Recent Consequences of Climate Change Have Affected Tree Growth in Distinct *Nothofagus Macrocarpa* (DC.) FM Vaz & Rodr Age Classes in Central Chile

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Abstract: Forests play an important role in water and carbon cycles in semiarid regions such as the Mediterranean ecosystems. Previous research in the Chilean Mediterranean forests revealed a break point in 1980 in regional tree-ring chronologies linked to climate change. However, it is still unclear which populations and age classes are more affected by recent increases in drought conditions. In this study, we investigated the influence of recent variations in precipitation, temperature, and CO_2 concentrations on tree growth of various populations and age classes of *Nothofagus macrocarpa* trees in Central Chile. We sampled 10 populations from five sites of *N. macrocarpa* through its whole geographic distribution in both Coastal and Andes ranges. We used standard dendrochronological methods to (i) group populations using principal component analysis, (ii) separate age classes (young, mature, and old trees), (iii) evaluate linear growth trends based on the basal area increment (BAI), and (iv) analyze the link between BAI and atmospheric changes using linear mixed-effects models. Results showed that young trees are more sensitive to climate variability. Regarding population grouping, we observed that all population clusters were sensitive to winter-spring precipitation, but only the Andes and Coastal populations were negatively correlated with temperature. The results of CO_2 fertilization analyses were controversial and unclear. Since young trees from all population clusters reacted positively in the phase with an increase of atmospheric CO_2 between 1980 and 2014, this behavior was not translated into growth for the last 15 years (2000–2014). However, it should be noted that the young trees of the highest elevation populations did not have a negative growth trend, so it seems that CO_2 counteracted the negative effect of recent regional climate change (increase in temperature and precipitation decrease) in these population trees. Further studies are needed to assess the effects of climate variability over other ecological and physiological processes.

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1. Introduction

Atmospheric CO_2 is the principal contributor to global warming [1]. This increase has been indicated as an impact factor on plant growth and function, as reflected in the 20th century increases of the internal water use efficiency (iWUE) [2] and as an inducer of changes in the health and dynamics of different forest ecosystems in multiple regions [3]. Thus, we should 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 CO_2 in some forest ecosystems of Europe and Asia [4–6]. Physiologically, it would be expected that the higher the concentration of atmospheric CO_2, the lower the degree of stomatal opening necessary to capture a certain amount of atmospheric carbon, which affects the efficiency tree water use [7]. Recent articles have shown that long-term trends vary with stand age, which also affects the response to climate temperature, precipitation, and CO_2 [8,9]. On the other hand, eco-physiological processes may influence tree growth in relation to tree age, where the hydraulic limitation is one of the main physiological variables that explains why there are differences in the sensitivity of trees to climate at different age classes [10–12]. Concerning physiological reactions according to ontogeny, increases in atmospheric CO_2 and air temperature during the 20th century have been related to increments in the iWUE and the intercellular CO_2 concentration, with adult trees showing higher iWUE values than young trees, which broadly indicates the incidence of climatic, environmental, and ontogenetic variability in the tree responses [13]. Therefore, understanding the response and forest resilience to atmospheric changes (i.e., temperature, precipitation, and CO_2 concentration) has become an important topic for its conservation [14].

Mediterranean environments are some of the most vulnerable to climate change [15]. Mediterranean vegetation in Chile is located in its Central region, and has a great interest worldwide due to its high levels of species' diversity, life forms, and endemism [16]. Central Chile is topographically characterized by a narrow valley between two mountains, the Coastal and the Andes ranges, with a Mediterranean-type climate of winter rainfall and summer drought [17]. Therefore, the geographical, geological, and climatic characteristics of this region have been the cause of the development of a large amount of endemic plants [18]. It is in this geographical setting where the Mediterranean deciduous forests of Central Chile (MDFC) occur. The forests dominated by *Nothofagus macrocarpa* ((DC.) Vásquez et Rodr.) (commonly called "Roble de Santiago or Santiago's oak") are among the most important and threatened species of these ecosystems [19,20].

The effects of climate change in Central Chile have been evident during the last century [17,21–23]. As a consequence of the reduction of precipitation beginning in the 1850s, in combination with significant warming, glaciers have significantly retreated [24]. A recent work has revealed a significant forest growth decline starting in 1980 in regional *N. macrocarpa* chronologies [25]. This decline is linked to climate change, primarily due to a reduction in rainfall from May to November (before and during the start of cambial activity) but is also linked to an increase in temperature from October to December (first months of cambial activity). However, the relationships associated with the populations as a whole have failed to discriminate whether recent climatic events have produced differential effects in relation to tree age or the geographical heterogeneity in which these forests are distributed. This current scenario is expected to be magnified, as climate models projected a temperature increase of about 3 °C to 4 °C and a precipitation decrease of about 10% to 30% in Central Chile (~ 30°S) over the next 100 years [26]. Furthermore, the region has suffered great environmental degradation due to anthropogenic factors, such as urban and agricultural expansion, cattle grazing, logging for firewood, and introduction of invasive species, which is a situation that still persist throughout the region [27].

The Coastal range is the most affected since it is closer to large urban areas [28], which is shown by a substantial decrease in the biological productivity of the land system. Therefore, both global climate change and human activities interact to place both the dynamics and the existence of the endemic flora of Central Chile at risk.

