

Environmental correlates of stem radius change in the endangered *Fitzroya cupressoides* forests of southern Chile



R. Urrutia-Jalabert^{a,c,*}, S. Rossi^b, A. Deslauriers^b, Y. Malhi^a, A. Lara^{c,d,f}

^a Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK

^b Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 Boulevard de l'Université, Chicoutimi, QC, G7H 2B1, Canada

^c Laboratorio de Dendrocronología y Cambio Global, Instituto de Conservación, Biodiversidad y Territorio, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, Independencia 641, Valdivia, Chile

^d Center for Climate and Resilience Research (CR)², Facultad de Ciencias Físicas y Matemáticas, Universidad de Chile, Santiago, Chile

^f Fundación Centro de los Bosques Nativos FORECOS, Valdivia, Chile

ARTICLE INFO

Article history:

Received 30 May 2014

Received in revised form 10 August 2014

Accepted 3 October 2014

Keywords:

Dendrometer
Stem daily cycle
Stem increment
Carbon accumulation
Dendrochronology

ABSTRACT

Relationships between environmental factors and stem radius variation at short temporal scales can provide useful information regarding the sensitivity of tree species' productivity to climate change. This study used automatic point dendrometers to assess the relationship between environmental variables and stem radius contraction and increment in ten *Fitzroya cupressoides* trees growing in two sites, the Coastal Range (Alerce Costero National Park) and the Andean Cordillera (Alerce Andino National Park) of southern Chile. The growing season in each site, determined using stem daily cycle patterns for each month, was longer in the Coastal Range site than in the Andes. Warmer and sunnier conditions were positively related with daytime tree radius contraction in both areas, and relationships were stronger in the Coastal Range site where more pronounced shrinking events were associated with prolonged warm and dry conditions compared to the Andes. Stem increment was positively related with precipitation and humidity in both sites, reflecting the positive effect of water on cell turgidity and consequent enlargement. Relationships between stem radius change and environmental variables considering longer temporal scales (7 to 31 days), confirmed a stronger association with humidity/vapor pressure deficit and precipitation, rather than with temperature. Although *Fitzroya* grows in particularly wet and cool areas, current and projected drier and warmer summer conditions in southern Chile may have a negative effect on *Fitzroya* stem increment and carbon accumulation in both sites. This effect would be more critical in the Coastal Range compared with the Andes though, due in part to more limiting soil conditions and less summer precipitation in this area. Long-term research is needed to monitor different aspects of the response of these endangered ecosystems to this additional threat imposed by climate change.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Climate change is likely to have considerable effects on tree growth and forest productivity (Boisvenue and Running, 2006); however, the directionality of these changes remains unclear. Positive effects on growth may occur due to CO₂ fertilization of photosynthesis (although there is an ongoing debate about the extent of this effect on forests), as well as because of an increase

in growing season length due to higher temperatures (Allen et al., 2010). Increases in productivity might be observed in cold climates due to warming, where water is sufficient to compensate for greater vapor pressure deficits, and also in water-limited systems due to precipitation increases. Negative effects on growth may occur due to increased evaporative demand due to warmer temperatures and deficits in precipitation (Fischlin et al., 2007). The specific response of forests is likely to vary from site to site, so the mechanistic assessment of current tree growth-climate relationships can inform our understanding of species' sensitivities to climate change.

In southern Chile, summer temperatures are projected to increase up to 4 °C and precipitation is projected to decrease up to 50% by 2100 in a medium-high greenhouse gas emission scenarios (Fuenzalida et al., 2007). In fact, a pronounced decrease in annual precipitation has been observed in the region during the last

* Corresponding author at: Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK. Tel.: +44 0 1865 275848; fax: +44 0 1865 275885.

E-mail addresses: rocio.urrutia@ouce.ox.ac.uk, chiourrutia@gmail.com (R. Urrutia-Jalabert).

century in combination with an increase in the frequency of droughts, especially during the last 50 years (Trenberth et al., 2007; Christie et al., 2011; González-Reyes and Muñoz, 2013). These changes are likely to have a particular impact on the growth of endemic tree species, commonly adapted to high precipitation and cool climate conditions.

Among the most compelling and least well-understood ecosystems in southern South America are *Fitzroya cupressoides* forests. *Fitzroya*, or alerce, is the second longest-lived tree in the world, with a maximum life span of >3600 years (Lara and Villalba, 1993). *Fitzroya* is endemic to the temperate rainforests of southern South America and mainly grows in the Andes of Chile and adjacent Argentina and in the Coastal Range of Chile between 39°50' and 43°S (Veblen and Schlegel, 1982; Lara et al., 2002). It is a giant conifer that can reach heights of >50 m and diameters >5 m (Donoso et al., 2006), thus representing a huge potential for long-term carbon sequestration and storage under undisturbed conditions. It is currently listed as endangered in the IUCN Red List of Threatened Species (IUCN, 2013).

Despite the importance of *Fitzroya* given its long lifespan, slow growth, and conservation status, it has been poorly studied in terms of its physiology and growth responses to environmental conditions and climate change. Dendroclimatological studies have found that *Fitzroya* tree-ring growth is positively related with summer precipitation, and mainly negatively related with summer temperature, especially from the previous growing season (Villalba, 1990; Villalba et al., 1990; Lara and Villalba, 1993; Neira and Lara, 2000; Barichivich, 2005). It is likely however, that these are not the direct drivers of stem productivity, since this type of study focuses on growth processes at long time spans, leaving a gap in the understanding of the causal chain between cellular and radial growth (Köcher et al., 2012). Since inter-annual radial growth variability is the result of a combination of average climate conditions, as well as specific events, it is clear that the effect of short duration climatic events on radial growth in this species cannot be detected using a dendrochronological approach (Duchesne and Houle, 2011).

Cell division and enlargement, which are the processes that generate growth, are considerably more sensitive to changes in water content than photosynthesis (Muller et al., 2011). Irreversible growth occurs in a cell when a certain pressure threshold in the tissue is exceeded, so when there is water deficit in the tree, this inhibits cell division and particularly cell expansion (Hsiao and Acevedo, 1974; Lambers et al., 2008). Besides the positive effects of water, it has also been reported that temperature would be important in determining the growth rate of metabolic processes in the cambium, as temperature is minimum at night, when hydraulic conditions are more suitable for growth (Drew et al., 2008). Probably the only straightforward way to monitor growth at a short time scale, and therefore assess the direct environmental correlates of radial increment in particular species, is through the use of high precision dendrometers. This monitoring can provide valuable information regarding subtle differences in climate sensitivity among species or populations, and potential long-term limitations to forest productivity caused by climate change (Pérez et al., 2009).

High precision automatic dendrometers can provide information on variation in water storage throughout the year, as well as seasonal growth (Deslauriers et al., 2007a), and they have been widely used to describe stem growth phenology and to evaluate growth-climate relationships in various ecosystems (e.g. Downes et al., 1999; Deslauriers et al., 2003, 2007b; Mäkinen et al., 2003; Bouriaud et al., 2005; Biondi and Hartsough, 2010; Köcher et al., 2012).

To date, the only study that has assessed *Fitzroya* stem increment-climate relationships at a daily time scale was carried out using band dendrometers in Chiloé Island (at the southern distribution of *Fitzroya* in the Coastal Range, Pérez et al., 2009). The

authors reported that daily stem growth was positively related to precipitation and negatively related to radiation. Nevertheless, it is not clear if these relationships hold for populations located toward the north in the Coastal Range, as well as in the Andes, where forests are much older and environmental conditions are different.

We investigated environmental correlates of stem radial contraction and increment of *Fitzroya* trees growing in two distinct environments in southern Chile (the Coastal Range and the Andean Cordillera). These sites were chosen because they contain the main populations of this species and the forests greatly differ in their structure, disturbance regime and environmental conditions.

The studied stands are representative of the widespread condition of forests in each range, with old and large trees in the less disturbed Andean area and younger and smaller trees in the Coastal Range, where there has been a multi-century influence of fires. We sought to resolve the following questions: (1) How do the stem radial change patterns compare between trees growing in these two areas?, (2) What environmental variables are related to daily stem radial contraction and increment in both sites?, (3) How can we better interpret the coarse-scale dendroclimatological relationships previously reported for this species?, and (4) Considering the findings from the previous objectives, what are the implications of climate change for *Fitzroya* stem growth and carbon sequestration in these two areas?

2. Methods

2.1. Study sites and tree selection

The study was conducted in the Alerce Costero National Park, close to the northern distribution of *Fitzroya* in the Coastal Range at 850 m.a.s.l (40°10'S, 73°26'W) and in the Alerce Andino National Park in the Andean Cordillera at 760 m a.s.l (41°32'S, 72°35'W, Fig. 1). Mean annual precipitation and temperature in 2012 were 4860 mm and 7.26 °C in the Coastal Range site and ca. 6600 mm and ca. 6.89 °C in the Andes (Urrutia-Jalabert, 2014).

The effective soil depth in Alerce Costero is generally thin (29 to 67 cm), and soils are brown-earths and severely podzolized (Veblen and Ashton, 1982; Urrutia-Jalabert, 2014). Soil texture in the upper horizon is mostly sandy-loam and organic matter content is ca. 10%. The studied forest is medium-age, dense (1415 trees ha⁻¹, considering trees ≥10 cm diameter at breast height (DBH)) and predominantly dominated by *Fitzroya*. Sampled trees were dominant and ranged between 35.5 and 47.9 cm DBH and 14.4 and 15.8 m height. In Alerce Andino, the effective soil depth is larger than in the Coast (56 to 100 cm), soils are derived from volcanic material (silty-loam texture) and contain a high amount of organic matter in the upper horizon (ca. 80%, Urrutia-Jalabert, 2014). The studied forest is old-growth, less dense than in the coast (782 trees ha⁻¹) and *Fitzroya* is the most important species in terms of basal area. Sampled trees were dominant and ranged between 82.5 and 161.5 cm DBH and 33.2 and 35.6 m height.

