)	1971-2014	33°40.8'	71°11.9'	168
Angostura de Paine ³ (ANP)	1988-2014	33°48.2'	70°52.6'	350
Carmen de las Rosas ^{3,4} (CDR)	1931-2014	33°45.5'	71°09.0'	165
Villa Alhue ^{3,4} (VAL)	1979-2014	34°02.1'	71°05.6'	197
Rapel ^{3,4} (RAP)	1940-2014	34°56.7'	71°05.1'	16
Barrera Loncha ⁴ (BAL)	1984-2014	34°04.9'	71°11.3'	144
Rancagua ⁴ (RAN)	1910-2014	34°11.4'	70°45.0'	515
Cocalan ⁴ (COC)	1978-2014	34°12.1'	71°16.5'	120
San Fernando ⁵ (LAR)	1910-2014	34°35.1'	71°00.0'	350
La Rufina ⁵	1930-2014	34°44.5'	70°45.1'	743
Temperature data from Royal Netherlands Meteorological Institute (KNMI Climate Explorer)				
CRU TS3.24 ¹	1901-2014	32°30'/33°00'	71°30'/71°00'	-
CRU TS3.24 ²	1901-2014	33°00'/33°30'	71°00'/70°30'	-
CRU TS3.24 ³	1901-2014	33°30'/34°00'	71°00'/70°30'	-
CRU TS3.24 ⁴	1901-2014	34°00'/34°30'	71°00'/70°30'	-
CRU TS3.24 ⁵	1901-2014	34°30'/35°00'	71°00'/70°30'	-

Numbers indicate sites where the meteorological station were used for analysis (¹PLC, ²SER, ³SAC, ⁴RRL, ⁵SAH)

To analyze the large-scale climate variability on tree growth, we analyzed two global atmospheric circulation indexes, El Niño/Southern Oscillation (ENSO) and Antarctic Oscillation (AAO). ENSO was analyzed by the Multivariate ENSO Index (MEI) for the time period of 1950-2014 (obtained from <http://www.esrl.noaa.gov/psd/enso/mei/table.html>). This index is based on six main observed variables over the tropical Pacific: sea level pressure, zonal and meridional components of the surface wind, sea surface temperature, air temperature, and total cloudiness fraction of the sky (Wolter and Timlin 2011). In the case of the tropospheric circulation south of 20° S, we used the Antarctic Oscillation index (AAO) for the time period 1948 to 2011 (obtained from <http://jisao.washington.edu/data/ao/slp/>). This index is based on principal components of geodynamic height anomalies at 850 hPa (Thompson and Wallace 2000) and represents the variability in the extratropical atmospheric circulation, accounting for ca. 1/3 climate variability of the Southern Hemisphere (Marshall 2003). The AAO positive phase is associated with decreased (increased) sea level surface pressure over Antarctica (mid-latitudes) in the austral summer (Garreaud et al. 2009).

3.2.4 Statistical analyses

To temporal correlations, we evaluated the effect of climate variables (precipitation, temperature, SPEI, MEI and AAO) on tree growth (ring-width index for each site and PC1 for regional chronology) using a correlation function analysis, i.e. tree growth was considered as an integration of climate influences occurring from prior to current growing periods (Fritts 1976). Thus, we correlated ring-width against the time period covering from previous January current March. We analyzed temporal trends in correlation coefficients between regional chronology and climate by bootstrapped moving correlation intervals of 30 years (Biondi 1997) using the Dendroclim2002 software (Biondi and Waikul 2004).

We explored the link between drought events in central Chile documented by Le Quesne *et al.* (2006), Garreaud *et al.* (2017)¹ and SPEI (1-month) with our ring-width chronology. We classified two types of lowest tree-growth (negative pointer years) related to drought; a threshold of ≤ 1.0 (strong effect) and ≤ 2.0 (severe effect) standard deviations below the mean of the residual regional chronology.

To spatial correlations on regional scale, we analyzed the relationship between PC1 and precipitation (CRU TS3.24 land), temperature (CRU TS3.24 land) and SPEI (1-month), using a resolution of $0.5^\circ \times 0.5^\circ$ gridded cell. On a global scale, we analyzed the link between PC1 and (i) ENSO using the sea surface temperature (SST) of the equatorial Pacific region (HadISST1 1.0° reconstruction), and (ii) AAO using the sea level pressure (SLP) across northern Antarctic Ocean (HadLSP2 5.0° reconstruction). We used spatial field correlations from the KNMI (Royal Netherlands Meteorological Institute) using the data available from the Climate Explorer Website (<http://climexp.knmi.nl/>). Finally, we performed a continuous Wavelet Transform analysis (Torrence and Compo 1998) for the regional chronology of *N. macrocarpa* to determine the main oscillatory cycles and to localize intermittent periodicities.

3.3 Results

3.3.1 Characteristics of tree-ring chronologies

We obtained cores from 146 trees with ages ranging between 22 to 248 years (Table 2). Tree-ring chronologies obtained from northern stands (PLC and SER) covered a shorter time period compared to southern stands (Fig. 2). We observed strongest amplitude of tree-ring width at the beginning of RRL and SAH chronologies probably due to small sample size. All five sites had high mean sensitivity and intercorrelation between series (>0.39 and >0.47 , $P < 0.01$, respectively). RBar varied between 0.19 (SAH) and 0.27 (PLC). The expressed population signal was ≥ 0.85 from 1930 (PLC), 1945 (SER), 1885 (SAC), 1910 (RRL) and 1860 (SAH), indicating that sampling replication was adequate in those periods (Table 2).

¹ Garreaud et al. 2017. The 2010-2015 mega drought in Central Chile: Impacts on regional hydroclimate and vegetation. Hydrology and Earth System Sciences *in revision*. <http://www.dgf.uchile.cl/rene/PUBS/hess-2017-191.pdf>

Table 2 - Descriptive statistics for the five *N. macrocarpa* chronologies developed in this study (see Table 1 for chronology code definitions). Site acronyms as in Table 1.

Variables	Sites					Regional
	PLC	SER	SAC	RRL	SAH	
No. trees (sampled)	30	30	27	24	44	155
No. trees (chronology/radii)	29/47	29/42	24/46	23/37	41/56	146/228
Mean ring width \pm SD (mm)	1.34 ± 0.88	1.81 ± 1.17	1.39 ± 0.78	1.69 ± 0.90	1.39 ± 0.73	1.49 ± 0.86
Time span (>5 trees)	1929-2014	1921-2014	1826-2014	1890-2014	1832-2014	1832-2014
Age \pm standard deviation	69 ± 17	72 ± 25	140 ± 73	88 ± 55	120 ± 110	98 ± 55
Mean sensitivity	0.45	0.50	0.47	0.4	0.39	0.44
Series intercorrelation	0.60	0.52	0.51	0.49	0.47	0.43
RBar (\pm SE)	0.27 ± 0.01	0.25 ± 0.02	0.25 ± 0.02	0.21 ± 0.03	0.19 ± 0.02	0.12 ± 0.01
First-order autocorrelation	0.60	0.49	0.47	0.54	0.60	0.54
Period with $\text{EPS} \geq 0.85$	1930-2014	1945-2014	1885-2014	1910-2014	1860-2014	1905-2014

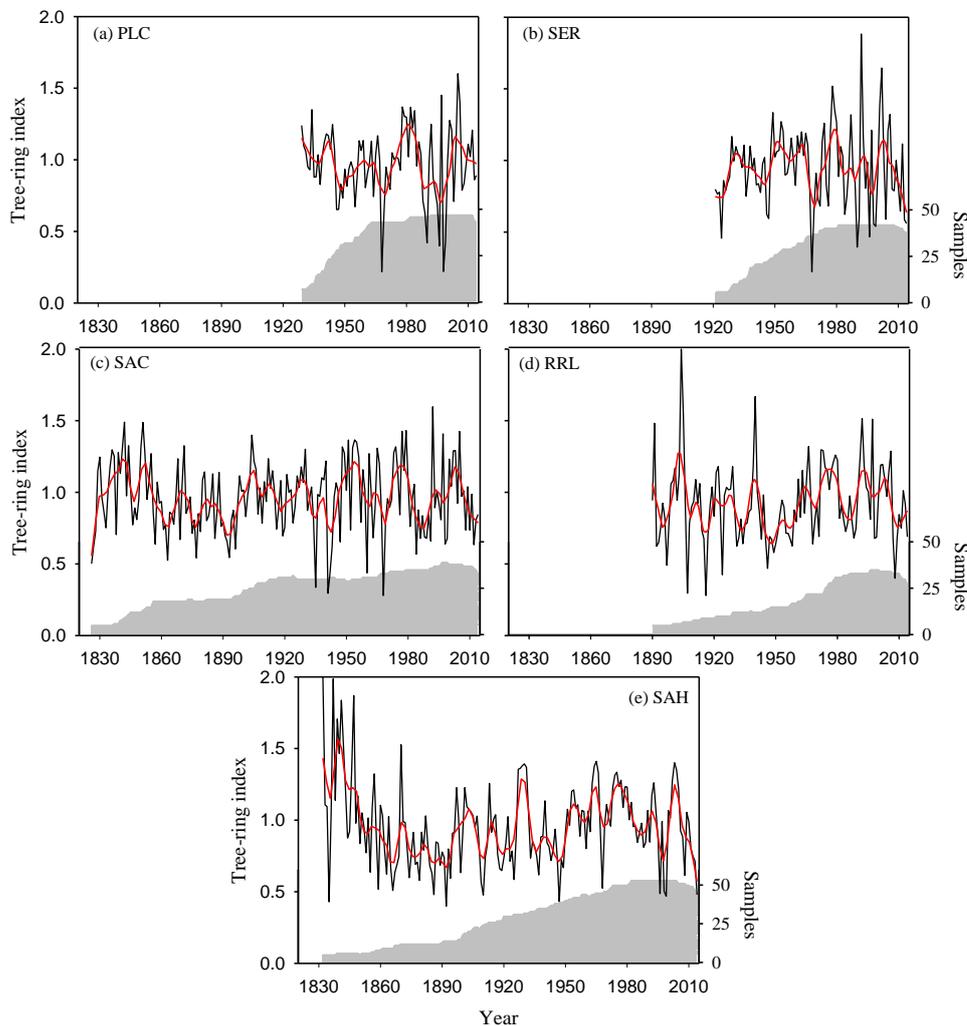


Figure 2 - Tree-ring residual chronologies of five study forest of *Nothofagus macrocarpa*: (a) National Park La Campana (PLC), (b) Nature Sanctuary El Roble (SER), (c) Nature Sanctuary Altos Cantillana (AC), (d) National Reserve Robleria del Cobre de Loncha (RRL), (e) Nature Sanctuary Alto Huemul (AH). Forest stands are ordered from northern to southern locations. The shaded area corresponds to the sample size of each chronology. The red line shows a cubic spline designed to reduce 50% of the variance in a sine wave with a periodicity of 10 years (Cook and Peters 1981).

3.3.2 Regional chronology and trends

We developed a regional chronology of 228 series (146 trees) for the whole distribution of *N. macrocarpa* covering the period 1832-2014 (>10 trees), with intercorrelation between series of 0.43 and mean sensitivity 0.44, and EPS most significant for the period 1905-2014 (≥ 0.85) (Table 2). The principal component analysis (PCA) of the five residual chronologies for the common period (1929-2014) showed that the first principal component (PC1) contributed to 60.8% of the total variance (the PC2 contributed 15.7% of the variance) with all sites showing positive loadings (see also Fig. 3).

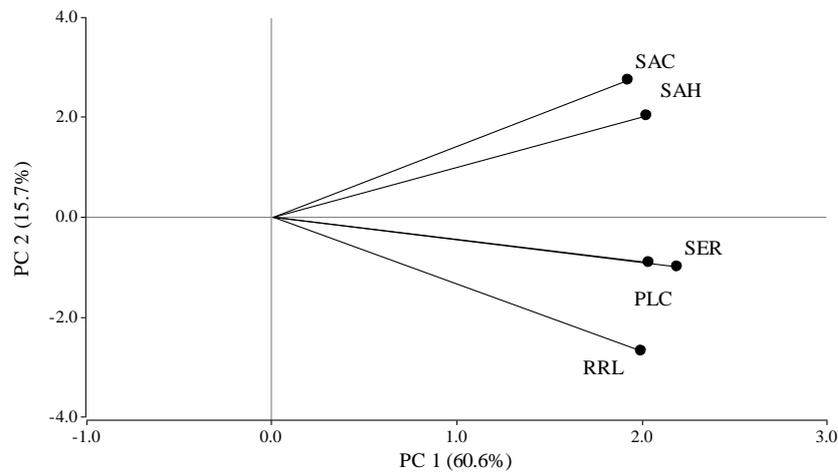


Figure 3 - Relative positions of five residual chronologies of *N. macrocarpa* according to the two principal components for the period 1929-2014 (common period of five chronologies). The first two principal components explained about 76.3% of the variance in the records.

Fig. 4 shows the radial growth variability with at least 30 trees covering the period 1890-2014. The piecewise regression model identified a significant decrease in the radial growth of *N. macrocarpa* trees after 1980 (Fig. 4a). Regional chronology shows negative pointer years that coincide with drought years identified by Le Quesne et al (2006) and Garreud et al (2017). The drought years that affected the regional chronology are 1892, 1924, 1946, 1967, 1968, 1988, 1996, 1998, 2007, 2013 and 2014 (Fig. 4b). We detected an increase of years with lowest tree growth linked to drought in the residual tree-ring chronology for the period 1980-2014. These responses represent the 55% of 11 years with lowest tree growth related to drought in central Chile. Three drought years had a severe effect on tree-ring growth (≤ 2.0 standard deviations below the mean of residual regional chronology) and two of them occurred in the 1990s.

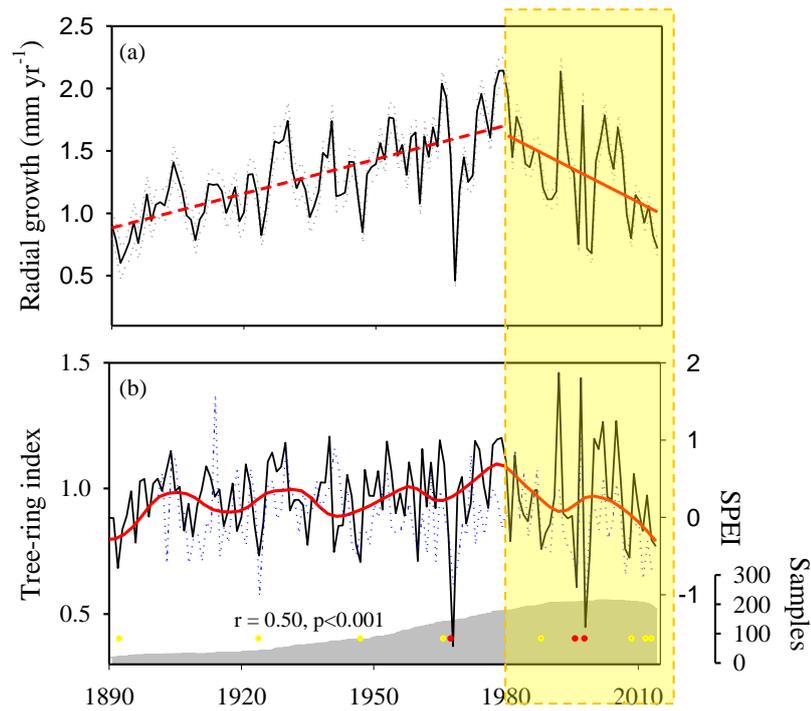


Figure 4 - (a) Mean radial growth rate (mm yr^{-1}) of the regional chronology of *N. macrocarpa* (black line). Piecewise regression model identified 1980 as a break year ($p < 0.001$, orange rectangle). (b) Residual regional chronology of *Nothofagus macrocarpa* (black) including the five sites for period 1890-2014 (> 30 trees) and SPEI chronology May-November calculated 1-month scale (blue) for the period 1901-2014. Circles represent the lowest tree growth that coincides with drought years identified also by Le Quesne et al (2006) and Garreud et al (2017). Yellow and red circles indicate growth departures ≤ 1.0 (strong effect) and ≤ 2.0 (severe effect) standard deviations below the mean of the residual regional chronology. Residual chronology smoothed are shown with a cubic spline (red line) designed to reduce 50% of the variance in a sine wave with a periodicity of 20 years (Cook and Peters, 1981). Number of samples is indicated by the grey shaded area.

3.3.3 Spatio-temporal climate-growth relationships (Local)

Overall, all chronologies correlated with climate (Fig. 5, 6). We detected significant correlations with monthly precipitation during the late austral autumn to austral spring (from May to November) and an inverse relationship with monthly mean temperature during the austral spring to early austral summer (October to December). We detected strongest correlations with monthly precipitation in June (all populations, $r \geq 0.30$, $P < 0.01$), while those for monthly temperature were observed in November (PLC, RRL and SAH, $r \geq 0.27$, $P < 0.05$) and December (SAC, $r \geq 0.23$, $P < 0.05$) (Fig. 5). Using seasonal means of Standardized Precipitation Evapotranspiration Index (SPEI, 1-month), we found a significant correlation of the five *N. macrocarpa* chronologies to wet conditions in winter ($r \geq 0.34$, $P < 0.01$) and spring ($r \geq 0.21$, $P < 0.10$) (Fig. 6a).

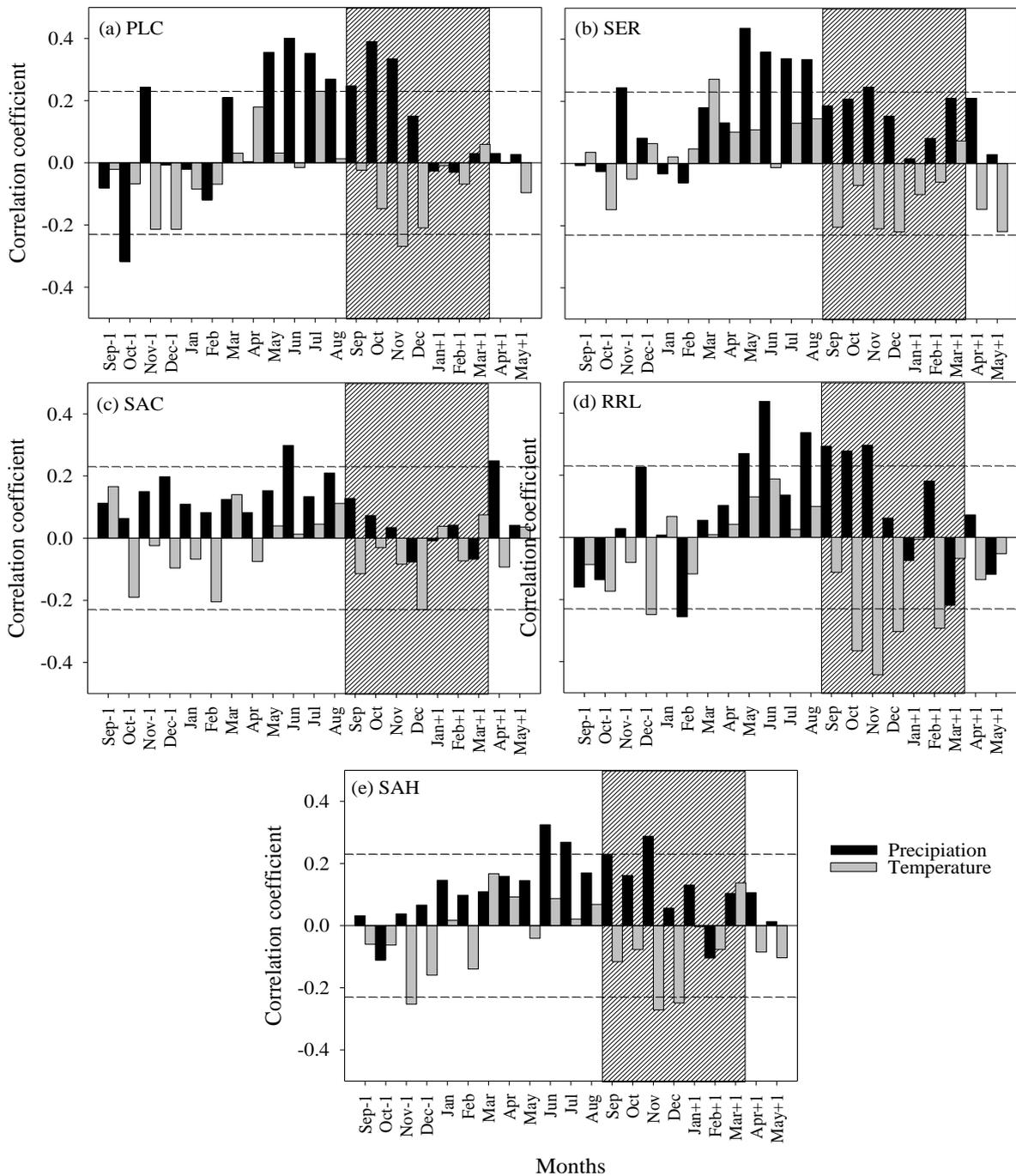


Figure 5 - Climate-growth relationships between residual chronologies of studied *N. macrocarpa* populations during the 1943-2014 common period. Dashed horizontal lines indicate statistical significance at the 95 % confidence level ($r = 0.23$). Shaded areas indicate current growth season. (+) and (-) months refer to the calendar year.