Nothofagus spp has proven to be an excellent tree to analyze human influences and climate change in forests from a long-term perspective in the south-central territories of Chile and Argentina [29,30]. However, the tree-rings response to increasing atmospheric CO_2 concentration, regional warming, and changes in precipitation pattern changes have been scarcely studied in the *N. macrocarpa* forest. In this case, we have evaluated a network of 10 *N. macrocarpa* forest stands at the extremes of its geographical distribution. The coastal range (northern limit, dry sites) and Andes range (southern limit, wet sites) to analyze growth trends in both young and adult trees in relation to CO_2 fertilization and recent changes in climate variability (i.e., precipitation and temperature). Our hypotheses were: (i) *N. macrocarpa* populations subjected to drier conditions in the Coastal range would have a lesser growth decline linked to climate change than wetter sites, since the former adapt better to arid conditions [31]. (ii) Overall, younger trees would be more sensitive to climate variability than older trees, considering that younger trees could better use the availability of resources [32], and the growing season period of older trees appear to be shorter, since these trees are well established [33]. (iii) The rise of atmospheric CO_2 will cause an increase in tree growth in some populations/age classes, as observed in other Mediterranean forests [8,34].

2. Materials and Methods

2.1. Study Area and N. Macrocarpa Populations

The study area is located in central Chile (from 32°57′ to 34°51′ S, and from 71°07′ to 70°40′ W) (Figure 1), with typical Mediterranean climate characterized by precipitation concentrated in winter (June to July) and a long, dry summer (December to March). The climate in the coastal range is drier than in the Andes range [35]. The inter-annual rainfall in this region is highly variable and very influenced by ENSO episodes, with warm (cold) events in central equatorial Pacific associated with wet (dry) conditions in Central Chile [36]. Along the Andes range, soils are developed from volcanic or granitic rocks and from glacial sediments, and are classified in the large group of forest brown soils, with a medium depth on slopes and greater depth in the high plains [37]. Along the Coastal range, soils are formed from granitic rocks in the Cordillera heights at the northern coast of the study region and are poorly developed, which are usually residual on rocky outcrops [20].

Nothofagus macrocarpa has been proposed as *Lophozonia macrocarpa* (A.DC.) Heenan & Smissen in a recent review of the generic taxonomy of the Nothofagaceae [38], but in this work we maintain the original taxonomic identity without prejudice to the proposed changes. The distribution of *N. macrocarpa* approximately covers the latitudinal distribution of MDFC [39]. This species is emblematic and endemic to Central Chile and represents the northernmost *Nothofagus* populations in America [40,41]. *Nothofagus macrocarpa* populations have been subjected to strong anthropogenic alterations, despite the fact that they are a potential biodiversity niche for the different communities that are living within them [40]. Additionally, given its sensitivity, the species represents an outstanding element for the monitoring of global climate changes. This endemic forest is considered a relic of the last glaciation period [18,37]. This situation is due to the particular evolutionary history of Mediterranean flora, characterized by the coexistence of elements of tropical, subtropical, and sub-Antarctic origins, as a result of geological and climatic changes that affected the territory during the Tertiary [37]. In addition, 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 [28].

The biogeographic action exerted by the Andes mountain range in MDFC, with higher elevations in these latitudes, has hampered the migrational dynamic of different species [28,37]. This region

has shown evidence of dynamic interactions between geomorphological and climatic phenomena throughout the post glacial period, with frequent earthquake success, volcanic eruptions, and alluviums, which influence the distribution patterns of the flora. The coastal range is characterized by islands of vegetation on top of the hills with high Andean flora [28]. These vegetation types would have been separated from the Andes populations due to the climatic changes that characterized the last glacial-interglacial cycle over the past 100,000 years in Central Chile [37]. This hypothesis is supported by the phytogeographic features of the hills El Roble, La Campana, and Altos Cantillana [28].

We selected *N. macrocarpa* trees from MDFC. These trees have deciduous leaves, which reach 25 m of height and > 60 cm of stem diameter at breast height (DBH) [40]. The structure of *N. macrocarpa* stands usually include a high arboreal stratum (over 16 m) of scattered individuals, which are remnants of a previous structure that was likely modified by fire or logging. Under this stratus, a monospecific layer of 8 to 16 meters in height is established, and, depending on the environmental situation, it can reach 50% to 75% of coverage. In situations with a lower canopy cover, it is possible to distinguish a sclerophyllous shrub stratus (1–2 m), with a high variability in density and composition, according to the altitudinal range (until 1000 meters). The tree growth is mainly sensitive to favorable moisture conditions from May to December [25].