2.2. Dendrometer data collection

From Spring 2011 (October–November) to Fall 2013 (May 2013), stem size variation was recorded in five dominant trees per site every 30 min and averaged over each hour using automatic point dendrometers (DR model, Ecomatik, Munich, Germany) installed at breast height. The instrument consists of a displacement transducer that is anchored to the tree using two screws. The instrument resolution is 2.6 μm and thermal expansion is <0.1 μm K⁻¹. The temperature variation does not affect the sensor measurements, and due to construction the thermal expansion of the framework is negligible. To reduce the influence of bark expansion and

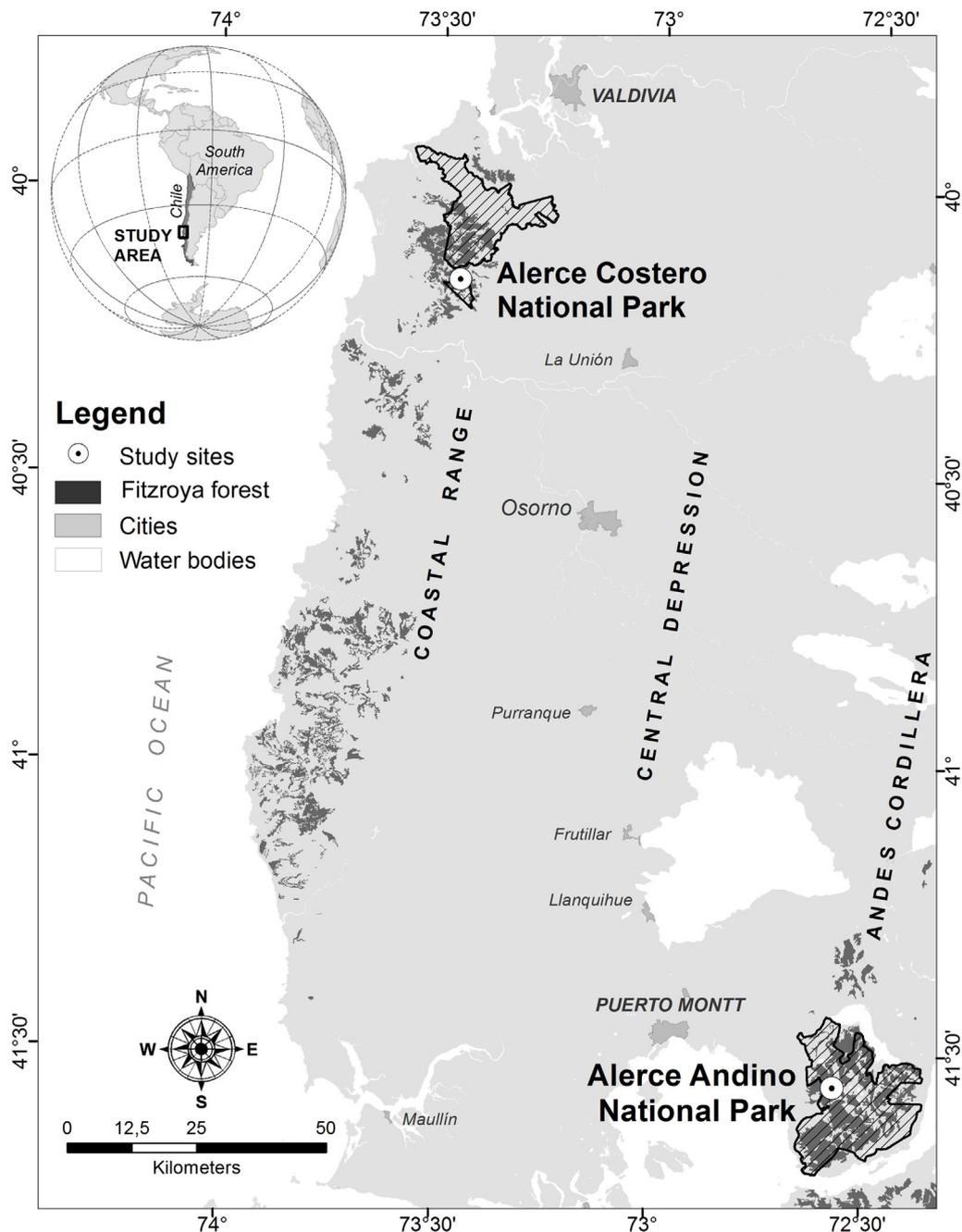


Fig. 1. Study sites in the Alerce Costero and Alerce Andino National Parks in southern Chile. The approximate location of the three major physiographic units in the area is shown (Coastal Range, Central Depression and Andean Cordillera). The distribution of *Fitzroya* forests north of 41°45'S is also displayed.

contraction, the outermost part of the bark was removed taking care to not damage the cambium. Raw measurements of every dendrometer were carefully checked and noisy or unexplained data, such as periods with constant or sudden extreme values, were removed for further analyses.

2.3. Environmental data

A weather station (Skye Instruments, Powys, UK) recording precipitation, temperature, relative humidity and total radiation was installed <1 km from the monitored trees at each site. In addition, one soil temperature sensor (Decagon EC-T, Pullman, USA) was installed close to the monitored trees in each site at 10 cm below the surface. Data were recorded every 30 min and hourly means

were calculated. Vapor pressure deficit (VPD, hPa) was calculated from the hourly means of temperature and relative humidity (Jones, 1992).

2.4. Growing season estimation

Since only the growing period is recommended to be used to examine correlations with environmental parameters (Deslauriers et al., 2007a), some studies have assessed this period using micro-coring techniques and subsequent cell analyses (Deslauriers et al., 2003; Rossi et al., 2006). Alternatively, growing season estimates have commonly relied on meteorological parameters (e.g. the period between the last spring and the first fall frost), phenological observations and satellite data, among others (Zhou et al., 2001;

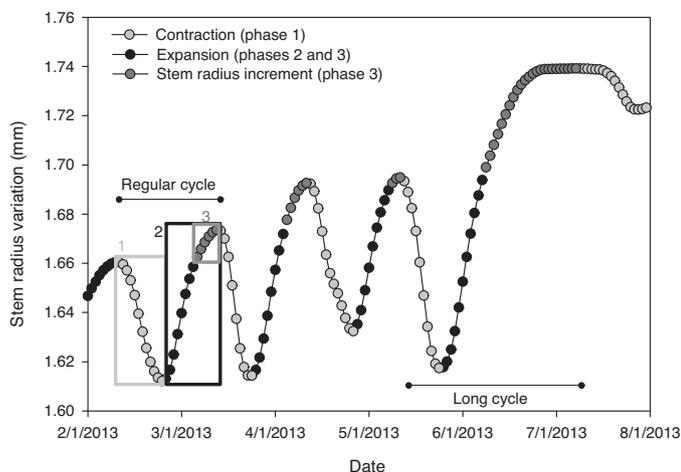


Fig. 2. Cycles in stem variation divided in three distinct phases: contraction (phase 1), expansion (phases 2 and 3) and radius increment (phase 3). Each dot represents an hourly measurement and the cycles are an example of data recorded during the first week of January 2013 (2nd to 8th of January) in one tree from the Coastal Range site.

Menzel et al., 2003). Here, in order to assess site-specific periods according to patterns of stem variation recorded by trees, an analysis of the daily cycle was performed. During the growing season, a clear pattern of daytime contraction and nighttime expansion (with high amplitudes) should be observed; while during the dormant season, amplitudes should be much lower in temperate climates or cycles can even be inverted in cold climates (Turcotte et al., 2009; Devine and Harrington, 2011; King et al., 2013). Therefore in each site, the amplitude of the daily cycle (from 0 to 23 h) was calculated for each month including the mean of all dendrometers for the whole sampling period.

The daily cycles of each month were scaled to start in zero and a K-means cluster analysis with $k = 2$ was used to divide the year in two periods: non-active and growing season. This clustering procedure is a partitioning method that finds a single partition for a group of objects; where objects within each cluster are more alike to one another than to objects assigned to other clusters (Legendre and Legendre, 2012). To confirm the definition of clusters, a hierarchical cluster analysis using the R package “pvclust” was performed (Suzuki and Shimodaira, 2006). Data recorded during the months defined as the growing period were used for subsequent analyses focused on the relationship between stem radius change and climate.

2.5. Extraction of stem radius variation

In order to extract the stem radius variation during the growing period, the stem cycle approach was used in this study (Downes et al., 1999 modified by Deslauriers et al., 2003). This approach uses stem shrinking and swelling to divide the stem cycle into three different phases: contraction, expansion and stem radius increment (Downes et al., 1999; Deslauriers et al., 2003; Fig. 2). Contraction (phase 1), includes the period between the morning radius maximum and the afternoon minimum and expansion (phase 2) includes the total period between the radius minimum to the next morning maximum. Stem radius increment (ΔR or phase 3) corresponds to the portion of the expansion phase from the time the stem radius surpasses the morning maximum until the following maximum, and has been considered as an estimate of growth (Deslauriers et al., 2003; Deslauriers et al., 2007a). When the previous cycle maximum was reached a positive stem radius change ($\Delta R+$) was calculated. When this maximum was not reached, a negative stem radius change ($\Delta R-$) was defined; however, only

positive values were used for further analyses. The duration of each phase (h, hours) was also estimated. Environmental variables were also processed according to each phase division in order to match them with stem data. Analyses were carried out using a routine specially developed for this purpose by Deslauriers et al. (2011) using the SAS software (SAS Institute, Cary, NC).

The stem circadian cycle commonly lasts around 24 h, but rain events can result in longer or shorter cycles (Deslauriers et al., 2003, 2007a,b, Fig. 2). To perform additional analyses, we defined regular ($24 \text{ h} \pm 3 \text{ h}$), short ($< 21 \text{ h}$) and long ($> 27 \text{ h}$) cycles (Deslauriers et al., 2007b; Turcotte et al., 2009).

