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Original article

Temporal changes in climatic limitation of tree-growth at upper treeline forests: Contrasted responses along the west-to-east humidity gradient in Northern Patagonia

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ABSTRACT

Over the last decades, gradual changes in summer climate in the Southern Hemisphere have affected forest growth in contrasting ways in moist and dry regions. Here, we use correlation analysis and a forward process-based model (Vaganov–Shashkin-Lite) to investigate changes in climate limitation of the interannual tree-ring growth of *Nothofagus pumilio* at the upper treeline along a precipitation gradient in northern Patagonia. Patterns of climate limitation vary consistently along the gradient. At mesic and humid treelines, tree-ring growth is positively related to growing season temperature and negatively to precipitation. At xeric treelines, the opposite is observed. Moreover, the climate-growth relations are not stationary. In particular, according to the model, the step decrease in precipitation in 1952 induced an increase of the moisture limitation at the dry edge of the gradient. Correlation analyses evidence that the dependence of growth on moisture after 1952 has enhanced since 1976. While the model consistently reproduces tree-ring width variations over the 1931–1975 period, it does not capture the growth patterns in the following years. Some environmental parameters (cloudiness, snowpack, atmospheric CO_2) affecting moisture, radiation and stomatal aperture may have reached thresholds beyond which the effect on tree-growth has become sizable.

1. Introduction

Changes in summer climate regimes associated with the anomalous positive trend in the Southern Annular Mode (SAM; Archer and Caldeira, 2008) have influenced the patterns of forest growth across much of the extra-tropical Southern Hemisphere (Villalba et al., 2012). Growing seasons in the temperate belt of the Southern Hemisphere have become warmer and drier as the mid-latitude westerly flow has weakened during recent decades (Gillett et al., 2006; Garreaud et al., 2009). Warming has stimulated tree growth in cool and moist subalpine forests of Tasmania and New Zealand (Allen et al., 2014, 2001; Cook et al., 2000; Villalba et al., 2012) whilst drying has reduced growth rates in mesic and dry forests of southern South America (Christie et al., 2011; Mundo et al., 2012; Villalba et al., 2012). Temporal stability of significant correlations between tree-ring chronologies and climatic variables suggest that forests growing at marginal locations, where growth is dominantly limited by either temperature or moisture, have responded consistently to this observed shift in growing season climate (Villalba et al., 2012; Muñoz et al., 2014). However, growth responses of mesic north Patagonian forests and at some treeline locations where temperature and moisture simultaneously co-limit tree-ring growth, appear to be more complex and time-dependent (Daniels and Veblen, 2004; Álvarez et al., 2015; Suarez et al., 2015 Suarez et al., 2015). Warmer conditions and large-scale changes in atmospheric circulation during the late twentieth century have reduced temperature limitation but might have increased moisture limitation, especially for species growing at mesic and humid environments along the north Patagonian precipitation gradient (Suarez et al., 2015).

The beech *Nothofagus pumilio* is the dominant subalpine tree species in northern Patagonia. The radial growth of the species at the upper treeline is typically controlled by spring–summer climate and has been used to reconstruct past temperatures and snow cover duration (Villalba et al., 1997; Lara et al., 2001;

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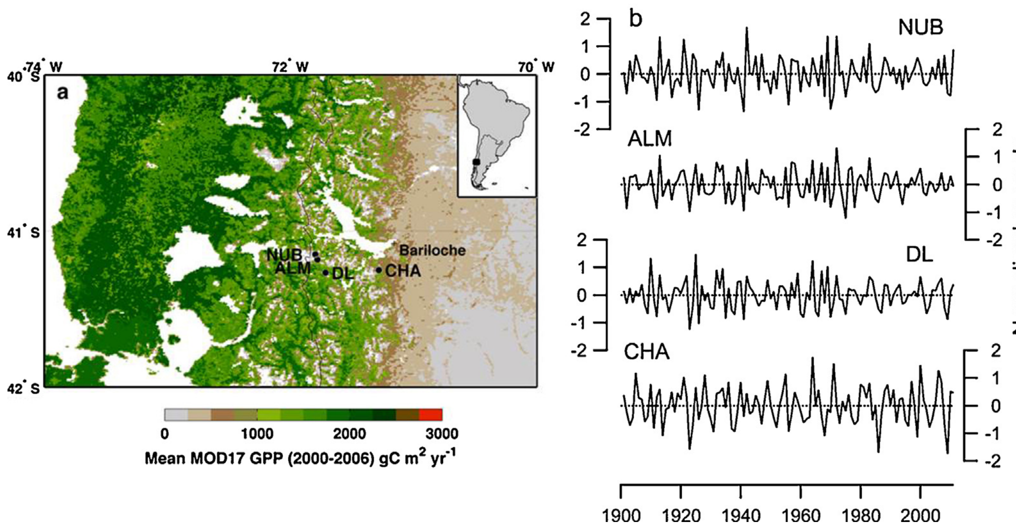

Fig. 1. (a) Location of the tree-ring sites and Bariloche meteorological station along the west-to-east climate and productivity gradient in northern Patagonia. Gross Primary Production (GPP) is based on the MOD17 product (Zhao et al., 2005). (b) Mean standardized tree-ring width chronologies of *Nothofagus pumilio* from northern Patagonia for each site along the west-to-east precipitation gradient (NUB, ALM, DL and CHA) between 1900 and 2011.

