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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 CO₂ 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 \pm 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 highlatitude 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 southfacing 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 $(50 \times 50 \text{ m})$ were established in both treeline forests. The stand basal area and mean tree height (mean \pm SD) were 39.7 m² ha⁻¹ and 10.2 \pm 1.0 m for Smith fir and 39.8 m² ha⁻¹ and 7.6 \pm 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 waterinduced 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-

Table 1

Parameters of the Gompertz models for the cumulative dynamics of stem increment across species and age-groups using daily maximum values of dendrometer data during 2008–2013. β/κ , the timing (day of year) of maximum stem growth rate.

Species & age	Year	Уо	а	β	κ (10 ⁻²)	β/κ	r ²	р
Smith fir trees								
Age (107-122 yr)	2008	925.46	737.12	9.41	5.50	171	0.99	< 0.0001
	2009	1814.70	1368.27	9.05	5.32	170	0.99	< 0.0001
	2010	1640.57	525.97	12.45	7.19	173	0.99	< 0.0001
	2011	1380.98	735.48	11.25	6.47	174	0.99	< 0.0001
	2012	894.51	899.64	10.38	6.14	169	0.99	< 0.0001
	2013	928.15	942.25	9.41	5.41	174	0.99	< 0.0001
Age (214–263 yr)	2008	562.92	528.97	6.92	4.07	170	0.99	< 0.0001
	2009	794.03	570.24	10.40	6.08	171	0.99	< 0.0001
	2010	1283.72	506.04	6.98	4.04	173	0.98	< 0.0001
	2011	833.49	384.27	11.48	6.64	173	0.98	< 0.0001
	2012	791.22	586.98	10.08	5.93	170	0.99	< 0.0001
	2013	853.14	558.16	13.33	7.58	176	0.99	< 0.0001
Juniper trees								
Age (175–195 vr)	2008	681.20	321.60	12.05	7.09	170	0.96	< 0.0001
	2009	1072.23	306.33	18.10	10.65	170	0.99	< 0.0001
	2010	1311.62	313.98	7.68	4.44	173	0.99	< 0.0001
	2011	720.04	244.41	15.83	9.26	171	0.94	< 0.0001
	2012	1006.44	278.78	13.63	8.02	170	0.98	< 0.0001
	2013	802.74	207.49	13.80	8.16	169	0.96	< 0.0001
Age (228–231 yr)	2008	287.60	142.77	15.37	8.94	172	0.86	< 0.0001
• •	2009	415.74	268.41	10.54	6.09	173	0.96	< 0.0001
	2010	612.35	133.24	7.43	4.37	170	0.96	< 0.0001
	2011	518.56	175.12	10.83	6.26	173	0.95	< 0.0001
	2012	683.43	197.15	16.65	9.68	172	0.95	< 0.0001
	2013	422.78	169.21	11.66	6.98	167	0.93	< 0.0001

weekly or tri-weekly stem radial increment, and then converted it into a weekly stem radial increment assuming that the stem radial increment proceeded linearly during each time interval. The frequency of "negative weekly stem increment" during the growing season was less than 2% in Smith fir trees but 14–19% in slow-growing juniper trees. To understand the extent to which stem growth signals can be extracted from dendrometer data, the estimates of annual stem increment (the sum of weekly increments over the growing season) by dendrometers were compared to the ring-width measurements of monitored trees during 2008–2013 as described below.

The onset of stem radial increment cannot be easily detected from dendrometer data because spring rehydration occurs simultaneously and causes an abrupt increase in dendrometer measurements. Wood formation of conifers in cold environments often occurs when a critical temperature of 4-5 °C is reached (Rossi et al., 2008). For Smith fir and juniper trees, the cambial activity generally started when daily minimum air temperature exceeded 1-2 °C for five consecutive days in spring (with daily mean temperature of 3-5 °C) (Li, 2015; Li et al., 2017). In this study, the onset date of stem radial increment was defined as the first day when daily mean air-temperature exceeded 4 °C for five consecutive days in spring. The end-date of stem radial growth was defined as the first day when the weekly stem radial increment continuously remained negative for 4 weeks. During 2007-2008, the temperature-defined onset dates (day of year, DOY) for stem radial growth of both species (Smith fir: 139-144 DOY; Juniper: 139-145 DOY) were typically consistent with the lower range of observed first cambial-cell emergence dates (Smith fir: 144-153 DOY; Juniper: 147-162 DOY) by repeated microscopic sampling of the developing tree ring (Li et al., 2013, 2017; Li, 2015).