2.6. Relationship between stem radius change and climate variables

In order to find the environmental correlates of stem radius change, bootstrapped correlations were calculated between stem contraction (magnitude of phase 1) and stem radius increment (magnitude of phase 3) and the environmental variables occurring during each phase (average or sum (precipitation) of values for the respective phase). The Kendall tau-b correlation coefficient (τ) was used since these relationships did not comply with all assumptions for a parametric test and the data contained tied observations (tied ranks). To make variables independent from each other and avoid using non-stationary data in the correlation analyses, the first difference was used for contraction and for all the climate variables, except precipitation. Mean correlations were significant if after 1000 bootstrapped iterations their absolute values were at least two times their standard deviations (SD) (Deslauriers et al., 2003). Data for the two estimated growing seasons (2011–2012, 2012–2013) were used.

Correlations were performed considering all cycles, as well as regular cycles alone, allowing to primarily assess the effect of long cycles on the relationship between climate and stem radius change. In addition, phase duration could be highly dependent on environmental factors and the effect of these factors on stem increment could be indirect through phase duration (Deslauriers et al., 2007b). As such, partial correlations were performed for all cycles’ data using duration as a partial correlate.

Finally, to examine the relationships between stem radius change and environmental variables at a longer time-scale, and thereby establish a better link with dendrochronological findings, correlations were also performed using time windows of 7, 21 and 31 days. For this purpose, the daily maximum radius was obtained and the first difference (difference between the maximum stem radii of two subsequent days) was used as a proxy of daily stem radius change (all data, including positive and negative values were used). A moving average for 7, 21 and 31 days was calculated for the mid-point of each window position and the deviations of each daily value from the mean average were calculated for the dendrometer and environmental data to perform correlations using these anomalies.

In order to better understand covariance and redundancy of the environmental variables mostly related with stem radial change, a principal components analyses (PCA) was performed using all the variables during each time period. Variables were logarithmically transformed as necessary to comply with linear relationships for the PCA.

3. Results and discussion

3.1. Patterns of stem radius change

Radius variation in all trees showed characteristic seasonal patterns in both sites (Fig. 3). Most of variation and stem increment

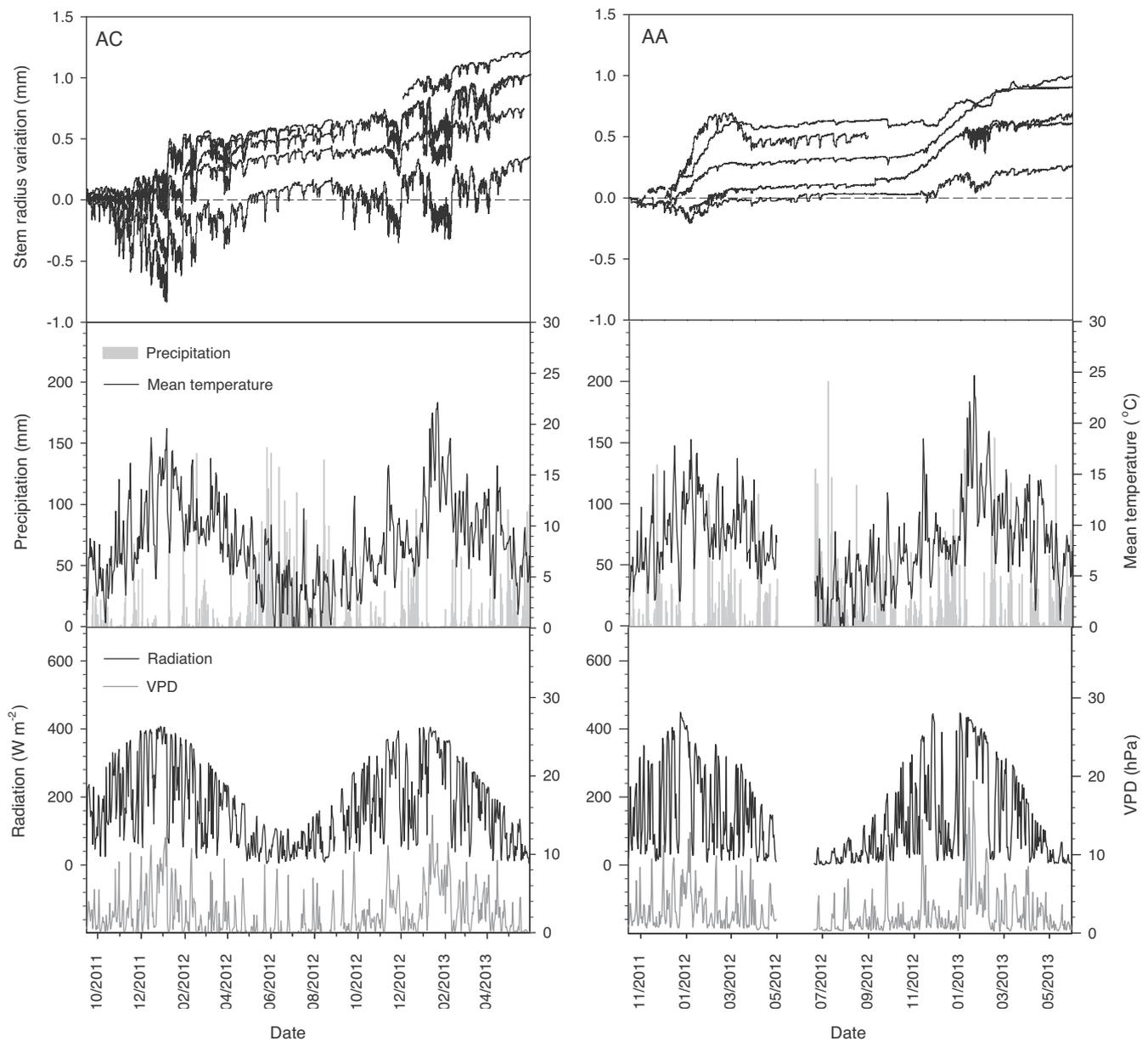


Fig. 3. Stem radius variation of the five trees monitored in each site and climate data from Alerce Costero (AC, left) and Alerce Andino (AA, right) for the whole studied period. Higher variability in stem radius is displayed during austral spring–summer months, when mean temperature, radiation and vapor pressure deficits (VPD) are higher and precipitation is slightly lower.

were observed during the period of higher temperature, radiation and VPD in spring and summer (~November–December through March). Precipitation was abundant all year long, with lower values recorded during summer (average of 839 and 1413 mm during December–February in Alerce Costero and Alerce Andino, respectively, Fig. 3). The amplitude of stem variations was lower during winter months in both sites and generally higher in the Coastal Range than in the Andes throughout the year. Trees responded synchronously in both study sites.

Stem radius especially in two trees from the Coastal Range site and in one tree from the Andes decreased during the summer of the first year, reaching the lowest values at the end of December 2011 and beginning of January 2012. This decrease corresponded with a rainless period of 15 days, accompanied with high values of radiation and temperature. The magnitude of this shrinking event was higher in the Coastal Range than in the Andes. An important

shrinking was also observed in most trees of both sites during the second half of January 2013. This corresponded to a period of very little precipitation during 17 days, with the warmest temperatures registered during the whole studied period (mean values of 16.9° and 16.1 °C in Alerce Costero and Alerce Andino, respectively). January was a particularly dry and hot month, where minimum and maximum temperatures in Valdivia (at a low altitude close to Alerce Costero) were up to 2 °C and 4.9 °C warmer than the climatological mean (1961–1990), respectively (Quintana and Aceituno, 2013). The amplitude of this decrease was also larger in the Coastal Range site than in the Andes, and the two periods with strong shrinking patterns were the longest ones with almost no precipitation and warm temperatures in both areas. Strong stem shrinking in the middle of the summer was also reported for *Fitzroya*, but not for other evergreen broadleaf species in Chiloé, when a strong El Niño event (1998) affected the region and a long rainless and warm

period (26 days) hit Southern Chile (Pérez et al., 2009). According to these authors, radial growth of *Fitzroya* is negatively affected by increased evaporative demand during rainless and sunny periods.

3.2. Growing season estimation, cumulative radial increment and cycle characterization

The evident higher stem activity during spring-summer compared to fall-winter resulted in a clear pattern of physiological activities suitable for wood formation and helped to estimate a potential period of growth in both study sites. According to the K-means cluster analyses, the growing season which was characterized by higher stem daily amplitudes, was estimated to occur from November to March in the Coastal Range and from December to February in the Andes (Fig. A1, Appendix). The remaining months in both sites were assigned to the second cluster and could be considered as part of a dormancy or “less active” period (Fig. A1). These results were confirmed by the hierarchical cluster analysis (results not shown). In spring and summer, the increases in temperature and radiation drive greater evaporative demand during the day that contribute to depletion of stem water reserves and, combined with the refilling at night, increase the amplitude of diurnal cycles (King et al., 2013). The lower daily amplitude observed during fall and winter seems characteristic of mild or maritime temperate regions, where there are no pronounced freeze-thaw events that could affect stem variation (Turcotte et al., 2009; Devine and Harrington, 2011; King et al., 2013).

The shorter growing season in the Andes agrees with the difference in climate between both sites, with air temperature, and particularly soil temperature and radiation being most of the time lower in the Andes than in the Coastal Range (Fig. A2, Appendix). Mean summer air temperature (December–February, 2012 and 2013) was 11.9° and 11.1 °C in Alerce Costero and Alerce Andino, respectively. Mean radiation was 259 and 218 W m⁻² and mean soil temperature was 11.1° and 9.4 °C in the Coastal Range site and the Andes, respectively. Latitude and a more Mediterranean climate influence in the Coastal Range site would explain these differences.

The shorter growing season in Alerce Andino is also in agreement with Donoso et al. (1990) who stated that the growing season should be significantly shorter in the Andes than in the Coastal Range due to more intense snow precipitation during winter and long-lasting snow cover in spring.

