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Research paper

Summer solstice marks a seasonal shift in temperature sensitivity of stem growth and nitrogen-use efficiency in cold-limited forests

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ABSTRACT

In boreal forests and alpine treelines, it is debatable how the temperature sensitivity of tree-ring growth should vary with changes in climate over time and the extent to which seasonal stem increments are controlled by leaf physiology. We aim to test the hypothesis that, in cold-limited forests, maximizing stem growth rate around summer solstice is closely related to foliage turnover, which generally results in high sensitivity of stem growth and less sensitivity of nitrogen-use efficiency (NUE) to early-season temperatures. Our analysis was based on repeat-census observations of stem radial increment (2008–2013; made with dendrometers) and monthly litterfall (2007–2015) as well as the measurements of tree-ring width series (1960–2015; made with tree-ring cores) in two Tibetan treeline forests. NUE was estimated as the inverse of leaf-litter nitrogen concentration. We further examined a global dataset of tree-ring chronologies (1931–1990) from 139 sites across temperate and boreal coniferous forests in the northern high-latitude region. Weekly stem increments across species and years synchronously peaked around summer solstice, with more than half of annual increment produced in the first 28–35 days of the growing season when air and soil temperatures were still low. Monthly stem increments were positively related to previous-month litterfall, and higher litterfall generally resulted in higher NUE. NUE was insensitive or less sensitive to soil temperature in the early growing season. Among years, pre-peak increments were positively correlated with pre-solstice temperatures while post-peak increments varied little. The annual increment was dominated by and coherent with the pre-peak increment and well correlated with the ring-width measurements of monitored trees during 2008–2013. Variations in tree-ring width chronologies from the two Tibetan treelines and the global 139 forest sites mainly reflected the change of early summer temperatures. The findings suggest a day-length control on the linkage between seasonal stem growth and nitrogen cycling in a cold-limited forest ecosystem, and provide the basic for predicting responses of tree-ring growth and NUE to climatic warming.

1. Introduction

Tree growth in cold environments is primarily constrained by low temperature (Briffa et al., 1990; Wieser and Tausz, 2007; Sullivan et al., 2015). In boreal forests and alpine treelines, however, there are divergent tree-ring growth responses to increasing summer temperatures over the past century (Briffa et al., 1998; Vaganov et al., 1999; Barber et al., 2000; Wilmking et al., 2004; D'Arrigo et al., 2008; Drobyshev et al., 2010; Zhang and Wilmking 2010; Galván et al., 2012; Girardin et al., 2014). Current understanding of this topic mainly relies on investigating correlations between annual ring-width series and climate variables, which may not truly capture the impacts of seasonal limiting factors on tree-ring growth. It is debatable how the temperature sensitivity of tree-ring growth should vary with changes in climate over time (Vaganov et al., 1999; Barber et al., 2000; Wilmking et al., 2004; D'Arrigo et al., 2008; Drobyshev et al., 2010; Galván et al., 2012; Girardin et al., 2014) and the extent to which seasonal stem increments are controlled by leaf physiology (Jarvis and Linder, 2000; Zweifel et al., 2010; Richardson et al., 2015; Sullivan et al., 2015), which is itself essential for understanding limitations to tree growth (Wieser and

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Tausz, 2007; D'Arrigo et al., 2008; Jarvis and Linder, 2000; Sullivan et al., 2015). Such uncertainties challenge the understanding of tree growth responses to warming in cold-limited forests.

Due to rotation of the planet, day-length represents a constant and reliable signal of seasonal change in the environment, and sensitivity to day-length protects plants from the potential risks (e.g. freezing damage, fitness losses associated with phenological mismatch) of simply tracking temperature (Jackson, 2009; Eriksson and Webb, 2011; Way and Montgomery, 2015). Day length is thought to control tree phenology, for example timing of flowering, bud set, growth cessation and leaf senescence (Jackson, 2009; Way and Montgomery, 2015), and also to regulate physiological factors such as circadian rhythms in leaf and canopy CO_2 exchange (Doughty et al., 2006; Bauerle et al., 2012; Resco de Dios et al., 2012). It has been suggested that maximizing stem growth rate around summer solstice would enable cold-limited trees to have enough time to safely complete secondary cell wall lignification before winter (Rossi et al., 2006). On the other hand, soil nutrient availability is also suggested to be another major constraint on growth of cold-limited trees (Jarvis and Linder, 2000; Sullivan et al., 2015), especially in the early growing season when soil temperature is low. The circadian signals perceived in the leaves (Jackson, 2009) may regulate the seasonality in foliage turnover to improve the nitrogen-use efficiency (NUE) of carbon gain through recycling nitrogen of older leaves prior to leaf shedding, in which higher litterfall results in higher nitrogen content and photosynthetic capacity of canopy leaves (Field, 1983; Hikosaka, 2005; Luo et al., 2011). Given that seasonal stem growth rate (Rossi et al., 2006) and photosynthetic capacity (Bauerle et al., 2012) tend to peak around summer solstice, there would be an intrinsic link between stem growth and foliage turnover to increase NUE in the early season. Thus, maximizing stem growth rate around summer solstice and linking stem growth to foliage turnover could be a mechanism by which plants strongly enhance NUE. To our knowledge, there are not observed data quantifying the temperature dependence of the link between seasonal stem increments (tree rings) and foliage turnover in cold environments.

