

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

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29 **Abstract**

30 Relationships between environmental factors and stem radius variation at short temporal scales
31 can provide useful information regarding the sensitivity of tree species' productivity to climate
32 change. This study used automatic point dendrometers to assess the relationship between
33 environmental variables and stem radius contraction and increment in ten *Fitzroya cupressoides*
34 trees growing in two sites, the Coastal Range (Alerce Costero National Park) and the Andean
35 Cordillera (Alerce Andino National Park) of southern Chile. The growing season in each site,
36 determined using stem daily cycle patterns for each month, was longer in the Coastal site than in
37 the Andes. Warmer and sunnier conditions were positively related with daytime tree radius
38 contraction in both areas, and relationships were stronger in the Coastal site where more
39 pronounced shrinking events were associated with prolonged warm and dry conditions compared
40 to the Andes. Stem increment was positively related with precipitation and humidity in both
41 sites, reflecting the positive effect of water on cell turgidity and consequent enlargement.
42 Relationships between stem radius change and environmental variables considering longer
43 temporal scales (7 to 31 days), confirmed a stronger association with humidity/vapor pressure
44 deficit and precipitation, rather than with temperature. Although *Fitzroya* grows in particularly
45 wet and somewhat cool areas, current and projected drier and warmer summer conditions in
46 southern Chile might have a negative effect on *Fitzroya* stem increment and carbon
47 accumulation in both sites. This effect would be more critical in the Coastal Range compared
48 with the Andes though, due in part to more limiting soil conditions and less summer precipitation

49 in this area. Long-term research is needed to monitor different aspects of the response of these
50 endangered ecosystems to this additional threat imposed by climate change.

51 **Keywords:** dendrometer, stem daily cycle, stem increment, carbon accumulation,
52 dendrochronology.

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1. Introduction

Climate change is likely to have considerable effects on tree growth and forest productivity (Boisvenue et al., 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 on 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 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.

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

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

115 Cell division and enlargement, which are the main processes that contribute to growth, are
116 considerably more sensitive to water changes than photosynthesis, having water availability a

117 direct effect on growth (Sala et al., 2012 See also Deslauriers et al. 2014). Irreversible growth
118 occurs in a cell when a certain pressure threshold in the tissue is exceeded, so when there is
119 water deficit in the tree, this inhibits cell division, and more sensitively cell expansion (Hsiao
120 and Acevedo, 1974, Lambers et al., 2008). Besides the positive effects of water, it has also been
121 reported that temperature would be important in determining the growth rate of metabolic
122 processes in the cambium, as temperature is minimum at night, when conditions are more
123 suitable for growth (Drew et al., 2008, Pantin et al. 2012 New Phytol). One of the only and
124 probably the most straightforward way to monitor growth at a short time scale and therefore
125 assess the direct environmental correlates of radial increment in particular species is through the
126 use of automatic dendrometers. This monitoring can provide valuable information regarding
127 subtle differences in climate sensitivity among species or populations, and potential long-term
128 limitations to forest productivity caused by climate change (Perez et al., 2009). High precision
129 automatic dendrometers can provide information on variation in water storage throughout the
130 year, as well as seasonal growth (Deslauriers et al., 2007a), and they have been widely used to
131 describe stem growth phenology and to evaluate growth-climate relationships in various
132 ecosystems (e.g. Downes et al., 1999, Deslauriers et al., 2003, Mäkinen et al., 2003, Bouriaud et
133 al., 2005, Deslauriers et al., 2007b, Biondi and Hartsough, 2010, Köcher et al., 2012).

134 To date, the only study that has assessed *Fitzroya* stem increment-climate relationships at a daily
135 time scale was carried out using band dendrometers in Chiloé Island (at the southern distribution
136 of *Fitzroya* in the Coastal Range, Perez et al., (2009)). The authors reported that daily stem
137 growth was positively related to precipitation and negatively related to radiation. Nevertheless, it
138 is not clear if these relationships hold for populations located towards the north in the Coastal

139 Range, as well as in the Andes, where forests are much older and environmental conditions are
140 different.

141 We investigated environmental correlates of stem radial contraction and increment of *Fitzroya*
142 trees growing in two distinct environments in southern Chile (the Coastal Range and the Andean
143 Cordillera). These sites were chosen because they contain the main populations of this species
144 and the forests greatly differ in their structure, disturbance regime and environmental conditions.
145 The studied stands are representative of the widespread condition of forests in each range, with
146 old and large trees in the pristine Andean area and younger and smaller trees in the Coastal
147 Range, where there has been a permanent influence of fires. We sought to resolve the following
148 questions: 1) How do the stem radial change patterns compare between trees growing in these
149 two areas?, 2) What environmental variables are related to daily stem radial contraction and
150 increment in both sites?, 3) How can we better interpret the coarse-scale dendroclimatological
151 relationships previously reported for this species?, and 4) Considering findings from objectives
152 1-3, what are the implications of climate change for *Fitzroya* stem growth and carbon
153 sequestration in these two areas?

154

155 **2. Methods**

156 **2.1. Study sites and tree selection**

157 The study was conducted in the Alerce Costero National Park, close to the northern distribution
158 of *Fitzroya* in the Coastal Range at 850 m.a.s.l (40° 10' S, 73° 26' W) and in the Alerce Andino
159 National Park in the Andean Cordillera at 760 m a.s.l (41° 32' S, 72° 35' W, Figure 1). Mean
160 annual precipitation and temperature in 2012 were 4,860 mm and 7.26° C in the coastal site and
161 ca. 6,600 mm and ca. 6.89° C in the Andes (Urrutia-Jalabert, 2014).