2.2. Characteristics of N. Macrocarpa Populations and Tree-Ring Analysis

Ten populations from five sites of *N. macrocarpa* were sampled, including four in the Coastal region and one in the Andes mountain. Coastal sites are located in PLC (National Park La Campana), SER (Nature Sanctuary 'El Roble'), SAC (Nature Sanctuary 'Altos de Cantillana'), and RRL (National Reserve 'Robleria Loncha'); while Andes sites are located in SAH (Nature Sanctuary 'Alto Huemul'). This represented almost the entire distribution of the species (Table 1, Figure 1). In each site, two or three forest stands were sampled from April to May 2015, except for Robleria del Cobre de Loncha where only one population was sampled. Most of the sampling sites are currently protected at different degrees, since they are in different types of protected wilderness areas (TPWA, Park, Reserve, or Sanctuary) for flora and fauna conservation. However, this protection status is very recent (YSP, Table 1) and most of the forest was disturbed by selective forest logging and man-made fires. We categorize the forests of the different sampling sites according to the diameter at breast high (DBH), the distance to a paved road (DPR), and the approximate time to get to the site of the regional capital (TGC). We considered a high intervened forest by selective forest logging if sites have trees with DBH < 30 cm, DPR < 10 km, and TGC < 1 h. We used this classification because it helped us to visualize which forest was affected by selective logging, which, in turn, may have impacted the natural dynamic of forests, both in regeneration and growth patterns [20,40]. In addition, this approach helped us to interpret the clustering of populations [35] (Table 1).
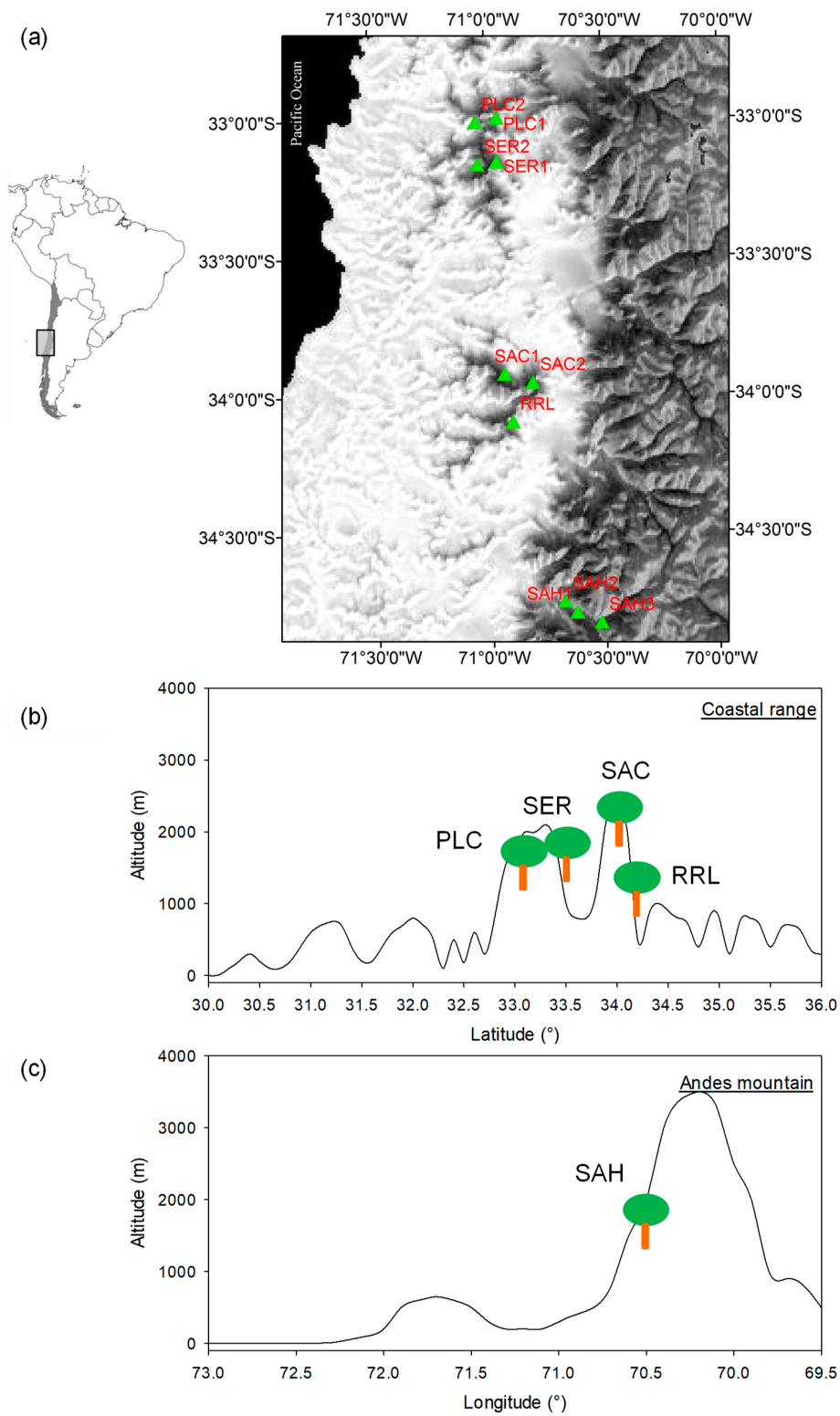
Figure 1. (**a**) Study area of *N. macrocarpa* sites sampled in this work. The populations represent the whole natural geographical distribution of *N. macrocarpa* in Chile (Amigo and Rodriguez-Guitan 2011). The digital elevation model shows the shape of the terrain (white showing the lowest elevation). (**b**) Relative positions of sites at the Coastal range (PLC, SER, SAC, and RRL) according latitudinal profile (° S). (**c**) Relative position of site SAH corresponding to the Andes group, according longitudinal profile (° W).

Table 1. Description of N. macrocarpa sites and wood sampling.

Range	TPWA [a]	YSP [b]	Site	Code	Elev. (masl)	No. trees [c] (chron.)	DBH ± SE [d]	DPR [e]	TGC [f]	Inter. [g]
Coastal	National park	1967	La Campana 1	PLC1	1350	15(15)	23.5 ± 0.7	10	1	High
			La Campana 2	PLC2	1210	15(14)	32.1 ± 3.1	7	1	High
	Nature Sanctuary	2000	El Roble 1	SER1	1590	15(15)	41.6 ± 3.63	6	1	Medium
			El Roble 2	SER2	1600	15(14)	29.6 ± 1.2	5	1	High
	Nature Sanctuary	2010	Altos Cantillana 1	SAC1	1810	15(13)	43.7 ± 5.4	*	9	Low
			Altos Cantillana 2	SAC2	1850	12(11)	51.4 ± 4.5	*	9	Low
	National reserve	1996	Robleria Loncha	RRL	1090	24(23)	35.4 ± 2.0	28	2	Medium
Andes	Nature Sanctuary	1996	Alto Huemul 1	SAH1	1500	20(18)	51.8 ± 10.5	50	4	Low
			Alto Huemul 2	SAH2	1600	14(13)	50.0 ± 4.2	53	4	Low
			Alto Huemul 3	SAH3	1550	10(10)	37.7 ± 4.7	47	4	Medium

[a] Type of protected wilderness area. [b] Year declared as protected area. [c] Number of trees sampled (number of trees considered in the chronology). [d] Diameter at breast height (DBH) ± standard error (SE) (cm). [e] Distance to a paved road (DPR) 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. [f] Approximate time to get the site from a regional capital in hour (TGC). PLC is Valparaíso. SER and SAC is Santiago. RRL and SAH is Rancagua. [g] Forest intervened by selective forest logging (high, medium, and low).

