RESEARCH ARTICLE

Key Points:
- Tree-ring width and carbon isotope chronologies for two contrasting *Fitzroya* sites are presented
- Tree growth has decreased in the drier site and increased in the rainier site in recent decades
- *Fitzroya* trees from both sites have become more efficient in their water use in recent decades

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Increased water use efficiency but contrasting tree growth patterns in *Fitzroya cupressoides* forests of southern Chile during recent decades

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Abstract Little is known about how old-growth and massive forests are responding to environmental change. We investigated tree-ring growth and carbon isotopes of the long-lived and high biomass *Fitzroya cupressoides* in two stands growing in contrasting environmental conditions in the Coastal Range (~300 years old) and Andean Cordilleras (>1500 years old) of southern Chile. The interannual variability in δ^{13}C was assessed for the period 1800–2010, and changes in discrimination and intrinsic water use efficiency (iWUE) were evaluated in relation to changes in climate and tree-ring growth during the last century. ^{13}C discrimination has significantly decreased, and iWUE has increased since the 1900s in both sites. However, these trends in isotopic composition have been accompanied by different growth patterns: decreasing growth rates in the Coastal Range since the 1970s and increasing growth rates in the Andes since the 1900s. Trees growing in the Coastal Range have become more efficient in their use of water, probably due to reduced stomatal conductance caused by increases in CO_2 and warming. Trees growing in the Andes have also become more water use efficient, but this has been likely due to increased photosynthetic rates. *Fitzroya* forests, including particularly old-growth stands, are responding to recent environmental changes, and their response has been site dependent. The growth of forests under a more Mediterranean climate influence and restrictive soil conditions in the Coastal Range has been more negatively affected by current warming and drying; while the growth of old stands in the wet Andes has been positively affected by changes in climate (decreasing cloudiness) and increasing CO_2. Permanent monitoring of these endangered forests under ongoing environmental changes is needed in order to reassure the long-term preservation of this millennial-aged species.

1. Introduction

The impacts of atmospheric change on forests vary from being potentially positive, such as benefits resulting from higher atmospheric CO_2 concentrations, to being negative, such as decreased growth and increased mortality due to increases in temperature and in the frequency and intensity of drought events [*Allen et al.*, 2010]. The rapid increase in atmospheric CO_2 from ~ 285 ppm in 1850 to 398 ppm in 2014 [*Robertson et al.*, 2001; *Keeling et al.*, 2015] has been one of the most prominent and consistent environmental changes in the last century. This ongoing increase may lead to a reduction in stomatal conductance and transpiration in plants, resulting in an improved water use efficiency, as well as in an enhancement of the rate of photosynthesis and tree growth [*Drake et al.*, 1997]. Despite ecophysiological arguments for CO_2 fertilization, there is still an ongoing debate about the actual and future effects of CO_2 increase on tree growth in natural ecosystems [*Jones et al.*, 2014]. Results from Free-Air CO_2 Enrichment add (FACE) experiments indicate that growth has not been always stimulated, that it can be constrained by nitrogen limitation in temperate forests, or that responses might be short lived [*Norby et al.*, 2010; *Bader et al.*, 2013; *Körner*, 2013].

The assessment of forest growth responses to environmental changes from seasonal to centennial timescales can be performed using tree rings. Dendrochronological studies in different species have reported divergent growth trends in recent decades, ranging from increases attributed to warming and CO_2 fertilization

[*Soulé and Knapp*, 2006; *Voelker et al.*, 2006; *Leal et al.*, 2008; *Salzer et al.*, 2009] to decreases mainly due to rainfall decline in water-limited systems [*Sarris et al.*, 2007; *Andreu-Hayles et al.*, 2011; *Linares et al.*, 2011].

Stable carbon isotopes in tree rings provide information on important physiological changes that can influence growth. They indicate the balance between stomatal conductance and the rate of photosynthesis, which is mainly determined by atmospheric relative humidity and soil water content in dry sites and by summer radiation and temperature in wet sites [*McCarroll and Loader*, 2004]. Stable carbon isotope ratios ($\delta^{13}C$) provide a metric of discrimination (Δ) against the heavier isotope (^{13}C) during stomatal diffusion and carboxylation [*Farquhar et al.*, 1982]. High $\delta^{13}C$ ratios (less discrimination) in tree rings indicate low concentrations of CO_2 in the intercellular air spaces, which can be caused by lower stomatal conductance or high photosynthetic rates [*McCarroll and Pawellek*, 2001].

$\delta^{13}C$ in tree rings is usually sensitive to water status in water-limited environments. Partial stomatal closure may occur during warm and dry conditions, reducing the rate of CO_2 diffusion into the leaf, and therefore decreasing the discrimination against ^{13}C, and increasing $\delta^{13}C$. Consequently, $\delta^{13}C$ is negatively related with precipitation or humid conditions and positively related with temperature [*Brienen et al.*, 2011; *Johnstone et al.*, 2013]. On the other hand, solar radiation can be the dominant driver of tree ring $\delta^{13}C$ in wet environments [*Gagen et al.*, 2011a; *Loader et al.*, 2013]. Higher solar radiation induces higher photosynthetic rates in light-limited environments, resulting in less discrimination and a positive correlation between sunshine and tree ring $\delta^{13}C$ [*Johnstone et al.*, 2013].

By using $\delta^{13}C$ in tree rings, potential changes in the intrinsic water use efficiency (iWUE), a proxy for the water used per unit carbon gain at the leaf level, can be detected [*Saurer et al.*, 2004]. Changes in iWUE result from changes in carbon assimilation (A) and stomatal conductance of water vapor (g_w). Therefore, an increase in this variable may be due to either an increase in A, a decrease in g_w, or both [*Andreu-Hayles et al.*, 2011].

A number of studies have reported an increase in iWUE in different forests around the world during recent decades [*Saurer et al.*, 2004; *Linares et al.*, 2009; *Brienen et al.*, 2011; *Nock et al.*, 2011; *Franks et al.*, 2013]. However, this increase has not always been accompanied by positive changes in tree growth, indicating that other environmental factors are limiting growth [*Peñuelas et al.*, 2008; *Andreu-Hayles et al.*, 2011; *Lévesque et al.*, 2014].

Most of the ecological studies assessing changes in water use efficiency and generally looking at the responses of forests to climate change have focused on Northern Hemisphere ecosystems. There have been very few studies on South American temperate forests [e.g., *Srur et al.*, 2008; *Villalba et al.*, 2012], and it has been 20 years since any study assessed changes in the isotopic composition of the longest-lived tree species that grows in this region (*Fitzroya cupressoides* [*Leavitt and Lara*, 1994]). These slow-growing trees have the second oldest recorded age after bristlecone pine (*Pinus longaeva* [*Lara and Villalba*, 1993]). Our studies of the Andean *Fitzroya* forests suggest they may be the slowest-growing and longest-lived high biomass forest stands in the world [*Urrutia-Jalabert et al.*, 2015a].

Due to the endemic character, endangered status, and the narrow distribution of *Fitzroya cupressoides* (Alerce) forests, this ecosystem may be highly vulnerable to climate change.

The tree-ring growth of *Fitzroya* has been found to be mainly negatively associated with summer temperature and positively related to summer precipitation [*Villalba*, 1990; *Lara and Villalba*, 1993; *Neira and Lara*, 2000; *Barichivich*, 2005]. In fact, the strong negative relationship between tree-ring growth and previous summer temperature allowed a 3622 year summer temperature reconstruction for southern South America [*Lara and Villalba*, 1993]. *Leavitt and Lara* [1994] developed a 290 year $\delta^{13}C$ chronology for *Fitzroya* growing in the Andes Cordillera, finding that the $\delta^{13}C$ trend in the rings mostly followed the $\delta^{13}C$ trend of atmospheric CO_2 and did not seem significantly affected by systematic changes in environmental factors.

Both climate and atmospheric CO_2 concentrations have been changing in recent decades, and new isotopic studies on this species can provide important insights into the response of old-growth systems to ongoing environmental changes. Changes in this millennial-aged species would demonstrate real physiological responses, beyond the intrinsic ontogenic effects that frequently influence isotopic studies in younger forests [*Franks et al.*, 2013]. The aim of this study is to understand how *Fitzroya* forests have responded to environmental

changes in recent decades through the investigation of radial growth and tree-ring carbon isotopes in two different stands growing in the Coastal Range (medium age) and the Andean Cordillera (old growth) of southern Chile. Environmental conditions differ in these two areas, with a more Mediterranean climate influence (drier summer) and restrictive soils in the Coastal Range, compared with the Andes. Our specific objectives are (1) to evaluate trends in tree growth (basal area increment, BAI) in *Fitzroya* forests from each site over recent decades; (2) to assess trends in $\delta^{13}C$, isotope discrimination, and iWUE in these forests over the same period; and (3) to determine tree ring (width/carbon isotope)-climate relationships and assess whether changes in climate have helped to modulate the observed trends in tree-ring growth and the isotopic composition in *Fitzroya* forests at each site.

To our knowledge this is the only such study (combining tree growth and isotopic composition) conducted so far on long-lived and particularly wet temperate forests, providing important information about the response of these unique ecosystems to global atmospheric change.

2. Methods

2.1. Study Sites

Our study sites are located in southern Chile in (a) the Alerce Costero National Park, close to the northern distribution of this species in the Coastal Range at 40°10′S–73°26′W, and (b) the Alerce Andino National Park in the Andean Cordillera at 41°32′S–72°35′W.