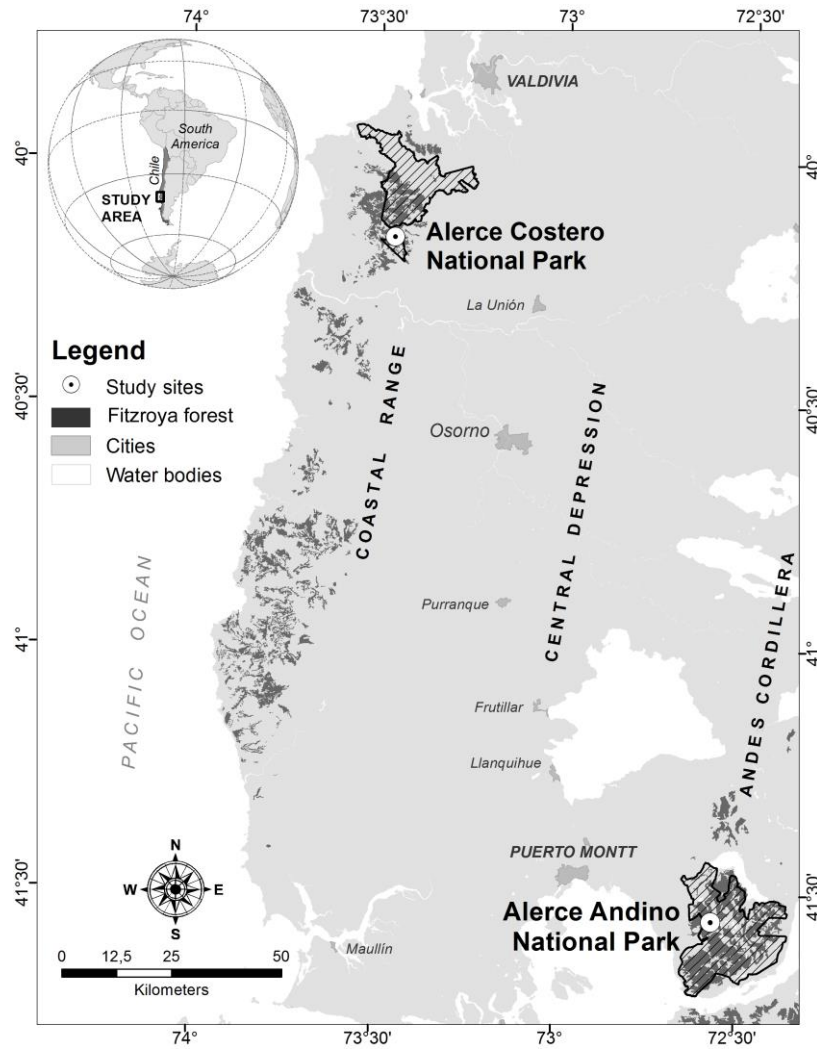
162 The effective soil depth in Alerce Costero is generally thin (29 to 67 cm), and soils are brown-
163 earths and severely podzolized (Veblen and Ashton, 1982, Urrutia-Jalabert, 2014). Soil texture in
164 the upper horizon is mostly sandy-loam and organic matter content is ca. 10%. The studied forest
165 is medium-age, dense (1415 trees/ha, considering trees ≥ 10 cm diameter at breast height (DBH))
166 and predominantly dominated by *Fitzroya*. Sampled trees were dominant and ranged between
167 35.5 and 47.9 cm DBH and 14.4 and 15.8 m height. In Alerce Andino, the effective soil depth is
168 larger than in the Coast (56 to 100 cm), soils are derived from volcanic material (silty-loam
169 texture) and contain a high amount of organic matter in the upper horizon (ca. 80%, Urrutia-
170 Jalabert, 2014). The studied forest is old-growth, less dense than in the coast (782 trees/ha) and
171 *Fitzroya* is the most important species in terms of basal area. Sampled trees were dominant and
172 ranged between 82.5 and 161.5 cm DBH and 33.2 and 35.6 m height.

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 178 **Figure 1.** Study sites in the Alerce Costero and Alerce Andino National Parks in southern Chile.
 179 The approximate location of the three major physiographic units in the area is shown (Coastal
 180 Range, Central Depression and Andean Cordillera). The distribution of *Fitzroya* forests north of
 181 41° 45' S is also displayed.

182

183 **2.2. Dendrometer data collection**

184 From Spring 2011 (October-November) to Fall 2013 (May 2013), stem size variation was
 185 recorded in five dominant trees per site every 30 minutes and averaged over each hour using
 186 automatic point dendrometers (DR model, Ecomatik, Munich, Germany) installed at breast

187 height. The instrument consists of a displacement transducer that is anchored to the tree using
188 two screws. The instrument resolution is 2.6 μm and thermal expansion is $< 0.1 \mu\text{m/K}$. The
189 temperature variation does not affect the sensor measurements, and due to construction the
190 thermal expansion of the framework is negligible. To reduce the influence of bark expansion and
191 contraction, the outermost part of the bark was removed taking care to not damage the cambium.
192 Raw measurements of every dendrometer were carefully checked and noisy or unexplained data,
193 such as periods with constant or sudden extreme values, were removed for further analyses.

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195 **2.3. Environmental data**

196 A weather station (Skye Instruments, Powys, UK) recording precipitation, temperature, relative
197 humidity and total radiation was installed $< 1 \text{ km}$ from the monitored trees at each site. In
198 addition, one soil temperature sensor (Decagon EC-T, Pullman, USA) was installed close to the
199 monitored trees in each site at 10 cm below the surface. Data were recorded every 30 minutes
200 and hourly means were calculated. Vapor pressure deficit (VPD, hPa) was calculated from the
201 hourly means of temperature and relative humidity (Jones, 1992).

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203 **2.4. Growing season estimation**

204 Since only the growing period is recommended to be used to examine correlations with
205 environmental parameters (Deslauriers et al., 2007a), some studies have assessed this period
206 using micro-coring techniques and subsequent cell analyses (Deslauriers et al., 2003, Rossi et al.,
207 2006). Alternatively, growing season estimates have commonly relied on meteorological
208 parameters (e.g. the period between the last spring and the first fall frost), phenological
209 observations and satellite data, among others (Zhou et al., 2001, Menzel et al., 2003). Here, in

210 order to assess site-specific periods according to patterns of stem variation recorded by trees, an
211 analysis of the daily cycle was performed. During the growing season, a clear pattern of daytime
212 contraction and nighttime expansion (with high amplitudes) should be observed; while during the
213 dormant season, amplitudes should be much lower in temperate climates or cycles can even be
214 inverted in cold climates (Turcotte et al., 2009, Devin and Harrington, 2011, King et al., 2013).
215 Therefore in each site, the amplitude of the daily cycle (from 0 to 23 hours) was calculated for
216 each month including the mean of all dendrometers for the whole sampling period.
217 The daily cycles of each month were scaled to start in zero and a K-means cluster analysis with
218 k=2 was used to divide the year in two periods: non-active and growing season. This clustering
219 procedure is a partitioning method that finds a single partition for a group of objects; where
220 objects within each cluster are more alike to one another than to objects assigned to other clusters
221 (Legendre and Legendre, 2012). To confirm the definition of clusters, a hierarchical cluster
222 analysis using the R package “pvclust” was performed (Suzuki and Shimodaira, 2006). Data
223 recorded during the months defined as the growing period were used for subsequent analyses
224 focused on the relationship between stem radius change and climate.

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226 **2.5. Extraction of stem radius variation**

227 In order to extract the stem radius variation during the growing period, the stem cycle approach
228 was used in this study (Downes et al., 1999 modified by Deslauriers et al., 2003). This approach
229 uses stem shrinking and swelling to divide the stem cycle into three different phases: contraction,
230 expansion and stem radius increment (Downes et al., 1999, Deslauriers et al., 2003, Figure 2).
231 Contraction (phase 1), includes the period between the morning radius maximum and the
232 afternoon minimum and expansion (phase 2) includes the total period between the radius

233 minimum to the next morning maximum. Stem radius increment (ΔR or phase 3) corresponds to
234 the portion of the expansion phase from the time the stem radius surpasses the morning
235 maximum until the following maximum, and has been considered as an estimate of growth
236 (Deslauriers et al., 2003, Deslauriers et al., 2007a). When the previous cycle maximum was
237 reached a positive stem radius change ($\Delta R +$) was calculated. When this maximum was not
238 reached, a negative stem radius change ($\Delta R -$) was defined; however, only positive values were
239 used for further analyses. The duration of each phase (h, hours) was also estimated.