An average of 15 trees were sampled per forest population distributed over an area not exceeding 0.5 to 1 ha. We sampled trees of all diameters in each stand with the aim to include individuals of different ages and sizes [42]. Two to three cores per trees were taken at 1.3 meters from the soil surface 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 their specific-site master chronology [43].

De-trended series were only used for performing principal components analysis (PCA) to identify common modes of variability in annual radial growth that allowed the order and classification of chronology populations (clusters) [35]. A 77-year common period (1938–2014) were used to identify these common modes of variability. A Hierarchical Clustering on Principal Components (HCPC) were used to identify the number of clusters, which were chosen visually from the hierarchical tree and were based on the inertia increase [44]. The 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'(version 1.42).

2.3. Tree-Growth Patterns

Tree growth of each tree at each analyzed site was converted into a basal area increment (BAI), according to the equation below.

$$\text{BAI} = \pi \left(r^2_t - r^2_{t-1} \right) \tag{1}$$

where r_t and r_{t-1} corresponds to tree radius at DBH calculated at the end and beginning of the annual increment in years t, respectively [45]. BAI is recommended to represent individual and stand-level changes [34,45,46]. Annual BAI for each tree were estimated from raw ring-width series using R (version 1.7.0) package dplR [47].

In the case of cores without pith, we used a geometric correction to estimate the number of missing rings and to adjust the inner-ring date, i.e., the pith was estimated by fitting a template of concentric circles with known radii to the curve of the innermost rings [48]. In the 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 an allometric model based on the DBH real of trees. We use direct data from BAI without standardizing since this methodology filters youth growth trends [45]. The piecewise regression model of growth rate (mm year^{-1}) were used to analyze significant changes in the temporal trend, using the 'segmented' R package [49]. We applied this analysis on radial growth data due to there being less data variability than the basal area increment data, since our study had many younger trees (30% of whole population with recruitment after 1950), so the common period to BAI analysis is short and showed a break point at the end of the chronology.

2.4. Avoiding Ontogenetic Problem

A biased sampling of big or fast-growing trees could produce spurious tree growth rates [14]. Therefore, it is important to sample coexisting trees of diverse sizes, growth rates, and ages [42]. We expect that BAI trends of *N. macrocarpa* and their climatic response varies with the stand age. Thus, trees were classified in three age classes, young trees (<80 years, which were established after 1935), mature trees (81–160 years, which were established between 1855 and 1936), and old trees (>161 years, which were established before 1855). Those age classes contain at least five trees by cluster. The 13 trees without pith had been classified as old trees because they had at least 161 years or missing distance to the pith higher than half the radius.

2.5. Effect of Climate and CO$_2$ on Tree Growth

We used the CRU TS3.24 datasets from for precipitation and temperature, gridded at 0.5° spatial resolution for the period between 1901 to 2014 [50]. Accumulated precipitation from May to November (P$_{M-N}$) and mean temperature from October to December (T$_{O-D}$) are the variables that better explain the growth variability in *N. macrocarpa* [25]. Annual atmospheric CO$_2$ values (C$_a$) were extracted from the Mauna Loa observatory in Hawaii for the period between 1958 and 2014 [51]. The piecewise regression model of the diameter growth rate (cm year^{-1}) showed a break point for regional chronology from approximately the three last decades (Figure S1a). 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 CO$_2$ (significance level of 90%) in the region (Figure S1b).

We performed a multilevel linear mixed model for modelling the effect of climate and atmospheric CO$_2$ concentration on tree growth (BAI after removing non-climatic and age-related trends) considering a year-to-year variability over the period from 1929 to 2014 by each cluster/age-class. The climatic variables P$_{M-N}$, T$_{O-D}$, and Ca were considered as fixed effects in the model, while tree and year were treated as random effects to properly account for their random variability. To identify the best predictors that included combinations of one, two, or three explanatory variables, we used an approach of multi-model inference [52]. This analysis shows the probability that a given model better explains the response variable than others [53]. 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 to its second-order Akaike information criterion (AICc). We selected the two best models that had ΔAIC < 2 [53], 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' (version 1.43.6) was used to perform the multi-model selection [52].

3. Results

Clustering analysis of annual radial growth of *N. macrocarpa* populations showed that the grouping could be associated with the intervention level of the forest (Table 1). We observed three specific clusters, which were called 'Coastal' (PLC1-PLC2-SER1-SER2-RRL), 'Highest' (SAC1-SAC2), and 'Andes' (SAH1-SAH2-SAH3) [35]. Coastal populations were more intervened by selective forest logging, trees were younger than the highest populations and Andes populations, and also represented the xeric sites (Table 1). In Coastal populations, 50% of the trees were approximately <80 years (younger), while in the highest populations and Andes populations, 50% were older (>161 years) (Figure S2). The highest populations represented the tree line in the coastal range, and Andes sites corresponded with the southern populations (wet sites). All populations showed a decline in the growth trend in the last several decades, which is more accentuated in Coastal and Andes populations (Figure S3). The origin of this decreasing trend was identified by the break points, which began to be significant in 1979 in Coastal populations and in 1978 in the Andes populations (Figure S3a,c), in coincidence with the regional chronology whose break point was observed for 1980 (Figure S1a). Highest populations did not show any significant break point (Figure S3b).