In Alerce Costero the studied stands (two nearby 0.6 ha plots with similar structural characteristics) are located at around 850 m above sea level (asl); the forest is medium aged, dense (1412 trees per hectare), and dominated by *Fitzroya cupressoides*. Mean tree diameter and height (of trees $\geq$ 30 cm diameter at breast height) is approximately 27 cm and approximately 14 m, respectively. According to tree ring samples most of the trees are at least 240 years old, with the oldest tree reaching a minimum age of 294 years old. Forests in this area have been affected by fires in the last few centuries, and the studied stands are aggrading probably following a stand-devastating fire that occurred in 1681 [*Lara et al.*, 1999; *Barichivich*, 2005; *Urrutia-Jalabert et al.*, 2015a]. Total stand biomass reaches around 113 Mg C ha^{-1}, of which the *Fitzroya* trees account for around 93 Mg C ha^{-1} (82% [*Urrutia-Jalabert et al.*, 2015a]). The studied forest stands present a structure that could be considered typical of the widespread condition of *Fitzroya* forests in this range where human intervention has been substantial in recent centuries. In Alerce Andino, the studied stands (two nearby 0.6 ha plots with similar characteristics) are located at 760 m asl. The old-growth studied forest has fewer stems than in the Coastal Range (752 trees per hectare) and *Fitzroya* trees are much larger and taller, reaching a mean of approximately 137 cm diameter and approximately 31 m height. Most of the *Fitzroya* trees are at least 500 years old (tree cores that do not reach the pith) and the oldest tree recorded is at least 1470 years old. Total stand biomass reaches 447–517 Mg C ha^{-1}, of which *Fitzroya* accounts for 329–401 Mg C ha^{-1} (74–78%) [*Urrutia-Jalabert et al.*, 2015a]. The size structure of the forest indicates that the *Fitzroya* trees form a single pioneer cohort that was established over 1500 years ago after a disturbance (probably a landslide) but that is not regenerating under current forest conditions and also showing no mortality. Underneath *Fitzroya* there is a high biomass subcanopy of *Nothofagus nitida* (Nothofagaceae) and other evergreen species (*Saxegothaea conspicua*, *Podocarpus nubigenus*, *Laureliopsis philippiana*, *Myrceugenia chrysocarpa*, among others) that have grown up between *Fitzroya* [*Urrutia-Jalabert et al.*, 2015a].

Both areas are characterized by high annual precipitation, reaching 4860 mm in the Coastal Range site and approximately 6600 mm in the Andes during 2012 [*Urrutia-Jalabert et al.*, 2015b]. The northern coastal site has a more Mediterranean climate influence that makes summers drier in this area (average of 839 mm for December–February 2011–2013) compared to the Andes (average of 1413 mm for the same period [*Veblen and Ashton*, 1982; *Urrutia-Jalabert et al.*, 2015b]). During 2012, mean annual temperature was 7.26°C and 6.89°C in the Coastal Range and Andes sites, respectively. Snowfall is common during winter (from May through September) and persists until spring especially in the Andean site [*Donoso et al.*, 1990]. Solar radiation is lower during most of the year in the Andes than in the Coastal Range (24% lower during 2012).

Soils in the Coastal Range are derived from pre-Cambrian to Paleozoic metamorphic rocks, have a sandy loam texture, and are generally shallow (approximately 40–60 cm depth), very poor in nutrients, and severely podzolized [*Veblen and Ashton*, 1982; *Urrutia-Jalabert et al.*, 2015a]. They have poor drainage due to the presence

of schist at shallow depths and can get particularly dry during rainless periods in summer, having a low water retention capacity [*Barichivich*, 2005; V. Gerding, personal communication, 2013]. Soils in the Andean site are derived from volcanic parental material; they have a silty loam texture, high C/N ratios and high organic matter content [*Peralta et al.*, 1982; *Corporación Nacional Forestal*, 1985; *Urrutia-Jalabert et al.*, 2015a]. Soils in this site are deeper (approximately 70–90 cm depth), have better water retention properties, and are wetter than those in the Coastal Range all year round (R. Urrutia-Jalabert et al., under review, 2015).

2.2. Tree-Ring Sampling and Tree-Ring Width Chronologies Development

We sampled 60 adult trees at each site. In the Coastal Range our sampling strategy was based on tree size, so the largest dominant trees (likely being the oldest ones) were chosen. In the Andes, the *Fitzroya* stand is even aged with most of the trees larger than 100 cm, so no specific sampling rule was followed. At each study site trees were double cored with a 5 mm diameter increment borer at approximately 1.3 m height. Cores were mounted, sanded and tree rings measured to 0.001 mm precision. Tree-ring series were visually dated, and cross-dating was verified using the computer program COFECHA [*Holmes*, 1983]. As the study site is in the Southern Hemisphere the growth season straddles two calendar years. For dating purposes we employed the Schulman convention [*Schulman*, 1956], which assigns to each tree ring the date of the year in which radial growth started. Ring width measurements of each tree-ring series were standardized to remove variability that is not related to climate (e.g., tree age) with a negative exponential curve or a linear regression using the ARSTAN44h2 program [*Cook and Krusic*, 2013]. The quality of the mean standard chronology (mean of standardized series) was evaluated using the expressed population signal (EPS) statistic. EPS is a measure of the similarity between a chronology and a hypothetical one that has been infinitely replicated [*Wigley et al.*, 1984]. When the EPS value is above a determined threshold (0.85), the chronology can be considered robust, and it is an indication of temporal stability, good quality, and a strong common signal [*Wigley et al.*, 1984]. Chronologies were as old as the length of the increment borer (50–60 cm), diameter of the tree, and quality of the samples allowed.

Basal area increments (BAI) for each forest stand were calculated as the mean of the basal area increment of each raw series. The basal area increment for every year in each series was calculated as

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

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

BAI is a proxy for aboveground woody biomass accumulation. Trends in unstandardized BAI, unlike trends in tree-ring widths, do not decline with age [*Silva et al.*, 2010]. Thus, a negative trend in BAI can be a true indication of a growth decline [*Jump et al.*, 2006; *Voelker et al.*, 2008; *Silva et al.*, 2010].

Trends in the BAI chronologies were computed for three different periods (1900–2010, 1950–2010, and 1970–2010) using the Mann-Kendall non-parametric trend test (*mkTrend* routine from the *fume* R package; Santander Meteorology group, 2012), which accounts for the effect of temporal autocorrelation on the significance. These periods were chosen to assess changes since the beginning and midcentury and also in more recent decades when important shifts in growth and isotopic composition have been reported in other studies [*Andreu-Hayles et al.*, 2011; *Gagen et al.*, 2011b].

2.3. Carbon Isotope Chronologies

Annual rings from five trees (five cores) for the last 210 years (1800–2010) in each site were analyzed for carbon isotopes. In order to maintain the temporal integrity of the isotopic signal in this study [*Loader et al.*, 2007] and due to strong correlations reported for the carbon isotope composition between wood and cellulose [*Borella et al.*, 1998; *Warren et al.*, 2001; *Loader et al.*, 2003; *Harlow et al.*, 2006; *Taylor et al.*, 2008; *Granados*, 2011], wood without extractives was used. Extractives were removed because they can vary within the same tree; they are soluble and mobile; and may then possibly move across ring boundaries [*Harlow et al.*, 2006; *Taylor et al.*, 2008]. Due to the small amount of wood available, resin extraction was performed on core samples (2.5 × 50 mm), as done by *Lévesque et al.* [2014], following the three-step method proposed by *Leavitt and Danzer* [1993]. Cores were treated under the 2:1 toluene/ethanol, 100% ethanol, and boiling water steps for 27 h (each phase). Annual rings were subsequently split using a razor blade and pooled for the five trees in each site in order to perform the isotopic analysis. The pooled sample was manually ground to 40 mesh and mixed using a razor blade and a ceramic mortar. An aliquot of 0.3–0.4 mg of each

sample was weighed in a tin capsule and was analyzed using a Carlo Erba NC1500 (Milan, Italy) elemental analyzer online with a Delta Plus XL (ThermoQuest, Bremen, Germany) mass spectrometer. This was performed at the Laboratorio de Biogeoquímica de Isótopos Estables at the Instituto Andaluz de Ciencias de la Tierra (Consejo Superior de Investigaciones Científicas-University of Granada, Spain). Due to the manual mixing, three replicates of each ring were analyzed with the objective of having a representative sample of the whole ring. To have an estimate of inter-tree variability, isotopic analyses were also performed separately for each tree every 10 years. Commercial CO_2 was used as the internal standard for isotopic analyses. Standards were systematically interspersed in analytical batches every ten samples and precision was better than ± 0.1‰ for $\delta^{13}C$.

The carbon isotope ratio ($^{13}C/^{12}C$) was expressed with reference to standard material for which the isotopic ratio is known. The ratio corresponds to $\delta^{13}C$ and is expressed as

$$\delta^{13}C\ (‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right)1000 \tag{2}$$

where R_{sample} and $R_{standard}$ are the carbon ratios of the sample and standard (Vienna Pee Dee Belemnite), respectively [*McCarroll and Loader*, 2004].

