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Rapid warming forces contrasting growth trends of subalpine fir (*Abies fabri*) at higher- and lower-elevations in the eastern Tibetan Plateau

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ABSTRACT

Tree radial growth is expected to increase at higher elevations under climate warming, while lower elevation tree growth is expected to decline. However, numerous studies have found tree radial growth responds consistently to climate along elevational gradients. Here, we sampled five plots across the subalpine *Abies fabri* forest belt on Gongga Mountain in the eastern Tibetan Plateau to determine tree radial growth trends and responses to climate. Three commonly used detrending methods all consistently showed that tree radial growth at high elevation (> 3100 m) increased, while tree growth declined at the lower elevations (2700 m–2900 m) over the last three decades. Increasing late-growing season temperature positively ($p < 0.05$) correlated to tree radial growth at higher elevations, but the sign of this relationship reversed to become negative at lower elevations. Moving-window correlation analyses indicated the difference between high and low elevations response to temperature variation increased strongly with warming. Placing our result into the global context, 62% of 39 published studies found that trees along elevation gradients respond divergently to warming, and that these are located in warmer and wetter regions of the Earth. Notably, 28% of studies found non-significant responses to temperature at both high and low elevations. Our findings in the subalpine mountain forest in the eastern Tibetan Plateau were consistent with the majority of published datasets, and imply increasing temperature benefit for tree populations at higher elevation, while warming dampens growth at lower elevations.

1. Introduction

Mountain forests are of particular importance in maintaining biodiversity, protecting from natural hazards, and in regulating the water and carbon cycle (IPCC, 2014). Ongoing climate warming in mountain areas is amplified with elevation (Mountain Research Initiative, 2015), and its impact on forest distribution is still a major question in global change biology (Lenoir and Svenning, 2015). Numerous studies have found that mountain forest belts have tracked climate warming and shifted their ranges to higher altitudes (Chen et al., 2011a; Feeley et al., 2011). Some studies suggest the upper elevation edge of mountain forests has not kept pace with the rapid warming (Harsch and Bader, 2011; Liang et al., 2016). Lastly, some forests are undergoing range contraction over their elevational ranges (McDowell et al., 2010), and modeling predicts that the average forest range will reduce almost 50% by the end of 21th century (Dullinger et al., 2012). Therefore, distinguishing how forest ranges respond to climate change is critical to the strategies of forest management.

Tree-ring widths are a sensitive index for forest response to climate change (Ettl and Peterson, 1995; Liang et al., 2010; McDowell et al., 2010; Sidor et al., 2015; Yin et al., 2016). Generally, tree growth at the upper treeline is limited by low temperature, while at the lower elevation water availability is often the limiting climate factor (Fritts, 1976; Salzer et al., 2009). Studies from multiple biomes have found that tree growth declined and mortality increased at lower elevations undergoing temperature increases, but at the upper treeline tree growth and tree density increased over the same periods (Adams and Kolb, 2005; Liang et al., 2011; Dang et al., 2012; Cai and Liu, 2013; Sidor et al., 2015; Ponocna et al., 2016; Conlisk et al., 2017). However, some studies have found consistent responses of tree growth to climate across entire elevational transects (Esper et al., 2007; Li et al., 2012b; Gao et al., 2013; Yang et al., 2013; Lyu et al., 2016). In the eastern margins of the Tibetan Plateau, the climate factors that limit tree growth along elevational gradients are still not well understood, as some results reported consistent growth responses across elevation (Liang et al., 2010; Li et al., 2012b; Lyu et al., 2016), while some report divergent

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responses with decreased growth at low elevation and increased growth at high elevation (Fan et al., 2009; Dang et al., 2012).

Age-effects and sampling strategy affect the accuracy of tree growth assessment and its climate response (Wu et al., 2013; Sun and Liu, 2014). Age-dependent climate-growth relationships were found in subalpine fir in the Olympic Mountains, USA (Ettl and Peterson, 1995), and also in the semi-arid region of Tianshan, China (Wu et al., 2013), however, Chinese pine growth is age-independent (Sun and Liu, 2014). Moreover, traditional sampling designs (focusing on the older, dominant trees only) could bias the growth trend more than 200% (Nehrbass-Ahles et al., 2014). Though previous dendroclimatic analysis has determined the climate response of Chinese subalpine fir (*Abies fabri*) using traditional sampling design and detrending methods along the elevational transect on Gongga Mountain (Duan et al., 2010), the subalpine fir population growth trends at different elevations, different detrending methods, age effects, and sampling strategy impacts on tree growth analyses are still not well understood.

Here, we sampled all of the individual subalpine fir trees within five large plots located across the elevation range of subalpine fir on Gongga Mountain within the Hengduan Mountains, eastern Tibetan Plateau. To better understand tree growth trends through time, we used three detrending methods to disentangle age/size trends in growth from long-term growth changes (Peters et al., 2015). We divided each plot's trees into two age classes: young (≤120 years) and mature (> 120 years) trees to explore whether age effects interpretation of subalpine fir growth in relation to climate. Moreover, we correlated the tree growth to climate variables to find which month(s) climate limits radial growth, then to determine if shifts through time in the relationship due to temperature rise occurred. Our objectives are: 1) to determine if any detrending methods and age effects exist on the fir tree radial growth trends; and 2) to determine how radial growth trends respond to climate change across the subalpine conifer elevation transect. To put our study into global context, we synthesized the existing ring-width studies across elevation transects to determine the frequency of observations that have found divergent versus consistent responses of growth to climate across elevation, and to examine the role of climatic factors in the pattern of results.