The mean cumulative radial increment in trees from Alerce Costero was 0.41 (±0.21) and 0.25 mm (±0.02) for the growing seasons 2011–2012 and 2012–2013, respectively. In Alerce Andino, the mean cumulative radial increment was 0.31 mm (±0.23) and 0.25 mm (±0.13) for 2011–2012 and 2012–2013, respectively. These results indicate that tree growth in both sites was lower during the second growing period (2012–2013), likely due to the strong decreases in stem radius recorded in most trees during January 2013 in both areas.

In terms of cycle characterization, in the Coastal Range site 75% of the cycles were classified as regular cycles, 17% as long cycles and 8% as short cycles. The longest cycle in this site lasted 128 h (Fig. A3, Appendix). In the Andes, 70% of the cycles were classified as regular cycles, 20% as long cycles and 10% as short cycles. The longest cycle event lasted 126 h (Fig. A3).

On average, the contraction phase was longer in Alerce Costero (9.3 h ± 2.5) than in Alerce Andino (8.3 h ± 2.8, $p < 0.05$). The mean time when this cycle started in the morning was 9:48 h (±2:04) in the Coastal Range site, and 8:48 h (±2:06) in the Andes; it was later in Alerce Costero mainly due to lower air temperatures and higher relative humidity conditions in the early morning in this site, because of the greater oceanic influence on this area.

The duration of the expansion phase varied considerably due to rainfall events, ranging from 1 to 118–119 h in the Coastal Range site and the Andes, respectively. The mean start time of this event was 19:24 (±1:48) in the coast and 17:12 h (±2:22) in the Andes. The longest increment phases were observed to last 108 and 115 h in Alerce Costero and Andino, respectively.

The longer contraction phase in Alerce Costero than Alerce Andino was mainly due to the higher radiation and air temperature experienced by trees during the day (from 09:00 to 19:00 h) in the former site (540 W m⁻² and 14.3 °C) compared with the latter (465 W m⁻² and 13.1 °C) during summer (December–February).

Additionally, a higher amplitude of contraction was found in the Coastal Range (0.06 mm) compared to the Andes (0.01 mm, $p < 0.05$), indicating that trees in the coast would utilize their internal stem water reserves faster than in the Andes (King et al., 2013). One possible explanation for this would be the difference in soil conditions between both sites: the Alerce Costero site is characterized by shallower soils with lower water retention capacity, which is accentuated by the sandy texture and less organic material in this area compared to Alerce Andino (Barichivich, 2005; Gerding, personal communication). These characteristics would result in a greater resistance to water flow from the soil, causing higher amplitudes of stem variation and a higher use of the stem water pool during the day (Sevanto et al., 2005). Soil volumetric water content measurements in each site during summer (at a monthly basis at 12 cm depth) partly reflect the differences that exist between areas: mean values reached 39% and 50% in Alerce Costero and Andino during 2011–2012 and 32% and 51% during the drier summer (2012–2013). A particularly strong drop in water content was observed during January and February 2013 in the Coastal Range site (Urrutia-Jalabert, 2014). An additional explanation for the difference between sites, would be that conditions are commonly cloudier and rainier (~40% more precipitation during December–February) in Alerce Andino than in Alerce Costero, and daily contraction amplitudes have been reported to be lower on overcast or rainy days (Devine and Harrington, 2011; King et al., 2013). The higher amplitude of contraction in the Coastal Range site could not be explained by a higher amount of bark in trees from this site, since trees have much thinner bark in the coast than in the Andes and in any case most bark was removed at the dendrometer contact point. Finally, an alternative explanation might be that larger and taller *Fitzroya* trees in the Andes have a greater sapwood capacitance compared to the trees from the Coastal Range which would depend more on soil water availability (Scholz et al., 2011).

3.3. Relationships between environmental factors and stem radius change

Considering all and just regular cycles, stem contraction during the day in both sites was positively related with mean and maximum temperatures, VPD and radiation (Fig. 4). Humidity on the other hand, was negatively related with contraction ($T = -0.58$) and precipitation also was negatively related with this variable, but just in Alerce Costero when considering all cycles (Fig. 4). This is in agreement with what was found by Devine and Harrington (2011) for young Douglas fir (*Pseudotsuga menziesii*) and supports the above reported statement that warmer and drier conditions are usually associated to strong stem shrinking patterns. Relationships were stronger in the Coastal Range site than in the Andes, meaning that trees in the former site would be more sensitive to environmental conditions that make the stem contract.

Stem radius increment mainly occurs at night or early morning, as was corroborated in this study. It has been reported that

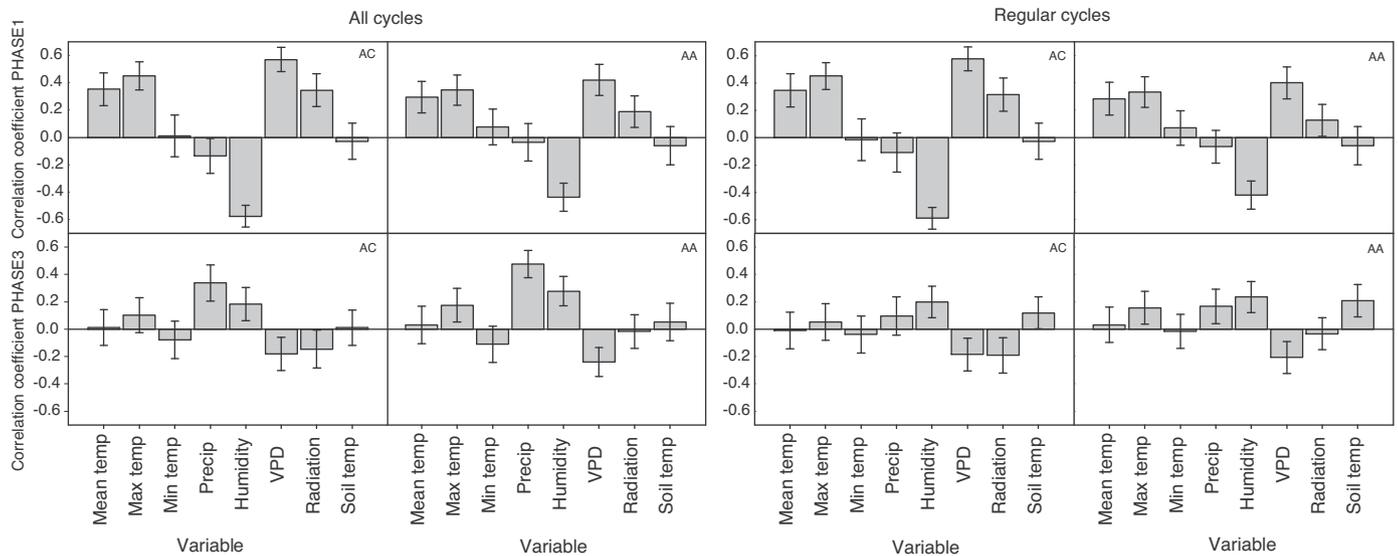


Fig. 4. Left panel: Kendall tau-b correlations between environmental variables in Alerce Costero (AC) and Alerce Andino (AA) and stem contraction (top panel) and increment (bottom panel) considering all cycles. Right panel: Kendall tau-b correlations between environmental variables in Alerce Costero and Alerce Andino and stem contraction (top panel) and increment (bottom panel) considering just regular cycles. Significant correlations are present when the error bar does not cross zero.

cell enlargement takes place mostly at night or on rainy days, when turgor is high and cambium is supplied with optimal water availability (Dünisch and Bauch, 1994; Downes et al., 1999; Deslauriers et al., 2003; Steppe et al., 2006; Gruber et al., 2009). During the day, more water is lost through transpiration than absorbed through the roots, so an internal water deficit affects trees and transpiration would negatively affect radial expansion (Tardif et al., 2001).

Stem increment had a significantly positive correlation with precipitation and humidity considering all cycles in the Coastal Range. VPD and radiation on the other hand, had a negative correlation with this factor. In the Andes, the pattern was more or less the same, but maximum temperature was also significantly and positively correlated with stem increment and radiation was not correlated with this factor (Fig. 4). Radiation was not important, probably because it is lower in this site. When performing correlations just considering regular cycles in the Coastal Range site, correlation with precipitation was not significant implying that the relationship between precipitation and stem increment is just seen when long precipitation events occur in this site. Additionally, a higher negative correlation with radiation was observed and a slightly significant positive relationship was obtained with soil temperature. In the Andes, relationships remained significant for the same variables, although correlation with precipitation decreased considerably. In addition, a positive correlation with soil temperature also appeared in this site ($T=0.21$, Fig. 4). Since VPD is derived from and strongly related to air humidity, relationships between these variables and stem radius change were usually similar in magnitude, but in opposite directions.

The positive relationship between maximum night temperature, soil temperature and stem increment particularly in the Andes, can be explained by generally colder conditions in this site compared to the Coastal Range. A number of studies have reported a positive relationship between night temperatures and stem increment (Deslauriers et al., 2003; Xiong et al., 2007; Drew et al., 2008). Night-time temperatures have been found to have a greater effect on tracheid expansion than daytime temperatures (Richardson and Dinwoodie, 1960; Richardson, 1964; Dünisch, 2010). Thus, low night temperatures were reported to negatively affect the

expansion of differentiating tracheids in *Podocarpus latifolius* (Dünisch, 2010). The positive relationship between soil temperature and stem increment on the other hand, could be associated to a positive effect of warmer soil temperatures on root water uptake and stem rehydration and the consequent beneficial effect on internal water balance (Tardif et al., 2001; Pérez et al., 2009).

Precipitation and humidity have been usually reported to positively affect stem increment in different conifer and broadleaved species (Deslauriers et al., 2003, 2007b; Duchesne and Houle, 2011; Krepkowski et al., 2011; Köcher et al., 2012). The direct effect of precipitation on radial growth is to increase the water status in the stem, inducing high water potentials that favor cell enlargement (Steppe et al., 2006). Humidity on the other hand, also contributes reducing the negative pressure in the conducting system, helping to increase turgor (Köcher et al., 2012). In the same sense, high VPD acts to inhibit cell enlargement and growth, due to its indirect effect on cell turgidity (Pantin et al., 2012).