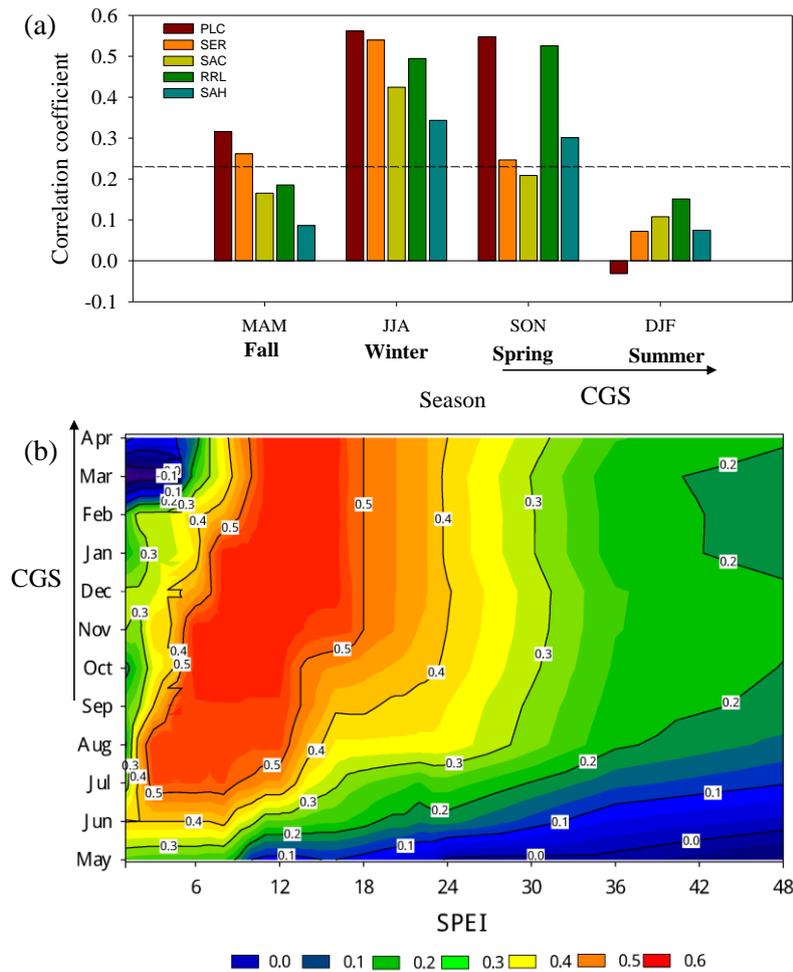


Figure 6 - (a) Relationships between residual chronologies of the five site study of *N. macrocarpa* and SPEI drought index (1-month) by season, during 1943-2014 (common period). Dashed horizontal lines indicate statistical significance at the 95 % confidence level ($r = 0.23$). (b) Correlations calculated between first principal component of *N. macrocarpa* sites. SPEI is calculated at monthly scales ranging from 1 to 48 months. Values of the correlation coefficients higher and lower than 0.20 or -0.20 ($P < 0.05$), respectively. CGS: Current growing season.

3.3.4 Spatio-temporal climate-growth relationships (regional)

First principal component of the tree-ring regional chronology of *N. macrocarpa* (PC1) was positively correlated to regional precipitation between May and November (austral winter/austral spring) of the current growing season ($P < 0.05$, Fig. 7a), with June precipitation having the highest correlation with PC1 ($r = 0.43$, $P < 0.001$). PC1 was negatively correlated to regional temperatures of late-spring/early-summer during the current growing season (i.e. October to December, $P < 0.05$) with November temperature having the highest correlation with PC1 ($r = 0.32$, $P < 0.01$, Fig. 7a). Drought-growth relationship shows that *N. macrocarpa* is a species very sensitive to long period of water deficit, since we observed higher correlation ($\sim r = 0.40$) between PC1 and SPEI at 1–24 months scale previous and current growing season (from May to April) (Fig. 6b). We found that regional chronology strongly responded to mean SPEI at 1-month scale of May to November to period 1901-2014 ($r = 0.50$, $P < 0.001$) (Fig. 4b). Spatial correlations verified the high sensitivity of *N. macrocarpa* forest to favorable humidity conditions of austral winter/austral spring in mid-latitudes of South America (30–45°S), for the period 1980-2014 (Fig. 9a).

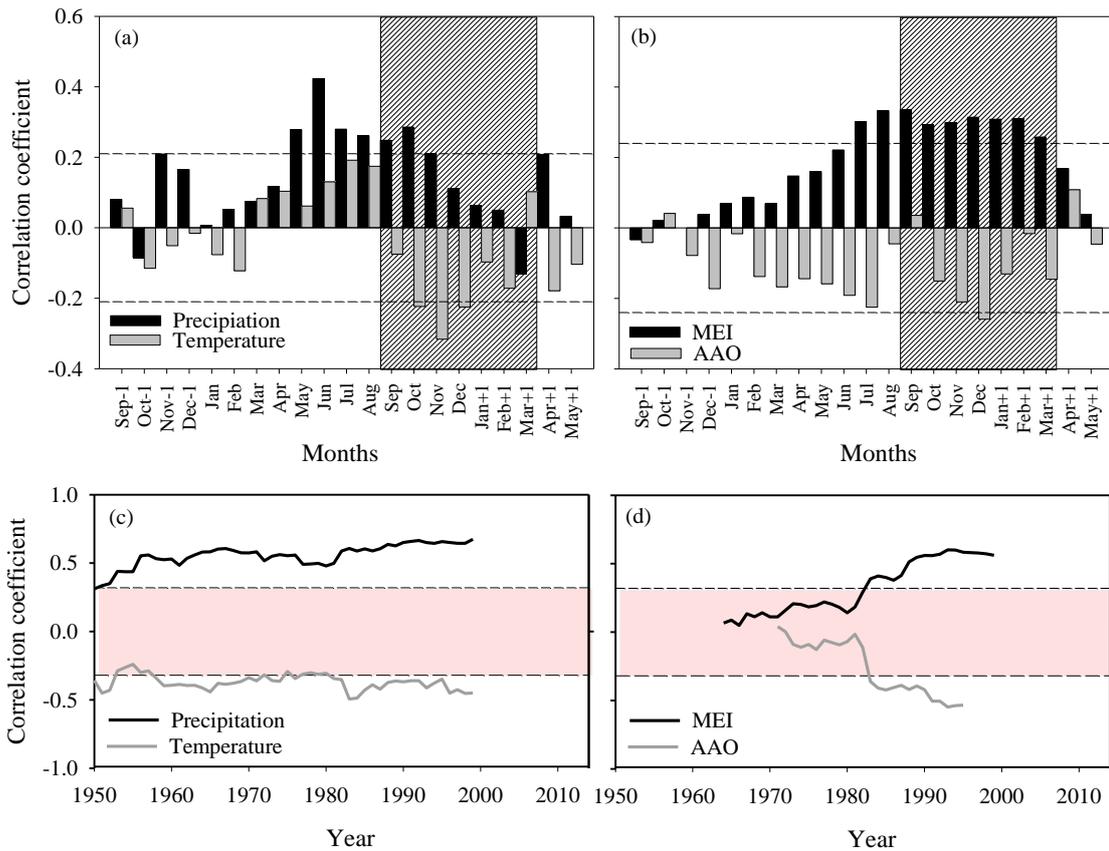


Figure 7 - (a) and (b) Correlations between the first principal component of the tree-ring chronology and anomalies of precipitation (May to November) and temperature (October to December) during the significant months of Fig. 4a, for the period with significant negative decrease trends (1980-2014). Blue and red line indicate the linear trends ($P < 0.10$ to precipitation and $P < 0.01$ to temperature). Note that for temperature, inverse values are used to improve visualization.

Moreover, moving correlations using a 30-year window confirmed that growth response to local and global climate variability increased since the last three decades of 20th century (Fig. 9c, d). We observed an increase of significant correlations after 1980 in local and large-scale climate variables. Regarding the local sensitivity, we observed positive correlation with precipitation anomalies ($r = 0.71$ and $P < 0.001$, Fig. 10a) and negative correlation with temperature anomalies ($r = -0.42$ and $P < 0.01$, Fig. 8b).

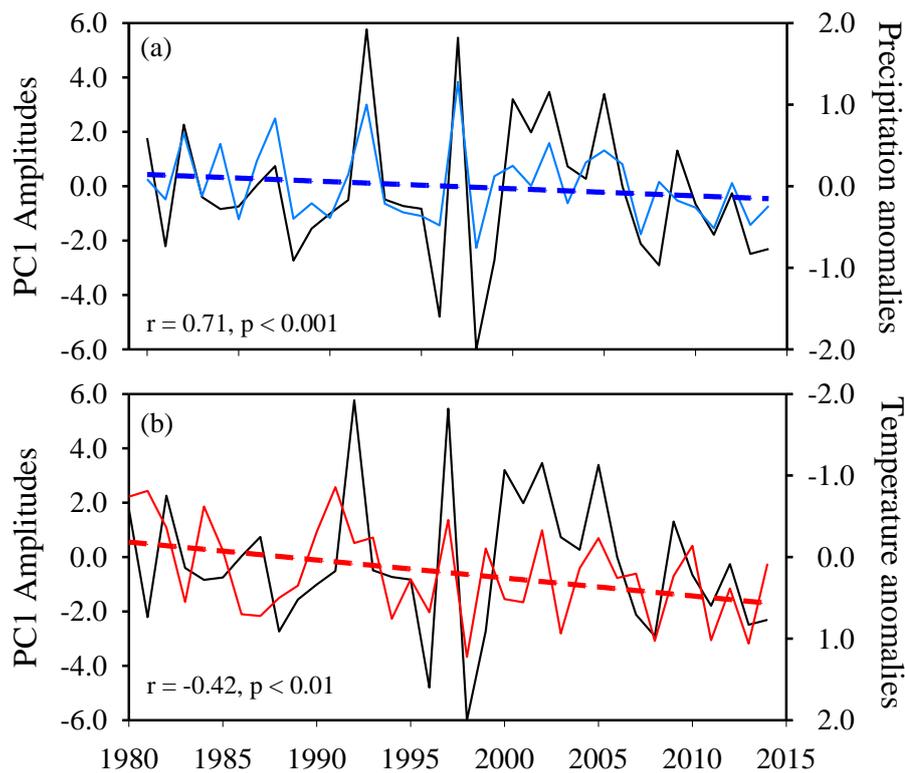


Figure 8 - (a) and (b) Correlations between the first principal component of the tree-ring chronology and anomalies of precipitation (May to November) and temperature (October to December) during the significant months of Fig. 6a, for the period with significant negative decrease trends (1980-2014). Blue and red line indicate the linear trends ($P < 0.10$ to precipitation and $P < 0.01$ to temperature). Note that for temperature, inverse values are used to improve visualization.

3.3.5 Spatio-temporal climate-growth relationships (global)

We found that PC1 was positively correlated to MEI and negatively correlated to AAO (Fig. 7b, $P < 0.05$). *N. macrocarpa* tree-ring width was strongly correlated to MEI particularly for the period from July to March+1 (late growing season). In contrast, tree-ring width was correlated to AAO only significant for December during current growing season ($r = -0.26$, $P < 0.05$).

Highest spatial correlations with sea surface temperature (SST) and sea level pressure (SLP) were observed for the time period after 1980 (Fig. 9b, 9c). We found a significant correlation of tree growth with atmospheric circulations of tropical Pacific and Antarctic regions ($r > 0.50$; $P < 0.05$). We found a positive association with the sea surface temperature (SST) in the equatorial Pacific, mainly at the Niño 3.4 region during July and March+1 (Fig. 9b). Also, we observed a dipole between the SST at the Equator region relative to mid-latitudes (10-40°S), with positive and negative correlations with our regional chronology after 1980. PC1 had a positive correlation with sea level pressure (SLP) throughout the Antarctic region south of 60°S, and negative correlation with SLP at mid-latitudes (Fig. 9c), indicating the inverse association between SLP south of 60° S and AAO.

Spectral analyses for the regional chronology (period 1850-2014) showed significant oscillations at sub-decadal frequencies (< 5 years) mainly during the time periods 1850-1900 and 1970 to present (Fig. 10). Other significant oscillations at sub-decadal (i.e. 2.5 and 4.6 years) and multi-decadal frequencies (13.1 and 24.9 years) were also detected.

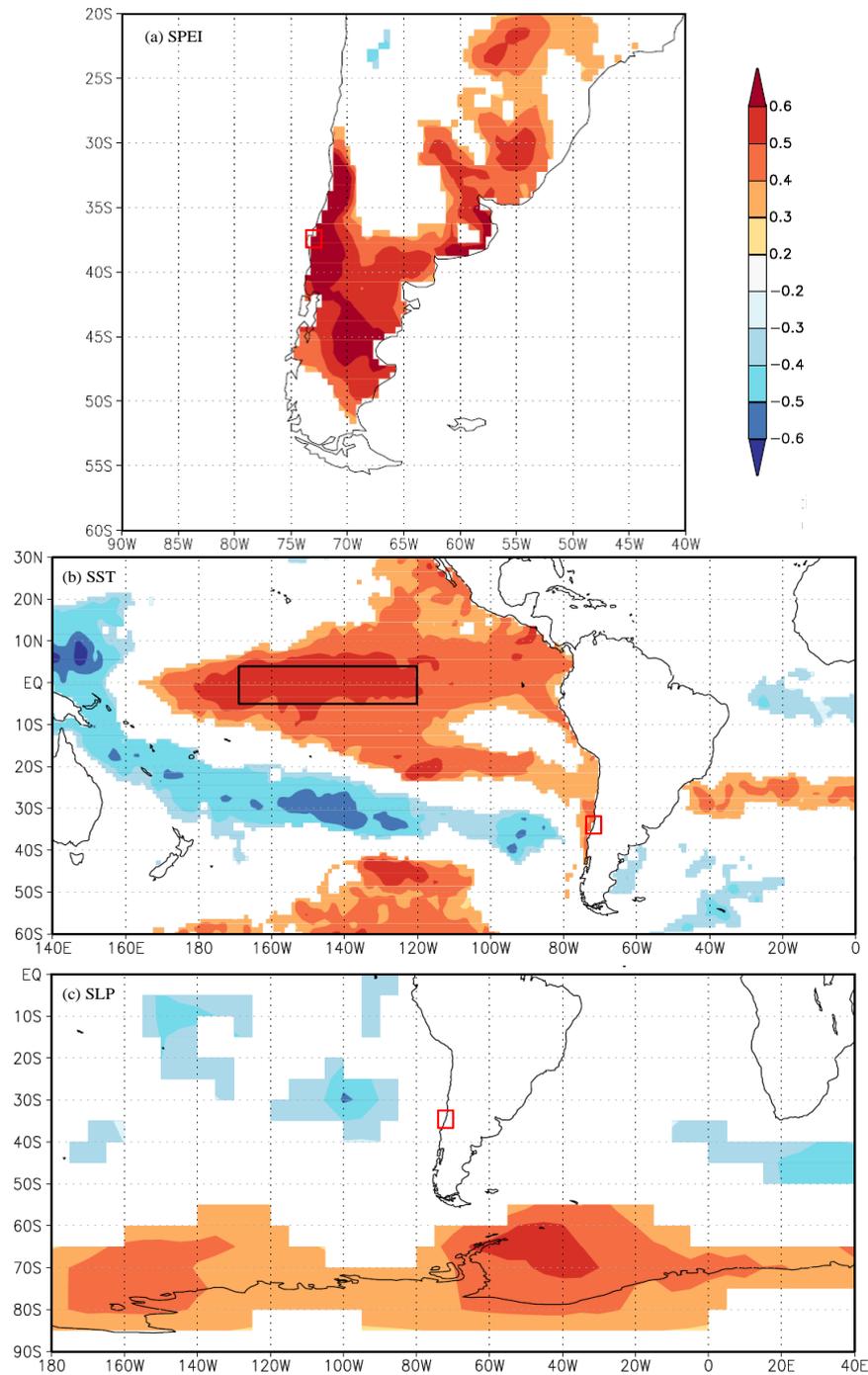


Figure 9 - Spatial correlation fields of regional chronology (PC1) of *N. macrocarpa* and gridded monthly climatic observations for the period 1980-2014: (a) Standardized Precipitation-Evapotranspiration Index (SPEI) (calculated 1-months scale) from May to November; (b) Sea surface temperature (SST $1.0^{\circ} \times 1.0^{\circ}$) from July to March and; (c) Sea level pressure (SLP $5.0^{\circ} \times 5.0^{\circ}$) of November and December. Colored areas are statistically significant at a 90% level. Study area is indicated by a red square. Niño 3.4 region is indicated by a black rectangle.