240 Environmental variables were also processed according to each phase division in order to match
241 them with stem data. Analyses were carried out using a routine specially developed for this
242 purpose by Deslauriers et al., (2011) using the SAS software (SAS Institute, Cary, NC).

243 The stem circadian cycle commonly lasts around 24 hours, but rain events can result in longer or
244 shorter cycles (Deslauriers et al., 2003, Deslauriers et al., 2007a, Deslauriers et al., 2007b, Figure
245 2). We defined regular ($24h \pm 3h$), short ($< 21h$) and long ($> 27h$) cycles (Deslauriers et al.,
246 2007b, Turcotte et al., 2009).

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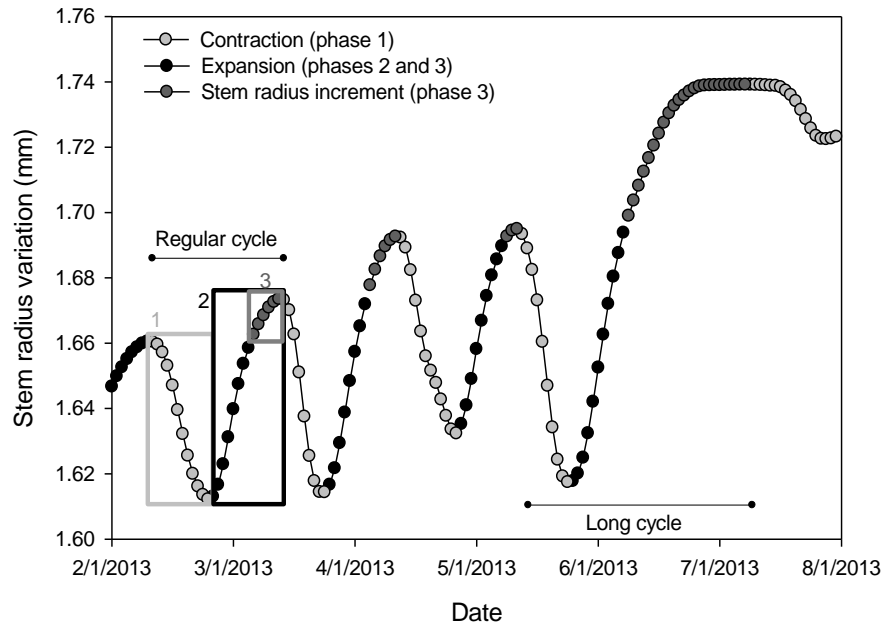
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254 **Figure 2.** Cycles in stem variation divided in three distinct phases: contraction (phase 1),
 255 expansion (phases 2 and 3) and radius increment (phase 3). Each dot represents an hourly
 256 measurement and the cycles are an example of data recorded during the first week of January
 257 2013 in one tree from the coastal site.

258

259 **2.6. Relationship between stem radius change and climate variables**

260 In order to find the environmental correlates of stem radius change, bootstrapped correlations
 261 were calculated between stem contraction (magnitude of phase 1) and stem radius increment
 262 (magnitude of phase 3) and the environmental variables occurring during each phase (average or
 263 sum (precipitation) of values for the respective phase). The Kendall tau-b correlation coefficient
 264 (T) was used since these relationships did not comply with all assumptions for a parametric test
 265 and the data contained tied observations (tied ranks). To make variables independent from each
 266 other and avoid using non-stationary data in the correlation analyses, the first difference was
 267 used for contraction and for all the climate variables, except precipitation. Mean correlations

268 were significant if after 1000 bootstrapped iterations their absolute values were at least two times
269 their standard deviations (SD) (Deslauriers et al., 2003). Data for the two estimated growing
270 seasons (2011-2012, 2012-2013) were used.

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

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

286 In order to have a spatial representation of the environmental variables mostly related with stem
287 radial change, and since most environmental parameters are strongly correlated, a principal
288 components analyses (PCA) was performed using all the variables during each time period.
289 Variables were logarithmically transformed as necessary to comply with linear relationships for
290 the PCA.

291 **3. Results and Discussion**

292 **3.1. Patterns of stem radius change**

293 Radius variation in all trees showed characteristic seasonal patterns in both sites (Figure 3). Most
294 of variation and stem increment were observed during the period of higher temperature, radiation
295 and VPD in spring and summer (~November-December through March). Precipitation was
296 abundant all year long, with lower values recorded during summer (average of 839 and 1413 mm
297 during December-February in Alerce Costero and Alerce Andino, respectively, Figure 3). The
298 amplitude of stem variations was lower during winter months in both sites and generally higher
299 in the Coastal Range than in the Andes throughout the year. Trees responded synchronously in
300 both study sites.

301 Stem radius especially in two trees from the coastal site and in one tree from the Andes
302 decreased during the summer of the first year, reaching the lowest values at the end of December
303 2011 and beginning of January 2012. This decrease corresponded with a rainless period of 15
304 days, accompanied with high values of radiation and temperature. The magnitude of this
305 shrinking event was higher in the Coastal Range than in the Andes. An important shrinking was
306 also observed in most trees of both sites during the second half of January 2013. This
307 corresponded to a period of very little precipitation during 17 days, with the warmest
308 temperatures registered during the whole studied period (mean values of 16.9° and 16.1° C in
309 Alerce Costero and Alerce Andino, respectively). January was a particularly dry and hot month,
310 where minimum and maximum temperatures in Valdivia (at a low altitude close to Alerce
311 Costero) were up to 2° C and 4.9° C warmer than the climatological mean (1961-1990),
312 respectively (Quintana and Aceituno, 2013). The amplitude of this decrease was also larger in
313 the coastal site than in the Andes and both periods with strong shrinking were the longest ones

314 with almost no precipitation and warm temperatures in both areas. Strong stem shrinking in the
315 middle of the summer was also reported for *Fitzroya*, but not for other evergreen broadleaf
316 species in Chiloé, when a strong El Niño event (1998) affected the region and a long rainless and
317 warm period (26 days) hit Southern Chile (Perez et al., 2009). According to these authors, radial
318 growth of *Fitzroya* is negatively affected by increased evaporative demand during rainless and
319 sunny periods.

