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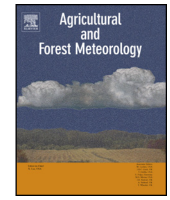

Environmental correlates of stem radius change in the endangered *Fitzroya cupressoides* forests of southern Chile

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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.

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 CO_2 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

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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