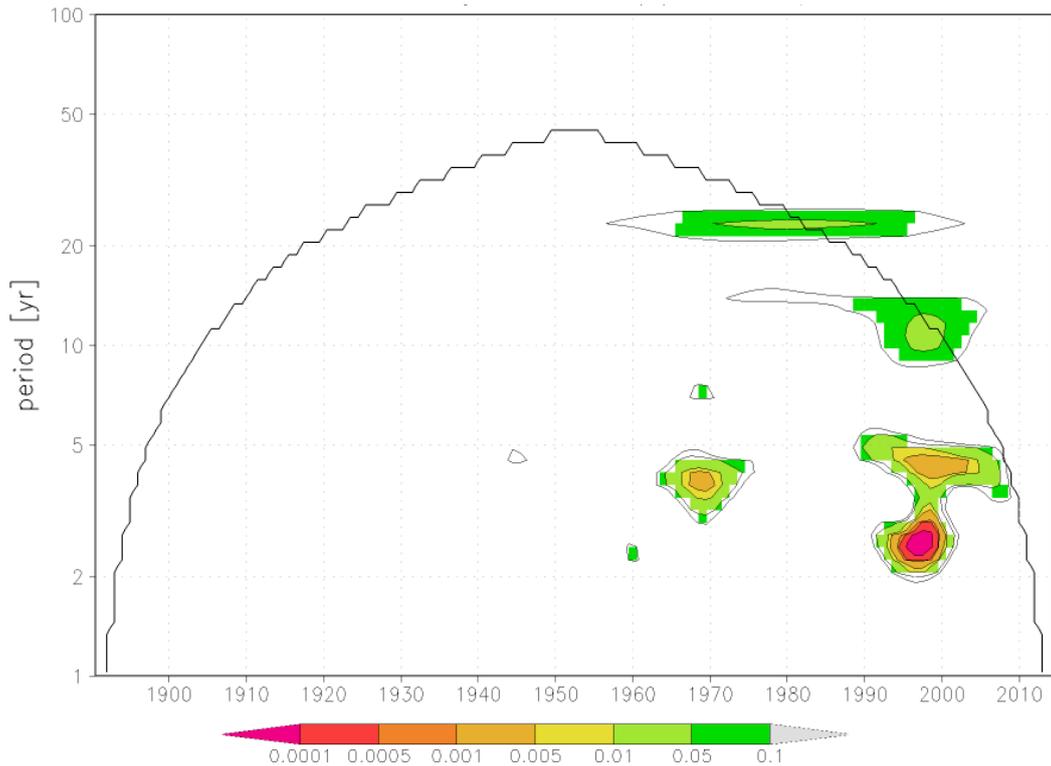


Figure 10 - The wavelet power spectrum. The contour levels were chosen at P -value < 0.1 . The cross-hatched region is the cone of influence, where zero padding has reduced the variance.

3.4 Discussion

3.4.1 Climate signals from tree-ring chronologies of *Nothofagus macrocarpa*

Our results demonstrate that radial growth of *Nothofagus macrocarpa* is sensitive to local and regional (to global) climatic variability. We found a decrease on tree-growth for this endemic and threatened forest, particularly from 1980 to present (Fig 4a). The decreasing growing trend resembled tendencies in winter-spring precipitation (Fig 6a) and late-spring/early-summer temperatures for the same time period in central Chile (Fig 6b).

The large proportion of common inter-annual variations in tree growth along the geographic distribution of *N. macrocarpa* (i.e. high percentage of common variance associated with the first principal component) reflects the regional influence of climate variability of central Chile on radial growth (Fig. S4). Accordingly, studied *N. macrocarpa* populations had comparable responses to climate. On one hand, winter and early spring rainfalls promotes tree growth in *N. macrocarpa* populations (Fig. 3, 5a) indicating a strong dependence of tree growth to soil water content. On the other hand, warm temperature constrained tree growth (Fig. 5a). We interpret this result as a negative response of tree growth to dry conditions during the growing season (see also Fig. S1, October to December). An increase in temperature during the growing season would promotes an increase in evapotranspiration, causing a decrease of tree growth in Mediterranean forest, mainly in species local dry edge, according growth projections under scenarios of global climate change (Gea-Izquierdo et al. 2013). This rising temperature would affect the physiology of plants, where trees would close their stomata to avoid excessive water loss, with a consequent reduction in CO_2 assimilation and less biomass production (Linares and Camarero 2012; Granda et al. 2014).

Such cross interaction between winter-spring precipitation and spring-summer temperature has been observed for other tree species within Chilean Mediterranean-type ecosystems both in northern and southern edge

of central Chile, such as *Austrocedrus chilensis*, *Kageneckia angustifolia*, *Pronstia cuneifolia* and *Fabiana imbricate* (Le Quesne et al. 2006; Barichivich et al. 2009; Christie et al. 2011; Urrutia et al. 2011). Therefore, these increased drought conditions have become important along the geographic distribution of *N. macrocarpa* in recent decades compared with previous centuries (Christie et al. 2011; González-Reyes 2016; Garreaud et al. 2017), a tendency that is significantly expressed in our study since 1980 (Fig. 2a), with consistent climate-growth relationship (Fig. 5c, d; 6a,b). In other Mediterranean regions was observed a similar climatic trend since the early 1970-1980s, with drier condition caused by enhanced temperature without increasing precipitation, that negatively affect the tree growth of endemic species, both of broadleaved and coniferous trees (e.g. Gea-Izquierdo et al., 2014; Gea-Izquierdo and Cañellas, 2014; Sarris et al., 2011). Based on our results and literature, we propose that water supply stresses and heat will exacerbate growth decline in *N. macrocarpa* trees if these climate trends continue in the future.

3.4.2 Impacts of drought conditions on tree-growth

The observed climate-growth relationships suggest that that drought events are the most proximate cause of years with lowest radial growth (negative pointer years) in forest of central Chile, since they have affected broadleaved (*N. macrocarpa*, our study) and coniferous trees (*Austrocedrus chilensis*, Le Quesne et al., 2006). For example, the severe droughts events occurring in 1968, 1996, and 1998 induced strong restrictions to radial growth in two species. Therefore, an increased drought conditions in central Chile would be impacting forest growth at both the Coastal and Andes mountain ranges. Moreover, a significant rainfall decline has been registered in central Chile since 2010 to date, which has decreased water reservoirs and increased the risk of wildfire hazards, among other effects (Garreaud et al. 2017). This last, long-lasting drought event has no precedents in local records and contributes to a drying trend in the region driven by climatic and anthropogenic change (Boisier et al. 2016).

Our results on declining growth rates are in line with findings from other temperate and Mediterranean regions with similar increases in extreme drought episodes during the last few decades. For example, the outstanding extreme heat wave and consequent drought experienced in 2003 produced extensive tree mortality and forest decline of tree species in different parts of Europe (Bréda et al. 2006; Venetier et al. 2007; Galiano et al. 2010; Rigling et al. 2013). Moreover, several forests across America have experienced extensive disease and mortality coincidently with droughts episodes during the 20th-century (Bigler et al. 2007; Negron et al. 2009). On the other side of the Andes (Argentina), it was observed negative influence of droughts to forest growth both broadleaved (*Nothofagus pumilio*) (Lavergne et al. 2015; Rodríguez-Catón et al. 2016) and conifer trees species (*Austrocedrus chilensis*) (Mundo et al. 2010) in northern Patagonia.

However, tree vulnerability to drought depends on a large number of physiological, genetic and adaptive factors, which are not yet fully understood in current scenarios of climate change (Franklin et al. 1987; Allen et al. 2015). The latter is particularly true for *Nothofagus macrocarpa* forests, thus future research addressing mortality caused by ongoing drought conditions in the region is necessary to understand ecological resilience of these forests to climate change.

3.4.3 Response of *Nothofagus macrocarpa* to large-scale climatic variability

Radial growth of *Nothofagus macrocarpa* was sensitive to the inter-annual climate variability in central Chile, which is influenced by two outstanding modes represented by El Niño-Southern Oscillation (ENSO) and the Antarctic Oscillation (AAO) (Garreaud et al. 2009). In central Chile (30-35°S), above-average precipitation in winter (June to August) coincides with El Niño episodes, while opposite rainfall anomalies are characteristic during La Niña

events (Quintana 2000; Montecinos and Aceituno 2003). In our study, we found a positive correlation between the SST anomalies of El Niño3.4 during the austral winter-spring seasons (July to November) and *N. macrocarpa* tree ring chronology (Fig. 5b, 7b). This result suggests that radial growth increases during El Niño episodes confirming other studies in the Mediterranean-subtropical forests of Chile (Christie et al. 2011; Muñoz et al. 2016). Thompson *et al.* (2011) suggested a dominance of a summer positive Antarctic oscillation (AAO) phase for the period 1950-2000 that may partially explain the observed downward trend in annual precipitation and temperature increase for central Chile, which caused a reduction in the frequency of wet days and intensity of precipitation (Garreaud et al. 2009; Quintana and Aceituno 2012). We found a strong and negative correlation between *N. macrocarpa* tree-ring chronologies and AAO during November-December (austral summer, Fig. 5b). Therefore, positive phases of AAO during summer would cause a rising temperature in December (warmer early-summer) and reduce precipitation in June (a declining trend of rainiest month), affecting negatively the tree growth in central Chile. This result is in line with other studies that showed the indirect influence of AAO on radial growth in temperate and Mediterranean-type forests from South America (Christie et al. 2011; Villalba et al. 2012; Álvarez et al. 2015; Lara et al. 2015)..

We observed stronger correlations since 1980 between radial growth of *N. macrocarpa* and MEI and AAO (Fig. 4d). This change in correlation strength is consistent for both in SST (Equatorial region) and SLP (Antarctic region) data (Fig. 7b,c). Furthermore, the spectral analysis of our regional tree-ring chronology showed a mean significant oscillatory mode around 4.3 years (Fig. 8) mimicking the oscillatory mode detected for the El Niño3 SST time series (Torrence & Compo, 1997). This high-frequency domain has also been detected in other tree species of the Mediterranean region of southern South America (Barichivich et al. 2009; Le Quesne et al. 2009; Christie et al. 2011; Álvarez et al. 2015), revealing a non-stationary periodicity at sub-decadal level. Wavelet power spectrum analysis (Fig. 8) confirmed that the spectral power at interannual time scales is more pronounced for the time period 1990-2010, possibly linked to 1997-98 ENSO event. Also, it was found teleconnections of atmospheric circulations patterns with tree growth in European Mediterranean-type species. Dorado-Liñan et al. (2017) and Camisón et al. (2016) found a general reduction of tree growth in populations of broadleaved (*Quercus spp.*, *Fagus sylvatica* and *Castanea sativa*) and coniferous trees (*Pinus spp.*) since 1970-1980s, that is linked to rising dry conditions during the growing season, being summer temperature linked to strengthening of Summer North Atlantic Oscillation and early-spring temperature related to negative phases of Western Mediterranean Oscillation, whereas Rozas et al. (2015) showed a significant positive association between tree growth of *Fagus sylvatica* over Northern Iberian Peninsula (transition between Eurosiberian and Mediterranean regions) and Niño 3.4 index. Therefore, the tree growth of Mediterranean-type ecosystems of the world depend indirectly of global atmospheric circulations patterns. It is predicted that more frequent La Niña events will occur by year 2100 (Cai et al. 2015) causing frequent and increased drought events in central Chile. Furthermore, in central Chile, global and regional climate models predict a reduction of rainfall for the 21st century under a business-as-usual scenario (Quintana and Aceituno 2012).

3.5 Conclusion

Here, we reported the climatic sensitivity of *Nothofagus macrocarpa*, an endemic tree species of broad-leaved Mediterranean-type forests in southern South America, with relictual distribution and the northernmost representative of the *Nothofagus* genus. Our results strongly suggest that radial growth of *N. macrocarpa* is sensitive to local and large-scale (i.e. regional to global) climatic variability, mainly for the period 1980-2014. We detected a significant decrease in radial growth during the last three decades related to a rainfall decline and temperature

increase registered in central Chile (increased drought conditions), and changes in high-frequency climatic oscillations (ENSO and AAO) that would be affecting indirectly the growth dynamic of Mediterranean-type forests in central Chile. This result is comparable to responses of Mediterranean-type forests in the Northern Hemisphere showing significant tree growth declines attributed to drought/heat stress, and thus contribute to climate change impact assessment on the Mediterranean-type forests biome.

According to our results, predicted climate conditions for this century would affect the growth of *Nothofagus macrocarpa* forests and can represent a major threat for the survival of these endemic, relict and endangered forest ecosystems, although their populations are protected (i.e. park, reserve or sanctuary). Therefore, increased drought conditions in the future could cause a growth decline in northernmost *Nothofagus* populations from South America. We based this conclusion on 1) *N. macrocarpa* growth decline following recent changes in the local and global climatic variability, and 2) its restricted geographic distribution found in a region with high human pressure. In order to assess forest persistence, further research is needed on the impact of climate change on mortality, recruitment patterns and genetic variability of these Mediterranean-type forests.

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4 WORRYING GROWTH RESPONSE TO CLIMATE CHANGE IN MEDITERRANEAN FOREST OF CENTRAL CHILE: EVIDENCE FROM YOUNGER, MATURER AND OLDER TREES *NOTHOFAGUS MACROCARPA*

Abstract

Forest play an important role in water and carbon cycles by means as regulators of hydric balance and large carbon pools, mainly in more arid regions such as Mediterranean ecosystem. Therefore, understanding Mediterranean forest responses to atmospheric changes (temperature, precipitation, CO₂ concentration) become important. CO₂ fertilization on tree growth is still unknown in Mediterranean deciduous forests of central Chile (MDFC). Here, we investigated the influence of precipitation, temperature and CO₂ concentrations on tree growth of *Nothofagus macrocarpa*, one of the most important species of MDFC. We sampled *N. macrocarpa* trees in ten sites covering its whole geographic distribution, which covers the entire latitudinal distribution of MDFC, both in Coastal and Andes range, central Chile (32°57'- 34°51'S/ 71°07'- 70°40'W). We used standard dendrochronological methods to (i) sites grouping by principal component analysis and separate by age class (younger, maturer and older trees); (ii) identify growth trends by piecewise regression of ring width and detrended basal area increment (BAI); and (iii) analyze the link between BAI and CO₂, precipitation and temperature by linear mixed-effects models. Piecewise regression model showed a break point from 1980, approximately, in Andes chronologies (Andes) and Coastal chronologies most intervened (Coastal); whereas sites with lower intervention did not show negative trends (Highest). However, BAI showed significant negative trends in all populations for the period 2000-2014, which seems to be related to decline precipitations and the increase of the temperatures in the last 15 years in *Nothofagus macrocarpa* forest. Overall, we did not found effects of rising CO₂ on BAI. We concluded that younger, maturer and older trees is being strongly affected by recent climate change in the central Chile – decreasing precipitation and increasing temperature –, and we did not observed a positive influence of rising CO₂ on stem biomass. *Synthesis.* Our results evidence that CO₂ fertilization does not compensate the regional warming and declining precipitation both in younger and older trees *Nothofagus macrocarpa* forest. Considering the worrying scenario for the future in central Chile, we expect these forests to continue declining, even though they are protected.

Keywords: Dendroecology; Global change ecology; Mid-latitude Southern Hemispheres; Plant–climate interactions; Rising atmospheric CO₂ concentrations; Roble de Santiago; Tree growth

4.1 Introduction

Climate change is a concern at global, national, regional and local levels, so that in Neotropical countries possess enormous challenges for forests and people. In this sense, trees play an important role in water and carbon cycles by means as regulators of hydric balance and large carbon pools, taking up and emitting enormous amounts of H₂O and CO₂ annually (Pan et al. 2011). Therefore, understanding response and forest resilience to atmospheric changes (temperature, precipitation, CO₂ concentration) become important (Brienen et al 2012). After the industrial revolution (last decades of nineteenth century) the planet has experienced a strong increase in atmospheric CO₂, which is associated with the global warming (Stocker et al. 2013). However, the present atmospheric CO₂ is not enough to saturate the photosynthesis of the forests (Norby and Zak 2011). Therefore, future trends in forest growth will depend on the response and adaptation of trees to this CO₂ enrichment and global warming (Körner 2004).

Atmospheric CO₂ increased from 280 ppm (before industrial revolution) to 400 ppm in 2014 (Pachauri et al. 2014), which would be affecting the plants development – and an indirect effect of increased water use efficiency (iWUE) (Wullschlegler et al. 2002) – and inducing changes in forest ecosystems. Thus, we should logically expect to be able to detect and, therefore, predict increases in tree growth of forest ecosystems. In this sense, plants generally respond positively to the increase of CO₂ in some forest ecosystem of Europe and Asia (Bert et al. 1997; Battipaglia

et al. 2013; Chen et al. 2015), so it would be expected that the highest concentration of atmospheric CO₂ reduces the degree of stomatal opening necessary to capture a certain amount of atmospheric carbon, affecting the efficiency of the use of tree water (Srrur et al. 2008). It seems that iWUE in dry sites is improved and the growth is not so constrained by temperatures as in the wettest sites (Huang et al. 2007). However, recent studies postulate that this process of CO₂ fertilization will hardly compensate for the losses in forest growth caused by climate change and discuss that in some cases their effect will be null in the long term (Körner et al. 2005). The consideration of ontogeny is also critical to detect any CO₂ fertilization effect on forest growth (Camarero et al. 2015a), i.e. growth trends are – at least partially – driven by underlying age distributions (Brienen et al. 2016). Therefore, it is still controversial whether this greater supply of CO₂ actually produces more forest biomass (Körner 2004; van der Sleen et al. 2015).

Recent articles have shown that long-term trends vary with stand age, which also affected the responses to climate temperature, precipitation and CO₂ (Camarero et al., 2015a; Konter et al., 2016; Pompa-García & Hadad, 2016). The ecophysiological processes that influence on tree growth change with age (Hinckley *et al.*, 2011), being the hydraulic limitation one of the main physiological variable that explains why there is difference in the sensitivity of trees to climate in different age class (e.g. Carrer & Urbinati, 2006; Yu et al., 2008; Pompa-García & Hadad, 2016).

Within the most threatened forest ecosystems by climate changes around the world there are the Mediterranean-type environments (Allen et al. 2010). In this sense, Chilean Mediterranean vegetation is of great interest worldwide due to its high diversity of species and life forms, as well as its high levels of endemism (Myers et al. 2000). Central Chile is characterized by a narrow valley between two great mountain cordilleras, Coastal and Andes range, with a Mediterranean-type climate of winter rainfall and summer drought (Le Quesne et al. 2006). Therefore, the geographic, geological and climatic characteristics of this region have been the cause of the development of large amount of endemic vegetation (Luebert and Plischoff 2006). Within this ecosystem are the Mediterranean deciduous forests of central Chile (MDFC), being the *Nothofagus macrocarpa* [(DC.) Vásquez et Rodr.] forest the most important (e.g. Donoso, 1982; Donoso et al., 2010). The distribution of *N. macrocarpa* covers approximately the latitudinal distribution of MDFC (Amigo and Rodríguez-Guitián, 2011). This species are emblematic and endemic from central Chile that is threatened and represents the northernmost *Nothofagus* populations in America (Vázquez and Rodríguez 1999; Gajardo 2001). This endemic forest is a relic of last glaciation period (Villagrán 1995; Luebert and Plischoff 2006). This situation is due to the particular evolutionary history of its flora, characterized by the coexistence of elements of tropical, subtropical and subantarctic origin, products of geological and climatic changes that affected the territory during the Tertiary (Villagrán 1995). In addition, the repeated cycles of expansion and isolation of the Andean flora, as a result of the climatic changes associated with the quaternary glaciations, have influenced the distribution of the current vegetation and floristic discontinuities between both ranges (Villagrán and Armesto 2005).

The effects of climate change in central Chile have been evident during the last century (Carrasco et al. 2005; Le Quesne et al. 2006; Garreaud et al. 2009; Christie et al. 2011). Was observed a reduction in precipitation from 1850s, in combination with a significant warming, which caused current glacier retreats in this region (Le Quesne et al. 2009). While it is expected that in the next 100 years the temperature will increase in about 3–4°C and precipitation will decrease in about 10–30% in central Chile, specifically in latitude ~ 30°S (Vicuña et al. 2011). Moreover, this region has suffered great environment degradation due to anthropogenic factors, such as urban and agricultural expansion, cattle grazing, logging for firewood, and introduction of invasive species, still persist

throughout the region (Schulz et al. 2010). The Coastal range is most affected by being near the big cities (Villagrán and Armesto 2005). Therefore, there is a substantial decrease in the biological productivity of the land system as a result of human activities and global climate change, which would endanger the natural dynamics of the endemic flora and ecological balance of central Chile.