The isotopic discrimination (Δ) resulting from the preferential use of ^{12}C over ^{13}C during photosynthesis was calculated using the following expression [*Farquhar et al.*, 1982]:

$$\Delta^{13}C = \frac{\delta^{13}C_{atm} - \delta^{13}C_{tree}}{1 + \frac{\delta^{13}C_{tree}}{1000}} \tag{3}$$

where $\delta^{13}C_{atm}$ corresponds to the isotopic value of atmospheric CO_2 and $\delta^{13}C_{tree}$ the measured isotopic ratio in tree rings. Following *Farquhar et al.* [1982], carbon discrimination was linearly related to the ratio intercellular (c_i) to ambient (c_a) CO_2 concentration through the expression:

$$\Delta^{13}C \cong a + (b - a)\frac{c_i}{c_a} \tag{4}$$

where a is the fractionation related to the diffusion of atmospheric CO_2 through stomata (4.4‰) and b the fractionation associated with the enzymatic carbon fixation (27‰). iWUE, which corresponds to the ratio between the net assimilation rate (A) and stomatal conductance to water vapor (g_w [*Ehleringer*, 1993]), was calculated as follows [*McCarroll and Loader*, 2004]:

$$iWUE = c_a\left(1 - \frac{c_i}{c_a}\right) \times 0.625 \tag{5}$$

$\delta^{13}C_{atm}$ and c_a were obtained from *McCarroll and Loader* [2004] for the period 1850–1997; values for 1998–2010 were obtained from the Scripps CO_2 website (http://scrippsco2.ucsd.edu/).

In order to establish relationships between the $\delta^{13}C$ chronology and climate variables in each site, $\delta^{13}C$ in tree rings was first corrected for its decreasing trend attributed to the rise of ^{13}C-depleted atmospheric CO_2 caused by the burning of fossil fuels and deforestation since industrialization (the Suess effect, $\delta^{13}C_c$). This correction was performed subtracting the difference between the atmospheric carbon isotope composition (for each year) and a pre-industrial standard value of -6.4% [*McCarroll and Loader*, 2004].

Changes in iWUE together with changes in BAI can provide insight into the natural responses of trees in both sites to increasing atmospheric CO_2 concentrations [*Waterhouse et al.*, 2004]. Leaving aside positive influences of climate, a positive relationship between changes in growth and iWUE could indicate CO_2 stimulation, while negative relationships would reflect the influence of stressors [*Silva and Anand*, 2013]. Since iWUE is a direct function of c_a, its trend may likely be positive over time [*Silva and Horwath*, 2013]; so trends in discrimination and c_i were also evaluated. The Mann-Kendall trend test was used to assess changes in isotopic variables during recent decades.

2.4. Trends in Climate Variables and Tree Rings-Climate Relationships

In order to assess changes in climate conditions, stations with the longest and more reliable climate records located close to both study areas were used. Monthly records from the Valdivia station, located at a low altitude approximately 45 km north of the Coastal Range site (9 m asl at 39°48′S, 73°14′W) and from Puerto Montt

Table 1. Characteristics of Tree-Ring Width Chronologies

Site	Alerce Costero	Alerce Andino
Total number of series	97	52
Time span (years)	1714–2010	772–2010
Mean series intercorrelation	0.464	0.453
Mean sensitivity	0.217	0.292
Period EPS ≥ 0.85	1739–2010	1355–2010

located at a low altitude approximately 43 km west of the Andean site (85 m asl at 41°25′S, 73°05′W) were used as proxies for the local climate of each site. No stations with long-term records exist at higher elevations close to both study sites; however, seasonal and longer term climate anomalies are likely to be strongly correlated between lowlands and highlands. Monthly temperature and precipitation in the Puerto Montt and Alerce Andino stations, for example, were strongly correlated over the common period November 2011 to May 2013 ($r = 0.93$ for precipitation and $r = 0.96$ for temperature). Both Valdivia and Puerto Montt meteorological stations recorded precipitation, mean, and maximum and minimum temperatures and spanned the 1960–2010 period (Universidad Austral de Chile [*Dirección Meteorológica de Chile* (*DMC*), 2014]). There was also a record of cloudiness from Puerto Montt measured in oktas (eighths), which refers to the proportion of the sky covered by clouds (1965–2010) [*DMC*, 2014].

Trends in climate records were evaluated for austral summer (December–February) and spring-summer (September–February) using the Mann-Kendall trend test. These seasons have been identified as the most important for tree growth processes in *Fitzroya* [*Villalba*, 1990; *Lara and Villalba*, 1993].

In order to determine the climate variables related to tree-ring growth, correlation analyses were performed between the standardized chronologies from each site and the associated climate data, both processed using a 20 year high-pass filter to isolate the year-to-year variability and avoid the effect of trends in the correlations. Furthermore, the tree-ring width chronology from the Coastal Range was also prewhitened due to a strong autocorrelation of first order ($r = 0.82$ for 1960–2010 period), even in the high-pass filtered series ($r = 0.43$, $p < 0.05$, for 1960–2010). Autocorrelation is likely to be present when photosynthate reserves from the previous year are used to produce the current ring, and since its presence violates the independence assumption of most statistical tests and biases hypothesis testing, it should be removed prior any correlation analysis [*Monserud and Marshall*, 2001]. Autocorrelation in the Andean chronology was significant only before detrending ($r = 0.48$, $p < 0.05$, for 1960–2010). Therefore, in the case of the Coastal Range chronology, residuals of a lag-1 autoregressive model were used for correlation analysis [*Monserud and Marshall*, 2001]. Bootstrapped correlations were calculated between monthly climate variables (ranging from January of the previous summer until March of the current summer) and tree ring data using the *cor* and the *boot* functions from the *stats* and *boot* R packages, respectively (R Development Core Team 2014). Only correlations significant at 95% confidence level were considered.

Bootstrapped correlation analyses for the isotopic data were performed between the corrected $\delta^{13}C$ ($\delta^{13}C_c$) chronologies from each site and monthly climate variables (also processed using a 20 year high-pass filter). The autocorrelation in both chronologies before detrending was 0.51 and 0.50 in the Coastal Range and Andes, respectively ($p < 0.05$, for the 1960–2010 period).

3. Results

3.1. Tree-Ring Width and BAI Chronologies

The tree-ring width chronologies spanned a period of 296 years in the Coastal Range and 1238 years in the Andes (Table 1). Descriptive statistics of these chronologies obtained from the COFECHA and ARSTAN44h2 programs are presented in Table 1.

The tree-ring width chronology from the Coastal Range site is characterized by two periods of high ring width values at the beginning of the 1800s and particularly the early 1900s. These events likely correspond to growth releases after fire events (Figures S1a and S1b in the supporting information). The Andean chronology seems more stable around the mean and has a lower mean ring width (0.34 ± 0.01 mm) compared with the coastal one (0.75 ± 0.01 mm) during the common period when the coastal chronology has an EPS value ≥ 0.85 (1739–2010, Table 1 and Figures S1c and S1d).

The Coastal Range BAI record shows a marked decreasing trend especially since the 1970s (slope = -0.07 cm^2 yr^{-1}, $p = 0.05$), indicating that trees in this forest are experiencing lower growth rates just
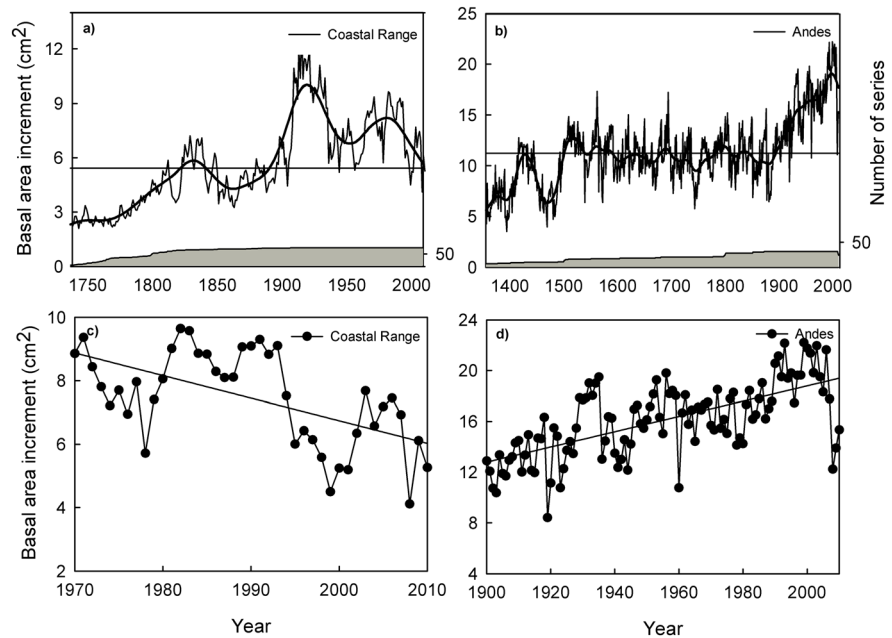
Figure 1. (a and b) Basal area increment chronologies (in cm^2) for the period 1739–2010 in Alerce Costero (Coastal Range) and 1355–2010 in Alerce Andino (Andes). A cubic spline version designed to reduce 50% of the variance in a sine wave with a periodicity of 25 years is also shown (bold black line [*Cook and Peters*, 1981]). (c and d) Basal area increment and its trend since 1970 in the Coastal Range and since 1900 in the Andes.

in recent decades (Figures 1a and 1c). This trend is also seen (and significant) in the standardized tree-ring width chronology from the site (not shown). The BAI trend for the 1900–2010 period is not meaningful due to the fire event at the beginning of the century, and the decreasing trend was not significant for the 1950–2010 period (slope = −0.0035, $p = 0.83$). On the other hand, in the Andean site the BAI record shows a consistent increasing trend since the 1900s (slope = 0.065, $p = 1.83 \times 10^{-7}$), with significant positive slopes also since 1950 (slope = 0.05, $p = 0.048$) and 1970 (slope = 0.118, $p = 0.033$, Figures 1b and 1d). The reported trends in the Coastal Range since the 1970s and the Andes since the 1900s are also observed in the raw tree-ring width chronologies from both sites and do not have any precedent considering the extent of each chronology (Figures S1a and S1c).