It is relevant to highlight the importance of precipitation and humidity conditions for maintaining the water status in the stem in order to induce cell enlargement and radial growth in *Fitzroya*. This occurs even in our very rainy sites which receive more than 800 mm of precipitation during summer.

Fig. 5 shows correlations between environmental factors and duration of the increment phase (phase 3), as well as partial correlations between environmental factors and stem radius increment using duration as the partial correlate (considering all cycles). Precipitation showed the highest correlation with duration in both study sites, so when rainfall was higher duration of the increment phase was longer. Humidity also had a significant positive correlation with duration of the increment phase in Alerce Andino, but not in Alerce Costero. VPD and minimum temperature had a negative correlation with duration of cycles in both areas. In the Coastal Range site, radiation also had a negative correlation with the duration of the increment phase (Fig. 5).

Partial correlations were performed given the positive and significant relationship between duration and stem radius increment ($T=0.52$ in both sites). Only humidity and VPD remained as variables with significant correlation with stem radius increment in the Coastal Range site.

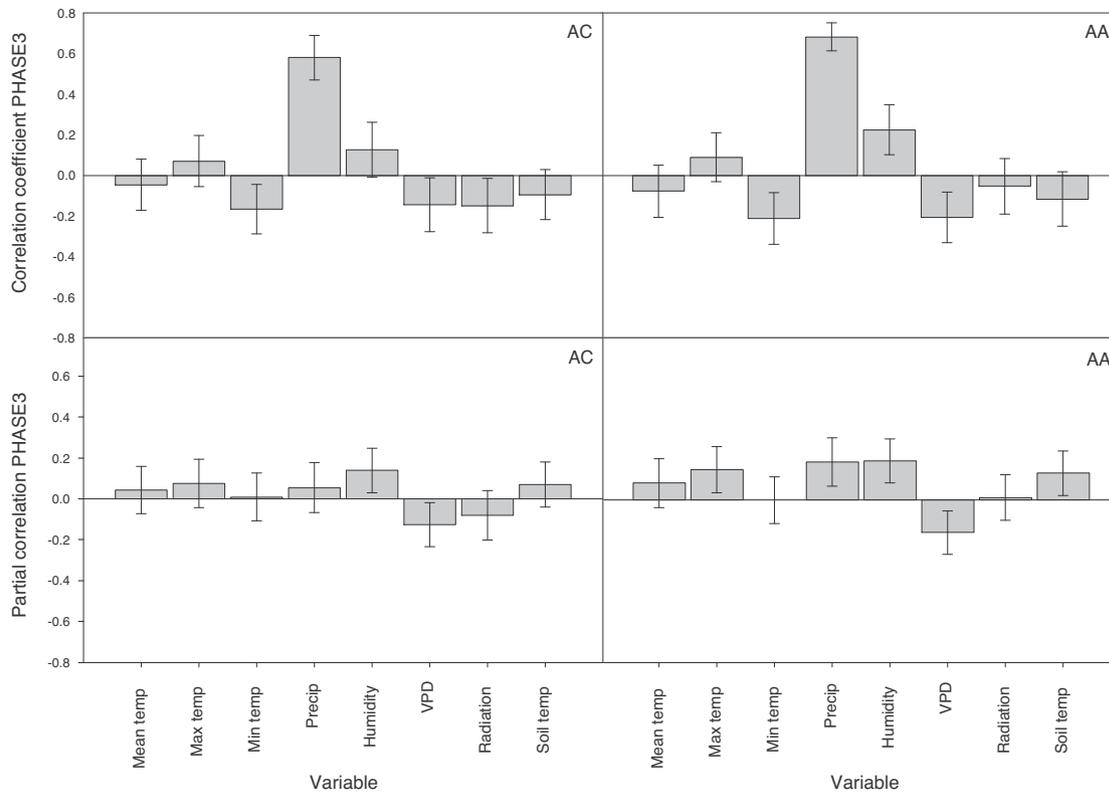


Fig. 5. Top panel: Kendall tau-b correlation coefficients between environmental factors and duration of the increment phase in Alerce Costero (AC) and Alerce Andino (AA). Bottom panel: Partial correlations between environmental factors and stem increment considering duration as the partial correlate. Significant correlations are present when the error bar does not cross zero.

The other variables that were reported as significant in Fig. 4 (precipitation and radiation) would have an indirect relationship with stem increment through phase duration. In the Andes, correlations remained significant for all the reported variables in Fig. 4 (Fig. 5). The fact that the positive effect of precipitation is mediated through duration in Alerce Costero, can be explained because soils do not have good water retention capacity, so more rainy days are needed in order to induce growth. On the other hand, the negative relationship between stem increment and radiation was mainly mediated through duration in this site. More radiation shortens the expansion/increment phases, reducing the favorable period for growth. Radiation increases transpiration and water loss from the tree, causing less cell turgidity and consequently less cell enlargement (Fritts, 1958).

Finally, since prevailing weather conditions mostly during the expansion phase have been shown to affect stem radial increment (Deslauriers et al., 2003), correlations were performed between environmental conditions during this phase and stem increment. This was done just using regular cycles to minimize the effect of large differences in duration between phases. The only variables that were related with increment were humidity ($T=0.24$) and VPD ($T=-0.19$) just in Alerce Andino, but these correlations were lower than when using environmental variables from the increment phase.

General findings in this study are in agreement with Pérez et al. (2009), who reported a positive effect of precipitation, soil hydration and temperature and a negative effect of photosynthetic active radiation on the radial increment of *Fitzroya* from Chiloé. Strong shrinkage events were equally experienced by trees from Alerce Costero and Chiloé, located in both extremes of the Coastal Range.

3.4. Insights and interpretation of findings in dendrochronological studies

Relationships between stem radius change and environmental variables considering longer time scales revealed that correlations with precipitation, humidity and VPD remained significant and even increased in the case of humidity and VPD, compared with correlations using the daily increment (considering all cycles) in both sites. Moreover, negative correlations with mean and maximum temperature were also significant, as well as with radiation in both areas (Table A1, Appendix).

The PCA plots (component 1 vs. component 2) for the different time scales highlight the close positive association between stem radius change and precipitation and humidity (Fig. 6). A negative association was particularly strong with radiation at longer time scales in both sites. For conciseness, and since patterns for 21 and 31 days were the same, Fig. 6 shows only the “daily”, 7 and 31 days results. “Daily” here and in the rest of the text refers to the time scale given by the stem cycle. Principal components 1 and 2, explained 58.5, 73.6 and 78.8% at a “daily”, 7 and 31 days scale in the Coastal Range site. In the Andes these values were 60.6, 76.3 and 79.5%, respectively.

Climate-tree growth relationships established in dendrochronological studies have a limited explanatory power in terms of an implicit growth mechanism (Zweifel et al., 2006), so a better understanding of the processes behind these relationships in *Fitzroya* can be obtained using this high-resolution study. The reported negative relationships of *Fitzroya* tree-ring width with summer temperature (Villalba, 1990; Villalba et al., 1990; Lara and Villalba, 1993; Neira and Lara, 2000; Barichivich, 2005) mainly appeared when longer time scales were considered in this

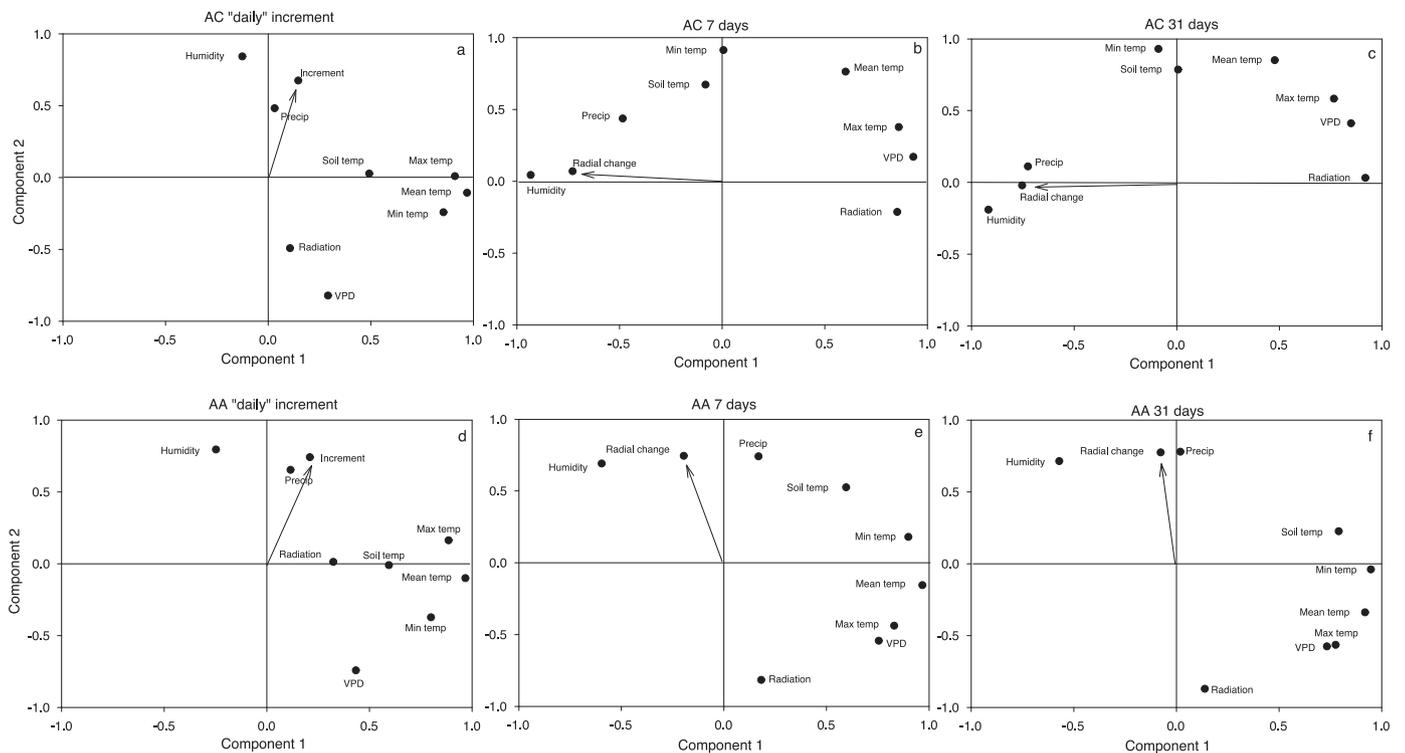


Fig. 6. Principal component analysis between (a) stem radius increment and environmental variables at a “daily” basis in Alerce Costero (AC), (b) stem radius change and environmental variables at a time scale of 7 days in the same site and (c) stem radius change and environmental variables at a time scale of 31 days also in Alerce Costero. (d)–(f) the same as (a)–(c), but for Alerce Andino (AA). Arrows in each plot point toward the stem increment/stem radius change variable. Environmental variables closely located to the stem radius variables or directly opposite covary more strongly with the response variables (closer variables are positively related and opposite variables are negatively related).

study. This relationship can be understood through the strong shrinking events recorded in *Fitzroya* when long warm, sunny and particularly dry periods occur. This would reduce the number of days with appropriate climate conditions for growth to take place, producing a smaller tree ring.