Long-term growth trends of BAI, according to cambial age, showed a sustained growth for all populations and three age classes (Figure 2). Therefore, it seems that all populations show a growth decline in recent decades. However, there was a noticeable increase in the first 50 years of life in younger trees of the highest population, which was better growth performance than any other trees (Figure 2a). Mature trees from Coastal populations and the highest populations showed a growth increase since ~100 years of cambial age, while, in Andes populations, showed a decline in growth for ~80 cambial years (Figure 2b). After 50 years, younger trees begin a decline in growth in the Coastal populations and the highest populations, while older trees from Andes showed a decline in growth from 150 years of cambial age in the tree populations (Figure 2c).
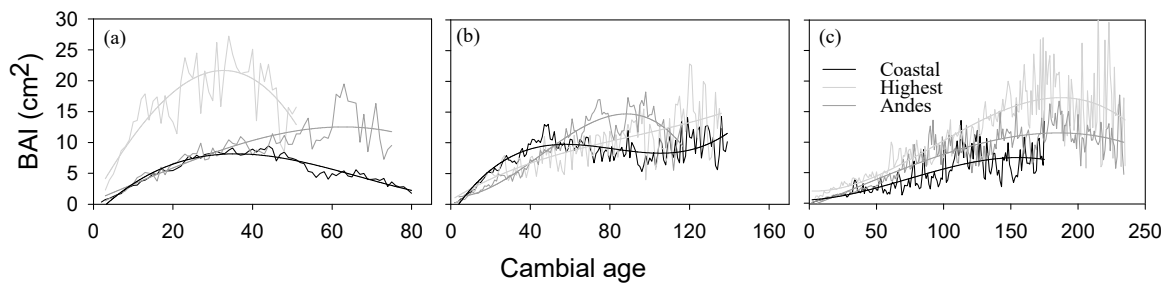
Figure 2. Basal area increment (BAI; cm^2 year^{-1}) of the three cluster populations according to cambial age. (**a**) <80 years, (**b**) 81–160 years, and (**c**) >161 years.

Mature and old trees of the three populations clusters showed a decline in the growth trend in the last several decades, mainly since 1980, except for the highest populations (Figure 3). Conversely, young trees showed a positive increase in the forest with lower intervention logging (highest and Andes). When trends were analyzed, a significant decline of BAI values by removing non-climatic and age-related trends were observed after 1980, with a notorious decrease after the 21st century (Figure 4). For the 1980-2014 period, only the Coastal population showed negative trends in mature and old trees, while young trees from the highest population and the Andes population showed a positive growth. However, for last 15 years (2000–2014), the trends in tree growth showed a notorious decline, except to young trees from the highest population, which seems to be less reactive to consequences of a global scale, as indicated by no significant trends.
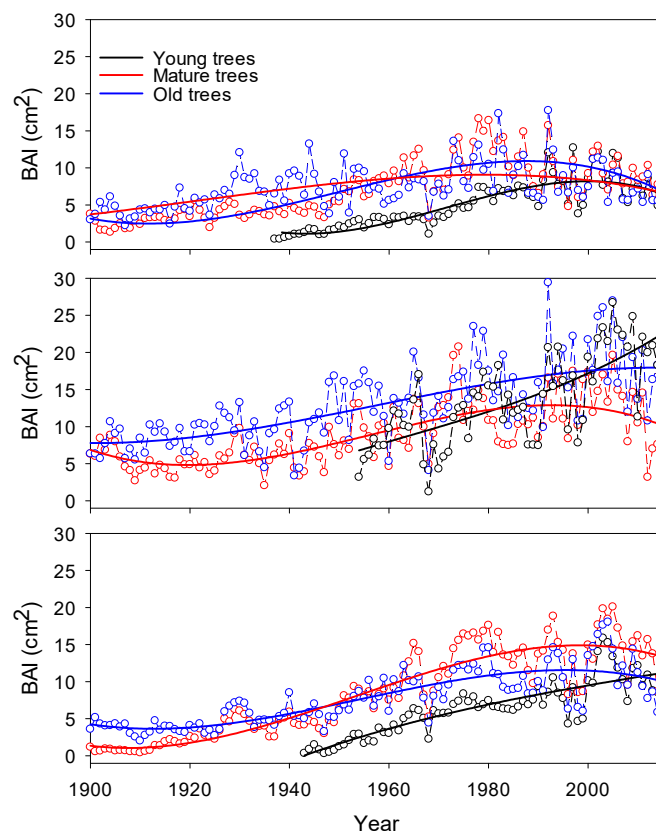

