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Authors: Lu, Xiaoming, Huang, Ru, Wang, Yafeng, Sigdel, Shalik Ram, Dawadi, Binod, et al.

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Summer temperature drives radial growth of alpine shrub willows on the northeastern Tibetan Plateau

Xiaoming Lu^{1,2}, Ru Huang^{1,2}, Yafeng Wang¹, Shalik Ram Sigdel^{1,2}, Binod Dawadi^{1,3}, Eryuan Liang^{1,4,*}, and J. Julio Camarero⁵

¹Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Building 3, Courtyard 16, Lin Cui Road, Chaoyang District, Beijing 100101, China

²University of Chinese Academy of Sciences, Beijing 100049, China

³Central Department of Hydrology and Meteorology, Tribhuvan University, Kathmandu, Nepal

⁴CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China

⁵Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana, 1005, 50059 Zaragoza, Spain

*Corresponding author's email: liangey@itpcas.ac.cn

ABSTRACT

Shrub willows (*Salix* species) are widespread beyond the latitudinal and altitudinal tree-lines. Their ring width has been shown to be a reliable ecological indicator for changes in the harsh cold conditions in the Arctic, but little is known on their growth in alpine conditions. The shrubby *Salix oritrepha* grows above the treeline on the northeastern Tibetan Plateau (TP), making it an interesting woody species to explore responses of alpine communities to ongoing climate warming in this area. Since precipitation increases with increasing elevation (until 4670 m) in the study area, we hypothesize that the growth of *S. oritrepha* is mainly constrained by cold summer temperature. We sampled 35 *S. oritrepha* individuals above the juniper treeline (4200 m), and took basal wood cross sections for dendrochronological analyses. Few missing rings were detected at the shoot base when serial sectioning was applied. Ring width (RW) and basal area increment (BAI) standard chronologies were established. We found that BAI reflected a stronger climatic signal than RW. The radial growth was constrained by low July to August temperatures. We expect that climate warming would enhance the growth of alpine willows, which could alter the services provided by these high-elevation ecosystems.

INTRODUCTION

Shrubby willows (genus *Salix*) are widely distributed beyond the treeline in high latitudinal and altitudinal regions (Wu, 1983; Blok et al., 2011; Schweingruber et al., 2013). In these treeless areas, shrubs are the only woody species that have been shown to record changes in climatic conditions in their growth rings (Walker, 1987; Srur and Villalba, 2009; García-Cervigón et al., 2012; Gazol and Camarero, 2012; Liang et al., 2012; Rayback et al., 2012; Myers-Smith et al., 2015). However, studies on willows have mainly focused on the High Arc-

tic where shrub encroachment has been taken as a response to climate warming (Sturm et al., 2001; Forbes et al., 2010; Schmidt et al., 2010; Blok et al., 2011). In contrast, little is known about the growth performance of alpine willow and their responses to climate (cf. Myers-Smith et al., 2015).

The Tibetan Plateau (TP) is considered to be one of the largest, little disturbed alpine regions showing a high responsiveness to ongoing climate change (Zheng and Yao, 2006). However, little is known on how the radial growth of alpine shrubs responds to climate warming in the large treeless areas of the TP. Since shrubs dominate above the

TP treeline, several studies have dealt with these woody species using their ring features as monitors of climate change effects on alpine ecosystem, particularly in the southeastern TP (Liang and Eckstein, 2009; Liang et al., 2012, 2015; Li et al., 2013; Lu et al., 2015; Wang et al., 2015). In the southeastern TP, July temperature is the key factor limiting the radial growth of alpine rhododendron shrubs under subhumid climate conditions (Liang and Eckstein, 2009; Li et al., 2013; Lu et al., 2015). However, along the monsoon margin of the central TP, low precipitation may constrain growth of alpine juniper shrubs (Liang et al., 2012). For instance, in the Qilian Mountains, northeastern TP, the growth of the shrub *Hippophae rhamnoides* is constrained by cold June temperature but also by low precipitation of February to March of the current year (Xiao et al., 2007). These biogeographical disparities in climate–growth associations show the need to analyze these relationships in detail, and to look at these associations among alpine shrub willows, as it is a species that is well distributed.

Salix oritrepha (hereafter called *Salix*) is one of the most common shrubby willow species in the northeastern TP, dominating in alpine communities occurring above the *Juniperus przewalskii* treeline (Fang et al., 2011). Here, we aim to determine if the radial growth and wood formation of alpine *Salix* is mainly limited by temperature or by precipitation. Understanding this relationship is important because climate warming could promote upward shrubline shifts but also enhance the growth of alpine shrubs and their ability to uptake carbon as wood. This could lead to shrub encroachment and changes in related services of alpine ecosystems such as the regulation of carbon and water cycles or the maintenance of high levels of plant biodiversity and endemism (Greenwood and Jump, 2014).