3.2. Carbon Isotope Chronologies

The raw $\delta^{13}C$ chronologies from both sites show the expected decreasing trend due to the rise of ^{13}C-depleted atmospheric CO_2 (Figures 2, 3, and S2). The mean standard deviation among trees for the whole period (1800–2010) was 0.47 and 0.59‰ in the Coastal Range and Andes, respectively; and the mean standard deviation of the three replicates for the total period was 0.31 and 0.23‰ in the coastal and Andean sites, respectively. An important feature is that the $\delta^{13}C$ values in the Coastal Range site were slightly lower at the beginning of 1800s (Figures 2a and 2b), and since the oldest sampled trees were < 300 years old, the first 50 analyzed years were not considered for further analysis to discard any potential juvenile effect. It has been reported that trees normally do not show any age-related $\delta^{13}C$ trend after an initial juvenile phase of approximately 50 years [*Gagen et al.*, 2007].

In contrast to the raw $\delta^{13}C$, a positive trend was observed in the $\delta^{13}C_c$ chronology from Alerce Costero since the 1900s (slope = 0.003‰ yr^{-1}, $p = 0.006$); while trends were also positive since the 1950s and 1970s (slope = 0.005, $p = 0.03$; slope = 0.001, $p = 0.53$, respectively, Figure 3a). Discrimination showed a negative-trend since the 1900s (slope = −0.003‰ yr^{-1}, $p = 0.009$) and also since the 1950s and 1970s (slope = −0.005, $p = 0.04$; slope = −0.001, $p = 0.61$, respectively, Figure 3b). There is also a positive slope in c_i (slope = 0.35 ppm yr^{-1}, $p = 6.68 \times 10^{-5}$, Figure 3d) and a very steep positive trend in iWUE since the 1900s (slope = 0.23 μmol mol^{-1} yr^{-1}, $p = 6.65 \times 10^{-5}$), which is especially evident since the 1970s (slope = 0.47, $p = 1.14 \times 10^{-7}$, Figure 3c). This indicates that trees from the drier Coastal Range site are being more efficient in the use of water especially in the last few decades.
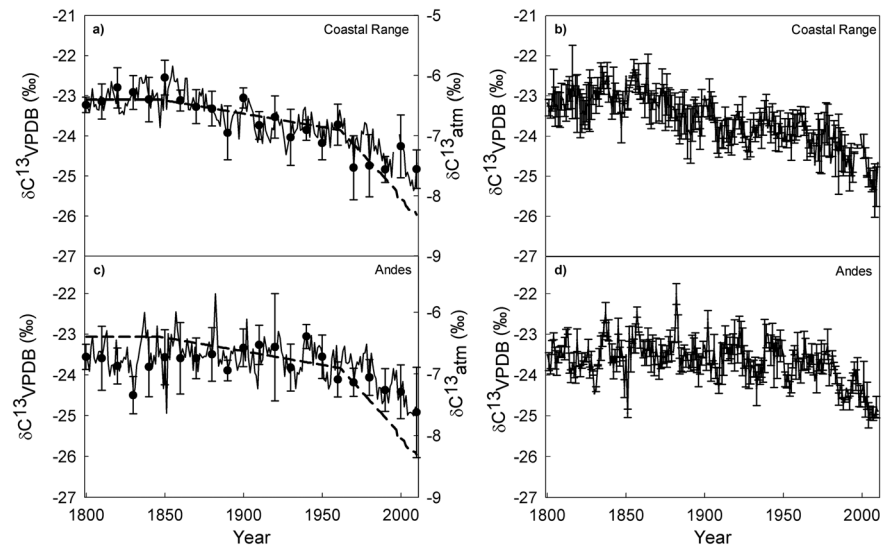
Figure 2. (a) Raw tree ring $\delta^{13}C$ chronology from Alerce Costero (Coastal Range) corresponding to the mean of three pooled replicates since 1800. Points and error bars every 10 years correspond to the mean and standard deviation of the five tree samples that form the chronology, respectively. This figure also shows the decreasing trend of the $\delta^{13}C_{atm}$ (dashed line, right axis). (b) Mean and standard deviation of the three $\delta^{13}C$ replicates in the Coastal Range. (c and d) The same as Figures 2a and 2b but for Alerce Andino (Andes).

In the Andes, the $\delta^{13}C_c$ trend was also significantly positive since the 1900s (slope = 0.004, $p = 4.76 \times 10^{-6}$), but not significant since the 1950s and 1970s (slope = 0.007, $p = 0.08$; slope = −0.003, $p = 0.46$, respectively, Figure 3e). The trend in discrimination was significantly negative since the 1900s (slope = −0.004, $p = 2.89 \times 10^{-6}$), but not significant since the 1950s and 1970s (slope = −0.007, $p = 0.12$; slope = 0.003, $p = 0.33$, respectively, Figure 3f). Positive trends were especially steep for c_i (slope = 0.35, $p = 2.58 \times 10^{-5}$, Figure 3h) and iWUE (slope = 0.24, $p = 2.34 \times 10^{-6}$) during the last century, and the trend in iWUE was even steeper and evident since 1950 (slope = 0.43, $p = 1.85 \times 10^{-17}$, Figure 3g). These trends indicate that trees from the Andes are also being more efficient in their water use, especially during the last few decades.

Comparing both sites, the $\delta^{13}C_c$ chronologies were somewhat similar with a significant correlation on an interannual basis ($r = 0.30$, $p < 0.05$, period 1900–2010). The trend in iWUE was also similar between sites (slopes of 0.23 and 0.24 in the Coastal Range and Andes, respectively). Comparison of non-detrended series are shown in Figure S3.

Standardized and high-pass filtered tree-ring width chronologies were also significantly correlated between sites, but only when considering the more recent period ($r = 0.23$ and $r = 0.27$, $p < 0.05$, for 1850–2010 and 1900–2010, respectively). Correlations between high-pass filtered tree growth and isotope chronologies were negative, but not significant in the Coastal Range ($r = −0.11$ and $r = −0.22$ for the period 1900–2010 and 1970–2010, respectively). In the Andean site, correlations were only significant and positive when considering the period with the steepest change in iWUE ($r = 0.32$, $p < 0.05$, for 1950–2010).

3.3. Trends in Climate Variables and Relationships With Tree-Ring Width and Isotope Chronologies

The climate records showed that spring-summer and summer precipitation have decreased in Valdivia and Puerto Montt over the period 1960–2010 (Figures 4a, 4d, S4a, and S4d). However, the precipitation decline has been stronger and significant only in Puerto Montt for both assessed periods ($p < 0.05$). Mean temperature records showed a warming trend during the same seasons, particularly in Valdivia ($p < 0.05$, Figures 4b, 4e, S4b, and S4e). This trend is driven only by rising maximum temperatures in both locations (Figures 4c, 4f, S4c, and S4f), with no significant trends in minimum temperatures at either site (not shown). Finally, cloudiness from Puerto Montt showed a significant negative trend in spring-summer and summer (1965–2010, Figures 4g and S4g). The rise in maximum temperatures but not in minimum temperatures is consistent with a trend of decreasing cloudiness and increasing insolation.
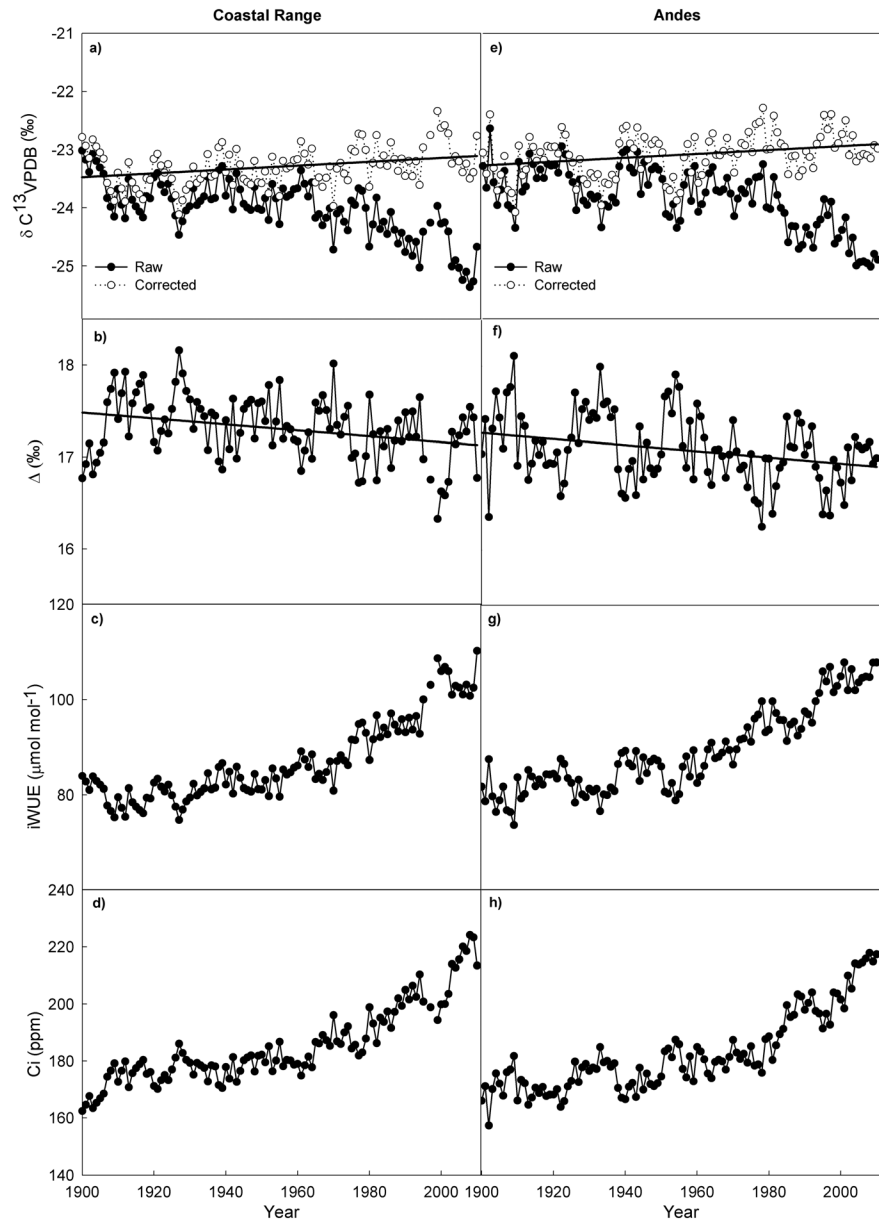
Figure 3. (a) Raw and $\delta^{13}C_c$ chronologies for Alerce Costero (Coastal Range) since 1900. The raw chronology presents the expected decreasing trend during the last century. (b) Discrimination against ^{13}C, (c) iWUE, and (d) changes in c_i (intercellular carbon) in Alerce Costero since 1900. (e–h) The same as Figures 3a–3d but for Alerce Andino (Andes). The trends in corrected $\delta^{13}C$ and discrimination are shown.