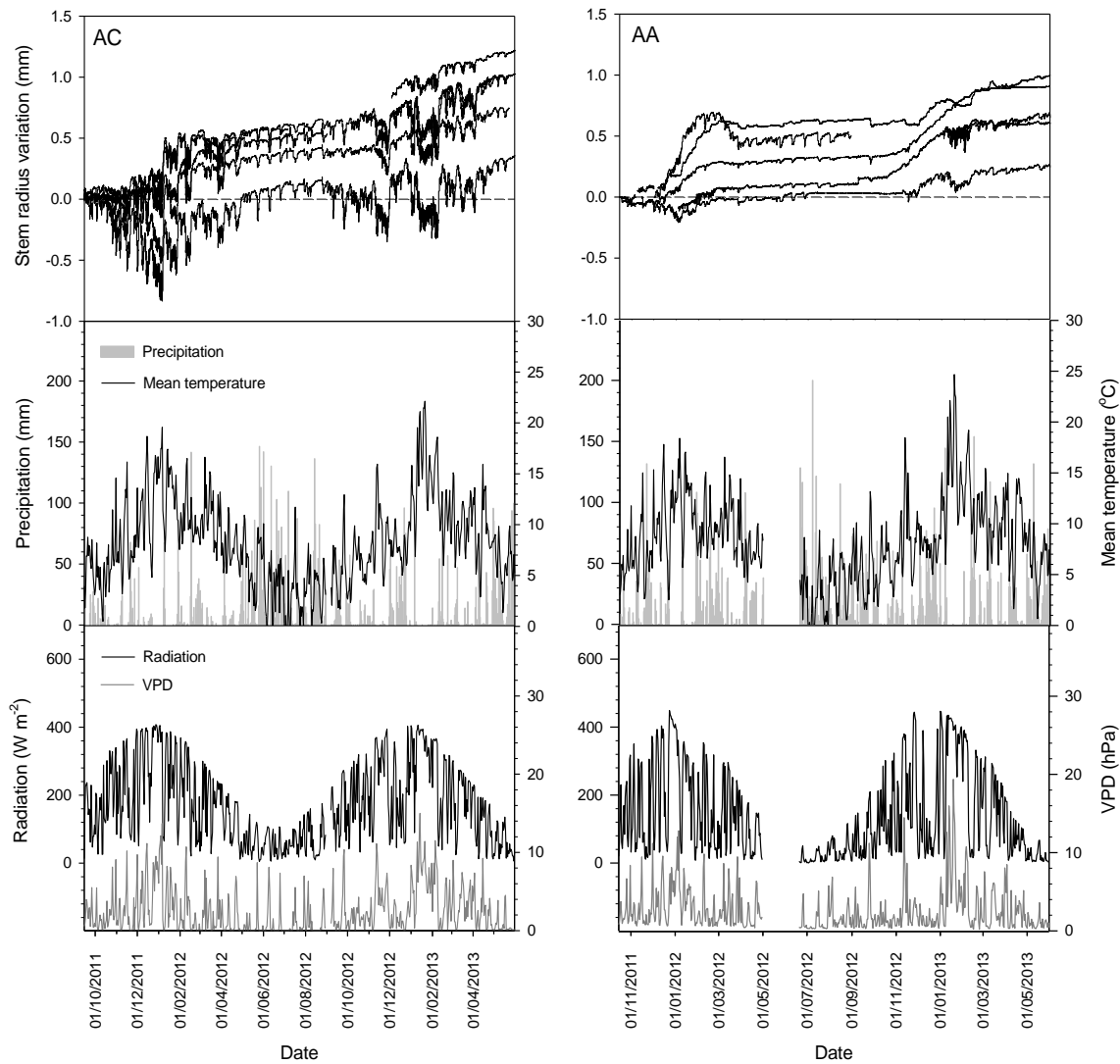
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326 **Figure 3.** Stem radius variation of the five trees monitored in each site and climate data from
 327 Alerce Costero (AC, left) and Alerce Andino (AA, right) for the whole studied period. Higher
 328 variability in stem radius is displayed during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

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332

333 **3.2. Growing season estimation, cumulative radial increment and cycle**
334 **characterization**

335 The evident higher stem activity during spring-summer compared to fall-winter resulted in a
336 clear pattern of physiological activities suitable for wood formation and helped to estimate a
337 potential period of growth in both study sites. According to the K-means cluster analyses, the
338 growing season which was characterized by higher stem daily amplitudes, was estimated to
339 occur from November to March in the Coastal Range and from December to February in the
340 Andes (Figure A1, appendix). The remaining months in both sites were assigned to the second
341 cluster and could be considered as part of a dormancy or “less active” period (Figure A1). These
342 results were confirmed by the hierarchical cluster analysis (results not shown). In spring and
343 summer, the increases in temperature and radiation drive greater evaporative demand during the
344 day that contribute to deplete stem water reserves and, combined with the refilling at night,
345 increase the amplitude of diurnal cycles (King et al., 2013). The lower daily amplitude observed
346 during fall and winter seems characteristic of temperate regions, where there are no pronounced
347 freeze-thaw events that could affect stem variation (Turcotte et al., 2009, Devine and Harrington,
348 2011, King et al., 2013).

349 These results agree with the difference in climate between both sites, with air temperature, and
350 particularly soil temperature and radiation being most of the time lower in the Andes than in the
351 Coastal Range (Figure A2, appendix). Mean summer air temperature (December-February, 2012
352 and 2013) was 11.9° and 11.1° C in Alerce Costero and Alerce Andino, respectively. Mean
353 radiation was 259 and 218 W m⁻² and mean soil temperature was 11.1° and 9.4° C in the coastal
354 site and the Andes, respectively.

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

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

365 In terms of cycle characterization, in the coastal site 75% of the cycles were classified as regular
366 cycles, 17% as long cycles and 8% as short cycles. The longest cycle in this site lasted 128 hours
367 (Figure A3, appendix). In the Andes, 70% of the cycles were classified as regular cycles, 20% as
368 long cycles and 10% as short cycles. The longest cycle event lasted 126 hours (Figure A3).

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

374 The duration of the expansion phase varied considerably due to rainfall events, ranging from 1 to
375 118-119 h in the coastal site and the Andes, respectively. The mean start time of this event was
376 19:24 ($\pm 1:48$) in the coast and 17:12 h ($\pm 2:22$) in the Andes. The longest increment phases were
377 observed to last 108 and 115 h in Alerce Costero and Andino, respectively.