2.3. Monthly litterfall measurements

To examine if seasonal stem increments are associated with foliage turnover and NUE, we collected monthly litterfall (including dead leaves and twigs) from five 2 m^2 litterfall traps in each of the two treeline forests during April and October in 2007–2015. The litter nitrogen concentration was analyzed by the Kjeldahl method (Kjeldahl,

1883). At a steady state, NUE can be measured as the inverse of the nitrogen concentration in dead leaves because the ratio of biomass production to nitrogen uptake is equal to the ratio of litterfall to nitrogen loss (Vitousek, 1982; Hikosaka, 2005).

2.4. Meteorological data at both treeline sites

Meteorological factors at the Smith fir and juniper treelines were continuously monitored with weather stations from August 2005. Air temperature and relative humidity at a height of 3 m above the ground were measured by a probe with vented radiation shield. Soil temperature and volumetric soil moisture content were measured at soil depths of 5 cm and 20 cm. Furthermore, solar radiation, photosynthetic active radiation, precipitation and snow depth were observed in low shrubland near to the Smith-fir treeline and in grassland nearby the juniper treeline. Data were recorded hourly with a HL20 data logger (Jauntering Inc., Taiwan). Detailed information on the sensors is found in Liu and Luo (2011).

Meteorological factors were calculated for a 7-day period consistent with that of the extracted weekly stem radial increment, including: weekly mean air-temperature (AT_{mean}), mean minimum air-temperature (AT_{min}), mean soil temperature at -5 cm (ST₅) and -20 cm (ST₂₀), mean soil moisture at -5 cm (SM₅) and -20 cm (ST₂₀), mean soil moisture at -5 cm (SM₅) and -20 cm (SM₂₀), mean solar radiation (SR) and photosynthetic active radiation (PAR), as well as weekly precipitation (Pr). We further calculated mean temperatures and total precipitation for the early season (from the onset date of stem radial increment as defined above to the 6 days later just after summer solstice given the calculation of weekly stem radial increment) and the later season after summer solstice.

2.5. Tree-ring width chronologies and related climate data

In October 2016, 60 tree-ring cores at breast height for each of both treeline species (Smith fir and Juniper) were collected from 30 trees (including the 8 monitored trees with dendrometers) with an increment borer (Haglöf, Sweden). The cores were processed following standard dendrochronological practices, and annual ring-widths were measured



Fig. 1. Two Tibetan treeline species generally maximized their stem growth rates around summer solstice (a and b) and typically produced > 50% of annual increment in the short pre-peak season (c and d) when the mean air-temperature (AT_{mean}) was still low (e and f). (a and b) Seasonal variations in weekly stem increments across two age classes of (a) Smith fir (Abies georgei var. smithii) and (b) juniper (Juniperus saltuaria) trees during 2008-2013; the vertical gray lines highlight the timing of summer solstice: error bars indicate + SD of mean. (c-d) Inter-annual changes in ratios of pre-peak to annual increments/durations in (c) Smith fir and (d) juniper; different letters between years indicate significant differences in pre-peak fractions of increment (capital) and duration (lowercase) at p < 0.05. (e and f) Inter-annual variations in pre- and post-peak mean air-temperatures (AT_{mean}) in (e) Smith fir and (f) juniper forests.

with a resolution of 0.01 mm (Liang et al., 2009). We performed the cross-dating check by using the COFECHA program (Holmes, 1983). The average correlation coefficients between the 60 ring-width series were 0.576 for Smith fir and 0.493 for juniper. The raw data of the 60 cross-dated ring-width series were transformed into indices by fitting a negative exponential function using the ARSTAN program (Cook and Kairiukstis, 1990). The instrumental climatic data of daily temperatures (mean, minimum and maximum) during 1960–2015 were obtained from Nyingchi weather station at 3000 m, ca. 10 km from our study sites.