We first performed correlations between tree-ring growth and climatic variables using individual months to understand broad patterns (Figure 5). The monthly correlations highlighted distinct relationships with late spring-early summer and mid-late summer conditions, and also possible correlations with preceding summer meteorological conditions. We therefore concentrated our analysis in these broad summer groups: previous mid-late summer (Jan-Mar_p), current late spring-early summer (Nov-Dec_c), and current mid-late summer (Jan-Mar_c; Figure 5).

Tree growth in the Coastal Range site was negatively correlated with late spring-early summer mean and maximum temperatures and positively correlated with precipitation over the same period (November–December, Figures 5a–5c). Partial correlations suggest that maximum temperature seems to have the strongest (negative and significant) influence on growth rate ($r = -0.50$, $p < 0.05$), with only a moderate positive influence of precipitation ($r = 0.12$–0.23, $p > 0.05$).
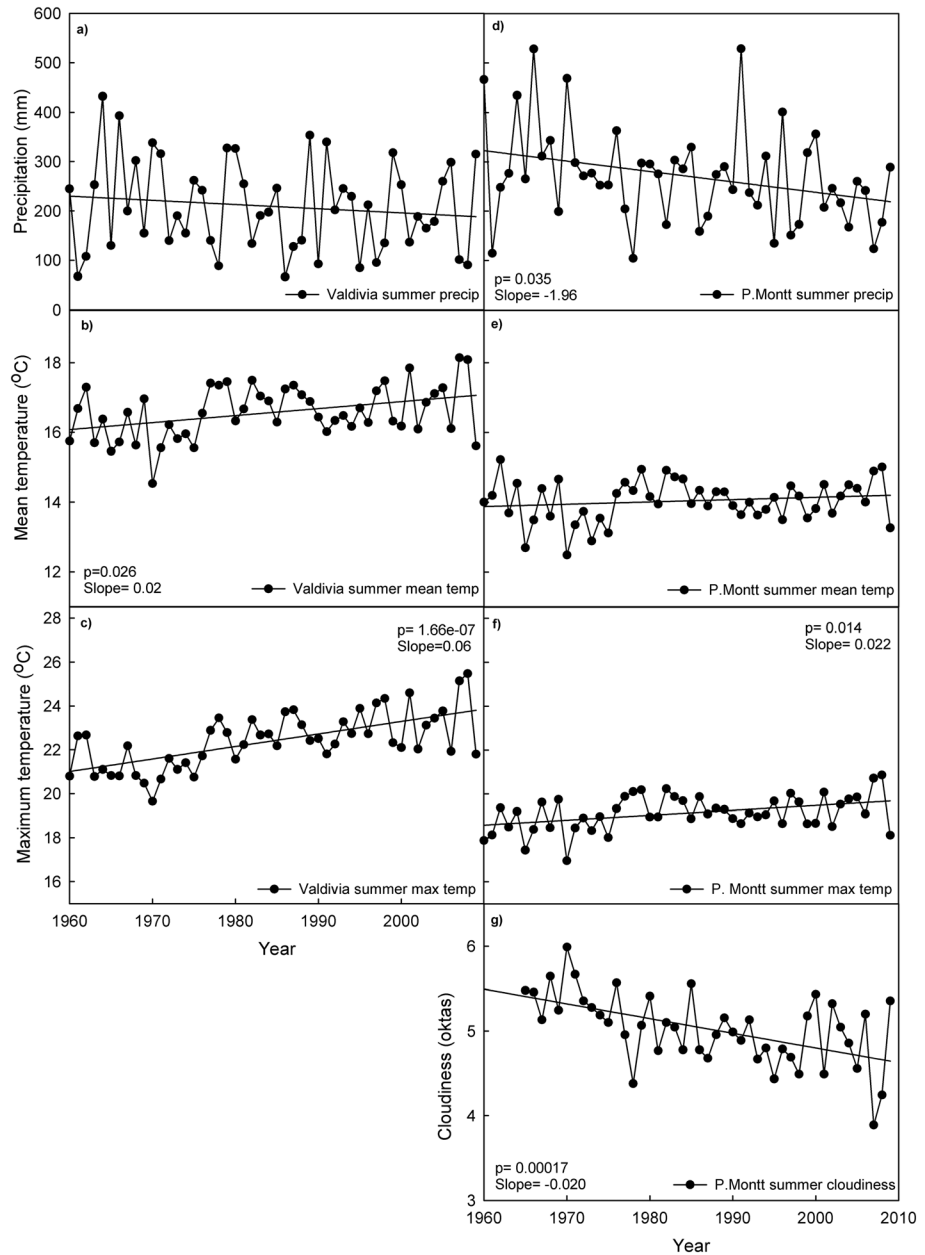
Figure 4. (a–c) Precipitation, mean temperature, and maximum temperature during summer (December–February) in Valdivia. (d–f) The same as Figures 4a–4c but for Puerto Montt. (g) Summer cloudiness in Puerto Montt. Only the significant slopes and p values are shown.

In the Andean site the most significant relationships for growth were negative correlations with the previous summer mean and maximum temperatures and a positive correlation with the previous summer cloudiness (Figures 5f, 5g, and 5i). Partial correlations with previous summer conditions show that when controlling for cloudiness, maximum temperature was the only variable significantly correlated with tree growth ($r = -0.31$, $p < 0.05$). In contrast to previous year relationships, correlations with current mid-late summer temperatures were positive but only significant for minimum and mean temperatures (Figures 5f–5h). Precipitation did not seem to have a significant effect on tree growth in this particularly rainy site (Figure 5e). Hence, in the Andean site warm temperatures in preceding years lead to less growth in the current year. Examples of tree growth-climate relationships in both sites are shown in Figure S5.
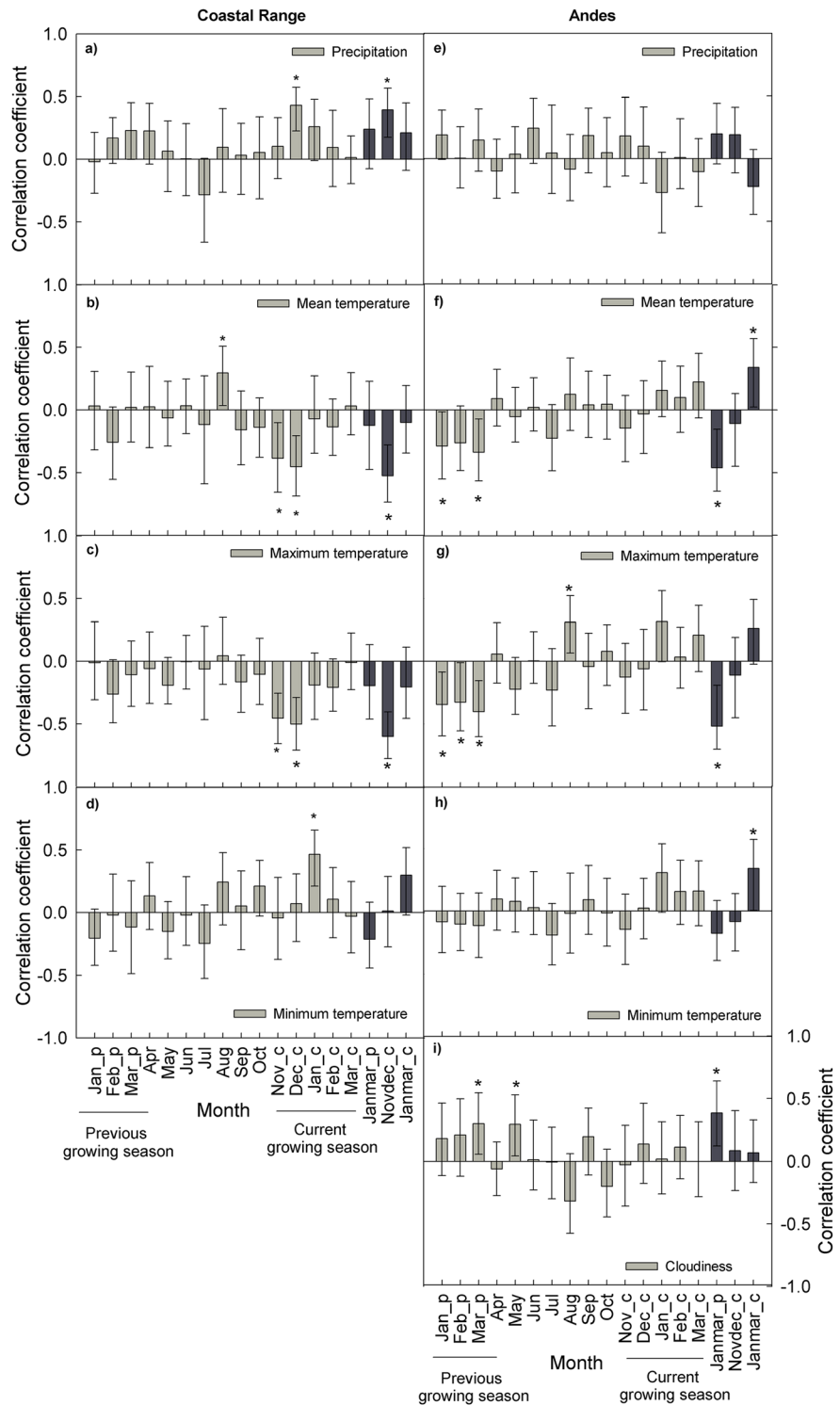
Figure 5. Correlations between the standardized chronology from the Coastal Range site and monthly (a) precipitation, (b) mean temperature, (c) maximum temperature, and (d) minimum temperature in Valdivia for the period 1960–2010. (e–h) As in Figures 5a–5d but for correlations between the standardized chronology from the Andean site and monthly climate variables in Puerto Montt. (i) Correlations between tree growth in the Andes and cloudiness in Puerto Montt. In all cases a 20 year high-pass filter was applied to the standardized chronologies and climate data, and prewhitening was additionally applied to the Coastal Range chronology (see section 2). Correlations with previous and current climate are indicated as "period_p" and "period_c," respectively. Mean correlations were significant if after 1000 bootstrapped iterations their confidence intervals do not cross zero. Significant correlations are marked with an asterisk.