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

382 Additionally, a higher amplitude of contraction was found in the Coastal Range (0.06 mm)
383 compared to the Andes (0.01 mm, $p < 0.05$), indicating that trees in the coast would utilize their
384 internal stem water reserves faster than in the Andes (King et al., 2013). One possible
385 explanation for this would be the difference in soil conditions between both sites: the Alerce
386 Costero site is characterized by shallower soils with lower water retention capacity, which is
387 accentuated by the sandy texture and less organic material in this site compared to Alerce
388 Andino (Barichivich, 2005, Gerding, 2013). These characteristics would result in a greater
389 resistance of water flow from the soil, causing higher amplitudes of stem variation and a higher
390 use of the stem water pool during the day (Sevanto et al., 2005). Soil water content
391 measurements in each site during summer (at a monthly basis at 12 cm depth) partly reflect the
392 differences that exist between areas: values reached 39% and 50% in Alerce Costero and Andino
393 during 2011-2012 and 32% and 51% during the drier summer (2012-2013). A particularly strong
394 drop in water content was observed during January and February 2013 in the Coastal site
395 (Urrutia-Jalabert, 2014). An additional explanation for the difference between sites, would be
396 that conditions are commonly cloudier and rainier (~40% more precipitation during December-
397 February) in Alerce Andino than in Alerce Costero, and daily contraction amplitudes have been
398 reported to be lower on overcast or rainy days (Devine and Harrington, 2011, King et al., 2013).
399 The higher amplitude of contraction in the coastal site could not be explained by a higher amount
400 of bark in trees from this site, since most bark was removed and trees have thinner bark in the

401 coast than in the Andes. Finally, an alternative explanation might be that larger and taller
402 *Fitzroya* trees in the Andes have a greater sapwood capacitance compared to the trees from the
403 Coastal Range which would depend more on soil water availability (Scholz et al., 2011).

404

405 **3.3. Relationships between environmental factors and stem radius change**

406 Considering all and just regular cycles, stem contraction during the day in both sites was
407 positively related with mean and maximum temperatures, VPD and radiation (Figure 4).

408 Humidity on the other hand, was negatively related with contraction ($T=-0.58$) and precipitation
409 also was negatively related with this variable, but just in Alerce Costero when considering all
410 cycles (Figure 4). This is in agreement with what was found by Devine and Harrington (2011)
411 for young Douglas-fir and supports the above reported statement that warmer and drier
412 conditions are usually associated to strong stem shrinking patterns. Relationships were stronger
413 in the coastal site than in the Andes, meaning that trees in the former site would be more
414 sensitive to environmental conditions that make the stem contract.

415 Stem radius increment mainly occurs at night or early morning, as was corroborated in this
416 study. It has been reported that cell enlargement takes place mostly at night or on rainy days,
417 when turgor is high and cambium is supplied with optimal water availability (Dünisch, and
418 Bauch, 1994, Downes et al., 1999, Deslauriers et al., 2003, Steppe et al., 2006, Gruber et al.,
419 2009). During the day, more water is lost through transpiration than absorbed through the roots,
420 so an internal water deficit affects trees and transpiration would negatively affect radial
421 expansion (Tardif et al., 2001).

422 Stem increment had a significantly positive correlation with precipitation and humidity
423 considering all cycles in the Coastal Range. VPD and radiation on the other hand, had a negative

424 correlation with this factor. In the Andes, the pattern was more or less the same, but maximum
425 temperature was also significantly and positively correlated with stem increment and radiation
426 was not correlated with this factor (Figure 4). Radiation was not important, probably because it is
427 lower in this site. When performing correlations just considering regular cycles in the coastal
428 site, correlation with precipitation was not significant implying that the relationship between
429 precipitation and stem increment is just seen when long precipitation events occur in this site.
430 Additionally, a higher negative correlation with radiation was observed and a slightly significant
431 positive relationship was obtained with soil temperature. In the Andes, relationships remained
432 significant for the same variables, although correlation with precipitation decreased considerably.
433 In addition, a positive correlation with soil temperature also appeared in this site ($T=0.21$, Figure
434 4). Since VPD is derived from and strongly related to air humidity, relationships between these
435 variables and stem radius change were usually similar in magnitude, but in opposite directions.
436 The positive relationship between maximum night temperature, soil temperature and stem
437 increment particularly in the Andes, can be justified due to generally colder conditions in this site
438 compared to the Coastal Range. A number of studies have reported a positive relationship
439 between night temperatures and stem increment (Deslauriers et al., 2003, Xiong et al., 2007,
440 Drew et al., 2008). Night-time temperatures have been found to have a greater effect on tracheid
441 expansion than daytime temperatures (Richardson and Dinwoodie, 1960, Richardson, 1964,
442 Dünisch, 2010). Moreover, low night temperatures were reported to negatively affect the
443 expansion of differentiating tracheids in *Podocarpus latifolius* (Dünisch, 2010). The positive
444 relationship between soil temperature and stem increment on the other hand, could be associated
445 to a positive effect of warmer soil temperatures on root water uptake and stem rehydration and
446 the consequent beneficial effect on internal water balance (Tardif et al., 2001, Perez et al., 2009).

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

455 It is relevant to highlight the importance of maintaining the water status in the stem, through
456 adequate precipitation and humidity conditions, in order to induce cell enlargement and radial
457 growth in this species. This occurs even in our very rainy sites which receive more than 800 mm
458 of precipitation during summer.

459

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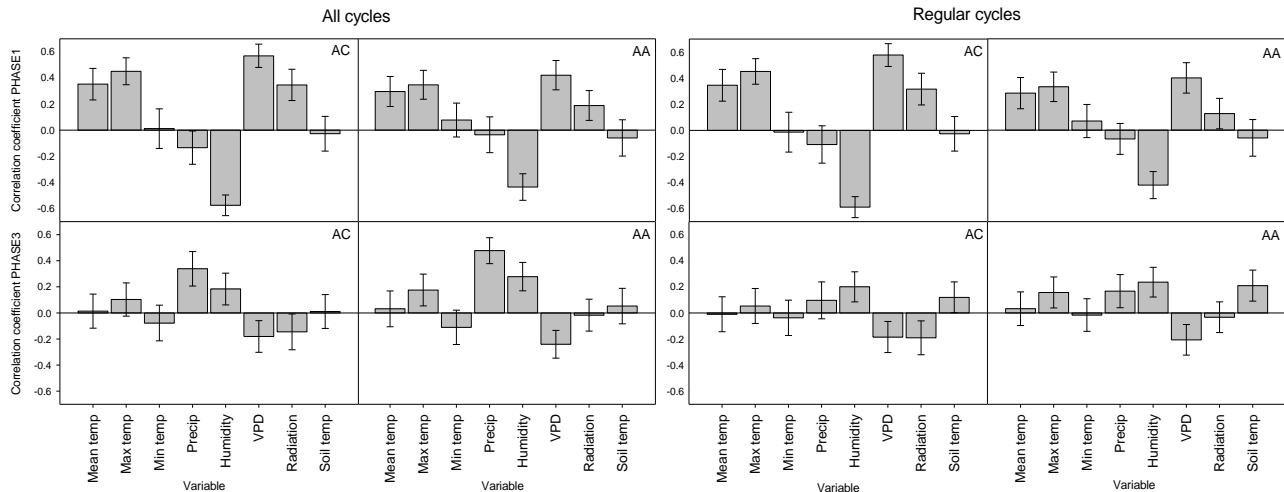
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467 **Figure 4.** Left panel: Kendall tau-b correlations between environmental variables in Alerce
 468 Costero (AC) and Alerce Andino (AA) and stem contraction (top panel) and increment (bottom
 469 panel) considering all cycles. Right panel: Kendall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