Nothofagus spp has demonstrated an excellent potential for retrospective analysis of the effect of the anthropogenic and climatic change in forests of south-central Chile and Argentina (Roig and Villalba 2008; Boninsegna et al. 2009). However, tree-rings response to increasing atmospheric CO₂ concentration, regional warming and precipitation patterns changes are poorly studied in *Nothofagus macrocarpa* forest (and hence in Mediterranean deciduous forests of central Chile). Here, we evaluate a network of 10 chronologies of tree-ring *N. macrocarpa* from northern limit in Coastal range and southern limit in Andes range (whole natural geographical distribution), analyzing their growth trends associated with CO₂ fertilization and recent changes in precipitation and temperature variability, considering different age class. Our hypotheses are: (i) *N. macrocarpa* populations from Andes range (wet site) would have a greater decline growth linked to climate change than dry sites, since Coastal populations would have an iWUE improved; it is based on the theory that in dry sites there is a positive effect of CO₂ fertilization on forest growth (Huang et al. 2007). (ii) However, most of the *N. macrocarpa* populations from Coastal range are disturbed, except in “Altos Cantillana hill” (Villagrán 1995; Gajardo 2001), so that this populations would have better resilience to the climatic change than others. (iii) Overall, younger trees are more sensitive to climate than older trees; considering that younger trees would use better of resource availability (Korner 2006) and vegetation period of older trees appear to be shorter, since these trees are well established (Rossi et al. 2008).

4.2 Materials and Methods

4.2.1 Study area and *N. macrocarpa* populations

The study area is located in Central Chile (32°57' to 34°51'S, and 71°07' to 70°40'W) (Fig.1, Table 1), with typical Mediterranean climate characterized by a rainy winter (June to July) and a long dry summer (December to March). The climate from the populations of Coastal range is drier than from the Andes range ones. The inter-annual rainfall in this region is highly variable and very influenced by the ENSO, with warm (cold) events in central equatorial Pacific associated with wet (dry) conditions in central Chile (Montecinos and Aceituno 2003). Along the Andean range, soils are developed from volcanic or granitic rocks and from glacial sediments, and classified in the large group of forest brown soils, with a medium depth in slopes and deep in the high plains (Villagrán, 1995). While along the Coastal range, soils are formed from granitic rocks in the Cordillera heights of the northern coast of this region and are poorly developed, usually residual on rocky outcrops (Donoso, 1982).

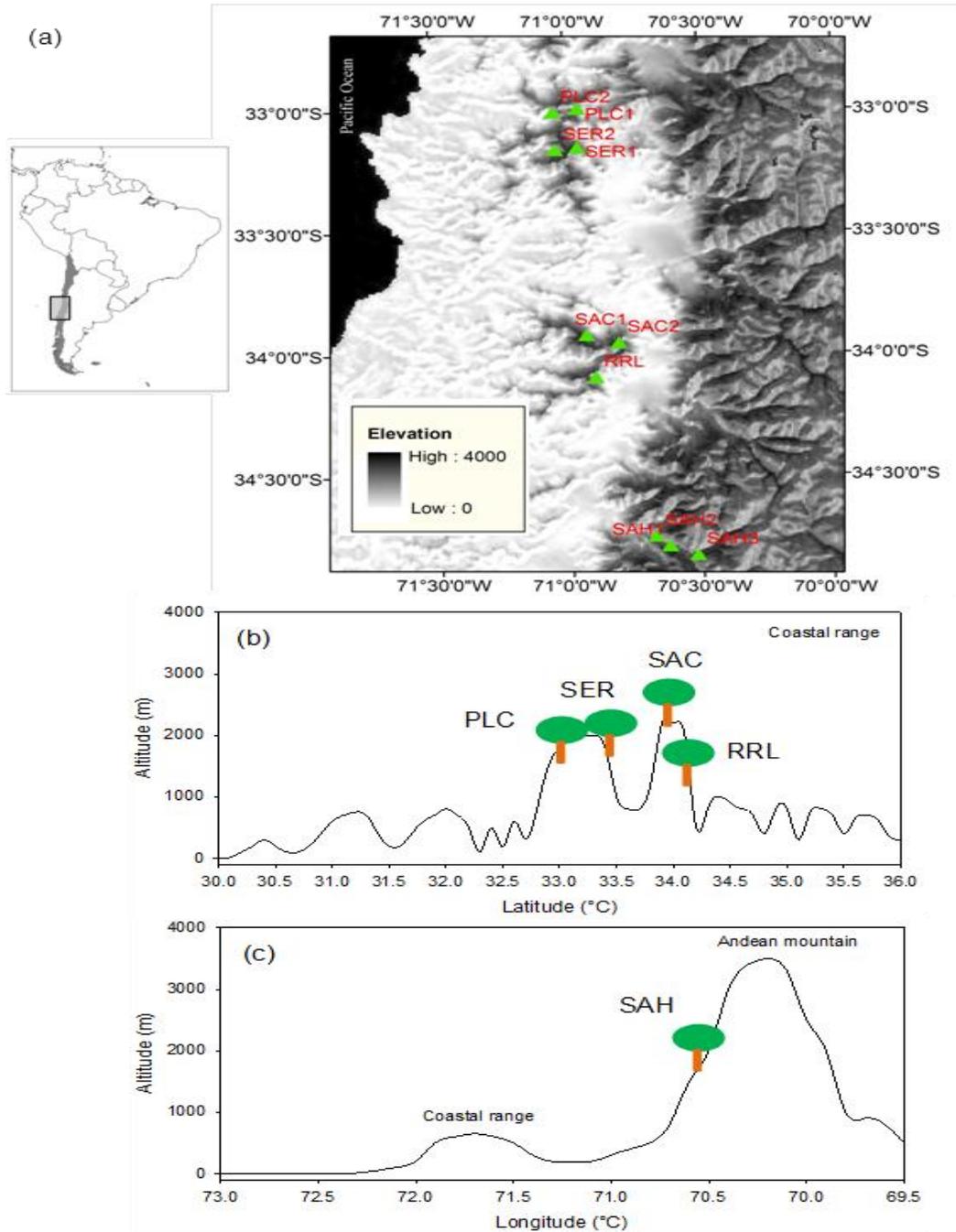


Figure 1 - (a) Study area of *N. macrocarpa* populations sampled in this work. The populations represent the whole natural geographical distribution of *N. macrocarpa* (Amigo & Rodríguez-Guitán 2011). (b) Sites of Coastal range (PLC, SER, SAC and RRL). (c) Site of Andes range (SAH).

Table 1- Description sites and trees sampled in each *N. macrocarpa* populations studied.

Range	TPWA ^a	YSP ^e	Site	Code	Elev. (masl)	No. trees ^b (chron.)	DBH \pm SE ^c	DPR ^d	TGC ^f	Inter. ^g
Coastal	National park	1967	La Campana 1	PLC1	1,350	15(15)	23.5 \pm 0.7	10	1	High
			La Campana 2	PLC2	1,210	15(14)	32.1 \pm 3.1	7	1	High
	Nature Sanctuary	2000	El Roble 1	SER1	1,590	15(15)	41.6 \pm 3.63	6	1	Medium
			El Roble 2	SER2	1,600	15(14)	29.6 \pm 1.2	5	1	High
	Nature Sanctuary	2010	Altos Cantillana 1	SAC1	1,810	15(13)	43.7 \pm 5.4	*	9	Low
			Altos Cantillana 2	SAC2	1,790	12(11)	51.4 \pm 4.5	*	9	Low
National reserve	1996	Robleria Loncha	RRL	1,090	24(23)	35.4 \pm 2.0	28	2	Medium	
Andes	Nature Sanctuary	1996	Alto Huemul 1	SAH1	1,500	20(18)	51.8 \pm 10.5	50	4	Low
			Alto Huemul 2	SAH2	1,600	14(13)	50.0 \pm 4.2	53	4	Low
			Alto Huemul 3	SAH3	1,550	10(10)	37.7 \pm 4.7	47	4	Medium

^a Type of protected wilderness area. ^a Number of trees sampled (number of trees considered in the chronology). ^b Diameter at breast height \pm standard error (cm). ^c Distance to a paved road in 2015 (km). * There is not a near dirt road, so we got on horse and it took us 8 hours to reach the *N. macrocarpa* populations. ^e Year of site protection. ^f Approximate time to get to the site of the regional capital (hr). PLC is Valparaiso; SER and SAC is Santiago; RRL and SAH is Rancagua. ^g Forest intervened (high, medium, low).

The biogeographic action exerted by the Andes mountain range in MDFC, with higher elevations in these latitudes, it has hampered the migrational dynamic of species (Villagrán 1995; Villagrán and Armesto 2005). This region has shown evidence of dynamics interactions of geomorphologic and climatic phenomena post glacial period, with frequency of cataclysm success, volcanic eruptions and alluviums, which would also be associated with the distribution patterns of the flora. While the Coastal range is characterized by islands of vegetation on top of the hills with high Andean flora (Villagrán and Armesto 2005). These vegetations would have been separated from the Andes populations due to the climatic changes that characterized the last glacial-interglacial cycle during the last hundred thousand years in central Chile (Villagrán 1995). This hypothesis is supported by the phytogeographic features of the hills El Roble, La Campana and Altos Cantillana (Villagrán and Armesto 2005).

We selected *N. macrocarpa* trees from Mediterranean deciduous forests of central Chile, commonly called “Roble de Santiago”. These trees have deciduous leaves, reaching 25m of height and > 60cm of diameter at breast height (DBH) (Gajardo 2001). The structure of *N. macrocarpa* formations usually includes a high arboreal stratum (over 16m) of scattered individuals, remnants of an anterior structure that was probably intervened by fire or logging. Under this stratus the dominant structure is established, an average arboreal floor (8-16m) of this same species, this depending on the environmental situation can reach 50-75% of coverage. In situations where there are lower densities of crowns, it is possible to distinguish a sclerophyllous shrubs stratus (1-2 m), highly variable in density and composition according to the altitudinal range (until 1000m). The tree growth is mainly sensitive to favorable moisture conditions from May to December (Table 2).

Table 2 - Descriptive statistics for the ten chronologies of *N. macrocarpa* considered (see Table 1 for chronology code definitions)

Code ^a	Record period ^b	Raw data		Residual chronologies		
		Mean sens. ^c	AR1 ^d	RBar \pm SE ^e	EPS ^f	SPEI ^g
PLC1	1929-2014	0.421	0.617	0.33 \pm 0,01	0.96	0.67
PLC2	1925-2014	0.490	0.599	0.30 \pm 0,02	0.94	0.68
SER1	1921-2014	0.482	0.561	0.42 \pm 0,01	0.93	0.38
SER2	1938-2014	0.527	0.400	0.40 \pm 0,01	0.95	0.47
SAC1	1837-2014	0.432	0.468	0.33 \pm 0,01	0.93	0.42
SAC2	1840-2014	0.513	0.480	0.28 \pm 0,02	0.92	0.44
RRL	1890-2014	0.401	0.537	0.25 \pm 0,01	0.95	0.53
SAH1	1851-2014	0.363	0.657	0.24 \pm 0,02	0.93	0.22
SAH2	1832-2014	0.395	0.569	0.27 \pm 0,01	0.92	0.41
SAH3	1910-2014	0.411	0.553	0.38 \pm 0,02	0.92	0.27

^a Localization of distribution region of *Nothofagus macrocarpa*. ^b Chronology time span considering at least five trees. ^c Mean sensitivity. ^d First-order autocorrelation. ^e Mean correlation coefficient between all the possible combinations of tree-ring series (radii) in the chronology. ^f First-order autocorrelation. ^g Correlations analysis between residual chronologies and mean SPEI index (calculated at 1-month scale) from May to December, except to SER2 that was significant from May to November. All correlations were performed for common period (1938-2014) and were significant at 95% confidence level.

4.2.2 Characteristics of *N. macrocarpa* populations and tree-rings analysis

Five populations of *Nothofagus macrocarpa* were sampled, four in Coastal and one in Andean range, and were selected to reach the entire species distribution (Fig. 2, Table 1), which represents the northernmost distribution of the genus in America (Gajardo 2001). In each population were sampled two or three sampling sites, with the exception of Robleria del Cobre de Loncha where one site was sampled, in April-May 2015 (Table 1). Most sampling sites are currently protected at different degrees, since they are (Park, Reserve or Sanctuary) in priority areas for flora and fauna conservation. However, this protection status is very recent and most of the forest is disturbed by human activity. We categorize the forests of the different sampling sites according to DBH, distance to a paved road (DPR) and approximate time to get to the site of the regional capital (TGC). We considered as high intervened forest if sites has trees with DBH <30 cm of, DPR <10 km and ATG < 1 hour. This classification helped to interpret the cluster grouping (see below).

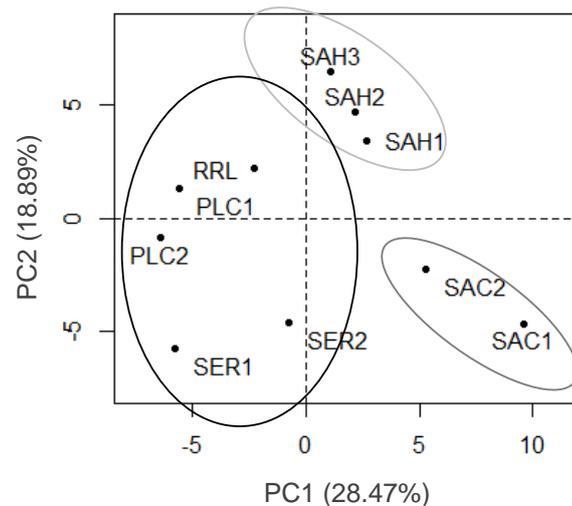


Figure 2 - (a) Relative positions of 10 residual chronologies of *N. macrocarpa* according to the two principal components for the period 1938-2014. Circles represent 95% confidence intervals of population groupings. We defined the clusters as Coastal (black), Highest (gray light) and Andes (gray) populations. Percentages by axes indicate how much variation is explained by the principal components.

An average of 15 trees were sampled in 0.5–1 ha areas by sampling site. We did a random sampling of trees with the aim of include individuals of different age and size (Nehrbass-Ahles et al. 2014). Two-three cores per trees were taken at 1.3m from each tree using a Pressler increment borer. Cores were prepared and cross-dated using classic methods of dendrochronology (Stokes and Smiley 1968). Cross-dating and measurement accuracy were checked with the program COFECHA, which calculates cross correlations between individual series of each core and a master chronology (Holmes et al. 1986a).

Ring width measurements were detrended to remove the biological age trend of individual trees and any other non-climate-related growth variation. We used a negative exponential or a linear regression of any slope, which allow to preserves common interdecadal and lower frequency variations. We used the residual chronology in order to prewhitened the standardized series and remove their autocorrelation (Table 2). To verify the quality of ring-width chronologies, we calculated the mean sensitivity (MS), which represents the change of mean percentage of year-to-year growth variability; RBar, which indicates the mean correlation coefficient for all possible pairings of ring width series over a common time; and the first order autocorrelation of tree-ring width series (AC1).

Principal components analysis (PCA) of the ring-width index, of 77 years of common period (1938-2014), were used to identify common modes of variability in annual radial growth, and allowed the order and classification of chronology sites (clusters). Hierarchical Clustering on Principle Components (HCPC) were used to identify the number of clusters, which were chosen visually from the hierarchical tree and were based on the increase of inertia (Husson et al. 2016). HCPC function makes use of Euclidean distances to define the distance between individuals, Ward's agglomeration method and 95% confidence interval to construct the hierarchical tree. We performed the HCPC with functions from package 'FactoMineR'. We observed three specific clusters, which were called 'Coastal' (PLC1-PLC2-SER1-SER2-RRL), 'Highest' (SAC1-SAC2) and 'Andes' (SAH1-SAH2-SAH3) (Fig.2), which would be correlated to forest types and more or less intervention (Table 1).

4.2.3 Tree-growth patterns

Tree growth was converted to basal area increment (BAI) according to the equation: $BAI = \pi(r_t^2 - r_{t-1}^2)$, where r_t and r_{t-1} corresponds to tree radius at DBH calculated at the end and beginning of annual increment in years t , respectively (Biondi and Qeadan 2008). BAI is recommended to represent individual and stand-level changes (Biondi and Qeadan 2008; Camarero et al. 2015b; Girardin et al. 2016). Annual basal area increments (BAI) for each tree were estimated from raw ring-width series using R package `dplR` (Bunn 2008).

In the cases of cores without pith, we used a geometric correction to estimate the number of missed rings and adjust the inner-ring date, i.e. pith was estimated by fitting a template of concentric circles with known radii to the curve of the innermost rings (Duncan 1989). In those trees in which the central core section could not be estimated because the innermost rings did not curve (last rings are parallels), we estimated missing rings with a model based on DBH of that trees without bark. For that, we took at least 10 trees in the sites with samples that crossed the tree, have both bark (two radius), and calculated the average (y). Then, the diameter (without bark) measured in field was divided by two (x). Subsequently, a linear regression was made between the radius x and y (i.e. $y = ax + b$). In radius without pith, we subtracted $x - y = z$, and z was divided by the number of rings in distance z from innermost (i.e. if $x - y = 5\text{cm}$, it lack 5cm to pith, so all rings in 5cm from the innermost ring were counted). All the model had $R^2 > 0.75$ and $p < 0.001$. We consider a tolerance until $z = 10\text{cm}$, because above this value results could be biased. After calculating the missing rings to the pith, we estimated the cambial age (at 1.3m). We could not estimate missing rings to pith in 13 trees (SER = 2, SAC = 1, SAH = 10).

BAI were standardized to remove non-climatic and age-related trends, and thus ensure that measurements of individual trees with different annual growth rates are calculated on a robust estimation of the mean value function (Cook 1985). BAI measurements were detrended with ARSTAN software, using a cubic spline with a 50% frequency response cutoff equal to 67% of the series length and horizontal line equal to the series mean followed by autoregressive time series modelling (Cook 1985). These models eliminate the long-term trends in tree rings and provide a better representation of the high-frequency variations in tree growth (Rodriguez-Canton et al 2016). We used the detrended BAI due to young trees (<50 years) (Fig. 3), avoiding the problem of growth overestimation. Piecewise regression model of growth rate (mm yr^{-1}) were used to analyze significant changes in temporal trend, using the 'segmented' R package (Muggeo 2008). We applied this analysis on diameter growth data due to there was lesser data variability than basal area increment data, since our study had many younger trees (30% trees with recruitment after 1950), so the common period to BAI analysis is small and did not show a break point.