For the isotope data (corrected $\delta^{13}C$ chronology) in the Coastal Range site, the strongest correlations were a positive correlation with current mid-late summer mean, maximum and minimum temperatures (only significant for mean temperature; Figures 6b–6d). This indicates that higher temperatures during mid-late summer lead to less discrimation and higher $\delta^{13}C$. There was also a significant negative correlation with previous mid-late summer mean temperature (Figure 6b). In the Andean site the strongest correlations were a negative correlation with mid-late summer cloudiness and a positive correlation with maximum temperature during the same period (Figures 6g and 6h). Thus, years with low summer cloudiness coincide with low discrimation and high $\delta^{13}C$ values. A significant negative correlation was also found with previous mid-late summer maximum temperature (Figure 6g). There were no significant correlations with summer minimum temperatures in this site (results not shown). Partial correlations between the $\delta^{13}C_c$ chronology and mean and maximum temperatures, controlling for cloudiness, indicate that temperature was the variable that mostly contributed to the relationships found for the previous summer, though no significant partial correlations were found. In contrast, for the current summer, cloudiness was the most important and significant factor when controlling for mean temperature. Examples of the isotopes-climate relationships are shown in Figure S6.

4. Discussion

4.1. Trends in Tree Growth and Carbon Isotope Chronologies

Since a negative trend in BAI is a strong signal of a genuine decline in tree growth [*Jump et al.*, 2006; *Silva et al.*, 2010], we are confident that biomass accumulation rates in Alerce Costero have been decreasing particularly since the 1970s. In the Andes, the sustained positive trend in tree growth is striking in this old stand, suggesting that the giant trees in this forest have been accumulating biomass at a faster rate since the beginning of the century.

The $\delta^{13}C_c$ chronologies showed significant positive trends since the 1900s in both sites; however, these trends appear to be weakening when analyzing the two more recent periods. Furthermore, discrimation has significantly decreased since the 1900s in both sites, which is in contrast with what was reported by *Leavitt and Lara* [1994] for an Andean site, who found a constant c_i/c_a since the 1700s and argued that the *Fitzroya* $\delta^{13}C$ was not being affected by changes in CO_2 or climate conditions. Differences in the trees' response between both studies may be partly caused by the different altitudes of the study sites (450 and 760 m asl in Alerce Andino in *Leavitt and Lara* [1994] and this study, respectively), which may lead to a different response of the species to climate because of differences in cloudiness and precipitation amounts.

Our discrimation calculations did not consider the mesophyll conductance of CO_2 from the intercellular space to the chloroplast, which is far more difficult to determine than stomatal conductance [*Gu and Sun*, 2014]. Although it has been argued that ignoring mesophyll conductance may underestimate the response of iWUE and c_i to increased CO_2 [*Seibt et al.*, 2008], we did not include this term in the calculation of isotopic discrimation because there is no such ecophysiological information for our species.

Following patterns in discrimation, iWUE has increased by 29% in Alerce Costero and 32% in Alerce Andino since the 1900s (increase between the period 1900–1910 and 2000–2010), indicating that trees are actually responding to environmental changes. These values compare relatively well with the range of values reported for forests in Europe and are higher than the mean reported just for conifers (25.7%) and for all species (27.8%) in this continent [*Saurer et al.*, 2014].

In order to further explore the response of trees in our study sites to environmental changes, and specifically to increases in CO_2, the observed changes in $\delta^{13}C_c$, discrimation and iWUE can be compared with the expected curves according to the three scenarios reported by *Saurer et al.* [2004]. These scenarios mainly diverge in the degree by which the increase in c_i follows the increase in c_a: (1) c_i constant, so $\delta^{13}C$ increases, c_i/c_a decreases, and iWUE increases strongly; (2) c_i increases in proportion to c_a, so c_i/c_a is constant, $\delta^{13}C$ decreases in parallel with $\delta^{13}C_{atm}$, and iWUE increases but not as strongly as in scenario 1; and (3) c_i increases at the same rate as c_a, so c_a-c_i is constant, $\delta^{13}C$ decreases more strongly than $\delta^{13}C_{atm}$, and iWUE is constant [*Saurer et al.*, 2004]. Trees from both sites showed an increasing trend in $\delta^{13}C_c$ and c_i, a decreasing trend in discrimation, and an increasing trend in iWUE since the 1900s, a response that is close to scenario 1 but that may well fit on the continuum between scenarios 1 and 2. Although c_i is not constant
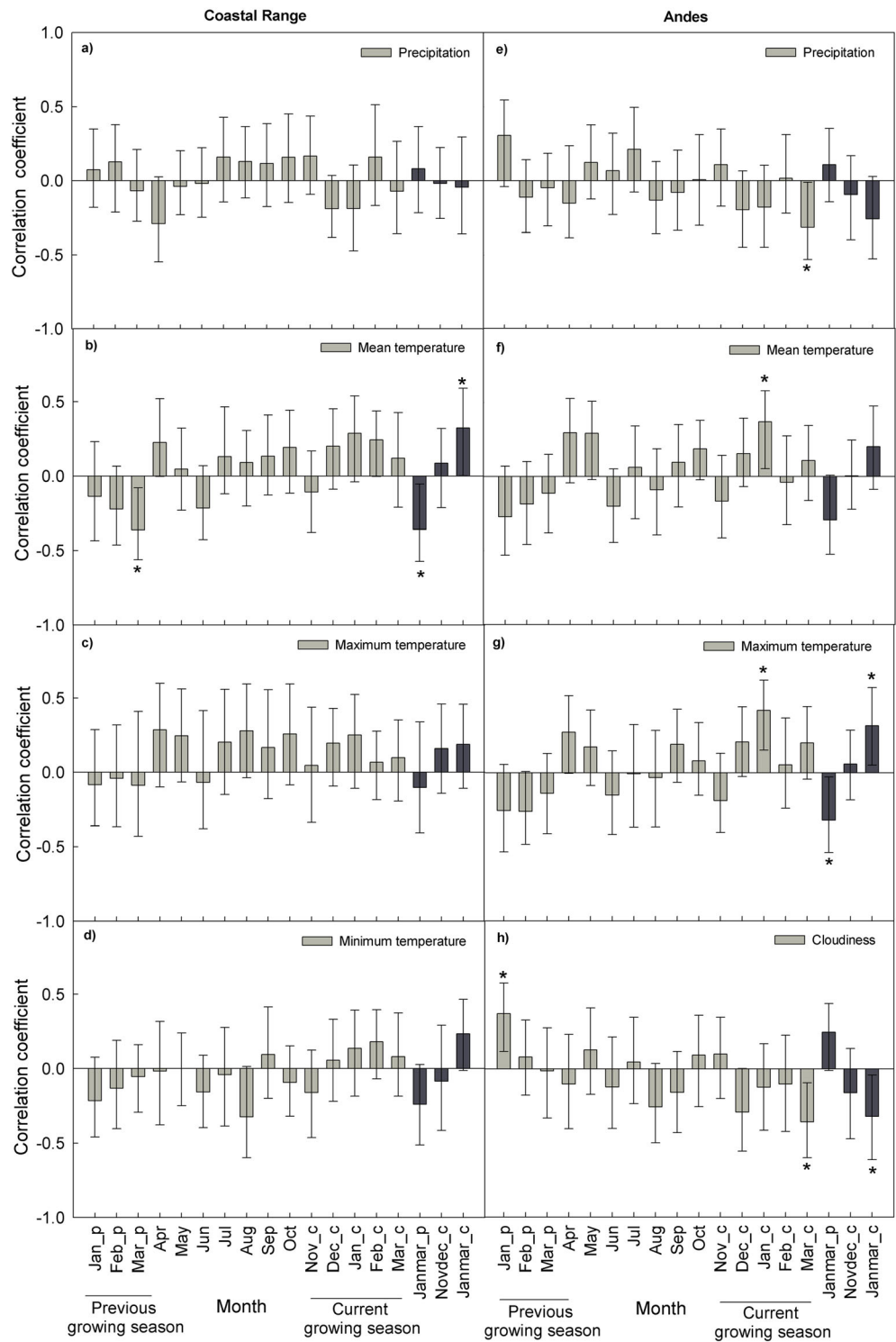
Figure 6. Correlations between the corrected $\delta^{13}C$ ($\delta^{13}C_c$) chronology from the Coastal Range site and monthly (a) precipitation, (b) mean temperature, (c) maximum temperature, and (d) minimum temperature in Valdivia for the period 1960–2010. (e–g) As in Figures 6a–6c but for correlations between the isotope chronology from Alerce Andino (Andes) and monthly climate variables in Puerto Montt. (h) Correlations between the Andean isotope chronology and cloudiness in Puerto Montt. In all cases a 20 year high-pass filter was applied to the isotope chronologies and climate data. Correlations with previous and current climate are indicated as period_p and period_c, respectively. Mean correlations were significant if after 1000 bootstrapped iterations their confidence intervals do not cross zero. Significant correlations are marked with an asterisk.