473

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

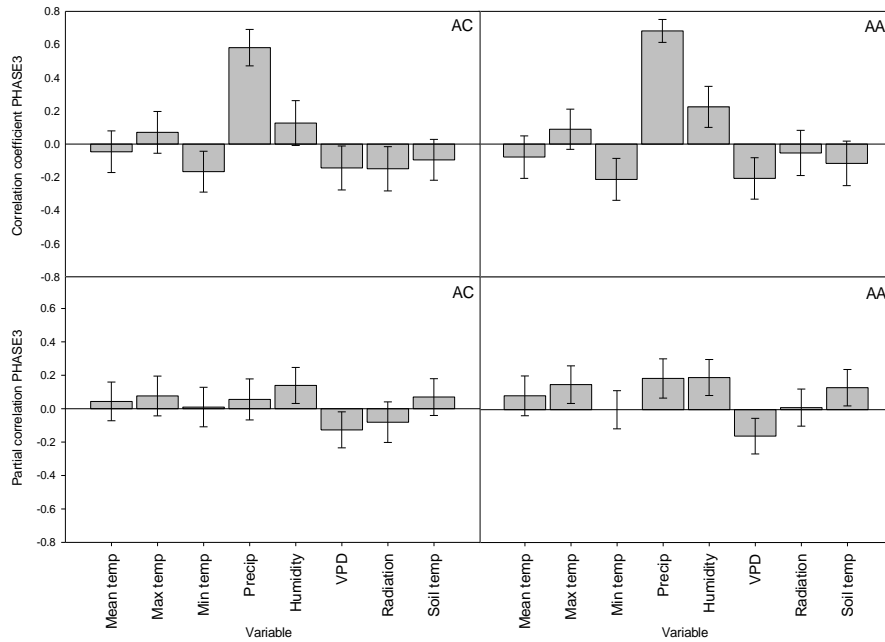
482 Partial correlations were performed given the positive and significant relationship between
483 duration and stem radius increment (kendall tau-b =0.52 in both sites). Only humidity and VPD
484 remained as variables with significant correlation with stem radius increment in the coastal site.
485 The other variables that were reported as significant in Figure 4 (precipitation and radiation)
486 would have an indirect relationship with stem increment through phase duration. The fact that
487 the positive effect of precipitation is mediated through duration, can be explained probably
488 because soils do not have good water retention capacity, so more rainy days are needed in order
489 to induce growth. On the other hand, the above reported negative relationship with radiation was
490 mainly mediated through duration in this site. More radiation shortens the expansion/increment
491 phases, reducing the favorable period for growth. Radiation increases transpiration and water
492 loss from the tree, causing less cell turgidity and consequently less cell enlargement (, add more
493 recent references such as Pantin or others).

494 In the Andes, correlations remained significant for all the reported variables in Figure 4 (Figure
495 5).

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

503 General findings in this study are in agreement with Perez et al., (2009), who reported a positive
504 effect of precipitation, soil hydration and temperature and a negative effect of photosynthetic

505 active radiation on the radial increment of *Fitzroya* from Chiloé. Strong shrinkage events were
 506 equally experienced by trees from these areas, located in both extremes of the Coastal Range.
 507



508
 509 **Figure 5.** Top panel: Kendall tau-b correlation coefficients between environmental factors and
 510 duration of the increment phase in Alerce Costero (AC) and Alerce Andino (AA). Bottom panel:
 511 Partial correlations between environmental factors and stem increment considering duration as
 512 the partial correlate. Significant correlations are present when the error bar does not cross zero.

513

514 3.4. Insights and interpretation of findings in dendrochronological studies

515 Relationships between stem radius change and environmental variables considering longer time
 516 scales revealed that correlations with precipitation, humidity and VPD remained significant and
 517 even increased in the case of humidity and VPD, compared with correlations using the daily
 518 increment (considering all cycles) in both sites. Moreover, negative correlations with mean and

519 maximum temperature were also significant, as well as with radiation in both areas (Table A1,
520 appendix).

521 The PCA plots (component 1 vs. component 2) for the different time scales highlight the close
522 positive association between stem radius change and precipitation and humidity (Figure 6). A
523 negative association was particularly strong with radiation at longer time scales in both sites. For
524 conciseness, and since patterns for 21 and 31 days were the same, Figure 6 shows only the
525 “daily”, 7 and 31 days results. “Daily” here and in the rest of the text refers to the time scale
526 given by the stem cycle. Principal components 1 and 2, explained 58.5, 73.6 and 78.8% at a
527 “daily”, 7 and 31 days scale in the coastal site. In the Andes these values were 60.6, 76.3 and
528 79.5%, respectively.