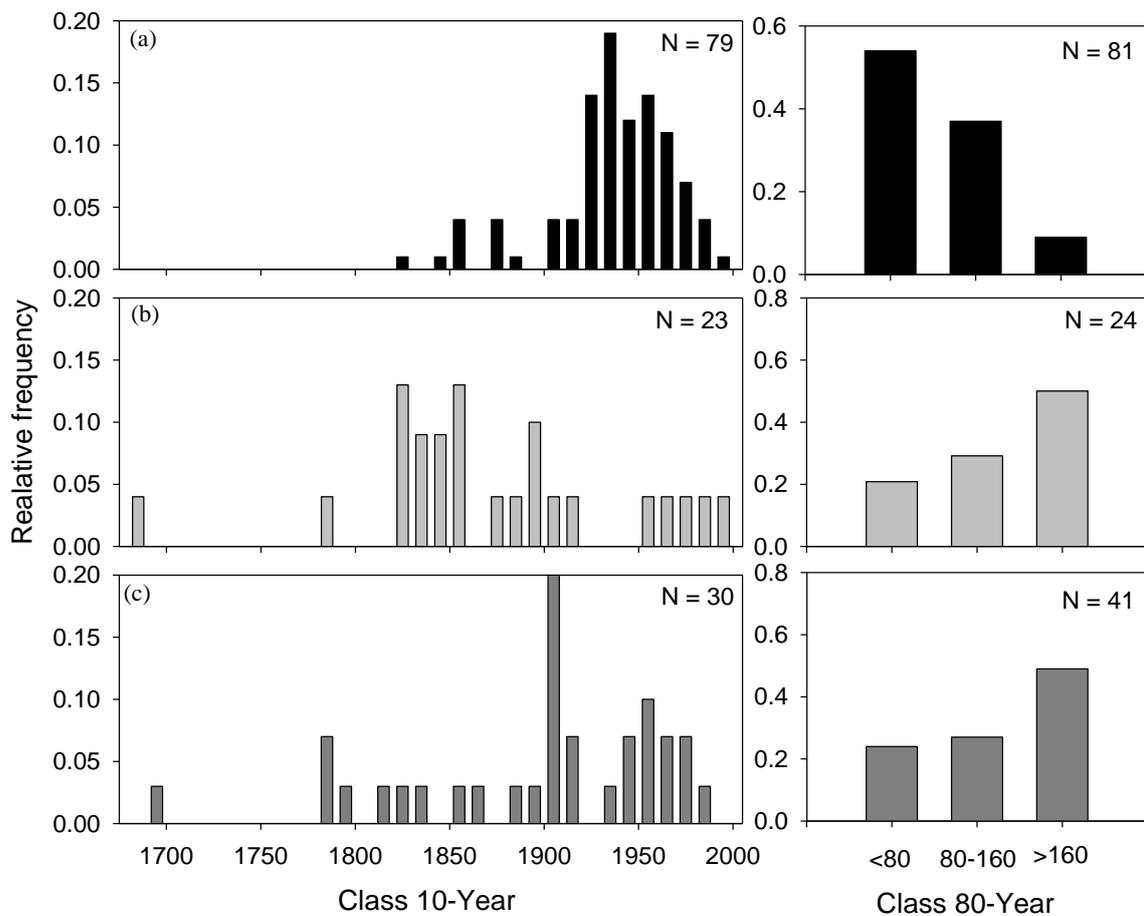


Figure 3 - Relative frequency of trees in the three populations (cluster) according three age class. (a) Coastal, (b) Highest, (c) Andes.

4.2.4 Avoiding ontogenetic problem

A biased sampling of big or fast-growing trees could produce spurious tree growth rates (Brienen et al. 2012). Therefore, it is important to sample coexisting trees of diverse sizes, growth rates and ages (Nehrbass-Ahles et al. 2014). We expect that BAI trends of *N. macrocarpa* and their climatic response varies with stand age. Thus, trees were classified in three age classes, younger trees (<80 years, which were established after 1935), maturer trees (80-160 years, which were established between 1855 and 1935) and older trees (>160 years, which were established before of 1855). Those age classes containing at least five trees by sites. The 13 trees without pith had been classified as older trees because they had at least 160 years or missing distance to pith higher than half the radius.

4.2.5 Effect of climate and CO₂ on tree growth

We used the CRU TS3.24 gridded datasets from the Royal Netherlands Meteorological Institute (<https://climexp.knmi.nl/>, accessed 5 December 2016) for precipitation and temperature, with 0.5° of spatial resolution for the period 1901-2014. Accumulated precipitation from May to November (P_{M-N}) and mean temperature from October to December (T_{O-D}) are the variables that explain better the growth variability in *N.*

macrocarpa (Venegas-González et al. *in press*). Annual atmospheric CO₂ values (C_a) were extracted from the Mauna Loa (Hawaii) observatory for the period 1958–2014 (<https://www.esrl.noaa.gov/gmd/ccgg/trends/>, accessed 10 December 2016).

We performed a multilevel linear mixed model to modelling the effect of climate and atmospheric CO₂ concentration on tree growth (BAI after removing non-climatic and age-related trends) considering a year-to-year variability over the period 1929–2014 by each cluster/age-class. The climatic variables P_{M-N}, T_{O-D} and C_a were considered as fixed effects of the model, while tree and year were treated as random effects to properly account for their random variability. We fitted the models using the ‘lme4’ R package with *lmer* function (Bates et al. 2014). To identify the best predictors that included combinations of one, two or three explanatory variables, we used an approach of multi-model inference (Bartoń 2013). This analysis shows the probability that a given model explains better the response variable than others (Burnham and Anderson 2002). This approach calculates the probability that a given model is more appropriate than others in explaining the response variable. Multi-model inference is being very used recently in dendroecology studies (e.g. Camarero et al., 2015a; Gazol et al., 2017). For each explanatory variable we calculated its relative importance, which is obtained by summing the Akaike weights of all models that include the predictor of interest and considering the number of models. Models were ranked according its second-order Akaike information criterion (AICc). We selected the two better models that had $\Delta\text{AICc} < 2$ (Burnham and Anderson 2002), i.e. the difference between AICc of each model and the minimum AICc found for all models. The relative weight of the best selected model is shown as probability (we only selected the best two models). The R package ‘MuMIn’ was used to perform the multi-model selection (Bartoń 2013). Piecewise regression model of the diameter growth rate (cm yr⁻¹) showed a break point from three last decades approximately (Fig. 4a). Therefore, our analysis was focused since the year 1980, where there was a significant decrease in precipitation and a significant increase of temperature and atmospheric CO₂ (significance level of 90%) (Fig. 4b).

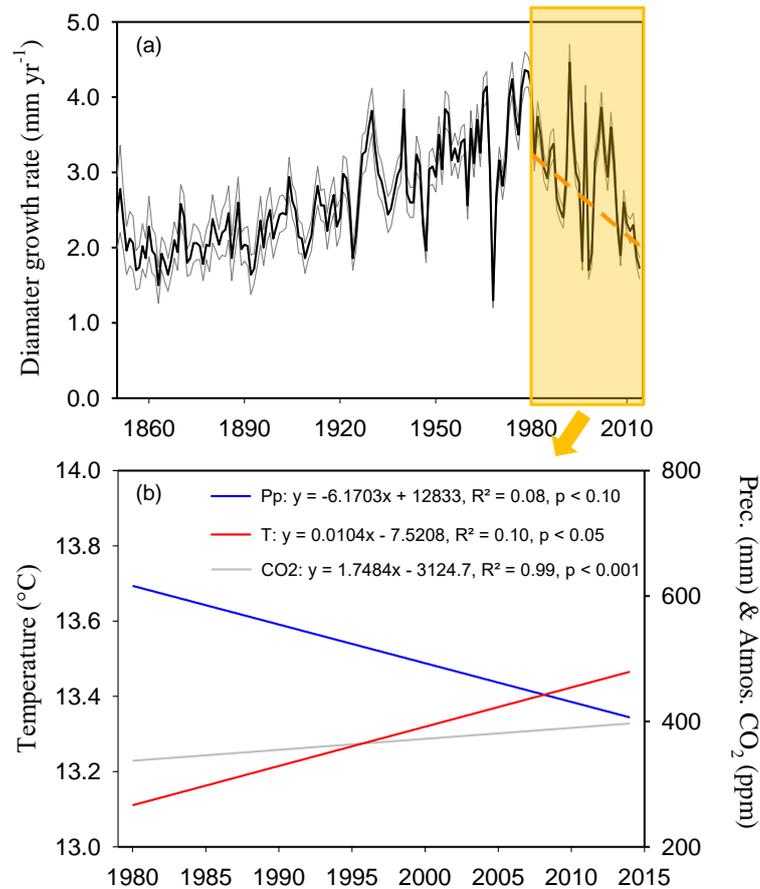


Figure 4 - (a) Mean diameter growth rate in mm yr⁻¹ (\pm SE in gray line) of regional chronology of *N. macrocarpa* populations (black line). Orange square represents the piecewise regression model that shows the break year from 1980 with $p < 0.001$. (b) Linear trends of climatic variables (precipitation [pp], temperature [T] and atmospheric CO₂ concentrations [CO₂]) to since 1980.

4.3 Results

Clustering analysis of annual radial growth of *N. macrocarpa* populations showed that the grouping would be associated with the intervention level of forest (Table 1). Coastal populations are more intervened and younger than Highest and Andes populations (Fig. 3, Table 2). In Coastal populations, 50% of the trees are approximately <80 years (younger), while in Highest and Andes populations 50% are older (>160 years) (Fig. 3). All populations showed a decreasing growth trend in the last decades, more accentuated in Coastal and Andes populations. This decreasing trend is caused by the break points, which began to be significant in 1979 in Coastal populations and in 1978 in Andes populations (Fig. 5a,c), coinciding with regional chronology, which had a break point in 1980 (Fig. 4a). Highest populations did not show significant break point (Fig. 5b).

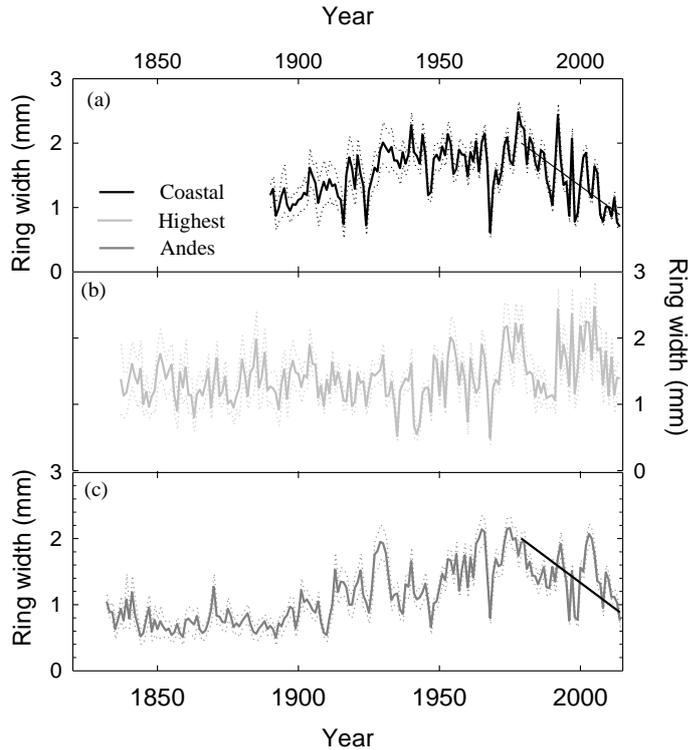


Figure 5 - Ring-width chronologies according population (cluster) grouping (a) Coastal, (b) Highest, (c) Andes. Shaded lines represent \pm SE. Black lines show the break year according piecewise regression model ($P < 0.001$), being from 1978 and 1979 to Andes and Coastal populations (Highest populations did not showed significant break point).

Long-term growth trends of BAI according cambial age have shown a forest decline in all populations in the three age classes (Fig. 6). Therefore, it seems that all populations show a decreasing growth in the last decades. However, there was a noticeable increase in the first 50 years of life in younger trees of Highest population, which was better than others trees (Fig. 6a). After 50 years, younger trees begin a growth decrease in Coastal and Highest populations, while older trees showed a decline from 150 years of cambial age in the tree populations (Fig. 6c). Maturer trees from Coastal and Highest populations had a growth increase since ~ 100 years, while in Andes populations showed a decrease growth since ~ 80 years (Fig. 6b).

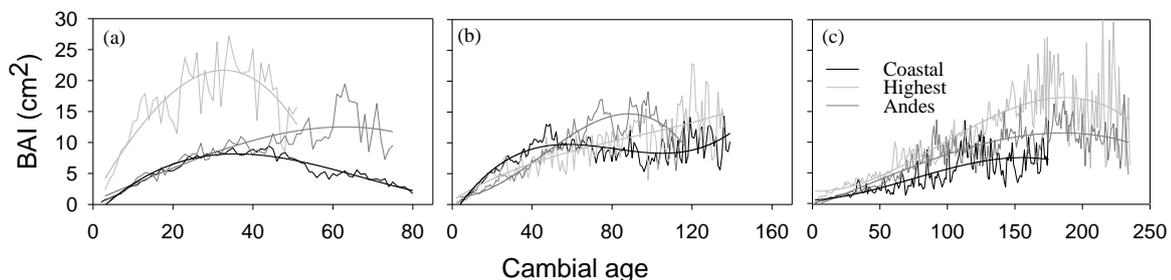


Figure 6 - Basal area increment ($\text{cm}^2 \text{yr}^{-1}$) of the three populations (cluster) according cambial age. (a) < 80 years, (b) 80-160 years, (c) > 160 years.

We observed a significant decline of BAI values by removing non-climatic and age-related trends after 1980, which decreased notoriously after the 21st-century (Table 3). For the period 1980-2014, we observed that only older trees from Coastal population showed negative trends, while maturer trees from Highest population were the

unique cluster that showed significant positive trends (considering all three analyzed periods (Table 3). However, in the last two decades the trends were maintained in older trees from Coastal population. For the period 1990-2014, we also observed negative trends in older trees from Andes and Coastal population (Table 3), and for the last analyzed period (2000-2014) all populations showed a forest significant decline (Table 3, Fig. 7).

Table 3 - Linear mixed-effects models represent the influence of climatic variables (precipitation, temperature, CO₂) on detrended basal area increment (BAI) for the three periods (1980-2014, 1990-2014 and 2000-2014), according population (cluster) grouping and age class. Grey cells show significant negative effects of CO₂ on BAI (*<0.05, **<0.01; ***<0.001).

	Cluster	Age class	Trends	P	Jun-Dec	T	Oct-Dec	CO ₂ (3)	Best	two	Delta	Relative
				(1)	(2)	models	AIC	weight				
1980-2014	Coastal	<80	(-)	1.12e-03***	-2.12e-01***	-	1 – 1,2	0 – 1.12	0.64 – 0.36			
		80-160	(-)	1.00e-03***	-1.70e-01*	-1.00e-03	1,2,3 – 1,2	0 – 0.01	0.42 – 0.42			
		>160	(-)*	1.00e-03***	-	-5.05e-03**	1,3 – 1,2,3	0	0.68			
	Highest	<80	(-)	1.11e-03***	-1.22e-01	-	1 – 1,2	0 – 0.07	0.36 – 0.35			
		80-160	(+)*	8.91e-04***	-3.12e-02	-	1 – 1,2	0 – 0.60	0.41 – 0.31			
		>160	(-)	8.87e-04***	-3.09e-02	-	1 – 1,2	0 – 1.73	0.51 – 0.21			
	Andes	<80	(+)	4.88e-04***	-9.82e-02*	-3.82e-04	1,2 – 1,2,3	0 – 1.80	0.54 – 0.22			
		80-160	(-)	7.65e-04***	-2.24e-01***	-6.53e-04	1,2 – 1,2,3	0 – 1.76	0.71 – 0.29			
		>160	(-)	9.29e-04***	-1.93e-01***	-7.58e-04	1,2 – 1,2,3	0 – 1.74	0.70 – 0.29			
	1990-2014	Coastal	<80	(-)	1.16e-03***	-3.08e-01***	2.36e-03*	1,2,3	0	0.77		
			80-160	(+)	1.03e-02***	-2.22e-01***	2.55e-02*	1,2,3	0	0.97		
			>160	(-)*	9.70e-04***	-1.12e-01	-5.86e-03**	1,2,3 – 1,2	0 – 0.32	0.43 – 0.36		
Highest		<80	(-)	1.14e-03***	-	-3.27e-03	2 – 1,3	0 – 0.77	0.41 – 0.28			
		80-160	(+)	9.30e-04***	-	-	1	0	0.55			
		>160	(-)	9.77e-04***	-	-2.68e-03	1 – 1,3	0 – 0.05	0.32 – 0.32			
Andes		<80	(+)	4.95e-04***	-1.43e-01*	-9.42e-04	1,2 – 1,2,3	0 – 1.63	0.57 – 0.25			
		80-160	(-)	6.42e-04***	-2.87e-01***	-9.26e-04	1,2 – 1,2,3	0 – 1.86	0.72 – 0.28			
		>160	(-)*	9.04e-04***	-2.27e-01**	-2.25e-04	1,2 – 1,2,3	0 – 1.31	0.63 – 0.33			
2000-2014		Coastal	<80	(-)*	9.81e-04***	-2.94e-01***	-4.61e-03	1,2 – 1,2,3	0 – 1.12	0.64 – 0.36		
			80-160	(-)*	7.09e-04***	-1.88e-01*	-1.05e-03	1,2 – 1,2,3	0 – 1.92	0.59 – 0.23		
			>160	(-)*	5.27e-04*	-	-1.10e-02*	3 – 1,3	0 – 0.75	0.30 – 0.21		
	Highest	<80	(-)*	6.33e-04***	1.45e-01	-	1 – 1,2	0 – 0.64	0.42 – 0.30			
		80-160	(-)*	5.42e-04*	-	-1.39e-02	1 – 1,3	0 – 0.61	0.30 – 0.22			
		>160	(-)*	5.48e-04*	1.53e-01	-	1 – 1,2	0 – 0.15	0.29 – 0.27			
	Andes	<80	(-)*	7.63e-05	-2.27e-01*	-1.49e-02***	2,3 – 1,2,3	0 – 1.05	0.53 – 0.31			
		80-160	(-)*	2.90e-04	-3.76e-01**	-1.22e-02**	2,3 – 1,2,3	0 – 1.49	0.58 – 0.27			
		>160	(-)*	4.47e-04*	-2.79e-01*	-3.14e-02***	1,2,3 – 1,3	0 – 1.36	0.57 – 0.29			

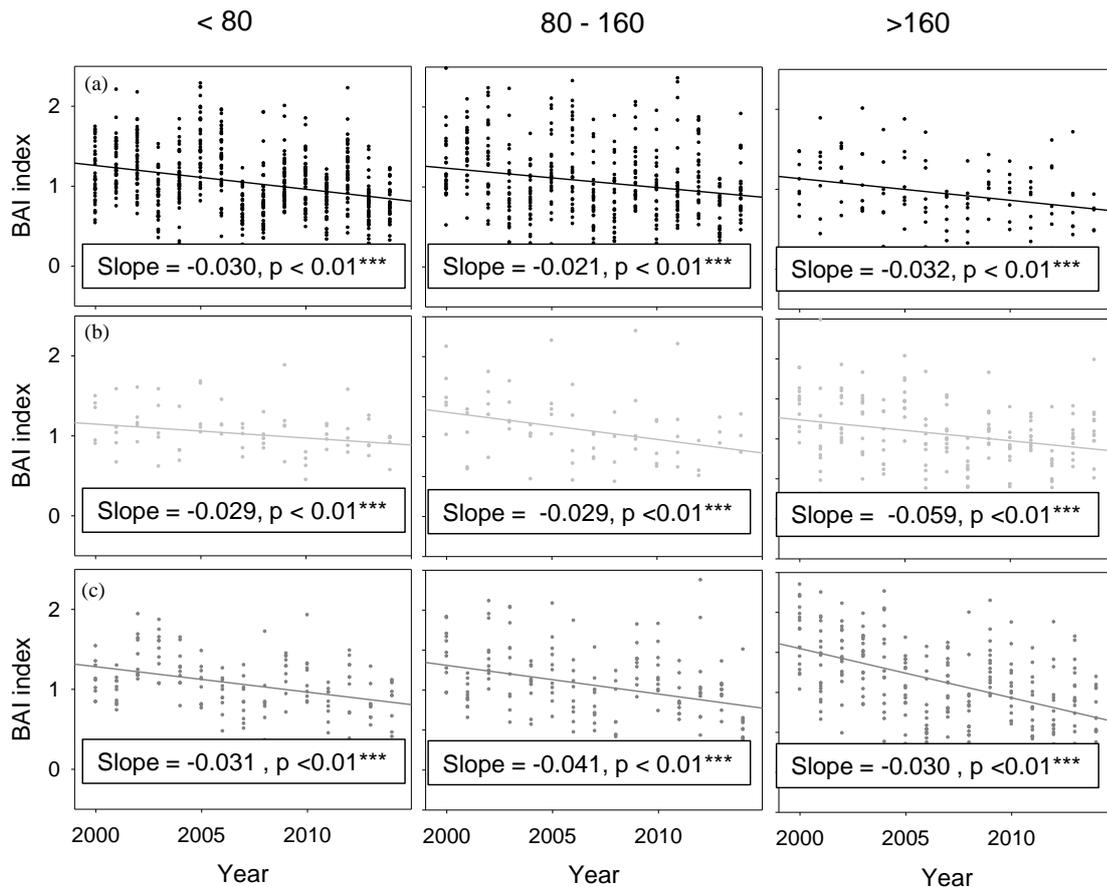


Figure 7 - Growth trends of detrended basal area increment of *N. macrocarpa* populations according population (cluster) grouping and age class for the period 2000-2014. 'sig' indicates only significant linear trends (*<0.1, **<0.05 and ***<0.01). (a) Coastal, (b) Highest, (c) Andes.