Globally, tree-ring width chronologies of temperate and boreal conifers with latitudes of > 45° N were obtained from the International Tree-Ring Data Bank (ITRDB) online available at the website (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring). In total, 139 age-detrended ring-width chronologies across 16 coniferous species and 139 sites were selected according to the significant correlation between ring-width index and summer mean temperature during 1931–1990 (Supplementary Table S1). Time series data of monthly mean temperatures for the 139 chronologies were obtained from the 0.5° \times 0.5° gridded dataset of CRU TS v. 3.23 online available at the website of Climatic Research Unit (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_3.23/).

2.6. Data analysis

Simple linear model (y = a + bx) was used for testing whether the

estimates of annual stem increment (the sum of weekly increments over the growing season) by dendrometers are well (positively) correlated with the ring-width measurements of monitored trees during 2008–2013. The timing of maximum weekly stem increments across tree species, stem ages and observed years was cross-checked by the fitting results of the Gompertz function with daily maximum dendrometer data. The daily maximum values calculated from hourly dendrometer data during 2008–2013 were fitted with the Gompertz function as described by Duchesne et al. (2012):

$$y = y_0 + a \times \exp[-\exp(\beta - \kappa \times t)]$$

Where y is the daily cumulative sum of stem increment; a is the upper asymptote; β is the x-axis placement parameter; κ is the rate of change parameter; and t is the time (expressed as day of year, DOY). The timing (DOY) of maximum radial growth rate can be calculated as the ratio of β to κ (Rossi et al., 2006). The Gompertz model includes a parameter (y_0 , the lower asymptote) indicative of the initial state at the beginning of growing season to avoid the arbitrary selection of initial settings of dendrometer data (Duchesne et al., 2012). The sensitivity analysis indicated that uncertainty in the temperature-defined growing season onset had a minor effect on the β/κ ratio (Supplementary Table S2). Given the possible age-related changes in the pattern of stem growth and the timing of maximum stem growth rate, the monitored trees per species were separated into two age-classes (107–122 yr in 3 trees and 214–263 yr in 5 trees for Smith fir, and 175–195 yr in 4 trees and 228–231 yr in 4 trees for juniper) for the data analyses of stem



Fig. 2. Seasonal stem increments of Smith fir and juniper were closely linked to canopy foliage turnover during the growing seasons of 2008–2013. (a and b) Monthly stem increments had a time lag with the litter production across (a) Smith fir and (b) juniper trees; error bars indicate \pm SD of mean. (c and d) There were positive correlations between monthly stem increment and previous-month litterfall for (c) Smith fir and (d) juniper trees in pooled data of years; the symbols are for seasonal stem increments.



Fig. 3. Relationships of seasonal nitrogen-use efficiency (NUE) to monthly litterfall and soil temperature in treeline forests of Smith fir and juniper during mid-April to mid-October of 2007–2015. (a and b) NUE increased with increasing monthly litterfall in a power pattern in Smith fir (a) and in a linear pattern in juniper (b). (c and d) With increasing soil temperature at -5 cm depth, NUE varied little (c, Smith fir) or declined slowly (d, juniper) in the early season of mid-April to mid-June (grey trend line), but quickly decreased in the later season (black trend line). NUE was measured as the inverse of leaf-litter nitrogen concentration.

increment.

To investigate if the temperature sensitivity of stem increment may differ before and after summer solstice, the whole growing season was subdivided into the pre- and post-peak growing phases by the timing of the stem growth peak. To examine the sensitivity of stem increment to meteorological factors (consistent responses or variable responses between pre- and post-peak growing phases), the correlations between weekly stem increment and meteorological factors as well as between annual variations of pre- and post-peak increments and seasonal mean temperatures were fitted with simple linear model. To understand relative effects of calendar dates (DOY, indicating seasonal change of day length) and climatic factors on seasonal stem increments during the observed years, we further examined if climate-based predictions across years have a higher correlation with observed data of pre- and postpeak increments than calendar-based predictions (being constant across years). Both predicted increments were calculated from the Gompertz models of cumulative stem increment vs. DOY in Table 1, and from regression models of weekly increments vs. climate factors (AT_{min}, except using Pr for juniper in the post-peak season because of its weak/no correlation with temperature) in Supplementary Table S3, respectively.