Aravena et al., 2002). Yet, correlations between climate and tree-ring growth at some treeline locations in northern Patagonia have been shown to vary substantially between early-20th century cool-wet and current warm-dry climate regimes (Raffaele et al., 1998; Daniels and Veblen, 2004). Furthermore, contrary to the expectation of enhanced growth rates with recent warming, tree growth at an adjacent high-elevation site in the western side of the Andes appears to have declined during recent decades (Álvarez et al., 2015). These observations could suggest a non-linear growth response to temperature or the emerging influence of other environmental controls at some high-elevation forests in the region. Similar site-level temporal instabilities in historical patterns of climate limitation of tree growth have been observed at treeline forests in North America (Ohse et al., 2012; Chavardès et al., 2013), where the so-called tree-ring divergence phenomenon has been described (Jacoby and D'Arrigo, 1995; D'Arrigo et al., 2004, 2008).

The recent development of generic forward models of tree-ring formation offer a new approach for studying the nature of growth responses to climate, overcoming some limitations of traditional linear correlation analyses (Anchukaitis et al., 2006; Boucher et al., 2014; Evans et al., 2013, 2006; Vaganov et al., 2011). These models can represent mixed and non-linear tree growth responses to changing climatic factors from daily to seasonal and decadal time scales. The Vaganov–Shashkin-Lite model (VS-Lite; Tolwinski-Ward et al., 2011) is perhaps the best model available for studying the nature of tree growth in regions were detailed daily climate data and field observations are not readily available. This model requires only monthly precipitation and temperature data to provide a representation of the climatic controls of tree-ring growth based on the principle of limiting factors and non-linear growth response functions (Fritts, 1976). VS-Lite has been used to simulate and evaluate regional patterns of climate limitation of tree growth in a range of environments from semi-arid to temperate and boreal regions (Breitenmoser et al., 2014; Evans et al., 2014; Tolwinski-Ward et al., 2011).

In this study, we combine linear correlation analysis with the VS-Lite model to investigate changes in the climate drivers of *N. pumilio* growth in upper treeline forests along the west-to-east precipitation gradient of northern Patagonia. We address the following question: is water limitation becoming more important than temperature limitation in recent decades with the drier and warmer SAM-driven climate regime, especially in the more moisture-limited environments? In cold and wet environments, we expect the typical pattern of temperature limitation described in previous studies (Villalba et al., 1997) whilst in cold and dry environments toward the east, tree growth should become more limited by water availability. With the persistent positive phase of the SAM, and the concomitant warming and drying in northern Patagonia, we also expect that water limitation should have become more important in recent decades (Daniels and Veblen, 2004; Suarez et al., 2015). This is the first detailed modeling study investigating the controls of tree-ring growth conducted in the region and thus provides novel mechanistic insights into the responses of these austral forests to recent climate change.

2. Material and methods

2.1. Regional setting and study species

Patagonia extends from about 37°S to 55°S and represents the southernmost portion of the South American continent. The regional climate is mainly driven by the interactions between the circum-Antarctic cyclonic belt to the south and the subtropical Pacific high-pressure cell to the northwest. The strong westerlies resulting from the large pressure differences between these semi-permanent circulation features in the atmosphere permanently interact with the north-south mountain range of the Andes (Aceituno, 1988; Villalba et al., 2003; Garreaud et al., 2009). The Andes Cordillera acts as a topographic barrier to the persistent westerlies bringing moisture from the South Pacific Ocean. The air masses discharge most of the humidity in the way up to the mountains on the western slopes of the Andes to descend drier on the eastern slopes. Therefore, the mountain range induces a dramatic decline in mean annual precipitation from 4000 mm at Lago Frías, near the continental divide, to about 500 mm toward the Patagonian steppe (Jobbagy et al., 1995; Veblen, 1979). Gross Primary productivity (GPP) follows the eastward decline in precipitation and ranges from around 2000 g C m^2 year $^{-1}$ in the most productive forests to about 500 g C m^2 year $^{-1}$ in the Patagonian steppe (Fig. 1; Muñoz et al., 2014; Zhao et al., 2005). In northern Patagonia, the annual migratory cycle of the Pacific anticyclone induces strong precipitation seasonality. Precipitation is largely concentrated from