It seems to be that these negative trends could be associated to climate change of the three last decades (Fig. 4b), where there was a temperature decrease and precipitation increase in the central region of Chile, together with the increasing of atmospheric CO₂ concentrations in the world. Linear mixed-effects models verified the climatic influence on BAI (Table 3). We found a positive strong influence of precipitation on BAI in all populations and age class for the period 1980-2014 and 1990-2014 (all significant levels at $P < 0.001$); however, its significance as a predictor decreased in the period 2000-2014. In general, the temperature had a negative influence in Coastal and Andes populations, being strongly correlated to BAI in younger trees from Coastal in the three analyzed periods (all significant levels at $P < 0.001$). Regarding atmospheric CO₂ concentrations, we found a significant negative influence of rising CO₂ on BAI, mainly in older trees from Coastal and Andes populations. In the case of Coastal population, we observed that CO₂ was a good predictor of BAI in the three analyzed periods ($P < 0.05$), while older trees from Andes population had a negative response to rising CO₂ in the last decade, besides of younger and maturer trees (all significant levels at $P < 0.001$).

4.4 Discussion

Based on ten unprecedented chronologies of *N. macrocarpa* in the whole distribution, we verified that there is no evidence of positive effect of CO₂ fertilization on tree-ring growth from, MDFC. The results provide new

knowledge about a poorly studied forest ecosystem, with high levels of endemism and very disturbed (Myers et al. 2000; Schulz et al. 2010). The significant decrease and increase of precipitation and temperature during the three last decades seems to be influencing tree growth, despite of the rising atmospheric CO₂ concentrations in the world (Fig. 4b). Theory says that dry sites would have an adaptation to rising CO₂, causing a positive effect on forest growth because their iWUE would have been most improved (Huang et al. 2007); however, the dry sites analyzed here (PLC, SER, RRL and SAC) from Coastal range did not corroborate our hypothesis I. In fact, although Coastal and Andes populations of *N. macrocarpa* have biogeography differences, all populations showed a forest growth decline in the last decades (Fig.7).

The Highest population seems to have the highest resilience to recent climate change, because their ring-width chronology did not show any break point (Fig. 5b). This population had higher mean growth rate than the other populations, both in ring width and BAI (Fig. 6). The high growth was maintained from the beginning of the chronology, which could be related with low anthropogenic pressure (Table 2). In addition, we found that younger trees showed higher growth rate during the initial 50 years (Fig. 6a), while maturer trees had significant positive trends for the period 1980-2014 (Table 2). Despite all those positive aspects of trees from Highest, we observed an imminently forest decline after the year 2000 both in younger, maturer and older trees, so our hypothesis II is rejected (Fig. 7).

We found that climatic variations would be correlated to decline of *N. macrocarpa* forests in the last decades, being the main predictor the precipitation from May to November in the most age class. There is a significant association of precipitation (positive) in the rainy period and temperature (negative) in spring/being-summer on tree growth of *N. macrocarpa* populations (see growth-SPEI relationship, Table 1) and others forest species in central Chile (Barichivich et al. 2009; Le Quesne et al. 2009; Christie et al. 2011). Thus, the decrease of precipitations and the increase of temperatures of the last 35 years would be conditioning the natural dynamics of *N. macrocarpa* forest. However, the climatic signal varies with age class (Table 3). Our hypothesis III is partially accepted because only younger trees from Coastal population (dry region) had a negative sensitivity to temperature (as second predictor) than older and maturer trees in three analyzed periods, so that its increase in the last decades caused a negative effect on BAI in this age class (Table 3). In this sense, this population was observed one main cohort (Fig. 3), which is characteristic of *Nothofagus* forests affected by disturbances (Cullen et al. 2001). Apparently, as these forests are more disturbed, the younger trees are more sensitive to rising temperatures and, therefore, possibly more sensitivity to drought (Rozas et al. 2009). Young trees with less efficient root systems are less able to access available water and become water-limited rather easily, while older trees with extensive root systems may tap into deeper water sources, allowing them to have higher rates of transpiration and photosynthesis (Bond 2000). Moreover, the decline of precipitations in the last decade affected the rainfall-growth relationship in the wettest population (Andes) in the three age classes, making the trees become more sensitive to the temperature (Table 3). Therefore, young, maturer and old trees from MDFC in Coastal and Andes range are being affected by recent climate changes.

We found that CO₂ fertilization did not cause a positive effect on tree-ring growth in *N. macrocarpa* populations, but rather a significant negative effect on older trees in Coastal and Andes populations from 2000 (Table 3). Other studies also observed a negative response to rising CO₂ in older trees (Girardin et al. 2014; Camarero et al. 2015a). Some authors note that tree-ring growth trends is more associated to high-low temperatures or high-low water availability than response to rising CO₂ (Körner et al. 2005). However, we cannot discard that CO₂

fertilization could lessen the negative impact of drought and warm period on tree growth in the driest sites, i.e. the negative BAI trends could have been more pronounced if atmospheric carbon is remained stable (Camarero et al. 2015b). Although younger trees from Highest population had higher tree growth than maturer and older trees for the same age, we cannot interpret that this higher postindustrial growth rates could be linked to rising atmospheric CO₂, since there is great data variability (Fig. S2), which would be related with selection of fast growing individuals. However, we observed significant negative trends in last the decade to detrended the BAI values in this population. Tree growth rate could also be the result of age-related selection against fast- and slow-growing trees within a population, which are not related to CO₂ fertilization (Voelker et al. 2006; Brienen et al. 2012).

If the warming trend continues in MDFC, trees would strategically prefer to close the stomata, avoiding excessive water loss, but capturing less CO₂, and then producing less trunk biomass (Linares and Camarero 2012). On the other hand, although there is more availability of atmospheric CO₂ concentrations, trees could show signals of changes on net photosynthetic rate by, mainly, light saturation and Rubisco (RuBP) regeneration capacity limitation (Azcon et al. 2008). Therefore, non-growth increase in *N. macrocarpa* trees under rising atmospheric CO₂ could be explained by water deficit and photosynthesis saturation.

Positive growth trends linked to CO₂ fertilization founded in other forest ecosystem are associated with an adaptation of the trees to climate by means iWUE (carbon fixed per unit of water transpired) (Wullschleger et al. 2002; Tognetti et al. 2014). However, available carbon is not always associated into enhanced basal area growth (Handa et al. 2006; Penuelas et al. 2008; Andreu-Hayles et al. 2011). Other studies in *Nothofagus spp* showed positive trends of iWUE mainly from 1950 in southern Argentina (Srur et al. 2008) and southern Chile (Tognetti et al. 2014). In Argentina, the authors concluded that in dry sites the strong water stress would reduce the photosynthetic rate to the maximum, so tree growth could not be offset by the iWUE increase. Whereas in Chile, they observed an increase of BAI, which could be associated to positive adaptation of iWUE; however, this study was based on dominant trees which could generate some interpretation biases (Brienen et al. 2012). Therefore, an iWUE improve could mean an increase of growth, storage, root exudation and metabolic respiration, but not necessarily linked to stem biomass. We must consider that carbon is also stored in leaves, roots and branches.

4.5 Conclusion

We concluded that *N. macrocarpa* populations from MDFC are being strongly affected by recent climate change in the region – decreasing precipitations and increasing temperatures –, and not observed a positive influence of rising CO₂ on stem biomass, both in younger, maturer and older trees. Although it would be important to complement these results with carbon stable isotope analysis (i.e. iWUE), this study gives us a first vision about the resilience to rising atmospheric CO₂ and recent changes in precipitation and temperature variability of a vulnerable forests in South America. Recent studies are demonstrating the potential use of BAI as a variable that reflects the growth stimulation (or not) of forests under 50 years of CO₂ fertilization and global warming (e.g. Camarero et al., 2015; Girardin et al., 2016).

Considering the worrying forecasts of climate change for central Chile (e.g. Vicuña et al., 2011; Allen et al., 2015), we would expect that the growth resilience of these forests will be affected in the future. In spite, all the studied populations are in protected forests (park, reserve or sanctuary), this does not guarantee the persistence of

the species. These results can contribute to strategies for adaptation and mitigation of climate change effects on deciduous forests of central Chile.

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5 REDUCTION OF ABOVEGROUND TREES BIOMASS OF TWO THREATENED BIOMES OF SOUTH AMERICA DUE TO CLIMATE CHANGE

Abstract

The biomes of Brazilian Atlantic Forest (BAF) and Chilean Mediterranean forest (CMF) are rich in biodiversity, however, historically they have been shaved by the anthropic pressure that has caused a considerable decrease of their forest surface, reason why they were classified as ‘hotspots’. On the other hand, an increase in drought conditions (mainly due to temperature increase and precipitation decrease) has reduced tree biomass in neotropical forests. The present study aims to (i) estimation of annual aboveground tree biomass (ATB), (ii) analyze the influence of climate on the accumulation of AB in both biomes, (iii) evaluate the growth projections under future climatic scenarios, (iv) determine which forest populations are most vulnerable to climate change by 2100. Five populations of *Cedrela spp* - cedro (MA, n = 116 trees) and five of *Notofagus macrocarpa* - roble (FM, n = 155 trees) were selected in a climatic gradient for a dendroecological analysis. We calculated the radial growth rate (classical dendrochronology), annual wood density (x-ray densitometry) and annual biomass accumulation for the period 1960-2014 (allometric equations based in radial growth and wood density). ATB response to climate variability was analyzed through correlation and regression analysis. Growth projections were designed with future climatic conditions (best and worst case scenario). The results show that the populations of cedro have local climatic response, while the populations of roble are under a regional climate pattern. The populations most vulnerable to future climate changes until 2100 are: (i) in MA, the populations of lower altitude and closer to the big city; and, (ii) FM, the driest and highest populations.

Keywords: Atlantic Forest; Mediterranean Forest; Tree growth; Carbon accumulation; Global warming; *Hotspot* biomes.

5.1 Introduction

Many studies have found that global warming has intensified and drought episodes have become more severe during the last decades in the world (e.g. Jones et al., 2001; Pachauri et al., 2014). This situation affects directly the availability of soil water, and hence strongly impact on net primary production (NPP) both in xeric and mesic forest (Yi et al. 2015). This NPP quantifies the amount of atmospheric carbon fixed by plants that is accumulated as biomass, being aboveground tree biomass (ATB) the component that contributes most to the PPN, and therefore, it is the most sensitive to the water deficit caused by climate variability (Brando et al. 2008; Vicente-Serrano et al. 2015). As evidence, it has been observed that severe droughts have reduced net primary productivity in neotropical forests (Phillips et al. 2010; Zhao and Running 2010), with stem growth being the most affected (Brando et al. 2008). Thus, changes in forest productivity will have economic, ecological and social impacts, especially if is accompanied by widespread dieback of the most vulnerable biomes (Allen et al., 2015; Anderegg et al., 2015).

Some of the most vulnerable biomes of South America are the Brazilian Atlantic Forest of Brazil (BAF) and the Chilean Mediterranean forest (CMF), with greatest fragmentation and high biodiversity so they were considered hotspot (Myers et al. 2000). It has been estimated that more than 50% of NPP of South America occurs in the tropical and subtropical forest region (such as the Atlantic forest), with an overall mean of 1170 g m² yr⁻¹, while that xeric forest (such as the Mediterranean forest) was estimated a NPP of 500 g m² yr⁻¹ (Raich et al. 1991). On the other hand, overall in South America (and in large parts of the world) was observed an experienced unprecedented high-impact climate extremes during the 2001–2010 decade, which was the warmest since the start of modern measurements in 1850 and continued an extended period of pronounced global warming (WMO 2011). As expected for the future (by 2100), more frequent warm nights in BAF region and a decrease of rainfall in CMF region (Marengo et al. 2009). Particularly, the scenarios from RCPs (Representative Concentration Pathways) considered a

wide range of possible changes in future anthropogenic glasshouse gas emissions, which forecasts an increase of global warming rates from +0.3° C (RCP 2.6) to +4.6°C (RCP 8.5), by the year 2100 (Collins et al. 2013).

For studies about growth projections and climate change the literature recommends the use a biogeographic approach (Sánchez-Salguero et al. 2016). This is justified because it allows us to analyze how forest growth and productivity change in response to environmental variation along geographical environmental gradients (Babst et al. 2013; Martin-Benito and Pederson 2015) and to know which trees populations are more vulnerable to climatic projections (Sánchez-Salguero et al. 2016). These results help to propose and develop new management and conservation strategies for warmer and drier climate scenarios (Lindner et al. 2014).

The combination of dendrochronological techniques, x-ray densitometry to estimate annual wood density and allometric equations can enhance understanding of carbon fluxes and their climatic sensitivity (Frank et al. 2010; Babst et al. 2014a), since assuming that the wood density is constant can deliver somewhat bias results (Taki et al. 2014; Pompa-García and Venegas-González 2016). In this study, we analyzed two South American hotspot forests (BAF and CMF) across a climatic-geographical gradient to examine the effects of climatic projections on aboveground biomass tree, by means dendrochronological techniques, x-ray densitometry, allometric equations and ensembles CO₂ emission scenarios. Although these biomes are different in structure, diversity and environmental condition; they have in common they are close to the largest urban centers of Brazil and Chile. We hypothesize that the tree populations most sensitive to temperature (negatively) and precipitation (positively) will be the most vulnerable to the projected rise in temperatures due to increased drier conditions. Specific objectives are (i) estimate the annual ATB from tree ring measurement (wood density and ring width), (ii) analyze that climate variables explain most of the variability in ATB at different spatial-temporal scales, (iii) projection annual ATB by 2100 under future climatic scenarios, (iv) find the populations that would be most affected by the temperature in the next 100 years. To reach our objectives, we selected forest species with dendrochronological potential in both biomes, *C. fissilis* and *C. odorata* (Brienen and Zuidema 2005) in Brazil and *Nothofagus macrocarpa* in Chile (Donoso et al. 2010).

5.2 Material and methods

5.2.1 Study areas

We selected two neotropical biomes Brazilian Atlantic Forest (BAF) and Chilean Mediterranean forest (CMF), located in Coastal region of São Paulo and central region from of Brazil and Chile, respectively (Fig 1). In both countries five studies sites were selected with populations of *Cedrela spp* (cedro: *C. fissilis* and *C. odorata*) and *Nothofagus macrocarpa* (roble) from Brazil and Chile, respectively. In Brazil (north to south, 22°-24°S), Park Campos de Jordão (CJ), Park Serra do Mar São Sebastião (SS), Juquitibá (JU), Park Carlos Botelho (CB) e Bom Sucesso de Itararé (BS). In Chile (north to south, 32.5-34.5°S), Park La Campana (PLC), Sanctuary El Roble (SER), Sanctuary Altos Cantillana (SAC), Reserve Roblería Loncha (RRL) e Sanctuary Alto Huemul (SAH). All tree populations are in public and private conservation areas.

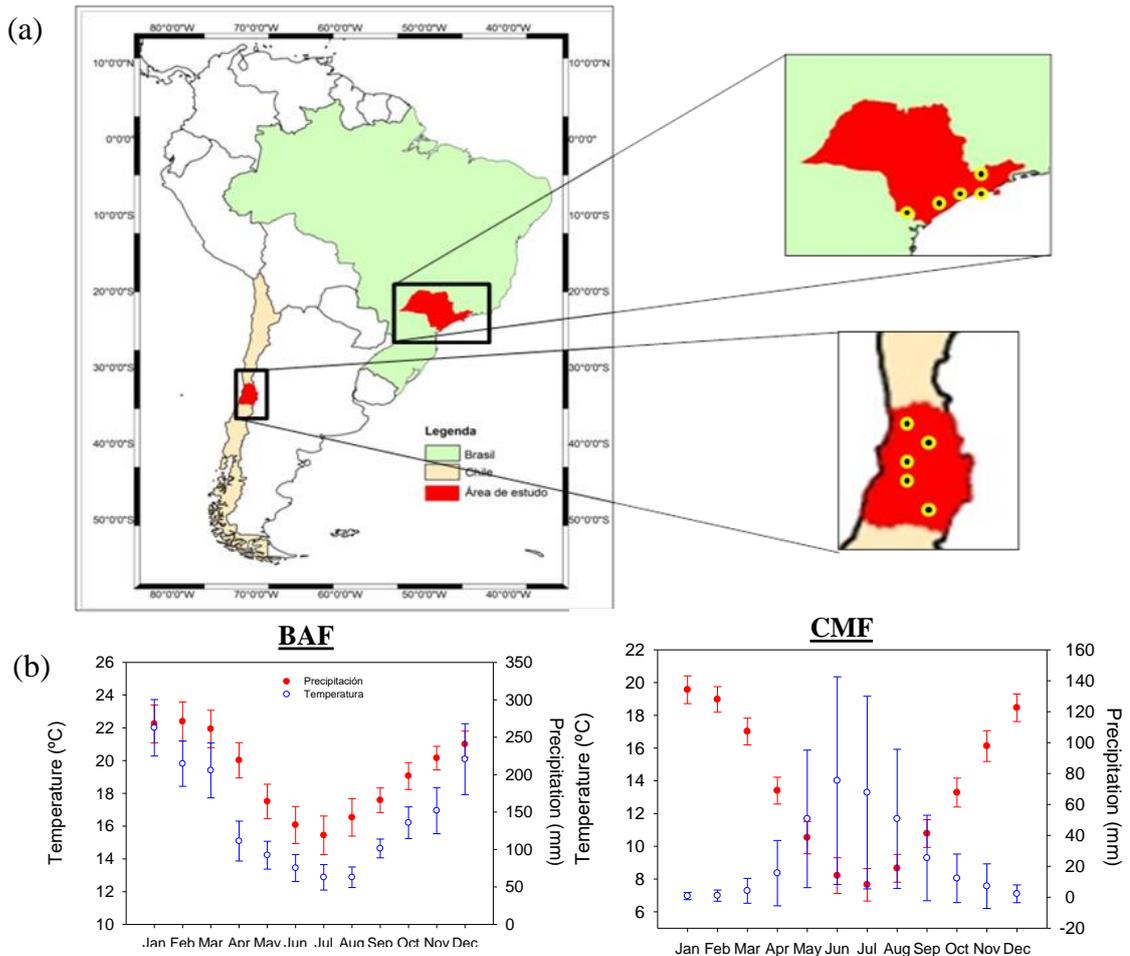


Figure 1 - (a) Studies populations studied in two countries. (B) Climogram of studies regions (mean \pm standard deviation). Winter is June to August, spring is September to November, and fall is March to May.