Differences in annual increments, pre- and post-peak increments and the ratios of pre-peak to annual increments/durations among observed years were assessed by one-way analysis of variance and the Turkey comparison. In pooled data of observed years, the correlations



Fig. 4. Annual stem increments (the sum of weekly increments over the growing season) by dendrometers were positively correlated with the ringwidth measurements of monitored trees at treelines of (a) Smith fir and (b) juniper during 2008–2013.

Fig. 5. The pre-peak stem increments of Smith fir and juniper generally paralleled annual increments (a and b) and were positively correlated with mean minimum air-temperatures (AT_{min}) of the early and later seasons (c and d) during 2008–2013. In contrast, the post-peak increments varied little among years (a and b) and showed no correlation with postpeak AT_{min} (c and d). (a and b) Inter-annual variations in pre- and post-peak and annual stem increments of (a) Smith fir and (b) juniper; different letters between years indicate significant differences in annual (capital) and pre-peak (lowercase) increments at p < 0.05. (c and d) Pre- and post-peak stem increments were correlated with pre- and postpeak AT_{min}, respectively.

of monthly stem increment to litterfall and of seasonal NUE to litterfall and soil temperature were fitted with simple linear/non-linear models.

Both datasets of age-detrended ring-width series obtained from this study and the ITRDB were used for examining if tree-ring width chronologies mainly respond to the changes of early-season temperatures. Simple linear model was used for assessing the correlations between tree-ring width indices of both treeline species and monthly temperatures at Nyingchi weather station during 1960–2015. In the global 139 chronologies, we calculated correlation coefficients between tree-ring width indices and mean temperatures of June (T₆), July (T₇) and August (T₈) for each site-specific chronology. We also calculated the occurrence frequency of the chronologies indicating significant correlations with T₆, T₇ and T₈ at p < 0.05, respectively. The interannual variation of global mean tree-ring width indices averaged from the 139 chronologies was compared to the changes in mean temperatures of T₆, T₇ and T₈ during 1931–1990, in which a 30-years moving correlation analysis was performed.

All statistical analysis were performed using the SPSS 15.0 for Windows (SPSS Inc., Chicago, USA), and all significant differences were taken at p < 0.05.

3. Results

Across tree species, stem ages and observed years, the timing of maximum weekly stem increments converged towards a narrow-range period around summer solstice regardless of great differences in the values of maximum stem increment (Fig. 1a and b), which was consistent with the fitting results of the Gompertz function with daily maximum dendrometer data (the β/κ ratio 171 ± 2 day of year, mean ± SD; Table 1). Weekly stem increments in juniper were tightly

correlated with those in Smith fir (r = 0.76-0.88, p < 0.001, Supplementary Fig. S2). The average growing-season length for Smith fir and juniper treelines was 108 ± 11 days and 104 ± 14 days, respectively (Fig. 1a and b). Both species typically produced 46%–75% of annual increment in the first 28–35 days of the growing season, with the exception of 2010 (32%–37%, Fig. 1c and d). In 2010, the early-season mean temperature was lowest (ca 5 °C) among the six observation years (Fig. 1e and f).

Monthly stem increments showed a time lag with litter production (Fig. 2a and b), exhibiting a positive correlation with the litterfall of the previous month (Fig. 2c and d). Higher litterfall was correlated with higher NUE (Fig. 3a and b). With increasing soil temperature, NUE (the inverse of litter N concentration) varied little or decreased slowly in the early season (mid-April to mid-June), but quickly decreased later in the season (Fig. 3c and d).

During 2008-2013, annual stem increments (the sum of weekly increments over the season) ranged from growing $440 \pm 74-865 \pm 429 \,\mu m$ (Smith fir) and from 200 \pm 100–294 \pm 54 μ m (juniper). In each of both species, annual stem increments of 2008-2013 were well (positively) correlated with the ring-width measurements of monitored trees though the tree-ring growth was systematically underestimated (r = 0.71-0.79, p < 0.01, Fig. 4). The variation of annual increments was in phase with that of pre-peak increments (Fig. 5a and b). Moreover, the pre-peak increments were positively correlated with pre-peak mean minimum temperature (p < 0.02, Fig. 5c and d) and with the mean temperature (r = 0.85-0.87, p = 0.02-0.03, data not shown). In contrast, the postpeak increments varied little among years (Fig. 5a and b) and had no obvious relationship with post-peak temperature (p = 0.55-0.97, Fig. 5c and d).