The correlation and the PCA examined together indicate that variables directly influencing the stem water status, namely humidity, precipitation and VPD, had a stronger relationship with stem radius change. In the second place, radiation and, to a lesser extent, maximum temperature were negatively related with this variable. It is likely that these negative correlations are a by-product of the strong correlation between humidity and radiation, and between VPD and maximum temperature, rather than a direct causal relationship among radiation/temperature and growth rate. It is noteworthy that mean temperature had a weaker relationship with stem radius change and minimum temperature did not have any significant relationship at all. This suggests that maximum temperature would matter, because of its links with VPD, rather than through direct effects on plant metabolism. Hence the results support the primary influence of humidity conditions on cell growth rates on the studied time scales. The negative association between tree-ring width chronologies and summer temperature appears to be mediated through the effect of temperature on VPD.

The reported negative effect of previous summer temperature and precipitation on the other hand, can be because warm temperatures are usually associated with dry conditions in the study area, and hence carbon assimilation can be reduced if stomata close (McDowell et al., 2008). Less carbon assimilation would result in less carbon reserves and a smaller tree-ring during the next season. Moreover, high temperatures during the previous growing season combined with higher respiration rates can reduce the

starch reserves that can be used for the following growth period (Deslauriers et al., 2014).

The use of multiple environmental variables in this study, although correlated among themselves, provided important insights that would not be possible to obtain with a priori restriction to a few variables.

3.5. Stem growth sensitivity to climate change

Findings of this study allow some tentative inferences to be made regarding the vulnerability of *Fitzroya*'s growth rates to climate variations. Current and projected climate change, characterized by decreased precipitation and warmer temperatures in southern Chile (González-Reyes and Muñoz, 2013; Fuenzalida et al., 2007), may have a negative effect on the carbon sequestration capacity and long-term storage of *Fitzroya* populations from both study sites. However, *Fitzroya*'s radius variation currently appears to be especially sensitive to dry and warm conditions in Alerce Costero, meaning that forests growing under similar restrictive site conditions in the Coastal Range are more vulnerable to experience stem shrinking and lower growth compared with trees from the Andes. Strong stem shrinking is experienced by *Fitzroya* trees in the Coastal Range site even during years that are not as extreme as El Niño years, which indicates that restrictive soil conditions and a more Mediterranean climate influence can make *Fitzroya* tree growth more vulnerable to future climate change. In addition, precipitation seems to be related with stem increment on a daily basis in the Coastal Range site only when long rainfall events take place, so less precipitation in the future, may negatively affect this variable. A significant negative trend in the tree-ring width (using detrended series to discount the effect of growth changes

due to tree aging, Fritts, 1976), as well as in the basal area increment chronology has been observed in this site especially in the last 40 years (Urrutia-Jalabert, 2014). This likely reflects the effect of decreased precipitation and increasing maximum temperatures on cell enlargement and consequent stem radial growth (significant trend in summer maximum temperature in Valdivia for the period 1960–2009, Urrutia-Jalabert, 2014). This negative trend in growth has not been seen so far in the older Andean forest, reinforcing the higher sensitivity of trees from the Coastal Range to current changes in climate (Urrutia-Jalabert, 2014).

It is important to emphasize, however, that further studies should address measurements of leaf water potential, sapwood capacitance and non-structural carbohydrates in *Fitzroya* trees, especially during dry periods, to assess to what extent they are affected by these conditions. In the case of trees from the Andes, and since it has been reported that absolute daily reliance on stored water across different species is higher in larger trees; stored water might help avoiding embolism in a future drier climate (Scholz et al., 2011).

4. Conclusions and implications

This study is the first to assess, at a high resolution level, the relationship between stem radius contraction and increment and environmental conditions in *Fitzroya* trees growing in the Andes and Coastal Range of southern Chile. The high resolution approach that we used was unique in allowing us to track the seasonal course of stem radius variation throughout the studied period and estimate a growing season for each area based on the definition of stem daily cycles. Moreover, we could explore the stem daily cycle in detail, understand the differences between sites and define the contraction and increment phases for subsequent correlation analyses. We found that stem radius contraction was positively related with radiation, temperature and VPD in both sites, so sunnier, warmer and less humid conditions conducive to higher transpiration rates, were associated to stronger stem contraction and shrinking events. The amplitude of these events was more pronounced in Alerce Costero than Alerce Andino, reflecting a higher sensitivity of this site to these growth-adverse conditions. Stem increment on the other hand, was primarily related with precipitation and humidity in both sites, reflecting the positive effect of water on stem water potential and especially cell enlargement. Relationships with humidity/VPD were stronger when considering longer time scales (7 to 31 days), and VPD appears to be the driver of the previously reported negative correlations between tree-ring width chronologies and temperature. Projected climate change in southern Chile is likely to impose restrictions to *Fitzroya*'s stem radius increment and carbon uptake, especially in the Coastal Range. This is somewhat surprising given the high amounts of annual precipitation that fall in *Fitzroya* sites. Long-term monitoring is needed in order to assess the responses of these forests total productivity to climate variations. Future research on *Fitzroya* forests should concentrate on multi-scale assessments ranging from cellular-scale analyses to determine the environmental variables that mostly influence xylogenesis, to ecosystem-scale studies to assess the actual condition of these forests and their interaction with climate (e.g flux towers). This knowledge is fundamental to better understand the vulnerability of these unique ecosystems and their carbon sequestration capacity to climate change.

Acknowledgements

This work has been funded by different sources: FONDECYT Project No. 1130410, the CRNII2047 project of the Inter-American Institute for Global Change Research supported by NSF (Grant

GEO-0452325), the Center for Climate and Resilience Research (CR)² funded by CONICYT/FONDAP/15110009, the Rufford Small Grants for Nature Conservation (Project 11371-1), the Royal Geographical Society (Monica Cole Research Grant), the ECI (University of Oxford) Small Grant and the Wolfson College Travel Grant. Especial thanks to the Merit Scholarship Program for Foreign Students of the Fonds de Recherche du Québec–Nature et Technologies for funding an internship at the University of Quebec at Chicoutimi to perform the analyses presented in this paper and to CONAF (National Forest Service) for their permission and support to work in the above mentioned National Parks. Finally, thanks to Aldo Farias for producing the map, to the field assistants Aldo Farias, Emilio Cuq, Oscar Concha and Waldo Iglesias, to the Park Ranger Marcelo Hernandez and family and to Nelson Garcia, Nixy Barra, Andres “Gallito” and Ruperto Mascareña from Alerce Mountain Lodge for supporting and facilitating fieldwork. Thanks to Dr. Mathieu Cusson for his advice provided in statistical analyses. This manuscript greatly benefited from the comments of Dr. Greg Goldsmith. Y.M. is supported by the Jackson Foundation and a European Research Council Advanced Investigator Grant.

Appendix A. Appendix

A.1. Results

Figs. A1–A3 and Table A1

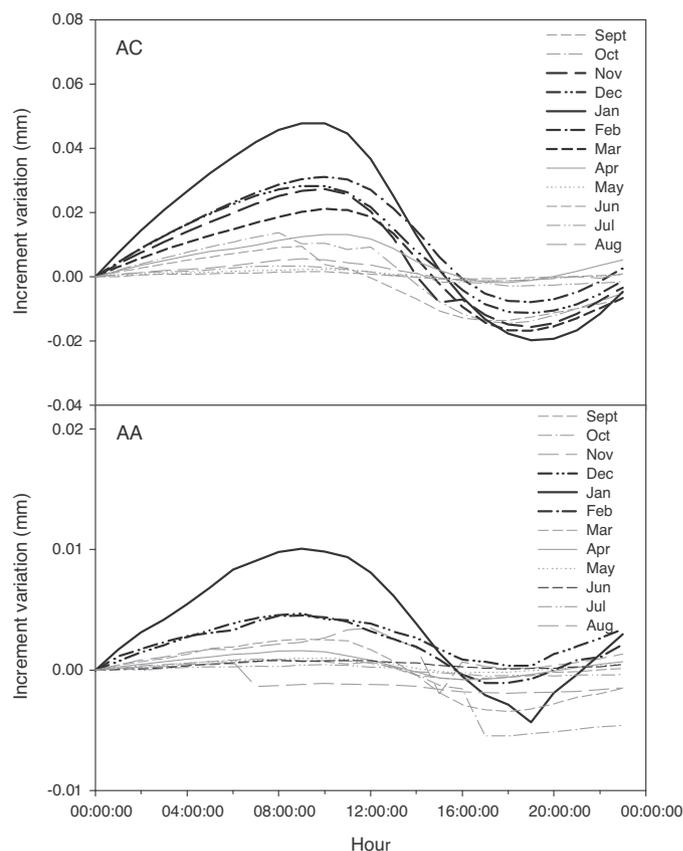


Fig. A1. Daily cycles found for the mean of the stem radius variation in Alerce Costero (AC, top) and Alerce Andino (AA, bottom). Months depicted in bold black, which present more defined and higher amplitude cycles, were the ones selected as the growing season according to K-means cluster analysis.