Cedrela spp populations are situated in the center of the biogeographic subregion of the Atlantic forest, ‘Serra do Mar’, while *N. macrocarpa* populations are located in Coastal range (northern) and Andes range (southern). The ecological niche in BAF is characterized by subtropical climate with cold/dry winter and hot/rainy summer; and in CMF is characterized by Mediterranean climate with cold/rainy winter and hot/dry summer. The climatic gradient is marked by altitude and latitude, since CB is the highest and coldest site, while that SS is the lowest and wet site, and southern sites are driest (CB, BS and JU). The climatic gradient is marked mainly by latitude and mountain, where northern sites driest (Coastal range) and southern site (Andes range) is wet.

5.2.2 Annual radial growth measurement

In the field, 12-44 trees of different age classes and apparently healthy were bored at 1.3 m in each site, using Pressler increment borers. Wood samples were air dried, glued onto wooden supports and polished with progressively finer sandpaper to visualize and cross-date them using characteristic narrow and wide rings. The ring widths were measured at 0.01 mm resolution using a software image (Rasband 1997). The dating was checked using the program COFECHA (Holmes et al. 1986a), which compares the ring-width series of each tree with a master chronology built for each site. We calculated the annual radial growth through the average of ring width series per years.

5.2.3 Annual wood density measurement

At each sites, one increment cores was collected by a non-destructive method from 10 trees per site (same trees used above). Wood cores were cut in the transverse direction, maintaining a thickness of 1.7 ± 0.02 mm, and were kept in a conditioning room at 20°C and 50% relative humidity until reaching a stable moisture content of 12% (Tomazello et al. 2008). Wood samples were scanned from bark to pith using an X-ray densitometry QTRS-01X Tree Ring Scanner (Quintek Measurement Systems, Knoxville, TN, USA) at 0.08-mm intervals. The demarcation zone among tree rings was automatically set up by the device and checked manually for every tree-ring scanned. We performed a linear regression to estimate annual wood density by years. The average of wood density per years delivered overestimated values sometimes, so we had problems building the annual values of aboveground tree biomass ($\text{year}_t - \text{year}_{t-1}$, see below). This situation can be explained because in some years the percentage of latewood is higher than in other years, so that increases the mean wood density (Babst et al. 2014b).

5.2.4 Aboveground tree biomass

The aboveground tree biomass (ATB) accumulated time t was determined using the formula: $\text{ATB} = V * \text{WD}$, where V is the trunk volume at time t and WD is the mean annual wood density at time t . For the calculation of V , we used formulas based only on diameter at 1.3 m (D), using the tree-ring width annual values (radial growth multiplied by 2). For *Cedrela spp.*, we used the equation for cedro from Ombrophilous Dense Forest: $\text{Ln}(V) = \beta_0 + \beta_1 * \text{Ln}(D)$, being $\beta_0 = -8.3315$ and $\beta_1 = 2.3004$ (Thaines et al. 2010). For *N. macrocarpa*, we used the equation for roble calculated in Sanctuary El Roble de $V = \beta_0 * D^{\beta_1}$, being $\beta_0 = 0.000115439$ and $\beta_1 = 2.48824$ (Donoso et al. 2010). This analysis allows a temporal evaluation in the accumulation of ATB, allowing ecological-climatic inferences throughout the life of the forest species. We estimated ATB for the period 1960-2014 (2005 to CJ and BS in cedro chronologies) because is common period of 10 chronologies. Annual ATB rates were derived from the difference of total ATB values between two consecutive years.

5.2.5 Climate-biomass relationships and growth forecasts

To remove non-climatic trends and related to stand age of ATB series, we used the program ARSTAN (AutoRegressive STANdardization) (Holmes et al. 1986a). Each series was detrended using a cubic spline with 50% frequency-response with a cutoff equal to 2/3 of series length, or lowest robust smoothing method. Those methods preserved high-frequency (yearly to sub-decadal) climatic information and removing low-frequency trends in the series. Detrending was followed by transforming tree-ring widths to dimensionless growth indexes, by dividing observed ring-width values by fitted ones.

The influence of climate on ATB was evaluated by Pearson's correlations. This analysis was calculated for each site using residual chronologies because values of first-order autocorrelation of the ten sites were overly large. Thus, series were pre-whitened by autoregressive models to remove temporal autocorrelation, and thus create the aboveground trees biomass indices ($\text{ATB}_{\text{index}}$) (Cook 1985). Those indices were used to investigate the climate-growth relationship from previous March to current April, using local climate variability, i.e., maximum temperature, minimum temperature and total monthly precipitation from 1961–2014. Climatic data was obtained from nearby meteorological stations to site and gridded dataset by Climate Research Unit.

5.2.6 Growth forecasts

We used a multiple regression analysis to determine which monthly variable (maximum temperature, minimum temperature and precipitation) is related to ATB on the observed data. Predictor variables were selected by stepwise model, allowing to an automatic selection of independent variables already included in the model and rejection of any variable that does not produce a *T-student* significant at the 0.90 level (Di Rienzo et al. 2001). We evaluated the existence of multicollinearity among explanatory variables by calculating the variance inflation factor (VIF), which was lower than two, confirming no redundancy problems with the data (O'brien 2007). The selected models were run to forecast the ATB of each site under the two CO₂ emission scenarios by 2100. We used two IPCC scenarios from Coupled Model Intercomparison Project (phase 5, CMIP5), the worst scenario (RCP 8.5) and lower-emission scenario (RCP 2.6). Monthly climatic variables for each species were transformed into normalized standard deviations to give them the same weight in the fitted models (Pompa-García et al. 2017). The validation was performed with a Pearson's correlation for the period 1961-2014 (2005-2005 for CJ and BS), using a significant of $P < 0.001$.

Finally, we compared three periods observed and ATB projected: 1963-2005, 2015-2057 and 2058-2100, by linear mixed-effects model (LMM). Those periods were selected due to ATB projected was divided in two equal periods, and in ATB observed was used the common period. LMM was used to analyze the statistical difference in trees biomass between observed and projected periods, sites and interaction (site x period). We used ATB_{index} due to meet assumptions of normality. Models were fit using the "lme4" package with lmer function in the R environment (Bates et al. 2014), using the interface implemented in InfoStat-Statistical Software (Di Rienzo et al. 2001). Later tests of multiple comparison were made between means with Fisher's Least Significant Difference test (LSD, $P < 0.05$).

5.3 Results

5.3.1 Aboveground tree biomass chronologies

Fig. 2 show the variations of data used to estimation of annual aboveground tree biomass. Wood density tended to increase with age in cedro populations with larger values for tree rings near bark (2005 for CJ and BS, and 2014 for SS, JU and CB), while that roble populations did not show a marked trend in five sites. Overall, in both biomes we observed higher data variability and a decrease of ring width in last 20 years.

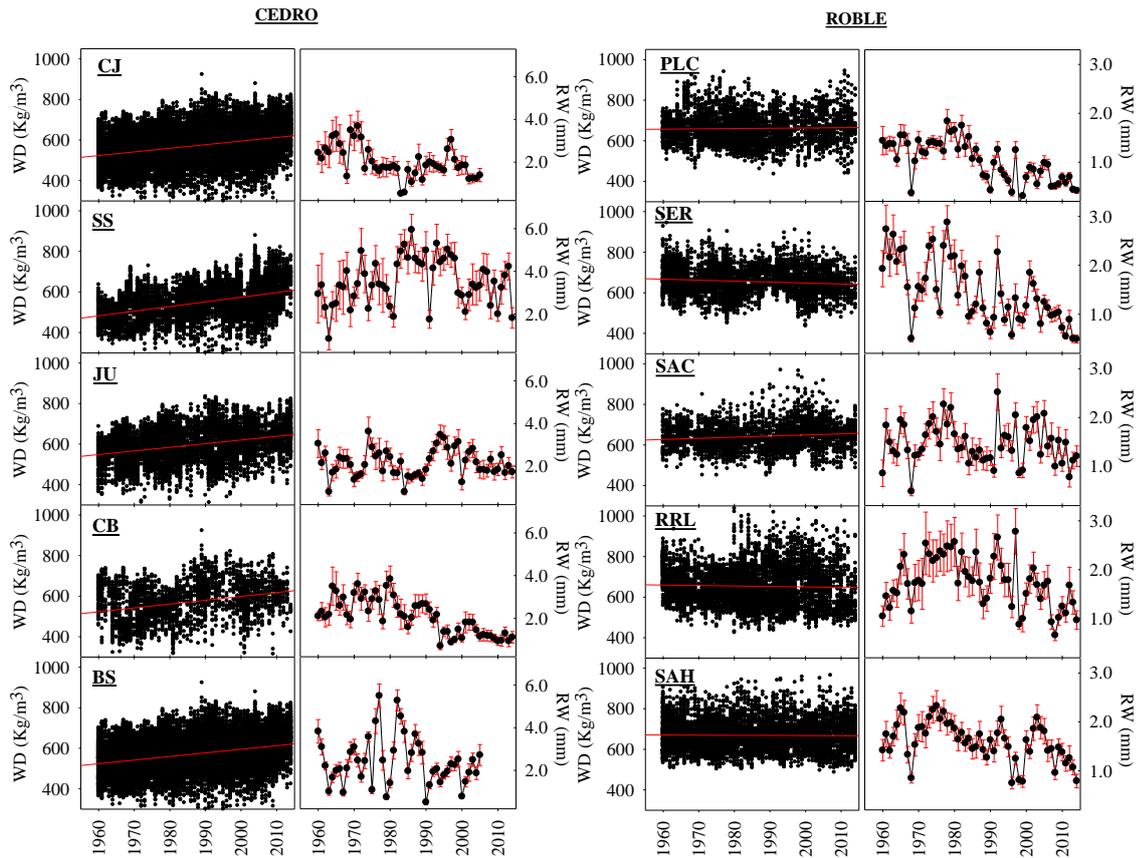


Figure 2 - Linear regression (WD) of mean wood density and ring width (RW) of cedro and roble populations. Wood density values are indicated by black points and red line represents linear trends (all $p < 0.05$). RW values represent mean \pm SE.

Overall, accumulated biomass for the period 1960-2014 was higher in cedro than roble. In this sense, rainiest site (SS) was the one that had higher values of accumulated biomass, with a mean of ~ 400 kg per trees and interannual biomass of ~ 10 kg per years. For roble populations, we observed that higher ATB was found at southern Coastal site (RRL), with a mean of ~ 200 kg per trees and interannual biomass of ~ 3.5 kg per years (Fig. 3).

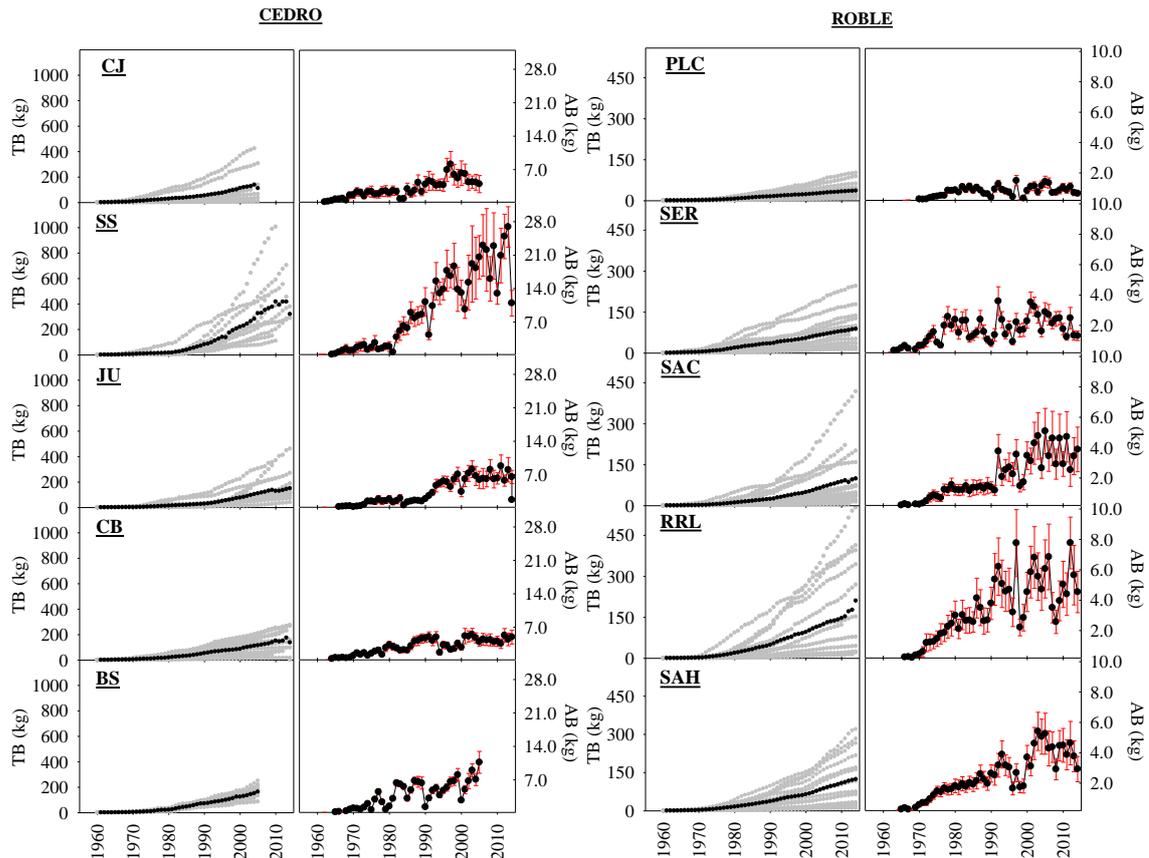


Figure 3 - Total (TB) and interannual (AB) variability of aboveground trees biomass. Gray lines represent TB values by trees and black line is the average. AB values represent mean \pm SE.

5.3.2 Climatic influence on aboveground tree biomass

Fig. 4 shows the climate-biomass relationship in latitudinal gradient in both biomes. In Brazilian Atlantic forest, ATB of cedro populations responded to climatic variability in different months. Highest and coldest site (CJ) has a positive correlation with maximum temperature and precipitation of summer, mainly December and February, respectively. While maximum temperature of July has a negative influence on ABT in this population. While the populations of intermediate altitude (JU, CB and BS = \sim 700 m.s.n.m) are very sensitive to winter precipitation (April to June), while lowest population (SS) is most sensitivity to precipitation from July to September. Maximum and minimum temperature is negatively correlated mainly with SS and JU from May to November, and from September to November, respectively. Driest site (BS) is negatively correlated with Maximum temperature in October.

In Chilean Mediterranean forest, it was observed greater similitude in the climatic response of ATB of roble populations both in precipitation and temperature. There is a strong influence of winter rains on all populations, while the minimum temperature has a positive effect in early winter at all five sites. The maximum temperature negatively affected the southern populations and SAC (highest altitude) during spring and winter, respectively.

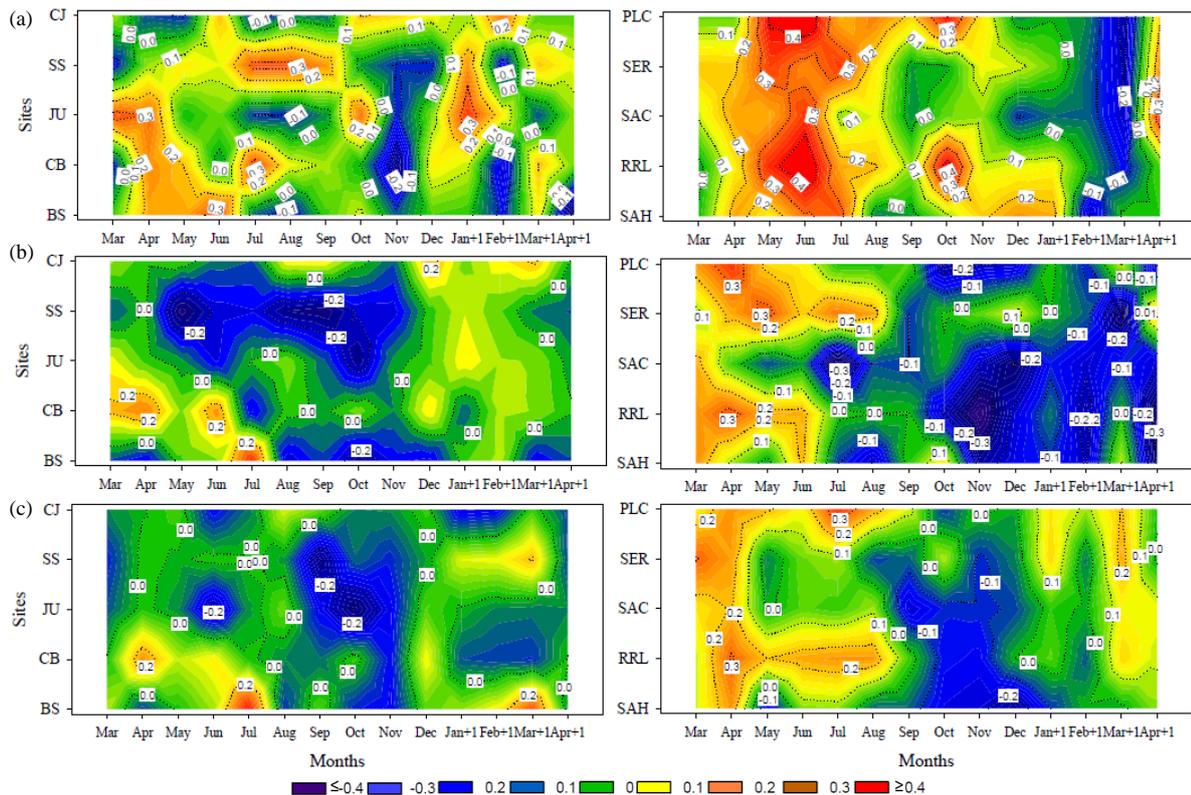


Figure 4 - Climate-biomass relationship in cedro and roble populations using data of (a) precipitation, (b) maximum and (c) minimum temperature. We consider as correlation coefficient ~ 0.20 ($r = 0.25$, $p < 0.05$). Left graphic is to cedro and right graphic is to roble.

5.3.3 Projected aboveground tree biomass

Overall, the percentage of explained ATBindex variance by stepwise models is higher in roble (R^2_{adj} varied between 0.34% and 0.58%) than cedro (R^2_{adj} varied between 0.21% and 0.42%) (Table 1). In all sites, the mean squared error were lower (< 0.06). The best and worst model in cedro projections was found in BS and CJ, while and in roble projections was observed in PLC and SAC. The number of climate predictors entering the stepwise models ranged from 5 to 7. All validations had a Pearson correlation coefficient ≥ 0.60 (Fig. 5, 6).

We observed a greater difference between the amplitude of RCP 2.6 (lowest scenario) and RCP 8.5 (worst scenario) in roble than cedro populations. For cedro, we observed a projected tree biomass similar with the two scenarios analyzed. We stand out a greater decrease ATBindex in SS and JU populations in the two scenarios since \sim year 2020 (Fig. 5). However, it seems that the severe increase (RCP 8.5) in temperature would have a positive effect on aboveground tree biomass in CJ and BS, mainly after 2080. For Roble, we found that an exacerbated temperature increase in a terrible scenario (RCP 8.5) would cause a strong forest decline in five sites, especially since 2040 (Fig. 6). However, biomass projections with RCP 2.6 show that are in the mean, except to SAC.