as scenario 1 predicts, it increases at a much lower rate than c_a, so c_i/c_a decreases. This indicates that trees may not only be responding to CO_2 but also that other environmental factors are influencing their stomatal conductance and photosynthetic rates, producing a decrease in discrimination in these sites [*Andreu-Hayles et al.*, 2011]. Trends in iWUE are especially strong since 1970 in the Coastal Range site, and since 1950 in the Andean site, when the decline in raw $\delta^{13}C$ is much less than the decline in $\delta^{13}C_{atm}$ in both sites (Figures 2a, 2c, 3c, and 3g).

The most common observed response at changing atmospheric CO_2 recorded in forests worldwide seems to be described by scenario 2, i.e., constant c_i/c_a. Examples include conifers in Eurasia and some species in Mediterranean areas [*Saurer et al.*, 2004; *Andreu-Hayles et al.*, 2011], as well as forests in China [*Wang et al.*, 2012]. A recent study in European forests also determined that trees were mostly exerting a moderate control on atmospheric CO_2 increases (toward a constant c_i/c_a [*Frank et al.*, 2015]). However, other species such as *Pinus sylvestris* in northwestern Spain [*Andreu-Hayles et al.*, 2011], *Abies alba* in the Spanish Pyrenees [*Linares and Camarero*, 2012], and a tropical dry forest species in Mexico [*Brienen et al.*, 2011] respond in a manner close to scenario 1, with stronger increases in iWUE.

The observed trends in the isotope series are certainly real responses of trees to environmental changes in the Andean site, due to the longevity and size of trees. In the Coastal Range, although trees are much younger (<300 years age), it is unlikely that an age/height effect has played a role in the last 100 years. The steepest increases in height are produced approximately until trees reach 20 cm in diameter, which according to the mean growth rate would correspond to trees of circa 130 years old (data not shown). Moreover, *Fitzroya* is a shade-intolerant species that tends to grow faster in height than diameter, which is reflected in the small height difference between trees 10–20 cm diameter (9 m) and trees 20–86 cm diameter (13 m) in this site.

4.2. Climate Relationships With Tree-Ring Width and Isotope Chronologies

The overall observed trends in climate are in line with climate change projections of warmer and drier summers in southern Chile, as summer rain belts migrate poleward in a warmer world [*Fuenzalida et al.*, 2007].

Tree growth was negatively correlated with temperature (especially maximum temperature) in both sites. The higher reliance on previous climate conditions in the Andean site could probably be explained by the shorter growing season, due to lower radiation and temperatures in the Andes compared with the Coastal Range [*Urrutia-Jalabert et al.*, 2015b]. This shorter growing season may result in the trees being more dependent on carbohydrate reserves from storage to initiate growth. Warmer and drier conditions during summer could cause stomata to close and, combined with higher respiration rates, could reduce the starch reserves that can be utilized in the following growing season [*Deslauriers et al.*, 2014; *Urrutia-Jalabert et al.*, 2015b].

In contrast, tree growth in the Coastal Range site is not correlated with the previous year climate yet presents a high lag-1 autocorrelation, which implies that current's year growth draws on carbon from the previous year. It has been reported that carbon investment in storage may help long-lived trees by giving them safety margins to keep hydraulic transport and metabolism under severe stress [*Epron et al.*, 2012; *Sala et al.*, 2012; *Palacio et al.*, 2014]. Moreover, it has been argued that the use of carbohydrates from storage enables resprouting, which seems important for trees exposed to recurrent disturbance [*Regier et al.*, 2010]. *Fitzroya* has the ability to resprout by root suckers, a strategy that is characteristic in the Coastal Range [*Veblen and Ashton*, 1982; *Donoso et al.*, 2006]. We hypothesize that growth at this site might be primarily limited by cambial dynamics (i.e., sink activity) rather than by carbon uptake (i.e., source). Thus, particularly hot and dry summers (less humid conditions and associated drier soils) will reduce growth, because of their primary effect on cell turgor and expansion. This is consistent with high-precision dendrometer observations showing that prolonged warm and dry conditions lead to strong stem contractions and reduced tree growth in this site [*Urrutia-Jalabert et al.*, 2015b]. The stronger Mediterranean influence (i.e., drier summers) and low soil water retention in the Coastal Range site would also make the tree growth relationship with summer precipitation much more likely to be significant at this site, as is observed.

The positive effect of current temperature on tree growth in the Andes might be partly given by the positive effect that night temperatures have on growth in this site [*Urrutia-Jalabert et al.*, 2015b], and also by higher radiation levels commonly associated with warmer conditions (this is concluded based on the isotopic response of trees).

The stronger tree growth relationships with maximum (diurnal) rather than with mean temperature in both sites indicate that vapor pressure deficit (VPD) may be the key variable negatively related with *Fitzroya* growth on a monthly-to-seasonal timescale, as also suggested by *Urrutia-Jalabert et al.* [2015b] using high-precision dendrometers.

Temperature seems to be the main factor modulating $\delta^{13}C$ in the Coastal Range site. The relationship with temperature is partly indirect, since hot summers are usually drier, so temperature is correlated with vapor pressure deficit and soil water content, which are the variables that more directly influence stomatal conductance, and consequently $\delta^{13}C$ [*McCarroll and Loader*, 2004]. Thus, high temperatures or low humidity reduce stomatal aperture and discrimination against ^{13}C (high $\delta^{13}C$ values [*Helle and Schleser*, 2004a]), which is consistent with the drier climate and poor soil water retention conditions observed in this site.

In the Andean site there was a negative relationship between $\delta^{13}C$ and current summer cloudiness, which can be explained by the direct positive influence that irradiance has on photosynthetic rate, and consequently on a decreased discrimination and increased iWUE [*McCarroll and Loader*, 2004; *Johnstone et al.*, 2013]. Although we did not have cloudiness data for the Coastal Range site, using the data from Puerto Montt did not give any significant correlation. The positive influence of radiation in the Andes may be due to the lower radiation and much higher precipitation in this site. As the Andean site is rarely if ever water limited, the trees are able to take advantage of the extra solar radiation during periods of low rain and cloud cover. In the Coastal Range site, the concurrent water stress prevents trees from taking advantage of higher insolation. A negative correlation between cloudiness and $\delta^{13}C$ has been reported especially in other sites that are usually not water limited, such as coniferous forests in Northern Europe [*Gagen et al.*, 2011a; *Loader et al.*, 2013] and coastal redwoods in Northern California (negative relationship with fog [*Johnstone et al.*, 2013]). The positive relationship between $\delta^{13}C$ and current temperature in the Andes would be mainly given by its correlation with cloudiness (e.g., less cloudy days are warmer).

The negative correlation between $\delta^{13}C$ and temperature from the previous growing season in both sites is difficult to justify in terms of the isotopic theory. One possible explanation could be related to the strong carryover effect of stored products in this species (significant lag-1 autocorrelation in growth and $\delta^{13}C$). It has been reported, especially for deciduous tree species, that there is a close correlation between the isotopic signature of the early wood of a year and the latewood of the previous year or simply that the carbon incorporated in early wood mainly comes from enriched stored starch from the previous season [*Helle and Schleser*, 2004b; *Offermann et al.*, 2011]. This effect has also been demonstrated for evergreen and conifer trees [*Jäggi et al.*, 2002; *Kagawa et al.*, 2006; *Vaganov et al.*, 2009].