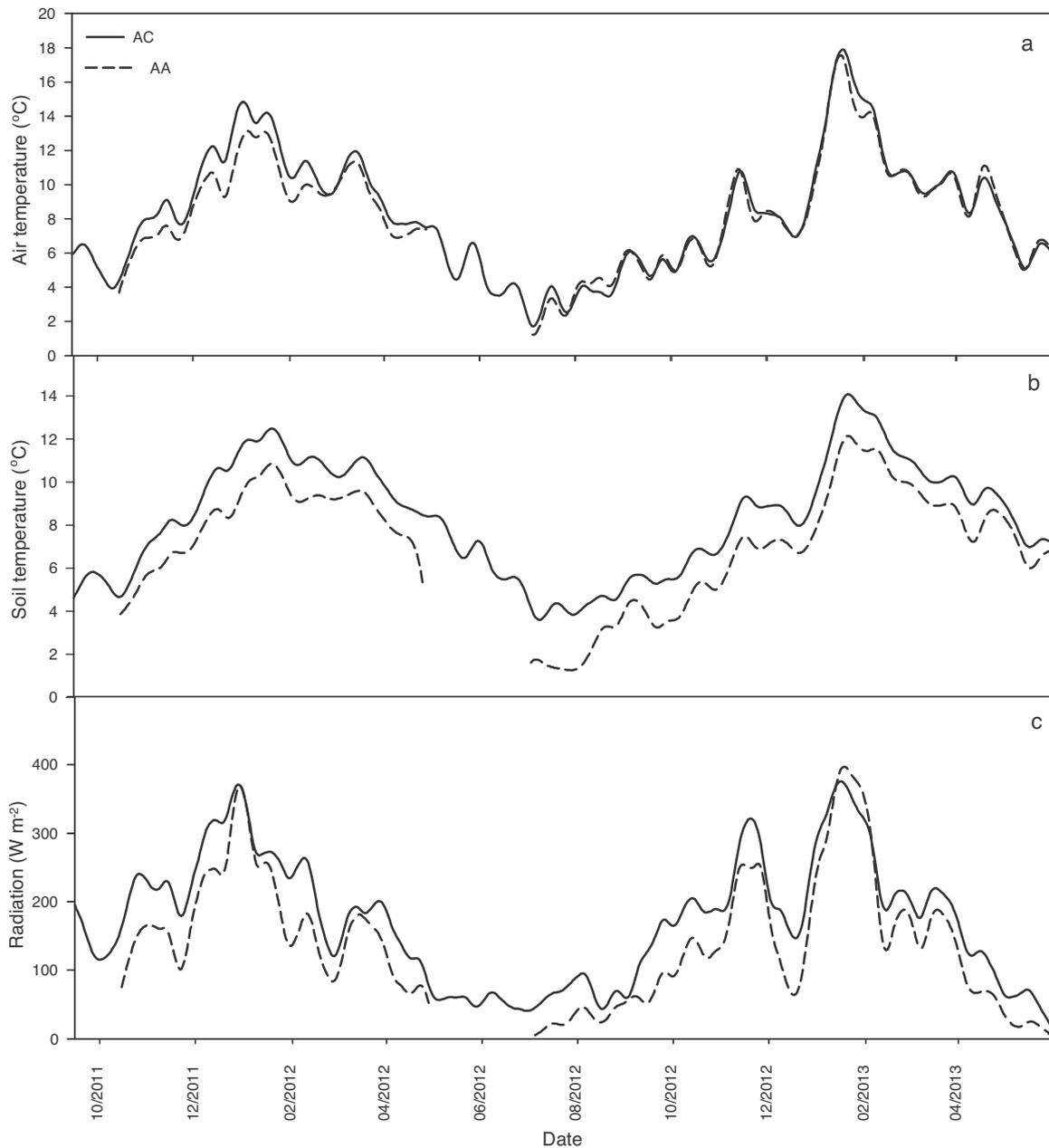


Fig. A2. (a) Daily mean air temperature for the period October 2011–May 2013 in both study sites (Alerce Costero, AC and Alerce Andino, AA), (b) daily mean soil temperature and (c) daily mean total solar radiation. For illustration purposes data were smoothed using a cubic spline designed to reduce 50% of the variance in a sine wave with a periodicity of 25 days. Soil temperature and radiation are clearly higher in Alerce Costero than Alerce Andino throughout the year, but the difference is less clear for air temperature.

Table A1

Kendall-tau b correlations between stem radius increment at a “daily” basis (considering short, regular and long cycles), stem radius change at 7, 21 and 31 days and environmental variables in Alerce Costero (AC) and Alerce Andino (AA). “Daily” refers to the time scale given by the stem cycle. Significant correlations are marked with an asterisk.

Site and time period	Mean temp.	Max. temp.	Min. temp.	Precip.	Humidity	VPD	Radiation	Soil temp.
AC “daily” increment	0.01	0.10	−0.08	0.34*	0.18*	−0.18*	−0.15*	0.01
AC 7 days	−0.21*	−0.32*	0.02	0.25*	0.47*	−0.45*	−0.34*	0.05
AC 21 days	−0.25*	−0.37*	0.01	0.30*	0.49*	−0.46*	−0.42*	0.01
AC 31 days	−0.26*	−0.38*	−0.01	0.28*	0.48*	−0.46*	−0.40*	−0.02
AA “daily” increment	0.03	0.18*	−0.11	0.48*	0.28*	−0.24*	−0.02	0.05
AA 7 days	−0.20*	−0.30*	−0.05	0.33*	0.45*	−0.41*	−0.38*	0.16*
AA 21 days	−0.18*	−0.29*	−0.05	0.30*	0.44*	−0.39*	−0.39*	0.11
AA 31 days	−0.19*	−0.29*	−0.05	0.28*	0.43*	−0.39*	−0.37*	0.07