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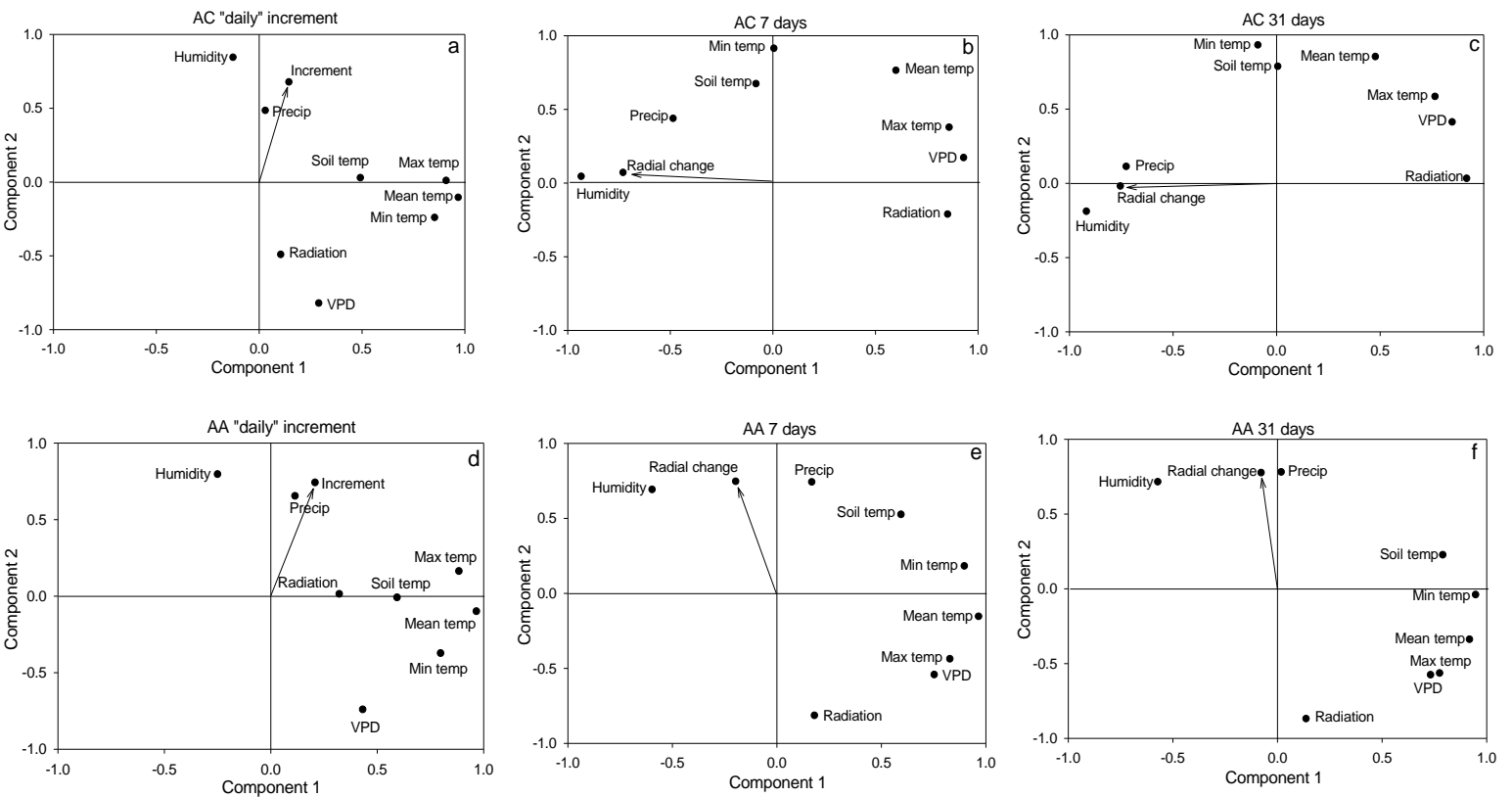
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537 **Figure 6.** Principal component analysis between a) stem radius increment and environmental
 538 variables at a “daily” basis in Alerce Costero (AC), b) stem radius change and environmental
 539 variables at a time scale of 7 days in the same site and c) stem radius change and environmental
 540 variables at a time scale of 31 days also in Alerce Costero. d),e), f) the same as a),b) c), but for
 541 Alerce Andino (AA). Arrows in each plot point towards the stem increment/stem radius change
 542 variable. Environmental variables closely located to the stem radius variables or in direct
 543 opposite direction are more strongly related to them (closer variables are positively related and
 544 opposite variables are negatively related).

545

546

547 Climate-tree growth relationships established in dendrochronological studies have a limited
548 explanatory power in terms of an implicit growth mechanism (Zweifel et al., 2006), so a better
549 understanding of the processes behind these relationships in *Fitzroya* can be obtained using this
550 high-resolution study. The reported negative relationships of *Fitzroya* tree-ring width with
551 summer temperature (Villalba, 1990, Villalba et al., 1990, Lara and Villalba, 1993, Neira and
552 Lara, 2000, Barichivich, 2005) mainly appeared when longer time scales were considered in this
553 study. This relationship can be understood through the strong shrinking events recorded in
554 *Fitzroya* when long warm, sunny and particularly dry periods occur. This would reduce the
555 number of days with appropriate climate conditions for growth to take place, producing a smaller
556 tree ring.

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

569 temperature on VPD. The use of multiple variables in this study, although correlated among
570 them, provided important insights that would not be possible to obtain with just a few of them.
571 The reported negative effect of previous summer temperature and precipitation on the other
572 hand, can be because warm temperatures are usually associated with dry conditions in the study
573 area, and hence carbon assimilation can be reduced if stomata close (McDowell et al., 2008, Sala
574 et al. 2012). Less carbon assimilation would result in less carbon reserves and a smaller tree-ring
575 during the next season. Moreover, high temperatures during the previous growing season
576 combined with higher respiration rates reduce the starch reserves in the stem that can be used for
577 the following growth period (Deslauriers et al. 2014).
578 Finally, the positive relationships between tree-growth and summer precipitation found here are
579 consistent with the findings of dendrochronological studies (Neira and Lara, 2000, Barichivich,
580 2005).

581

582 **3.5. Stem growth sensitivity to climate change**

583 Findings of this study allow some tentative inferences to be made regarding the vulnerability of
584 *Fitzroya*'s growth rates to climate variations. Current and projected climate change,
585 characterized by decreased precipitation and warmer temperatures in southern Chile (González-
586 Reyes and Muñoz, 2013, Fuenzalida et al., 2007), might have a negative effect on the carbon
587 sequestration capacity and long-term storage of *Fitzroya* populations from both study sites.
588 However, *Fitzroya*'s radius variation currently appears to be especially sensitive to dry and warm
589 conditions in Alerce Costero, meaning that forests growing under similar restrictive site
590 conditions in the Coastal Range are more vulnerable to experience stem shrinking and lower
591 growth compared with trees from the Andes. Strong stem shrinking is experienced by *Fitzroya*

592 trees in the coastal site even during years that are not as extreme as El Niño years, which
593 indicates that restrictive soil conditions and a more Mediterranean climate influence can make
594 *Fitzroya* tree growth more vulnerable to future climate change. In addition, precipitation seems
595 to be related with stem increment on a daily basis in Alerce Costero only when long rainfall
596 events take place, so less precipitation in the future, may negatively affect this variable. A
597 significant negative trend in tree-ring growth and basal area increment has been observed in this
598 site especially in the last 40 years, likely reflecting the effect of decreased precipitation and the
599 indirect effect of increasing maximum temperatures on stem radial growth (increasing trend in
600 summer maximum temperature in Valdivia for the period 1960-2009, Urrutia-Jalabert, 2014).
601 These environmental conditions are probably leading to more frequent or more pronounced stem
602 shrinking events and consequently to lower radial increment in trees from this site. This trend has
603 not been seen so far in the older trees from the Andean site (Urrutia-Jalabert, 2014).
604 It is important to emphasize, however, that further studies should address measurements of
605 leafwater potential, sapwood capacitance and carbon reserve in *Fitzroya* trees, especially during
606 dry periods, to assess to what extent they are affected by these conditions. In the case of trees
607 from the Andes, and since it has been reported that absolute daily reliance on stored water across
608 different species is higher in larger trees; stored water might help avoiding embolism conduits in
609 a future drier climate (Scholz et al., 2011).