2. Materials and methods

2.1. Study area

Our study area (Fig. 1) is on the eastern slope of Gongga Mountain, located in the central Hengduan Mountains of the eastern Tibetan Plateau. Gongga Mountain is the highest peak (7556 m) of the Hengduan Mountains. Due to its high elevation, most of the water vapor from East Asia monsoon falls in the eastern slope, which leads to a humid moderate climate characterized by both low latitude glaciers and abundant forests. From the nearest national Kangding meteorological station (30°03′N, 101°58′E, 2615.7 m), the mean annual temperature is 7.2 °C from 1952 to 2015, and the mean annual precipitation is 834 mm in the same period (Fig. 2a). Mean annual temperature has increased significantly (0.012 °C yr^{-1}, $p < 0.001$, for a total rise of 0.75 °C) during the period 1952–2015, and monthly total precipitation also increased slightly but significantly (1.43 mm yr^{-1}, $p < 0.05$, for a total rise of 91.6 mm over the period). Vapor pressure deficit (VPD) rose significantly (0.0008 kPa per year over the period), with a particularly large rise in the last two decades (Fig. 2). Gongga Mountain has subalpine coniferous forest distributed from 2700 to 3600 m. *Abies fabri* is the dominant tree species in this subalpine forest and extends to the local treeline.

2.2. Field sampling and dendrochronological methods

During October 2015, and May 2016, we established five large dendrochronology plots (about 500 m^2) along an elevational transect of subalpine fir (Table 1) with elevation between plots ranging from 200 to 300 m. The plots crossed the entire elevation range of subalpine fir locally, from the high (~3600 m) to the low (2700 m) elevation ecotones. At each plot, we sampled two cores for every living tree at breast height from the *Abies fabri* trees at DBH > 10 cm in each plot using diameter increment borers. Tree cores were taken to laboratory to measure the ring widths with a precision of 0.01 mm, after air-drying and sanding each core. Because *Abies fabri* exhibits decay symptoms in the heartwood, some of the tree cores were abandoned. To confirm the accurate of dating, we used the COFECHA software to check the results (Holmes, 1983). We sampled to the pith of each tree, which allowed records up to ~200 years in length, however climate data for this region is only available starting in the 1950s, so much of our analysis are conducted using the data from 1952 to 2015.

To remove the ontogenetic effect of the age trend, we used three detrending methods: conservative detrending (CD), regional curve standardization (RCS) and basal area index (BAI) (Peters et al., 2015). The CD method was used a negative-exponential model to detrend the age series for each tree and developed the tree-ring width chronology using the ARSTAN software (Cook, 1985). The RCS method was first aligned with cambial age of individual ring width series to produce the "regional curve", then we calculated the ratios of each ring width to the regional curve (Briffa and Melvin, 2011). The BAI was calculated based on measuring tree-ring width as the equation (Jump et al., 2006): $BAI = \pi \times (R_n^2 - R_{n-1}^2)$, where R is the radius of the averaged ring width and n is the year of tree-ring formation. The RCS and BAI series were calculated from R package.

2.3. Data analysis

Our experimental design used all five sites and both age classes (≤120 and > 120 years old) but varied in temporal length for the six tests we conducted to fulfill our objectives. In the detrending and age-class methods tests, the mature tree records we analyzed extended 1800–2015, but the initial year varied by site (Table s1). The younger tree records extended from 1897 to 2015, again with variable start years between sites (Table s1). There were four additional growth tests we conducted. To examine correlations among sites (Table 2), and trends over time as a function of elevation (Table 3), we analyzed three, thirty-year periods (1926–1955, 1956–1985 and 1986–2015). Because temperature records in this region only go back to 1952, our tests of correlations of growth with temperature (as a function of elevation) used data from 1952 to 2015. Likewise, our tests for changes in the strength of the growth/climate relationships over time using the moving window analysis utilized only data from 1952 to 2015.

The nearest weather station is the subalpine meteorological station (3000 m) at Gongga Mountain, however, the short duration of its meteorological data (only available from 1988 to 2015) makes it difficult to perform reliable calibration with the targeted tree-ring data. Therefore, we used the nearby national meteorological station (Kangding station, about 65 km from the study site) and the gridded Climatic Research Unit, East Anglia, UK (CRU TS 3.24, Mitchell and Jones, 2005) for climate-growth correlation analysis. The annual mean temperature correlated significantly ($r = 0.75$, $p < 0.001$) of Kangding and CRU dataset. Climate variables include monthly mean temperature, monthly total precipitation, and monthly precipitation-potential evapotranspiration (P-PET) from 1952 to 2015 for growth-climate correlation analysis. To detect the regional climate and tree growth trends, the Mann-Kendall trend tests were used. We tested their significance using the Theil-Sen trend estimate (http://www.singlecaseresearch.org/calculators/theil-sen). We also used a 31-year moving-window correlation analysis to calculate the temporal stability of the growth-climate series to allow testing if the difference between high and low elevations' response to temperature variation increased with rapid warming. Correlation analyses were conducted using the SPSS 16.0 statistical package (SPSS, Chicago, IL, USA).