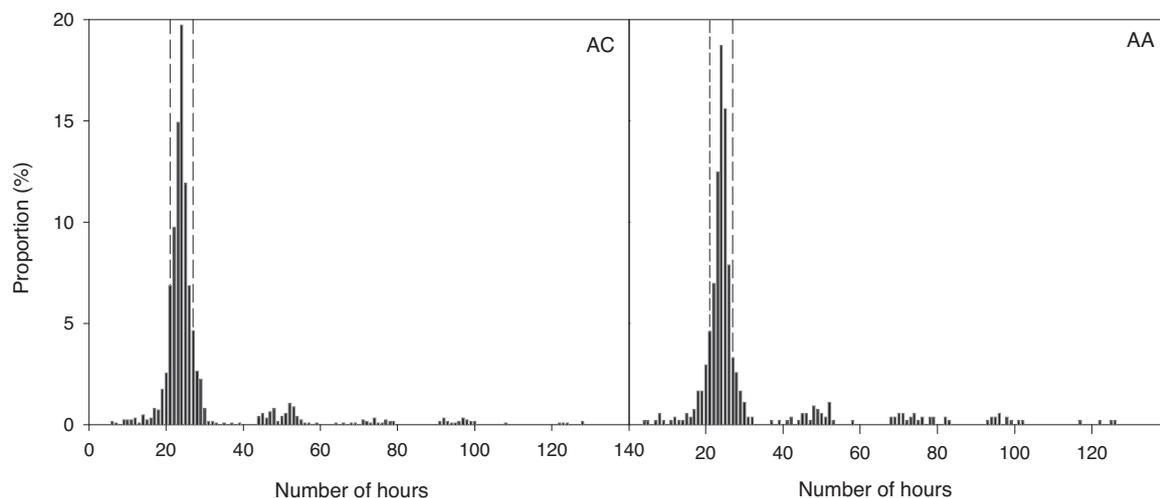


Fig. A3. Distribution (in percentage) of the number of hours of stem circadian cycles in Alerce Costero (AC) and Alerce Andino (AA). Regular cycles (24 ± 3 h), representing the highest proportion of cycles, are delimited by dashed lines.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Barichivich, J., 2005. Muerte apical episódica en bosques de alerce (*Fitzroya cupressoides* [Mol.] Johnston) de la Cordillera de la Costa de Valdivia. Facultad de Ciencias Forestales, Universidad Austral de Chile, Valdivia (Thesis).
- Biondi, F., Hartsough, P., 2010. Using automated point dendrometers to analyze tropical tree stem growth at Nevado de Colima. *Mexico Sens.* 10, 5827–5844.
- Boisvenue, C.E.L., Running, S.W., 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. *Global Change Biol.* 12, 862–882.
- Bouriaud, O., Leban, J.M., Bert, D., Deleuze, C., 2005. Intra-annual variations in climate influence growth and wood density of Norway spruce. *Tree Physiol.* 25, 651–660.
- Christie, D.A., Boninsegna, J.A., Cleaveland, M.K., Lara, A., Le Quesne, C., Morales, M.S., Mudelsee, M., Stahle, D.W., Villalba, R., 2011. Aridity changes in the temperate-Mediterranean transition of the Andes since AD 1346 reconstructed from tree-rings. *Clim. Dyn.* 36, 1505–1521.
- Deslauriers, A., Morin, H., Urbinati, C., Carrer, M., 2003. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). *Trees-Struct. Funct.* 17, 477–484.
- Deslauriers, A., Rossi, S., Anfodillo, T., 2007a. Dendrometer and intra-annual tree growth: what kind of information can be inferred? *Dendrochronologia* 25, 113–124.
- Deslauriers, A., Anfodillo, T., Rossi, S., Carraro, V., 2007b. Using simple causal modeling to understand how water and temperature affect daily stem radial variation in trees. *Tree Physiol.* 27, 1125–1136.
- Deslauriers, A., Rossi, S., Turcotte, A., Morin, H., Krause, C., 2011. A three-step procedure in SAS to analyze the time series from automatic dendrometers. *Dendrochronologia* 29, 151–161.
- Deslauriers, A., Beaulieu, M., Balducci, L., Giovannelli, A., Gagnon, M.J., Rossi, S., 2014. Impact of warming and drought on carbon balance related to wood formation in black spruce. *Ann. Bot.* 114, 335–345.
- Devine, W.D., Harrington, C.A., 2011. Factors affecting diurnal stem contraction in young Douglas-fir. *Agric. For. Meteorol.* 151, 414–419.
- Donoso, C., Grez, R., Sandoval, V., 1990. Caracterización del tipo forestal alerce. *Bosque* 11, 21–34.
- Donoso, C., Lara, A., Escobar, B., Premoli, A., Souto, C., 2006. *Fitzroya cupressoides* (Molina) I.M. Johnston. In: Donoso, C. (Ed.), Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología. Maria Cuneo Ediciones, Valdivia, Chile, pp. 68–81.
- Downes, G., Beadle, C., Worledge, D., 1999. Daily stem growth patterns in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Trees-Struct. Funct.* 14, 102–111.
- Drew, D.M., O'Grady, A.P., Downes, G.M., Read, J., Worledge, D., 2008. Daily patterns of stem size variation in irrigated and unirrigated *Eucalyptus globulus*. *Tree Physiol.* 28, 1573–1581.
- Duchesne, L., Houle, D., 2011. Modelling day-to-day stem diameter variation and annual growth of balsam fir (*Abies balsamea* (L.) Mill.) from daily climate. *For. Ecol. Manage.* 262, 863–872.
- Dünisch, O., Bauch, J., 1994. Influence of soil substrate and drought on wood formation of spruce (*Picea abies* [L.] Karst.) under controlled conditions. *Holzforchung—Int. J. Biol. Chem. Phys. Technol. Wood* 48, 447–457.
- Dünisch, O., 2010. Low night temperatures cause reduced tracheid expansion in *Podocarpus latifolius*. *IAWA J.* 31, 245–255.
- Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J., Velichko, A.A., 2007. Ecosystems, their properties, goods, and services. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., et al. (Eds.), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 211–272.
- Fritts, H.C., 1958. An analysis of radial growth of beech in a central Ohio forest during 1954–1955. *Ecology* 39, 705–720.
- Fritts, H., 1976. *Tree Rings and Climate*. Academic, San Diego, CA.
- Fuenzalida, H., Aceituno, P., Falvey, M., Garreaud, R., Rojas, M., Sanchez, R., 2007. Estudio de la variabilidad climática en Chile para el siglo XXI. In: Informe Final CONAMA. Gobierno de Chile, Santiago, Chile.
- González-Reyes, A., Muñoz, A., 2013. Cambios en la precipitación de la ciudad de Valdivia (Chile) durante los últimos 150 años. *Bosque* 34, 200–213.
- Gruber, A., Zimmermann, J., Wieser, G., Oberhuber, W., 2009. Effects of climate variables on intra-annual stem radial increment in *Pinus cembra* (L.) along the alpine treeline ecotone. *Ann. For. Sci.* 66, 1–11.
- Hsiao, T.C., Acevedo, E., 1974. Plant responses to water deficits, water-use efficiency, and drought resistance. *Agric. Meteorol.* 14, 59–84.
- Jones, H.G., 1992. *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge.
- King, G., Fonti, P., Nievergelt, D., Büntgen, U., Frank, D., 2013. Climatic drivers of hourly to yearly tree radius variations along a 6 °C natural warming gradient. *Agric. For. Meteorol.* 168, 36–46.
- Köcher, P., Horna, V., Leuschner, C., 2012. Environmental control of daily stem growth patterns in five temperate broad-leaved tree species. *Tree Physiol.* 32, 1021–1032.
- Krepkowski, J., Bräuning, A., Gebrekirstos, A., Strobl, S., 2011. Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. *Trees* 25, 59–70.
- Lambers, H., Chapin, I.F.S., Chapin, F.S., Pons, T.L., 2008. *Plant Physiological Ecology*, second ed. Springer, New York, USA.
- Lara, A., Villalba, R., 1993. A 3620-year temperature record from *Fitzroya cupressoides* tree rings in southern South America. *Science* 260, 1104–1106.
- Lara, A., Donoso, C., Alarcon, D., 2002. *Fitzroya cupressoides* (Molina) I.M. Johnston. In: Schutt, P., Weisgerber, H., Schuck, H.J., Lang, U., Roloff, A. (Eds.), *Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie. Ergänzungslieferung, Landsberg*, pp. 1–8.
- Legendre, P., Legendre, L., 2012. *Numerical Ecology*, third english ed. Elsevier, Amsterdam.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.
- Mäkinen, H., Nöjd, P., Saranpää, P., 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiol.* 23, 959–968.
- Menzel, A., Jakobi, G., Ahas, R., Scheifinger, H., Estrella, N., 2003. Variations of the climatological growing season (1951–2000) in Germany compared with other countries. *Int. J. Clim.* 23, 793–812.
- Muller, B., Pantin, F., Genard, M., Turc, O., Freixes, S., Piques, M., Gibon, Y., 2011. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *J. Exp. Bot.* 62, 1715–1729.

- Neira, E., Lara, A., 2000. Desarrollo de cronologías de ancho de anillos para alerce (*Fitzroya cupressoides*) en Contao y Mirador, Chile. *Rev. Chil. Hist. Nat.* 73, 693–703.
- Pantin, F., Simonneau, T., Muller, B., 2012. Coming of leaf age: control of growth by hydraulics and metabolics during leaf ontogeny. *New Phytol.* 196, 349–366.
- Pérez, C.A., Carmona, M.R., Aravena, J.C., Farina, J.M., Armesto, J.J., 2009. Environmental controls and patterns of cumulative radial increment of evergreen tree species in montane, temperate rainforests of Chiloé Island, southern Chile. *Aust. Ecol.* 34, 259–271.
- Quintana, J., Aceituno, P., 2013. Boletín Climático Enero Febrero 2013. Universidad de Chile, Santiago, Chile.
- Richardson, S., Dinwoodie, J., 1960. Studies on the physiology of xylem development. I. The effect of night temperature on tracheid size and wood density in conifers. *J. Inst. Wood Sci.* 6, 3–13.
- Richardson, S., 1964. The external environment and tracheid size in conifers. In: Zimmermann, M.H. (Ed.), *The Formation of Wood in Forest Trees*. Academic Press, pp. 367–388.
- Rossi, S., Deslauriers, A., Anfodillo, T., 2006. Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the Alpine timberline. *IAWA J.* 27, 383–394.
- Scholz, F.G., Phillips, N.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., 2011. Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size. In: *Size- and Age-related Changes in Tree Structure and Function*. Springer, Dordrecht, Netherlands, pp. 341–362.
- Sevanto, S., Holttä, T., Markkanen, T., Peramäki, M., Nikinmaa, E., Vesala, T., 2005. Relationships between diurnal xylem diameter variation and environmental factors in Scots pine. *Boreal Environ. Res.* 10, 447–458.
- Steppe, K., De Pauw, D.J., Lemeur, R., Vanrolleghem, P.A., 2006. A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree Physiol.* 26, 257–273.
- Suzuki, R., Shimodaira, H., 2006. Pvcust: an R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics* 22, 1540–1542.
- Tardif, J., Flannigan, M., Bergeron, Y., 2001. An analysis of the daily radial activity of 7 boreal tree species, northwestern Quebec. *Environ. Monit. Assess.* 67, 141–160.
- Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., et al., 2007. Observations: surface and atmospheric climate change. In: Solomon, S., Qin, D., Manning, M., et al. (Eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Turcotte, A., Morin, H., Krause, C., Deslauriers, A., Thibeault-Martel, M., 2009. The timing of spring rehydration and its relation with the onset of wood formation in black spruce. *Agric. For. Meteorol.* 149, 1403–1409.
- IUCN, 2013. The IUCN Red List of Threatened Species 2013. IUCN, (<http://www.iucnredlist.org/details/30926/0>) 29 August, 2013.
- Urrutia-Jalabert, R., 2014. Primary Productivity and Soil Respiration in *Fitzroya Cupressoides* Forests of Southern Chile and Their Environmental Controls. University of Oxford, Oxford (DPhil Thesis).
- Veblen, T.T., Ashton, D.H., 1982. The regeneration status of *Fitzroya cupressoides* in the Cordillera Pelada, Chile. *Biol. Conserv.* 23, 141–161.
- Veblen, T., Schlegel, F., 1982. *Reseña ecológica de los bosques del sur de Chile. Bosque* 4, 73–115.
- Villalba, R., 1990. Climatic fluctuations in northern Patagonia during the last 1000 years as inferred from tree-ring records. *Quatern. Res.* 34, 346–360.
- Villalba, R., Leiva, J.C., Rubulls, S., Suarez, J., Lenzano, L., 1990. Climate, tree-ring, and glacial fluctuations in the Rio Frias Valley, Rio Negro, Argentina. *Arct. Alp. Res.* 22, 215–232.
- Xiong, W., Wang, Y., Yu, P., Liu, H., Shi, Z., Guan, W., 2007. Growth in stem diameter of *Larix principis-rupprechtii* and its response to meteorological factors in the south of Liupan Mountain, China. *Acta Ecol. Sin.* 27, 432–440.
- Zhou, L., Tucker, C.J., Kaufmann, R.K., Slayback, D., Shabanov, N.V., Myneni, R.B., 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *J. Geophys. Res.: Atmos.* 106, 20069–20083.
- Zweifel, R., Zimmermann, L., Zeugin, F., Newbery, D.M., 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J. Exp. Bot.* 57, 1445–1459.