610

611 **4. Conclusions and implications**

612 This study is the first to assess, at a high resolution level, the relationship between stem radius
613 contraction and increment and environmental conditions in *Fitzroya* trees growing in the Andes
614 and Coastal Range of southern Chile. The high resolution approach that we used was unique in

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

638

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655

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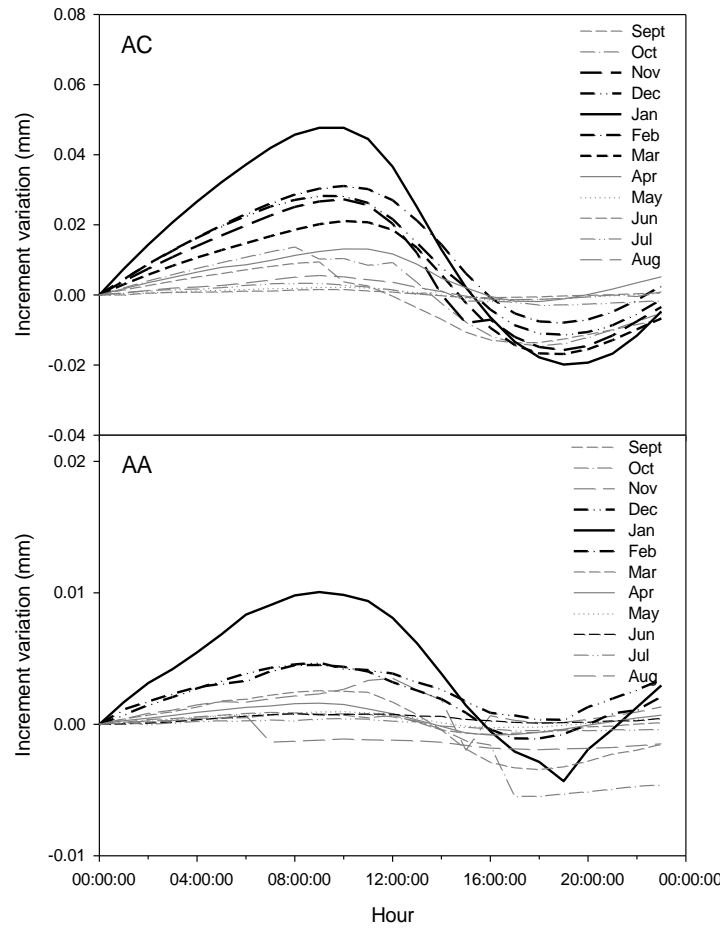
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816 **Appendix**

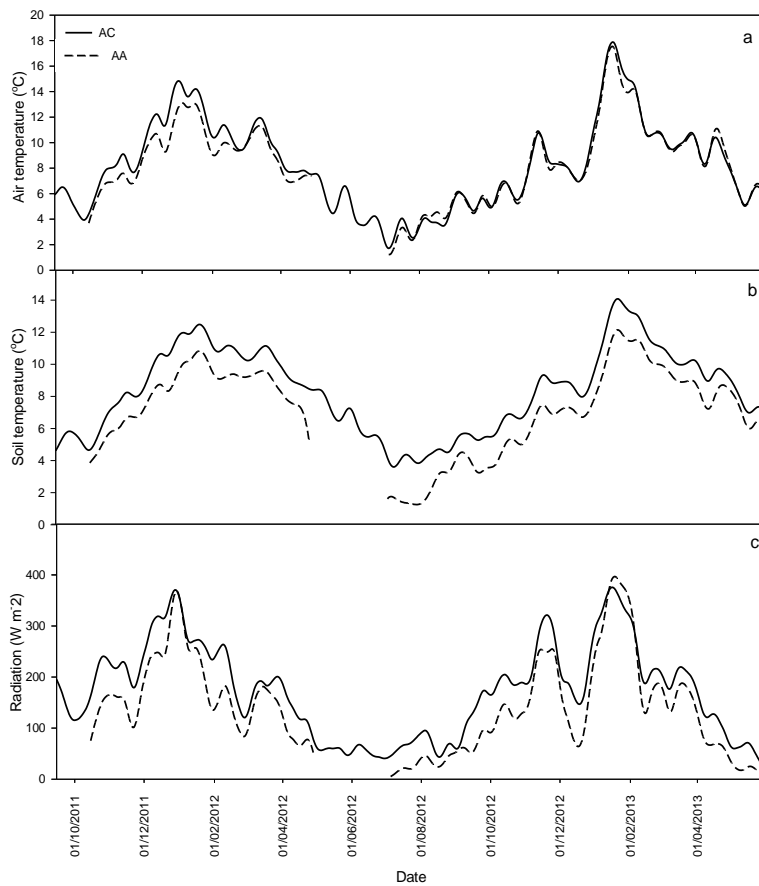
817 **Results**



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

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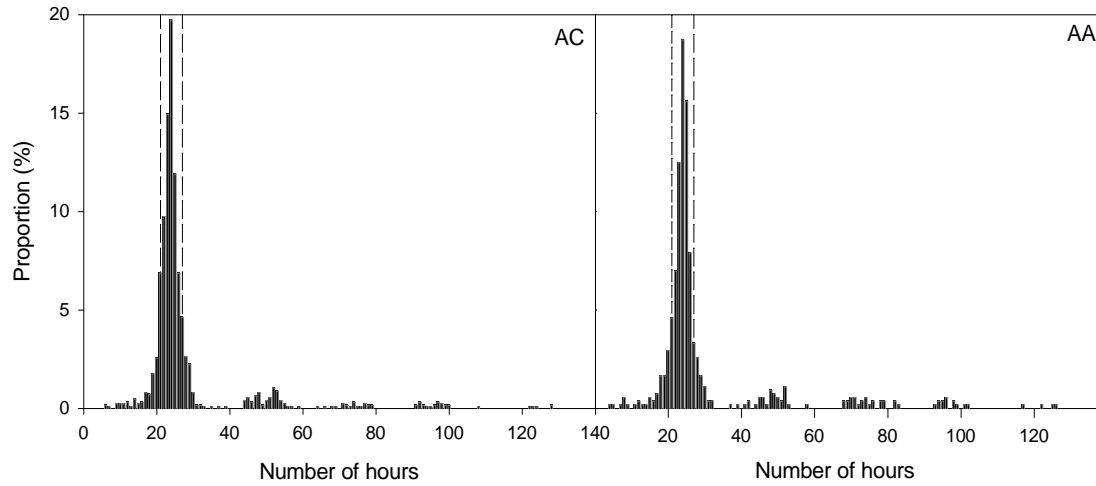
826 Figure A2. a) Daily mean air temperature for the period October 2011-May 2013 in both study
 827 sites (Alerce Costero, AC and Alerce Andino, AA), b) daily mean soil temperature and c) daily
 828 mean total solar radiation. For illustration purposes data were smoothed using a cubic spline
 829 designed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

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

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852 Table A1. Kendall-tau b correlations between stem radius increment at a “daily” basis
 853 (considering short, regular and long cycles), stem radius change at 7, 21 and 31 days and
 854 environmental variables in Alerce Costero (AC) and Alerce Andino (AA). “Daily” refers to the
 855 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 |

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