In both biomes, we observed a greater decrease of ATBindex for the period 2058-2011 with RCP 8.5 scenario, being SS and JU the sites most affected for cedro with mean ATBindex = 0.75 (F-value = 7.33, df = 16, $P < 0.001$), while for the more vulnerable sites were PLC and SAC, with mean ATBindex = 0.61 (F-value = 9.88, df = 16, $P < 0.001$) (Fig. 7).

Table 1 - Summary of the stepwise multiple linear regressions models used to forecast species chronologies of trunk biomass indices. R^2_{adj} indicate the percentage of variance explained by climate based models, and SQM represent the mean squared error. Abbreviations: Pt, total precipitation; Tmax, mean maximum temperature; Tmin, mean minimum temperature. Letters after climate variables indicate months (i.e. Pt_{apr} = total precipitation of April). We analyzed from April (previous growing season) to March (current growing season).

Species	Sites	Best predictors*	R^2_{adj}	SQM
Cedro	CJ	(+)Pt _{jun} (+)Pt _{feb} (-)Tmax _{jul} (+)Tmax _{dec} (+)Tmin _{ago}	0.21	0.05
	SS	(+)Pt _{jul} (+)Pt _{sep} (-)Tmax _{sep} (-)Tmax _{may} (+)Tmin _{mar}	0.35	0.05
	JU	(+)Pt _{apr} (-)Pt _{jul} (+)Pt _{jan} (-)Tmin _{oct} (-)Tmin _{may}	0.39	0.02
	CB	(-)Pt _{nov} (-)Pt _{feb} (-)Tmax _{jun} (-)Tmax _{jul} (+)Tmax _{aug} (-)Tmin _{nov}	0.31	0.03
	BS	(+)Pt _{jun} (+)Pt _{dec} (-)Tmax _{aug} (-)Tmax _{oct} (-)Tmax _{dec} (+)Tmin _{jun}	0.42	0.06
Roble	PLC	(+)Pt _{apr} (+)Pt _{may} (+)Pt _{jun} (+)Pt _{oct} (+)Pt _{dec} (-)Tmax _{oct}	0.58	0.04
	SER	(+)Pt _{jul} (+)Pt _{may} (-)Pt _{mar} (-)Tmax _{jul} (+)Tmax _{oct} (+)Tmin _{jan}	0.39	0.05
	SAC	(+)Pt _{apr} (+)Pt _{jun} (+)Pt _{jul} (-)Tmax _{jul} (-)Tmin _{sep} (+)Tmin _{oct}	0.34	0.04
	RRL	(+)Pt _{apr} (+)Pt _{jun} (+)Pt _{oct} (+)Tmax _{apr} (-)Tmax _{nov} (+)Tmax _{jan}	0.51	0.03
	SAH	(+)Pt _{jun} (+)Pt _{jul} (+)Pt _{jan} (+)Tmax _{jun} (-)Tmin _{sep}	0.37	0.02

* '+' or '-' indicates positive or negative estimate values respectively

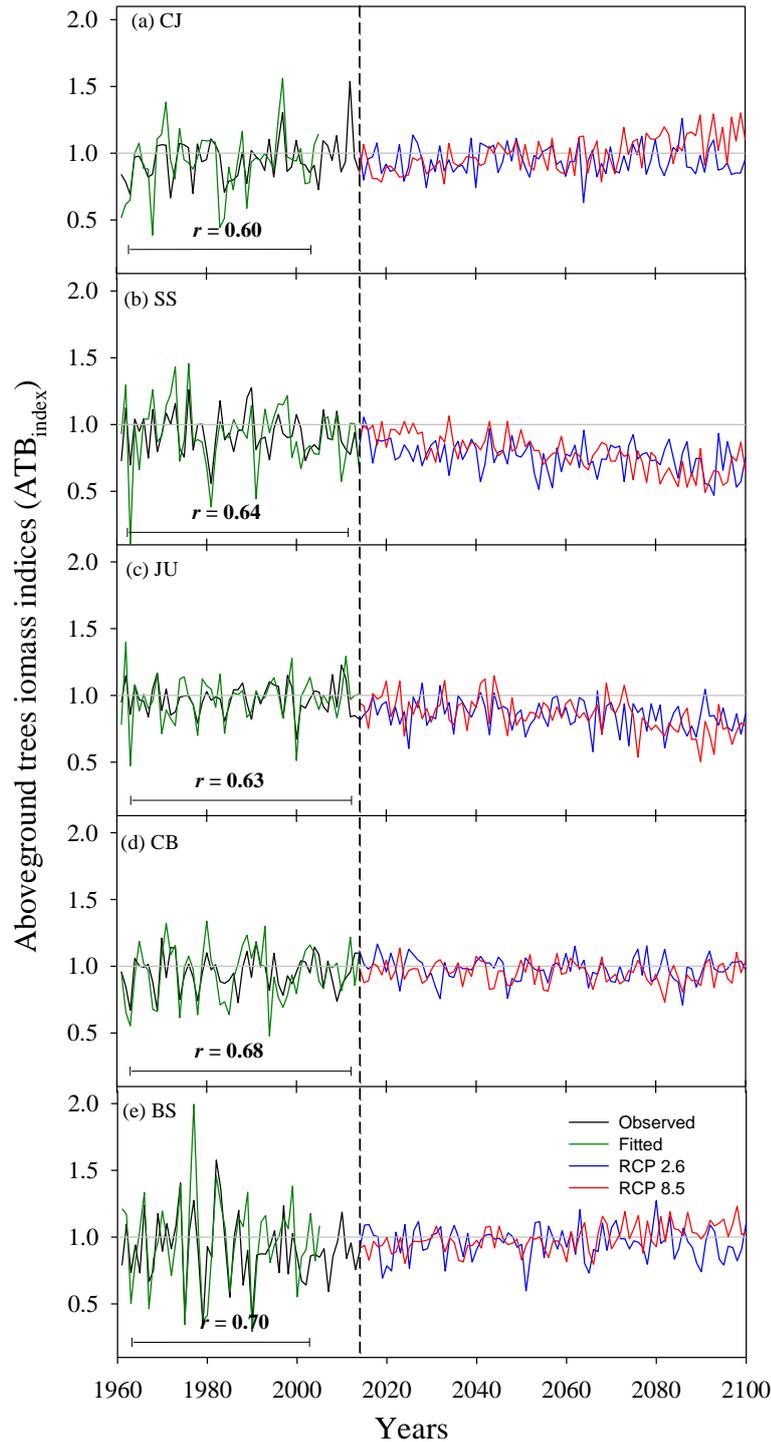


Figure 5 - Observed, fitted and projected ATB_{index} for *Cedrela spp.* populations. The observed and fitted period was 1961–2014 for SS, JU and CB; and 1961–2005 for CJ and BS. Correlation coefficient indicate the model validation (all sites with $r \geq 0.60$, $P < 0.001$). Projected indices are based on two IPCC AR5 emission scenarios for the 2015–2100 period (RCP 2.6 and RCP 8.5). Segmented line indicate the change between observed/fitted and projected growth.

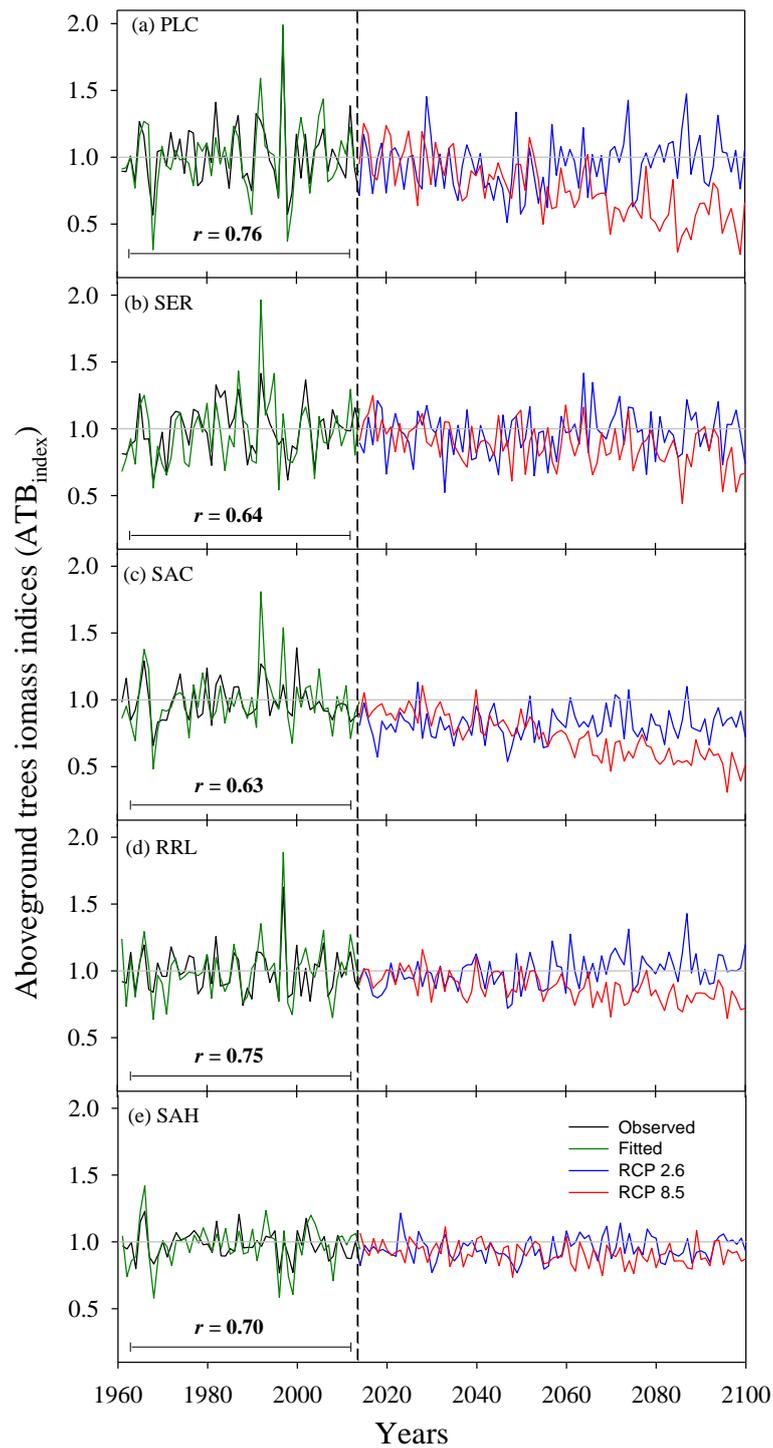


Figure 6 - Observed, fitted and projected ATB_{index} for *N. macrocarpa* populations. The observed and fitted period was 1961–2014 for five sites. Correlation coefficient indicate the model validation (all sites with $r \geq 0.60$, $P < 0.001$). Projected indices are based on two IPCC AR5 emission scenarios for the 2015–2100 period (RCP 2.6 and RCP 8.5). Segmented line indicate the change between observed/fitted and projected growth.

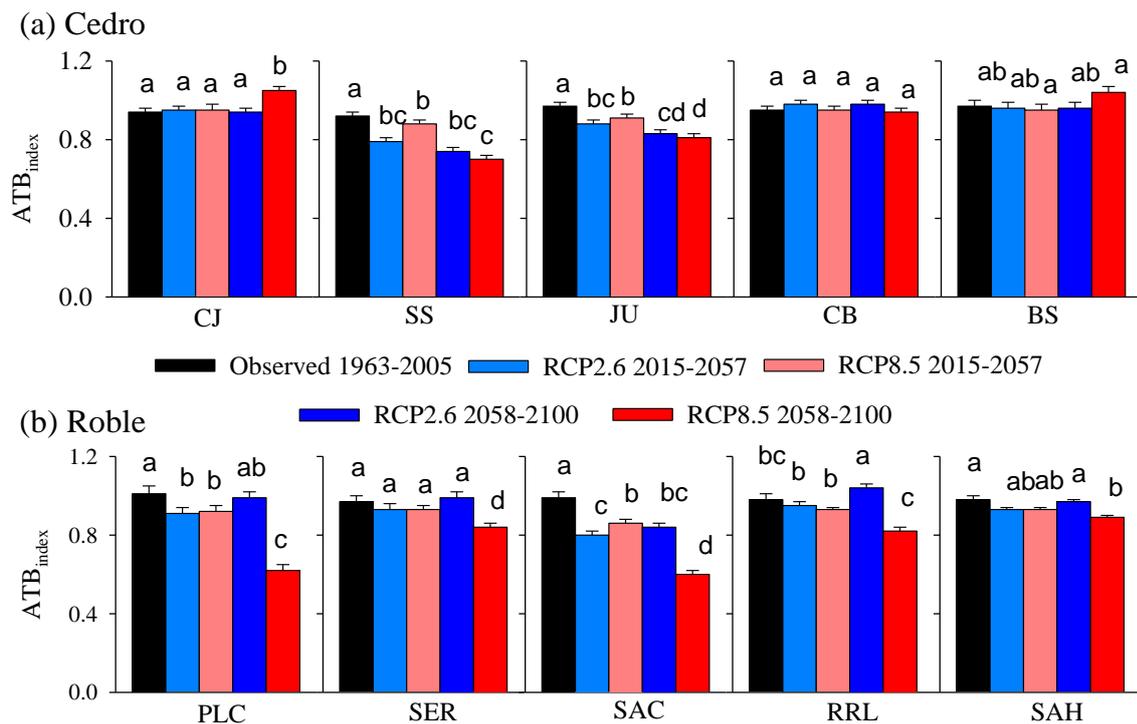


Figure 7 - Mean (\pm SE) aboveground trees biomass indices (ATB_{index}) between observed and projected periods, (a) cedro populations, (b) roble populations. Different letters indicate if there are significant differences ($P < 0.05$).

5.4 Discussion

This study shows us the potential of use of tree-ring width and mean wood density to annual rates estimate of aboveground trees biomass in different forest ecosystem. Moreover, growth projections are becoming increasingly important to forecast forest resilience to climate change, especially in threatened biomes. We applied a novel approach that provides detailed insights into the biomass accumulation dynamics of trees populations over their entire lifetime in Brazilian Atlantic Forest of Brazil (BAF) and Chilean Mediterranean forest (CMF). We found that SS from BAF, and PLC and SAC from CMF are de most vulnerable trees population to worst scenario of anthropogenic CO₂ emissions, which would cause a rising temperature of +4.6°C (RCP 8.5) by 2100.

5.4.1 Estimation of annual trees biomass

Studies on annual estimation of trees biomass have increased recently using dendrochronological techniques (Pompa-García and Venegas-González, 2016; Taki et al., 2014), since this allows to have a more accurate retrospective view of forest carbon dynamic (Babst et al., 2014a; Köhl et al., 2017). The incorporation of the variation of wood density improves aboveground biomass estimation (i.e. carbon uptake from trees), since this variable varies temporally, depending on tree age (Hietz et al., 2013; Knapic et al., 2007) and diameter class (Chave et al., 2004). Annual trees biomass provides a more relevant measure than ring width and basal area increment for assessing climate impacts on forest productivity and carbon cycling (Hember et al., 2015; Hogg et al., 2017). Here, we verified the importance of considering the temporal variation of wood density in studies about forest carbon dynamics.

5.4.2 Influence of climate on aboveground trees biomass

Overall, we found that climate-biomass relationship is similar to results of climate-ring width relationship (see chapter I and III). We observed that the importance environmental gradient on forest growth is more marked in Brazilian Atlantic Forest (BAF) than Chilean Mediterranean forest (CMF), since cedro populations are sensible to predominantly local climatic influence, while roble populations are under a more regional climate pattern. In both biomes, we observed a greater influence of precipitation on trees biomass, mainly months before the beginning of growing season. These results coincide with others studies around the world, which indicate that the increase of trees biomass is favored with months without water deficit at the beginning of the growth (Babst et al., 2014b; Hogg et al., 2017).

Overall, maximum temperature had higher correlation values and greater number of predictor variables than minimum temperature in two biomes (Table 1, Fig. 4). Maximum temperature is negatively correlated with trees biomass in winter/spring to BAF (SS, lowest site) and summer to CMF (southern roble populations). In the first case (BAF), it is related to the increase of the water deficit at the beginning of growing season, would affect specially the division of cambial cells in *Cedrela* forest (Marcati et al., 2006); while that in the second case (CFM) maximum temperature in summer would cause a higher rate of trees evapotranspiration that trigger small latewood vessels and stop radial growth in tropical trees (López and Villalba, 2011). Thus, we verified the importance of knowing the key months related to tree biomass accumulation, which could be used in studies of modeling, conservation and forest restoration.

5.4.3 Most vulnerable forests

We found that climatic scenarios showed a higher risk in dry biome (Chilean Mediterranean forest). The projected models showed that the most vulnerable sites to future climate scenarios are SS and JU in BAF, while that PLC and SAC in CMF. In cedro populations, this result is explained by the increase of maximum and minimum temperature of September and October for SS and JU, respectively. Moreover, worst scenario (RCP 8.5) would increase the trees biomass accumulation due to positive effect of maximum temperature of December. In roble populations, both vulnerable sites are negatively linked to maximum temperature of October and July for PLC and SAC, respectively. However, considering the percentage of variance explained by climate based models ($R^2_{adj} \geq 0.40$), we propose that JU and PLC sites are most vulnerable to rising temperature, mainly after 2058.

JU populations are located closer to the Sao Paulo capital, which would increase its risk due to a greater presence of trace elements (Baes and McLaughlin, 1984). While PLC is the northern and driest *Nothofagus* population in South America, so that it will increase evapotranspiration and water use efficiency in trees (iWUE) mainly in dry sites (Körner, 2006). In this sense, Sanchez-Salguero et al. (2016) forecasted mean growth reductions after 2050 in some Mediterranean pines that would cause dieback and a contraction of their species distribution due to potential local extinctions of the southernmost populations (i.e. dry warm distributional edge). Nevertheless, other studies have found that those species that have their distribution at warmer sites are genetically more capable of adapting to drought (Carsjens et al., 2014; Chen et al., 2010). These results allow to identify which populations of BAF and CMF are most vulnerable to climate change, and help to propose and develop new management and conservation strategies for warmer and drier climate scenarios (Lindner et al., 2014).

5.5 Conclusions

This study presented a vision of the ecological importance of the Brazilian Atlantic Forest and the Chilean Mediterranean Forest in the accumulation of biomass (and CO₂ fixation), and how its populations would adapt to future climate changes. Although biomes are very different in structure and biodiversity, both have a fundamental ecological role as a carbon sequestration in their countries, considering that both biomes are in important economic and populational poles of Brazil and Chile.

In the case of cedro populations, we found that similar autoecology species located in different habitats depend on soil water conditions in different months; therefore, any change in precipitation/temperature will specifically affect each population, being SS site very vulnerable to increase of minimum temperature of October. While roble populations, we observed a regional climate pattern that affect trees biomass, so the projected climatic scenarios have affected almost all the *N. macrocarpa* distributions, being dry edge (northern limit) the site most vulnerable. Thus, we can understand the vulnerability of threatened forests in South America to global warming that, although they are in protected areas, does not guarantee their persistence.

Our modelling approach mixing dendrochronology, biogeography and climatic scenarios could help to know the similarity in resilience to the rapid anthropocene warming in different hotspot forest around the world.

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