Figure 3. Basal area increment (BAI, cm^2 year^{-1}) chronologies of the three cluster populations and age classes. Trends are enhanced by a cubic polynomial curve ($R^2 > 0.75$). (**a**) Coastal, (**b**) Highest, and (**c**) Andes.
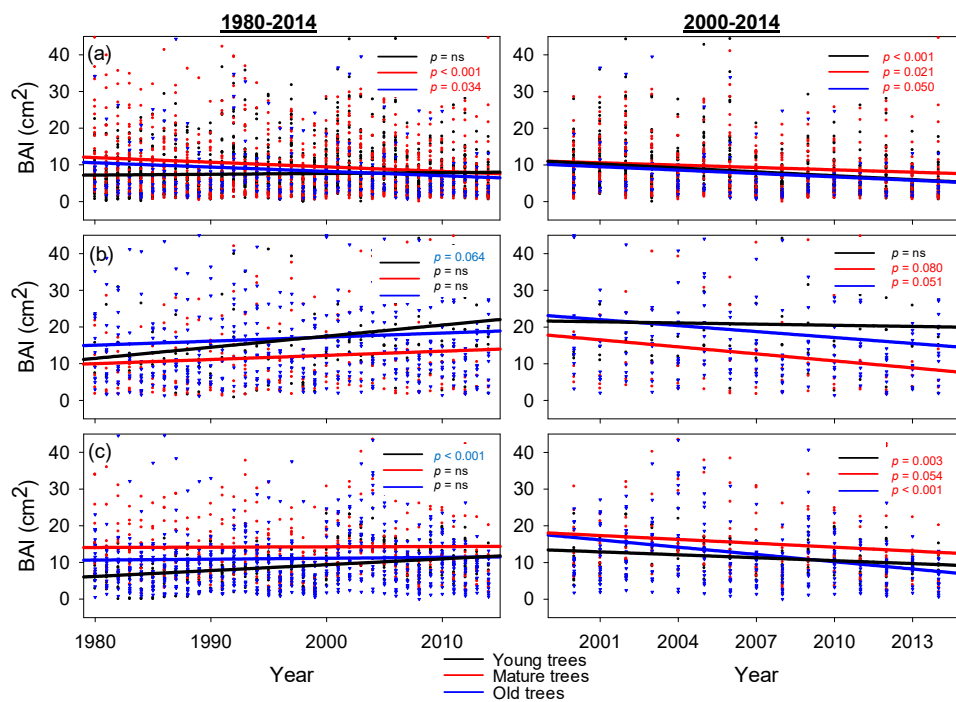
Figure 4. Growth trends of the basal area increment (BAI) of *N. macrocarpa*, according to the cluster population and age classes for the period from 1980 to 2014 and 2000 to 2014. Values of '*p*' in blue indicate positive significant linear trends (at a significant level of 90%), and, in red, the negative linear trends. (**a**) Coastal, (**b**) Highest, and (**c**) Andes.

It seems that these negative trends could be associated with climate change of the last three decades (Figure S1), where there was a temperature increase and precipitation decrease in the central region of Chile, with the increase of atmospheric CO_2 concentrations in the world. Linear mixed-effects models verified the climatic influence on BAI (Table 2). We found a positive strong influence of precipitation on BAI in all populations and age classes for the period of 1980 to 2014, since this variable was always found within the best two models, which is a significant predictor for the Coastal and Andes populations. Overall, the temperature had a negative influence in Coastal and Andes populations, which is strongly correlated to BAI in younger trees from Coastal populations in the three analyzed periods ($p < 0.001$). Regarding atmospheric CO_2 concentrations, we found a significant positive influence of rising CO_2 on BAI in young trees in the three populations grouping ($p < 0.001$). In the case of the Coastal population, we observed that CO_2 was a good predictor of BAI in young trees ($p < 0.001$).

Table 2. Linear mixed-effect models represent the influence of climatic variables (precipitation, temperature and CO_2) on basal area increment (BAI) for the periods 1980–2014, according to the cluster population and age classes. Grey cells show significant negative effects of CO_2 on BAI (* $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$).

Cluster	Age Class	Trend Sign	*p* May–Nov (1)	T Oct–Dec (2)	CO_2 (3)	Best Two Models	Delta AIC	Relative Weight
	<80	(+)	0.00267 ***	−12.0 ***	0.0260 ***	1,2,3	0	0.87
Coastal	80–160	(−) *	0.00221 ***	−0.112 *	−0.0115 *	1,2,3–1,2	0–0.16	0.31–0.29
	>160	(−) *	0.00155 **	-	−0.0117	2–1,3	0–1.20	0.34–0.19
	<80	(+) *	0.00286	-	0.175 ***	3–1,3	0–0.53	0.39–0.30
Highest	80–160	(−)	0.00220	-	0.0630	1–1,3	0–0.27	0.20–0.17
	>160	(-)	0.00121	-	0.0585	1–1,3	0–1.9	0.26–0.24
	<80	(+) *	0.00148 **	−10.8	0.0985 ***	1,3–1,2,3	0–0.22	0.48–0.43
Andes	80–160	(−)	0.00116	−22.4 *	-	2–1,2	0–0.43	0.23–0.18
	>160	(−)	0.00156 *	−15.4 *	-	1–1,2	0–0.75	0.23–0.16