We hypothesize that increasing summer temperatures would cause higher maintenance respiration rates [*Adams et al.*, 2009], which could reduce the starch reserves that can be used for the following growth period [*Deslauriers et al.*, 2014; *Urrutia-Jalabert et al.*, 2015b]. This reduction in carbon reserves would cause that less growth during the following year would rely on the enriched starch, and therefore, the $\delta^{13}C$ in this ring wood would be more depleted. The opposite pattern would also hold true, if lower temperatures are present. This explanation would be especially supported in the Andean site, with lower tree growth following a warmer preceding summer. In the Coastal Range site this mechanism is less supported; however, if carbohydrates are easily transferred from one year to another (high autocorrelation in growth), the isotopical signal in carbon can be also transferred.

The use of whole-ring wood in this study is a constraint for deciphering a clear climate signal in carbon isotopes in *Fitzroya* and prevents higher correlation coefficients. The use of stored carbon in early wood and the mixing of carbohydrate pools of different origin and age have been reported to prevent or dampen the relationship between $\delta^{13}C$ and climate [*Keel et al.*, 2007; *Offermann et al.*, 2011; *Gessler et al.*, 2014]. Further isotopic studies should attempt to separate early and late wood components, although the narrow rings of *Fitzroya* may be a limitation.

Finally, the weak (negative) correlation between tree growth and isotope records in the Coastal Range can be explained because the months with a significant climate effect were different for tree-ring width and $\delta^{13}C$. This can also be due because wood growth is often disconnected from carbon assimilation caused by variable allocation to other tissues and remobilization of carbohydrate reserves [*Mölder et al.*, 2011; *Härdtle et al.*, 2013]. It is noteworthy, however, that when 10 year running correlations between detrended ring width
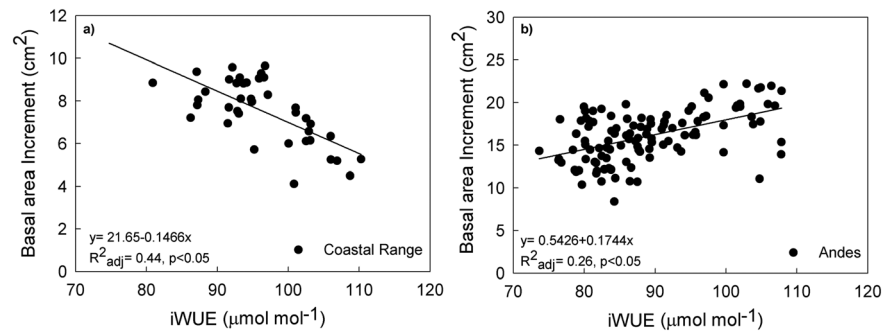
Figure 7. (a) Relationship between the basal area increment chronology from Alerce Costero (Coastal Range) and intrinsic water use efficiency (iWUE) in trees from this area (period 1970–2010). (b) Relationship between the basal area increment chronology from Alerce Andino (Andes) and iWUE in trees from this area (period 1900–2010). The linear regression equation and the adjusted R^2 are presented as an approximate indicator of the relationship, but these statistics are not accurate due to temporal autocorrelation.

and isotope chronologies were performed in both sites since the 1850s, the trend in correlations was significantly negative (correlations have become more negative) in the Coastal Range site and significantly positive in the Andes (results not shown). Thus, according to what has been proposed by *Voelker et al.* [2014], tree growth in the coastal site has become more moisture limited in recent decades, while assimilation rates have been mostly constrained by low radiation and/or wet conditions in the Andes. In Alerce Andino, positive correlations between growth and carbon isotopes are in agreement with what could be expected, since lower discrimination and high $\delta^{13}C$ values are associated with higher growth in this site.

4.3. Changes in Tree Growth and Water Use Efficiency

A positive correlation between non-detrended BAI and iWUE changes in the Andean site (Figure 7) suggests that an increment in the photosynthetic rate, rather than a decrease in stomatal conductance, has been taking place [*Silva et al.*, 2010]. The increase in tree growth reported for the last century in this site is somewhat unexpected given the climate response of the species and the increasing trends in temperature in the area. We believe that this increasing growth trend has been produced by a raise in photosynthetic rates, which has likely been driven by some combination of CO_2 and/or surface radiation increases. A regional rainfall decline in southern Chile has been recorded since the beginning of the twentieth century (1901–2005 [*González-Reyes and Muñoz*, 2013]), so pronounced changes in CO_2 have occurred in parallel with changes in climate, making it difficult to distinguish between both effects. The positive effect of cloudiness reduction (more surface radiation) on tree ring development was inferred looking at the isotope-climate response, because current summer cloudiness is not significantly correlated with tree growth, probably because this variable is strongly correlated with precipitation (positively) and maximum temperature (negatively) and none of these variables are significantly related with growth in the current season. The positive correlation of growth with mean and mainly minimum temperature in the current summer is less likely to be playing a role on the *Fitzroya* increasing growth trend, since minimum temperatures are not increasing in the last decades. Further research is certainly needed to better understand the effects of previous and current climate conditions on the growth of Andean *Fitzroya* forests.

A similar positive growth response under current warming conditions has been reported for *Sequoia sempervirens* during recent decades, which has been attributed to increasing insolation due to reduced summer fog frequency in Northern California [*Sillett et al.*, 2015]. *Sequoiadendron giganteum* has also shown an increase in tree level productivity early this century compared with early twentieth century: trend that was attributed to different causes such as extended growing seasons, CO_2 fertilization, and/or nitrogen deposition [*Sillett et al.*, 2015]. Positive tree growth trends in long-lived and old trees, including the trend also observed in *Pinus longaeva* in California, emphasize that these trees are indeed able to respond to environmental changes [*Salzer et al.*, 2009; *Sillett et al.*, 2015].

Growth rates have also been reported to increase in recent decades especially in some other moist temperate sites [*Cole et al.*, 2010; *McMahon et al.*, 2010] and also in Mediterranean species, where the increase was mainly attributed to CO_2 fertilization [*Martinez-Vilalta et al.*, 2008; *Koutavas*, 2013].

A significant negative relationship between iWUE and BAI in the Coastal Range site since the 1970s reflects an increasingly stressed environment especially in most recent decades [*Silva and Anand*, 2013, Figure 7] and suggests that a reduction in stomatal conductance rather than an increase in photosynthetic rates has prevailed [*Lévesque et al.*, 2014]. The decreasing trend in growth may be produced by a negative effect of warmer temperatures (higher VPD and evapotranspiration under drier conditions) on cell growth and enlargement, with the increase in iWUE not being sufficient to counteract this effect. It is important to mention that dieback and tree mortality events have been observed in this site in recent years [*Barichivich*, 2005]. These events have been likely caused by an amplification of recent drought stress by shallow soils and physical damage by past fires [*Barichivich*, 2005]. Furthermore, significant decreasing trends in growth have also been observed in *Fitzroya* stands growing in the Central Depression and Coastal Range farther south in recent decades (chronologies not shown), implying that this behavior is not unique to the studied Coastal Range site.

Numerous studies have reported increases in iWUE, but no increases or even decreases in tree radial growth in Mediterranean [*Andreu-Hayles et al.*, 2011; *Linares et al.*, 2011], high altitude forests [*Gómez-Guerrero et al.*, 2013] and recently in tropical forests [*Van der Sleen et al.*, 2014]. Furthermore, no increases in growth have been recently reported for mesic sites in Europe, where temperature-induced drought stress has stimulated stomatal closure and consequently reduced carbon uptake and growth [*Lévesque et al.*, 2014]. Two global studies concluded that tree growth has not increased as expected due to CO_2 increases during the last 40 years and that other factors (e.g., warming-induced stress, nutrient limitation, and long-term acclimation) have played a role in this pattern [*Peñuelas et al.*, 2011; *Silva and Anand*, 2013]. In the case of southern South America, a decreasing trend in tree growth has been observed in dry-mesic forest species in Patagonia. This decrease in growth has mainly been attributed to drier conditions associated to the positive trend of the Southern Annular Mode (SAM) in recent decades [*Villalba et al.*, 2012]. This trend in SAM, especially since the 1950s, has been unprecedented in the last 600 years, and it is still uncertain how it will evolve in the future, so its projected effects on forests remain to be understood [*Villalba et al.*, 2012].

Hence, our results indicate that the long-term response of one of the longest-lived tree species in the world to recent environmental changes has mainly been site dependent, despite the small geographical range of the species. Lower summer precipitation in the Coastal Range site compared with the Andes may be limiting growth under current warmer and drier conditions. This sensitivity is amplified because of the shallower and lower water retention capacity soils in the Coastal Range site [*Urrutia-Jalabert et al.*, 2015b]. Finally, it is also possible that gradual shifts in allocation to other tissues (e.g., roots or canopy) and that the extremely poor nutrient conditions of these soils may also be contributing to the absence of any potential CO_2-driven woody growth signal in this site [*Lapenis et al.*, 2013; *Van der Sleen et al.*, 2014].

5. Conclusions

Fitzroya trees from the drier Coastal Range site, or growing under similar conditions, are more susceptible to reduce their growth rates due to climate change, so priority should be given to monitor and protect these populations that have been most strongly affected by fires and human interventions in the past. The unprecedented growth increase in the rainier Andean site might stall or reverse with projected drier and warmer conditions in the future, as water supply restrictions dominate over increased sunshine effects. Our study provides evidence that tree growth in very wet temperate forests can be positively or negatively affected by ongoing environmental changes depending on site conditions. Given the endangered status of *Fitzroya*, national efforts are needed to monitor the growth of these forests throughout their distribution and further studies are needed to assess the physiological implications of current changes in climate beyond their potential effects on growth.

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