Fig. 6. Seasonal variations in observed vs. predicted weekly stem increments and their correlations during 2008-2013. (a and b) Seasonal variations in observed vs. predicted weekly increments of (a) Smith fir and (b) juniper; both predictions were calculated from the Gompertz models of cumulative increment vs. day of year in Table 1, and from linear regression models of weekly increments vs. climate factors (ATmin, but Pr for juniper in the post-peak season) in Table S3; the vertical gray lines highlight the timing of summer solstice. (c and f) Correlations between observed and predicted weekly increments separated for two growing phases of (c, e) before and (d, f) after the timing of maximum stem growth rate around summer solstice (171 ± 2 day of year), respectively.

To further understand the relative effects of calendar dates (day of year, indicating seasonal change of day length) and climatic factors (weekly temperature or precipitation) on seasonal stem increments, we compared the performance of the calendar- and climate-based regression models for predicting the weekly increment measurements (Fig. 6). During 2008–2013, the climate-based models accounted for more variation in weekly stem increment (Fig. 6a and b), and also resulted in better predictions for pre-peak increments (Fig. 6c and e). The calendar-based models, however, made better predictions for the post-peak increments (Fig. 6d and f). In addition, we found that the pre-peak increments had strong and significant positive correlations with both air and soil temperatures, while the post-peak increments (Supplementary Table S4).

During 1960–2015, the age-detrended ring-width series of Smith fir were mainly correlated with June and July mean minimum temperatures, indicating a higher correlation coefficient in June (r = 0.53) than in July (r = 0.46) (Fig. 7a). In juniper trees, the series of ring-width indices were mainly correlated with mean minimum temperatures of March to September, showing higher correlation coefficients in April (r = 0.69) and June (r = 0.63) than in July (r = 0.59) and August (r = 0.51) (Fig. 7b).

To cross-check our findings in Tibetan treelines we examined a

global dataset of 139 site-specific tree-ring chronologies (1931–1990) that included 16 coniferous species from high-latitude northern regions (Fig. 8). Among them, 104 chronologies (75%) showed significant correlations between tree-ring width index and June mean temperature (T₆), compared to 81 significant correlations for July (58%; T₇) and 21 significant correlations for August (15%; T₈) (Fig. 8a). Further, the mean correlation coefficient of all the 139 chronologies was significantly higher with T₆ than with T₇ or T₈ (Fig. 8b). The mean tree-ring width indices of 1931–1990, averaged from the global data of 139 chronologies, correlated rather well with the change of T₆ (r = 0.52, p < 0.001) comparing to the low or no correlation with T₇ (r = 0.25, p = 0.03) or T₈ (r = 0.03, p = 0.40) (Fig. 8c). Similar patterns were found in the 30-years moving correlations between ring-width indices and mean temperatures (T₆, T₇, T₈) during 1931–1990 (Supplementary Table S5).

4. Discussion

At high latitudes and high elevations, cold environments are generally characterized by a short growing season, which is one of main filters for woody plant survival and distribution (Rossi et al., 2006; Moser et al., 2009). In this study, seasonal change of stem growth signals can be extracted from dendrometer data (Fig. 4). The average



Fig. 7. Correlation coefficients between age-detrended ring-width series of (a) Smith fir and (b) juniper at 4300–4400 m and monthly mean minimum temperatures of Nyingchi weather station at 3000 m during 1960–2015.