In southeast Tibet, the growing season mean soil temperatures of alpine treelines fall within the threshold temperature of 6.7 ± 0.8 °C found in global climatic treelines (Körner and Paulsen, 2004; Liu and Luo, 2011). Instrumental climatic data indicate a significant warming trend since the 1960s, which has been recorded in tree-ring width chronologies of *Abies* trees (Liang et al., 2009) and *Rhododendron* shrubs (Kong et al., 2012). At and above treelines, age-detrended ring width chronologies of the *Rhododendron* shrubs across ten altitudes are positively correlated with June mean temperature but varied little with precipitation and other monthly mean temperatures (Kong et al., 2012). This provides us an ideal system to examine the controls on intra- and inter-annual variations in stem growth. In this study we aim to test the hypothesis that, in cold-limited forests, maximizing stem growth rate around summer solstice is closely related to foliage turnover (litter production), which generally results in high sensitivity of stem growth (Rossi et al., 2006) and less sensitivity of NUE to early-season temperatures. Our analysis was based on repeat-census observations of stem radial increment (2008–2013; made with dendrometers) and monthly litterfall (2007–2015) at treeline sites of Smith fir (*Abies georgei* var. *smithii*) and juniper (*Juniperus saltuaria*) in southeast Tibet. NUE was estimated as the inverse of leaf-litter nitrogen concentration (Vitousek, 1982; Hikosaka, 2005). We also measured tree-ring width series (1960–2015; made with tree-ring cores) of both treeline species to test the extent to which stem growth signals can be extracted from dendrometer data and whether the age-detrended ring-width indices are more sensitive to the change of early-season temperatures. To further test the generality of the Tibetan treeline data, we examined a global dataset of tree-ring chronologies (1931–1990) from 139 sites across temperate and boreal coniferous forests in the northern high-latitude region.

2. Materials and methods

2.1. Study sites

This study was conducted on the opposing slopes (north-facing vs. south-facing) of a U-shaped valley at the peak of the Sergyemla Mountains (29°36′N, 94°36′E, 4300–4400 m elevation) in the southeast of Tibet. The dominant tree species of treelines on the north- and south-facing slopes are *A. georgei* var. *smithii* (Smith fir) and *J. saltuaria* (juniper), respectively. Along the slopes vegetation changes from sub-alpine and treeline forests (tree height > 4 m and canopy coverage > 40%) to an open mosaic of alpine shrublands and grasslands. In 2005, two long-term plots (50 × 50 m) were established in both treeline forests. The stand basal area and mean tree height (mean ± SD) were 39.7 m^2 ha^{-1} and 10.2 ± 1.0 m for Smith fir and 39.8 m^2 ha^{-1} and 7.6 ± 0.5 m for juniper. Four weather stations (HL20, Jauntering Inc., Taiwan) were installed at the sites for treeline forests of Smith fir (4320 m) and juniper (4425 m), and above both treelines. The meteorological data of 2008–2013 indicated that there was similar annual precipitation (850–940 mm) and growing-season mean air temperature (6.5–6.6 °C) across both treelines, but annual mean air-temperature above both treelines differed by 2.0 °C, with a warmer climate on the south-facing slope. Spring soil warming dates (when soil temperatures began to be continuously above 0 °C) differed by up to 20–30 days between north- and south-facing slopes, while daily mean soil moisture content across both slopes was typically > 35% during the growing season (Supplementary Fig. S1).

2.2. Measurements of seasonal stem radial increment with dendrometers

At each treeline site, eight mature and healthy trees were selected. The monitored Smith fir and juniper trees had an average height of 9.6 ± 1.8 m and 8.6 ± 0.9 m, diameter at breast height (DBH) of 37.2 ± 14.0 cm and 22.4 ± 3.1 cm, and stem age of 188 ± 61 yr and 207 ± 24 yr, respectively. Automatic dendrometers of diameter and circumference (including 2 DD and 6 DC dendrometers, Ecomatik, Munich, Germany) mounted at breast height were used for continuously monitoring stem radial growth. To minimize the influence of swelling and shrinkage of the bark on dendrometer measurements, and also to ensure a close contact with stem, the outer parts of the bark were carefully removed before installation. In addition, we periodically adjusted the tension of dendrometer sensor rods or wire bands to remain within the measurement range as suggested by the manufacture's specifications. Raw data were hourly recorded by a HL20 data logger (Jauntering Inc., Taiwan).

To calculate a stem increment in radius, the data measured by DD and DC types of dendrometers were divided by 2 and 2π, respectively. Dendrometer measurements started in August 2005, but the data loggers were broken in 2007. In this study, we used the continuous observation data during 2008–2013. We obtained 6-years of continuous observation data for 4 Smith-fir trees and 7 juniper trees, and 2–5 years data for 4 other Smith-fir trees and 1 juniper tree in which part of data were lost in some of observed years because of sensor failure.

The raw dendrometer data are a combination of growth- and water-induced stem variations, which needs an appropriate method to extract the information of stem radial increment. Stem growth information is based on the changes of daily maximum values, in which the weekly stem radial increment is always extracted to minimize water-induced stem variations (Rossi et al., 2006). In this study, weekly stem radial increments for each tree, year and species were extracted using the method as described by Rossi et al. (2006). First, the daily maximum value was calculated from the 24 h values within a day. Secondly, the weekly stem radial increment was calculated as the difference of daily maximum values between the consecutive seventh day and the first day. When the calculated weekly stem radial increment was negative, we prolonged the time interval to 2 or 3 weeks and calculated the bi-