We observed differences of BAI values among the cluster population and age classes for the more pronounced period of global warming in central Chile (1980–2014, Figure 5). In Coastal and Andes populations, the young trees had lower growth than mature and old trees (mean of <10 cm^2 year^{-1}), while, that in Coastal populations, the results were inverse. The young trees had the lowest growth (mean of >10 cm^2 year^{-1}). For the period from 2000 to 2014, the results were similar, except for Coastal populations, where the trees of all age classes did not show significant differences. Regarding differences among clusters for the same age classes, similar results to both analyzed periods were observed. Costal populations had the lowest growth in BAI in all age classes, while, in the Highest population, this showed the highest growth in both young and old trees. The higher growth in mature trees were found in the Andes population.
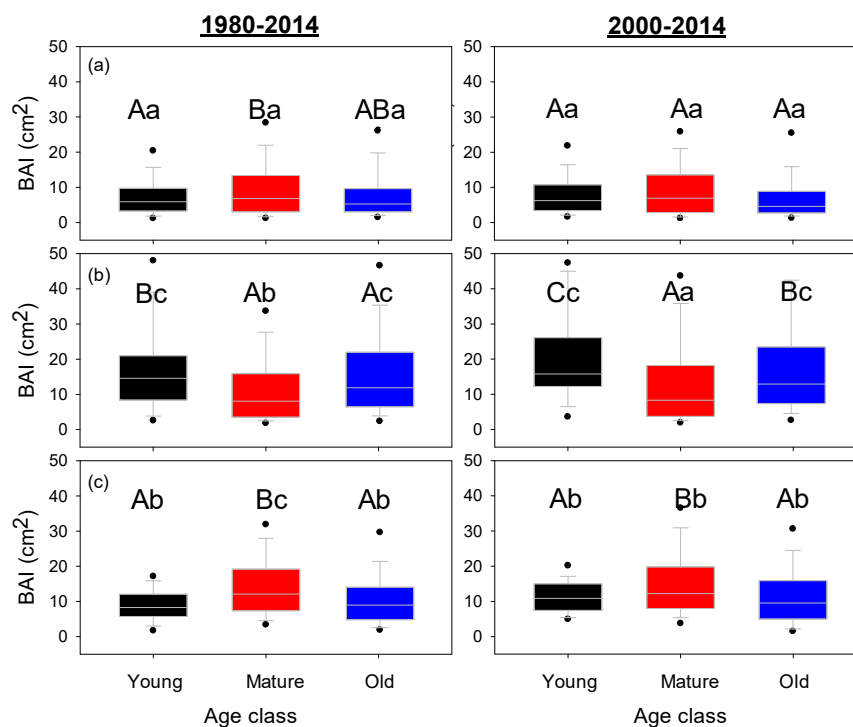
Figure 5. Difference of the basal area increment (BAI) of *N. macrocarpa* populations among clusters and age classes for the period of 1980 to 2014 and 2000 to 2014. Uppercase letters indicate a difference among age classes by cluster. Lowercase letters indicate a difference among population clusters by age classes (Kruskal-Wallis test using *p* < 0.05). (**a**) Coastal, (**b**) Highest, and (**c**) Andes.

4. Discussion

Based on the analysis of ten tree-ring chronologies of *N. macrocarpa* covering the species' natural distribution in the Mediterranean deciduous forests of Central Chile (MDFC), we verified that the growth of the species is highly sensitive to climatic variability both among populations and age classes. The results provide new knowledge about a poorly studied forest ecosystem, with high levels of endemism but also high disturbance rates [16,27]. The significant decrease in precipitation and increase in temperature experienced in the MDFC region during the last three decades seems to have influenced the growth of trees, despite the worldwide rising atmospheric CO_2 concentrations (Figure S1b). There are indications that dry sites would express adaptations to rising CO_2, which causes a positive effect on forest growth due to an iWUE stimulation [31]. However, the dry sites analyzed in this case (PLC, SER, RRL, and SAC) from the Coastal range did not corroborate our hypothesis. In fact, although Coastal and Andes populations of *N. macrocarpa* have bio-geographical differences Figure 1b, [27,28], all populations showed a forest growth decline since the year 2000 (Figure 4).

The highest population seems to have the highest resilience to recent climate change, as shown by any recent break point in their ring-width chronologies (Figure S3). This finding would be related to a high growth of their trees, indiscriminately expressed as ring widths or BAI (Figure 3, Figure S3). The high growth was maintained from the beginning of the chronology in all age classes (Figure 4), which could be related with low anthropogenic pressure (Table 1). However, this finding seems to be related to young trees, which had a higher growth rate during the initial 30 years (Figure 2a), and showed the highest growth inter-populations for the period from 1980 to 2014 (Figure 5). In other Mediterranean forests, Camarero et al. (2015) observed that *Pinus uncinata*, which are younger trees, display significantly larger values of BAI than trees in the rest of the age classes. Despite the positive aspects of trees from the highest sites, we observed a sharp forest decline after the year 2000, both in mature and old trees, but not for young trees (Figure 4), which indicates that the growth of these trees were impacted by the increase in drought conditions during the last 15 years. Moreover, both the Andes and the other Coastal populations showed a significant decline for the period from 2000 to 2014. This decline was also observed since 1980 in mature and old trees, so we must reject our hypothesis I. We give, therefore, evidence that young, mature, and old trees from MDFC from both Coastal and Andes sites were affected by recent climate changes. Although all areas of our study are under some protection regime, this would not ensure their forest decline nor their complete control of these forests.

We found that climatic variations correlated with the decline in *N. macrocarpa* growth during the last several decades (Table 2). The precipitation from May to November (before and during the austral growing season) was the main growth predictor for all age classes and populations, while temperature from October to December (beginning of cambial activity) was positively related to only Coastal and Andes populations. A significant association was found between precipitation (positive) during the rainy period, temperature (negative) during the spring/early-summer, and tree growth of *N. macrocarpa* populations (see growth-SPEI relationship, Table S1), which is a similar model reported for other tree species in Central Chile [21,24,54]. However, the significance of the climatic signal varies with age class (Table 2), which shows that young trees are more sensitive to climate variability than mature and old trees. Therefore, our hypothesis II is partially accepted. This would seem to indicate that younger trees are more sensitive to rising temperatures and, therefore, possibly more sensitive to drought [55]. Young trees with a less widespread root system may be committed to exploring greater diversity of moisture niches in soils and becoming more water-limited, while older trees with extensive root systems may tap into deeper water sources, which allows them to maintain higher rates of transpiration and photosynthesis [56]. In European Mediterranean forests, younger trees exhibited negative growth trends in recent years and these trends were often different and more abrupt than those detected in older age-cohorts [57].

