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Poor acclimation to current drier climate of the long-lived tree species *Fitzroya cupressoides* in the temperate rainforest of southern Chile

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ABSTRACT

Climate change and rising atmospheric CO_2 concentrations (c_a) are expected to affect forests worldwide. The effects of climate change, however, have not been deeply assessed in humid forest biomes from the southern Hemisphere where climate is not warming but drying. This is the case of the temperate rainforest in southern Chile, where the endemic and threatened long-living gymnosperm *Fitzroya cupressoides* occurs. We assessed how radial growth, intrinsic water-use efficiency (iWUE) and tree-ring $\delta^{18}O$ responded to increasing c_a and decreasing precipitation in *F. cupressoides* and companion species. We hypothesized that *F. cupressoides*, a long-lived and probably less plastic species, will show less acclimation to global-change effects than co-occurring *Nothofagus* species which show broader climatic niche. Thus, *F. cupressoides* should display iWUE increases different from the c_i/c_a constant scenario, which represents an active mechanism to increase intercellular CO_2 concentrations (c_i) as c_a rises. Although cool and wet conditions during the growing season enhanced growth of all species, particularly in *F. cupressoides*, growth of *F. cupressoides* declined noticeably since the 1980s in response to a decrease in precipitation. Current drier conditions led to increased iWUE in *Nothofagus* species. According to $\delta^{18}O$ values, this increased in iWUE should be due to a decrease in stomatal conductance. *Fitzroya cupressoides*, however, displayed a decrease in iWUE in response to drier conditions, shifting from an active c_i/c_a scenario to a more passive c_i/c_a scenario, and maintaining a relatively constant stomatal conductance. Using multiple bodies of evidence, our findings indicate a poor adaptability of the long-lived *F. cupessoides* to drier conditions despite rising c_a. Thus, not all species are having similar and expected responses to increasing c_a, which should be a call of attention in the case of long-lived, endangered and narrow-distributed species, like *F. cupressoides*.

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1. Introduction

In 2015, the Mauna Loa observatory recorded atmospheric CO_2 concentrations (c_a) over 400 ppm and global air temperatures were +1.0 °C warmer than during preindustrial times (Blunden and Arndt, 2016). These two global-change milestones may be biased towards the much intensive carbon-emitter northern Hemisphere as compared with southern latitudes. Despite c_a over the Antarctica reached also a record value of 399 ppm in 2016 (see http://www.esrl.noaa.gov/gmd/obop/spo/), some austral regions as southern South America are among the few land areas where temperature records did not show a clear warming trend (Bidegain et al., 2016). Such understudied regions may provide valuable information to disentangle long-term forest responses to changes in c_a and temperatures.

In principle, forests were expected to show enhanced growth rates in response to rising c_a and warmer temperatures. This expectation was based on the assumption that trees would exhibit improved photosynthesis and hence growth rates due to an increase in their intrinsic water-use efficiency (iWUE, i.e. the carbon fixed per unit of water transpired through stomata) through a CO_2-fertilization effect (Norby et al., 2005). These relationships, however, were mostly constructed in short-term experimental studies. A much integral approach to understanding the response of plant to changes in c_a and temperatures is by comparing decadal to centennial tree-ring records of growth and iWUE through the use of C isotopic ratios (e.g. Linares and Camarero, 2012; Saurer et al., 2004). Such long-term approaches have indicated that despite for-

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est water-use efficiency has generally increased during the 20th century—inferred from tree-ring C isotopes (Saurer et al., 2004) or from eddy-covariance flux data (Keenan et al., 2013), this increase has not led to enhanced forest growth (Lévesque et al., 2014; Peñuelas et al., 2011; Silva and Anand, 2013). Additionally, warmer temperatures may also lead to higher water deficit in drought-prone areas translating this into growth declines or a lack of response to rising c_a in some tree species (Camarero et al., 2015; Gómez-Guerrero et al., 2013). Despite this knowledge, we know little about how forest communities less used to dry conditions (e.g. temperate rainforests) will respond to changes in c_a and temperature. In fact, increasing concern about the potential negative effects of global change on trees has shifted from semi-arid areas to wet forests that were initially not considered at drought risk.

Inferring how changes in c_a and temperature will affect forests may become challenging given that some species are more susceptible or resistant-tolerant to drought than others (Granda et al., 2014). In particular, it is not clear at all how long-lived tree species will react to global change. In principle, long-lived tree species could become more susceptible to sudden changes in climate as dry spells because they are expected to have a rather narrow climatic niche. In contrast, we could also expect that long-lived tree species may be more resilient to rather recent changes in c_a and temperature. In this respect, long-lived tree species could also function as long-term monitors (*sentinels*) of global-change components (rising c_a and warmer air temperatures) given that long-living tree species respond differently to these two environmental drivers (Voelker et al., 2006).

The iWUE of trees can be retrospectively inferred using the $^{13}C/^{12}C$ ($\delta^{13}C$) isotope ratio from tree-ring wood or cellulose which simultaneously tracks changes in assimilation rates and stomatal conductance under increasing c_a (Francey and Farquhar, 1982; McCarroll and Loader, 2004). In normal conditions, C_3 carbon fixation plants photosynthesis discriminates against ^{13}C (the heaviest isotope), but if gas exchange is constrained by stomatal closure (e.g. during warm and dry conditions), ^{13}C is used along with ^{12}C and the $\delta^{13}C$ becomes less negative (Farquhar et al., 1989). In most tree-ring based studies assessing long-term c_a and iWUE associations, the temporal variation in $\delta^{13}C$ supports the prevalence of an active plant mechanism that maintains a constant ratio between intercellular (c_i) and atmospheric (c_a) CO_2 concentrations (Leonardi et al., 2012; Saurer et al., 2004). Recently, the analysis of the $^{18}O/^{16}O$ ($\delta^{18}O$) isotope ratio has also been applied to tree-ring based studies since $\delta^{18}O$ reflects the changes in stomatal conductance (g) and it is considered a proxy for evaporative flux, relative humidity and $\delta^{18}O$ source-water signal (Anderson et al., 1998; Barbour, 2007; Voltas et al., 2013). The use of $\delta^{18}O$ has been helpful to clarify whether the rising iWUE trends are more related to increasing photosynthesis assimilation rates (A) or to decreasing g rates (Saurer et al., 1997).