growing season length for alpine treelines of Smith fir (108 \pm 11 days) and juniper (104 \pm 14 days) is close to the threshold of minimum growing days (ca. 100 days) for stem growth found in global treelines (Moser et al., 2009; Rossi et al., 2008). To safely complete secondary cell wall lignification before winter (Rossi et al., 2006), both treeline species typically produced more than half of annual increment in the first 28-35 days of the growing season even though the mean temperature was generally less than 7 °C (Fig. 1c-f), which is the low temperature threshold that significantly limits plant growth and photosynthesis (Wieser and Tausz, 2007). Because the early-season air and soil temperatures varied greatly among years (Fig. 1e and f, Supplementary Fig. S1a and b), there was high inter-annual variation in maximum stem growth rate (Fig. 1a and b) and early-season increment (Fig. 5a and b). Hence, temperatures prior to summer solstice are the most crucial factor defining intra-annual increment as well as annual increment (Fig. 5c and d), which explains why the age-detrended ringwidth series of both treeline species (Fig. 7) and the global 139 chronologies (Fig. 8) were more sensitive to the change of early-season temperatures. In juniper trees on the south-facing slope, the pre-peak increments were also sensitive to the early-season precipitation prior to summer solstice (Supplementary Table S4). In contrast, the post-peak increment varied little with the temperatures after summer solstice (Fig. 5c and d). Instead of temperature or precipitation, the models suggested that day of year (indicating seasonal change of day length) could be a better predictor for the post-peak stem increment (Fig. 6d and f). In mid to late summer when the mean temperature is generally above 7 °C (Fig. 1e and f), the relatively sufficient supply of photosynthates makes the plant easier to meet the demand of the secondary wall cellulose synthesis, resulting in a one-month lag between woody biomass production and stem-girth increase (Cuny et al., 2015). Thus, our data supported the previous suggestion by Rossi et al. (2006), indicating that maximizing stem growth rate around summer solstice generally results in a high sensitivity of ring-width growth to earlyseason temperatures.

The close relationships between monthly stem increments and previous-month litterfall (Fig. 2), and between seasonal NUE and litterfall (Fig. 3a and b), also reflect the effect of day-length on foliage turnover and nitrogen cycling, resulting in less sensitivity of NUE to the early-season soil temperature (Fig. 3c and d). Plant circadian clocks may have evolved to synchronize physiological and developmental events with seasonal changes of the environment by anticipating differences in day length (Dodd et al., 2005; Doughty et al., 2006; Jackson, 2009; Eriksson and Webb, 2011; Resco de Dios et al., 2012). At canopy level, the fast turnover of labile carbon and nitrogen pools in leaves may be driven into an approximate steady state fitting to a general seasonality in foliage turnover and productivity (Field, 1983; Hikosaka, 2005; Luo et al., 2011), which could be constrained by photoperiod (Bauerle et al., 2012; Way and Montgomery, 2015). There is evidence that optimal increases in photosynthesis, growth, survival rate and competitive advantage in plants are often achieved by correctly matching the circadian clock period with that of the external light-dark cycle (so called circadian resonance) (Dodd et al., 2005; Graf et al., 2010). Since the rotation of the Earth occurs with an approximately 24 h period throughout the year, the inherent plasticity within the circadian system will cause phenology and physiology to adapt to alterations in photoperiod. There would be an intrinsic link between seasonal stem increment and canopy productivity and NUE through circadian resonance relating to summer solstice. As a result, seasonal limiting factors to NUE may shift from foliage turnover in the early growing season to soil temperature in the later season, which explains why NUE was insensitive or less sensitive to soil temperature in the early season (Fig. 3c and d). In the later season when soil temperature is generally above 5 °C (the critical temperature for wood formation of conifers, Rossi et al., 2008; Fig. 3c and d), higher soil temperature may result in higher nitrogen uptake by roots and then lower NUE (Hikosaka, 2005; Luo et al., 2011). The mechanisms linking stem growth to canopy productivity and NUE would also explain previous findings that annual ring widths of Rhododendron shrubs along elevations are well correlated with plant-level relative growth rate, maximum photosynthetic rate and simulated productivity (Kong et al., 2012). The intrinsic link between stem growth and foliage turnover to enhance NUE in the early season (Figs. 2 and 3) might also provide a new explanation for the special observation in the Rocky Mountains where the largest fraction of annual canopy CO2 uptake of spruce-fir forests occurs in the early part (first 30-35 days) of the growing season (Monson et al., 2002). At global scale, there is evidence that incorporating a day-length correction of photosynthetic capacity into a global terrestrial carbon-cycle model can significantly improve predictions of seasonal atmospheric CO2 cycling and forest ecosystem productivity (Bauerle et al., 2012).