We found that CO_2 fertilization caused a positive effect on the tree-ring growth in young trees of *N. macrocarpa* populations, for the period from 1980 to 2014 (Table 2). However, there was no net effect on tree growth for the last 15 years, so our hypothesis III is rejected (Figure 4). A recent work verified that rising CO_2 fertilization under future climatic scenarios (RCP 4.5 and RCP 8.5) does not guarantee an increase in tree growth in a Mediterranean forest in the Southwestern Pyrenees [58]. It should be noted that young trees at tree lines (Highest) do not show a negative significant trend, so the CO_2 seems to play a compensate role against the effect of precipitation/temperature incidence. Some authors note that tree-ring growth trends are more associated with high-low temperatures or high-low water availability than with the atmospheric increase in CO_2 [58]. However, we do not discard that CO_2 fertilization could lessen the negative impact of drought and temperature increases on tree growth at the driest sites, i.e., the negative BAI trends could have been more pronounced if atmospheric carbon remained stable [34]. Although young trees from the highest populations showed higher tree growth than mature and old trees for the same age (Figure 2), we cannot interpret that these higher growth rates could be directly linked to the instrumentally measured rising atmospheric CO_2 (Figure S1b). The tree growth rate could also be the result of age-related selection against fast-growing and slow-growing trees within a population, which is not necessarily linked to CO_2 fertilization [14,59].

If the warming trend continues in the MDFC region, trees could strategically increase their stomata closure, avoiding excessive water loss, but capturing less CO_2 and then producing less trunk biomass [60]. On the other hand, although there is more availability of atmospheric CO_2 concentrations, trees could show signals of changes on the net photosynthetic rate mainly by light saturation and Rubisco (RuBP) regeneration capacity limitation [61]. Therefore, the absence of growth increase in *N. macrocarpa* trees under rising atmospheric CO_2 would be explained by a water deficit and photosynthesis saturation.

Positive growth trends linked to CO_2 fertilization reported for other forest ecosystems were associated with an adaptation of trees to the climate by means of the iWUE, as an expression of the carbon fixed per unit of water transpired [2,62]. However, available carbon is not always associated with an enhanced basal area growth [63–65]. Other studies concerning *Nothofagus spp* showed positive trends of iWUE mainly from 1950 in southern Argentina [7] and southern Chile [62]. In Argentina, the authors concluded that, in dry sites, the strong water stress would reduce the photosynthetic rate to the maximum, so a tree growth decrease could not be offset by the iWUE increase [7]. Whereas in Chile, they observed an increase of BAI, which could be associated with a positive adaptation of iWUE [62]. However, their study was based on dominant trees, which is a fact that could generate some interpretation biases [14]. Therefore, an improved iWUE could mean an increase of growth, storage, root exudation, and metabolic respiration, but not necessarily linked to stem biomass. Field experiments are necessary to understand how adult trees of different ages and their dynamic processes are responding to the new drier and hotter climate conditions. Only recently a few forest micrometeorological monitoring sites have started to operate in southern Chile and Argentina [66], including measurements of water and carbon exchange, soil respiration, radial stem growth, and the transpiration flow to understand how climate change is affecting temperate forests. In addition, our dendroecological approach could be combined with tomography and growth simulation models to help with decision-support for management and conservation of forest ecosystems [67]. No such ecological monitoring activities have been conducted in the Mediterranean forests at this moment, even though these forests are highly endangered by human pressure, land use changes, and climate drying.

5. Conclusions

We concluded that the growth of *N. macrocarpa* populations from Mediterranean deciduous forests of Central Chile (MDFC) are being strongly affected by recent climate change in the region, as expressed by decreasing precipitations and increasing temperatures, but not due to the influence of rising atmospheric CO_2 on stem biomass, regardless of the age of trees. Even when it would be desirable to complement these results with carbon stable isotope analysis (i.e., iWUE), this study gives us the first appraisal about the resilience of rising atmospheric CO_2 and recent changes in precipitation and temperature variability of longleaf MDFC forests in South America. Recent studies demonstrated the potential use of BAI as a variable that reflects the growth stimulation (or not) of forests under 50 years of CO_2 fertilization and global warming, as a good complement to studies with stable isotopes [8,46].

Considering the worrying climate change projections for Central Chile [68], we would expect that the growth resilience of these forests will be affected in the future. Although all the studied populations are located in protected forests (park, reserve, or sanctuary), this does not guarantee the persistence of the species as climate conditions become more stressful. Field monitoring of the forest are necessary to understand more deeply how trees of different ages and regeneration status are responding to the new climate conditions. We hope these results will be considered as input for the agenda of policymakers and for the awareness of society against the risks of the ongoing climate change on the Mediterranean forests of Central Chile.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/8/653/s1, Figure S1. (a) Mean radial growth rate in mm year^{-1} (± SE in shaded gray line) of regional chronology of *N. macrocarpa* populations (black line). The orange square represents the piecewise regression model that shows the

break year since 1980 with $p < 0.001$. (b) Linear trends of climatic variables (precipitation (pp), temperature (T), and atmospheric CO_2 concentrations [CO_2]) since 1980. Figure S2. Relative frequency of trees in the three cluster populations according to age classes. (a) Coastal, (b) Highest, and (c) Andes. Figure S3. Ring-width chronologies according to each population cluster: (a) Coastal, (b) Highest, and (c) Andes. Shaded lines represent ± SE. Black lines show the break year according to the piecewise regression model ($p < 0.001$), between 1978 and 1979 in the Andes and Coastal populations (Highest populations did not show a significant break point). Table S1. Descriptive statistics for the ten tree-ring chronologies of *N. macrocarpa* (see Table 1 for chronology code definitions).

Conflicts of Interest: The authors declare no conflict of interest.

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