In this study, we were interested in determining how increasing c_a, temperature and dryness are impacting the growth (in the form of basal area increment, BAI) and the intrinsic water use efficiency (iWUE) of tree species in a temperate rainforest. We focused on the temperate rainforest (TRF) of western southern South America (Chile), which is known to harbour a relatively high number of tree species, including the endangered, long-lived and high-biomass conifer *Fitzroya cupressoides* (Cupressaceae) (Armesto and Figueroa, 1987; Urrutia-Jalabert et al., 2015b; Veblen and Schlegel, 1982). This temperate rain forest also includes many endemic species, all adapted to wet and cool conditions (annual precipitations can surpass 4000 mm), which are suitable *sentinels* to assess how tree species are responding to global-change components throughout the late 20th century, when c_a and temperatures have rapidly increased (e.g. Salzer et al., 2009). In contrast to most other regions, the Southern South American temperate rain forest is not experiencing a clear warming trend but a decrease in precipitation during the second half of the 20th century accompanied by the occurrence of more severe droughts (Fuenzalida et al., 2007; Quintana and Aceituno, 2012). Although Urrutia-Jalabert et al. (2015a) found that growth and iWUE responses to rising c_a varied in *F. cupressoides* between sites and populations, we still do not know how this long-lived species reacts to global warming effects when it is compared to other tree species members of the temperate rain forest under a scenario of lower precipitation. We assessed here the temporal change in tree secondary growth (BAI), iWUE ($\delta^{13}C$) and $\delta^{18}C$ during the last 50–100 years of *F. cupressoides* as compared to other tree species in a temperate rain forest in southern Chile. Given that this temperate rain forest is subjected to wet and cool conditions, we first expected than c_a-induced changes in iWUE will mainly correspond to changes in photosynthesis rates (A) and not in stomatal conductance (g). Second, since selection pressures for long-lived, tall tree species, such as *F. cupressoides*, are very strong (Lanfear et al., 2013), and must therefore, select for greater specialization or less plasticity—narrower climatic breadth, we also expected that *F. cupressoides* will display less acclimation to global-change effects than other companion species with greater climatic breadth; i.e. an increase of iWUE more different from the constant c_i/c_a scenario, which represents an active mechanism to increase c_i as c_a rises, than other companion species. Marked differences in how different tree species face drier conditions and rising c_a, especially in temperate rainforests, will have consequences for the future structuring of these unique communities where species with low acclimation may be outcompeted by other more resilient species.

2. Material and methods

2.1. Study sites and tree species

Temperate rainforests in southern Chile are characterized by a cold-temperate and super-humid climate (Alaback, 1991; Luebert and Pliscoff, 2006), with mean annual temperature of ~10 °C and annual precipitation of 2500 mm or more, regularly distributed throughout the year (Appendix, Fig. S1). We worked in the Huinay Private Park (42° 23′S, 72° 25′W, sea level), near the Comau fjord in southern Chile. Here, the topography and geomorphology are characterized by fjords, steep slopes and glacial valleys. The annual precipitation ranges from 2000 to 6500 mm, with a very wet winter and a less wet summer (Dávila et al., 2002). Soils are rather acid (mean pH = 4.7), well developed (mean N concentration = 0.96%). The aspect of the study area is W–NW (270–335°), where slopes ranged from 5 to 40°.

The vegetation at Huinay is typical of the temperate rain forest; a dense understory of bamboos (*Chusquea* spp.) and ferns (*Blechnum* spp., *Lophosoria* spp.) (Donoso, 1993; Tecklin et al., 2011), broadleaf evergreen angiosperms as dominant tree species, and the presence of the long-lived conifer species, *Fitzroya cupressoides* I.M. Johnst (Veblen and Schlegel, 1982; Villagrán, 1985; Lara and Villalba, 1993; Donoso et al., 2006). At low-elevation (140 m a.s.l.), the dominant tree species include *Nothofagus dombeyi* Mirb. Oerst. and *N. nitida* (Phil.) Krasser (Nothofagaceae), *Weinmannia trichosperma* Ruiz & Pav., *Eucryphia cordifolia* Cav. (Cunoniaceae), *Laureliopsis philippiana* (Looser) R. Schodde (Atherospermataceae) and *Luma apiculata* (DC.) Burret (Myrtaceae). At mid-elevation (560 m a.s.l.), the dominant tree species are *N. dombeyi* and *Saxegothaea conspicua* Lindl. (Podocarpaceae), *N. betuloides* (Mirb.) Oerst., and *Podocarpus nubigena* Lindl. (Podocarpaceae). Finally, at high-elevation (780 m a.s.l.), *N. betuloides* and *F. cupressoides* (Cupressaceae) dominate, along with *W. trichosperma*, *P. nubigena*, *N. antarctica* (G.Forst.) Oerst., and *Desfontainia spinosa* Ruiz & Pav. (Columelliaceae). In short, the low-elevation site is compositionally similar to a TRF *sensu stricto*, without conifers present and

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