Several previous studies demonstrated the reduced sensitivity of cold-limited tree growth to summer temperature in recent decades (Briffa et al., 1998; Barber et al., 2000; Wilmking et al., 2004; Girardin et al., 2014), and some possible causes were proposed according to the correlations between annual ring-width series and climate factors (Vaganov et al., 1999; D'Arrigo et al., 2008; Drobyshev et al., 2010; Galván et al., 2012). Some studies suggested that the limiting factors of tree-ring growth might have shifted from low temperature to other environmental factors under global warming, such as the warming induced drought stress on tree physiology (Barber et al., 2000), changes in snowfall pattern and snow melt timing which affects initiation of cambial activity (Vaganov et al., 1999), decreased solar radiation for photosynthesis (D'Arrigo et al., 2008), and the warming-induced decrease of soil organic layer that affects soil temperature, moisture and nutrient availability (Drobyshev et al., 2010). Other studies have also suggested that the reduced sensitivity of annual ring-width growth to summer temperature is likely due to the non-linear responses of tree growth to climate variability (Wilmking et al., 2004) or the age-related decline of sapwood production (Galván et al., 2012). Our study, however, illustrates that maximizing stem growth rate around summer



Fig. 8. Global mean tree-ring width indices averaged from 139 site-specific chronologies across temperate and boreal coniferous forests mainly indicated the change of June mean temperature during 1931-1990. (a and b) Latitudinal and longitudinal variations in correlation coefficients between treering width index and mean temperatures of June (T₆), July (T₇) and August (T₈); (insert, a) the occurrence frequency of the chronologies indicating significant correlations with T6, T7 and T8 at p < 0.05, respectively. (c) Inter-annual changes in global mean tree-ring width indices and mean temperatures of T₆, T₇ and T₈ during 1931-1990; the mean indices were significantly correlated with T₆ (r = 0.52, p < 0.001) but showed low or no correlations with T_7 (r = 0.25, p = 0.03) or T_8 (r = 0.03. p = 0.40). The species and site conditions are found in Supplementary Table S1.

solstice generally resulted in a high sensitivity of ring-width growth to early-season temperatures (Figs. 5,7 and 8), and there was an increasing trend in the 30-years moving correlation coefficients between global mean tree-ring width series and June mean temperature during 1931-1990 (Supplementary Table S5). Some previous studies have noted that the ring-width chronologies of arctic and subarctic trees (Gostev et al., 1996) as well as subarctic and alpine shrubs (Blok et al., 2011; Kong et al., 2012) are good indicators of changes in mean temperature of May to June. Furthermore, two earlier experiments with locally heated and cooled stem portions of lowland Norway spruce (Gričar et al., 2007) and treeline Pinus uncinata (Lenz et al., 2013) consistently indicated that the heating or cooling treatment can respectively increase or decrease the xylem cell production rate at the beginning of growing season, but have no effect of heating on the cambial activity in the second part of growing season. Thus, our observations in the Tibetan treelines are generally consistent with these literature results and the global data of tree-ring chronologies deployed in this work, indicating that cold-limited stem increments mainly respond to temperature variations of the early growing season approximately prior to summer solstice.

In conclusion, our data provide evidence that there is a seasonal strategy-shift in temperature sensitivity of stem growth and NUE in cold-limited forests. The early growing season prior to summer solstice is the most important period for ring-width growth and leaf physiology. Annual ring width series should mainly record the changes of pre-solstice limiting factors, compared to the mid to late summer conditions. This study advances the knowledge for identifying crucial factors constraining woody plant growth and nitrogen cycling in cold environments, and highlights the importance of distinguishing seasonal growing phases marked by summer solstice in detecting the sensitivity of tree-ring growth and NUE to climatic warming. Under strong warming at high latitudes and high elevations where water limitation will not become an issue in the near future, our results imply that increasing temperatures in the pre-solstice growing season could mostly affect the pre-solstice and annual stem increments with a link to high NUE, while the warming in late summer would have a minor influence on the post-solstice stem increments with a link to low NUE.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.10.029.

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