The specific objectives of this study are (1) to test the dendrochronological potential of *Salix* by comparing the radial-growth patterns along the shoot of the same individual (serial sectioning), and (2) to quantify the climate–growth relationships using ring width (RW) and basal area increment (BAI) mean series (chronologies). We hypothesize that the radial growth of alpine *Salix* is mainly limited by growing-season temperatures, that is, summer thermal conditions.

MATERIAL AND METHODS

Study Species

Salix oritrepha is a deciduous and shrubby willow that is widely distributed on the TP and usually grows polycormic (Fang et al., 2011). This species may also grow in a more erect shape attaining heights of 0.6–1.2 m. The *Salix* stems are usually round at the base. In the species' xylem, one to several rows of thick-walled fiber cells formed a well-defined ring boundary (Fig. 1). The wood anatomy is semidiffuse to diffuse-porous.

Study Area and Climate

The study site (36°00'N, 98°11'E, 4270 m a.s.l.) is situated in the northeastern TP, about 32 km southeast from Dulan County (Fig. 2). This region is located at the eastern edge of the Qaidam Basin where *J. przewalskii* grow from 3850 m to 4200 m (Shao et al., 2005), and *Salix* appear above 4000 m elevation.

The study area is characterized by a typical continental arid climate. The annual mean temperature is 3.2 °C (1954–2014) at the meteorological station in Dulan (3191 m). July and January are the warmest and coldest months with mean temperatures of 15.8 °C and –9.8 °C, respectively. The mean annual total precipitation is 201 mm and 80% of the rainfall occurs between May and September. The annual mean pan (20 cm in diameter) evaporation is 1760 mm.

Meteorological data from the Qilian Mountains demonstrates that precipitation increases uphill and reaches a maximum at about 4670 m a.s.l. (Wang et al., 2009). Based on climatic data recorded in 2014 by an automatic weather station near the study site (4200 m a.s.l.), the annual mean temperature was –1.6 °C and the annual precipitation was 396 mm. The mean temperature from May to September was 5.9 °C and the total precipitation for that period was 331 mm. The mean temperatures in July and January were 9.2 °C and –12.0 °C, respectively.

Shrub Sampling and Chronology Establishment

In April 2015, we selected a well-drained site above the uppermost *J. przewalskii* individuals. A to-

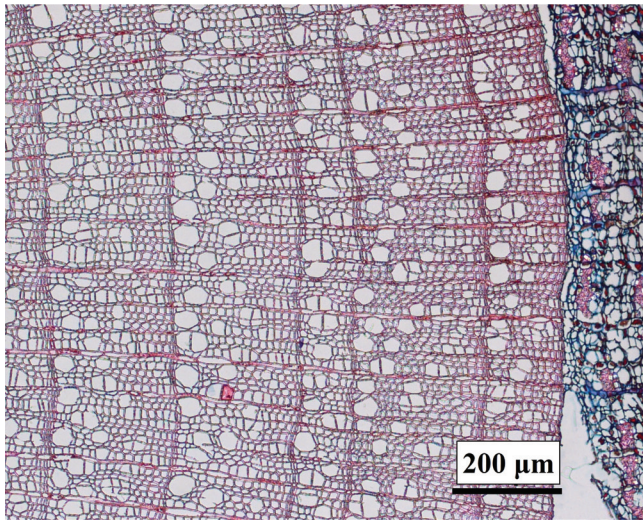


FIGURE 1. Microscopic cross section of *Salix oritrepha* wood.

tal of 35 *Salix* individuals were randomly selected and 2- to 3-cm-thick cross sections were cut at their bases. The samples were air dried and polished using sand papers of different grains until the ring boundaries were clearly visible. Then, the wood disks were visually cross-dated (Stokes and Smiley, 1996). The ring widths (RW) were measured along three radii per disk (every 120°) with a precision of 0.01 mm using the Lintab system (Rinntech, Heidelberg, Germany). The quality of the visual cross-dating was checked by the program COFECHA (Holmes, 1983). Digital photographs were taken under the microscope for each disk, and the shrub ring boundaries were vectored in each photograph

in ArcGIS 10. Then the area of each shrub ring polygon was calculated as the BAI. By avoiding the effects of irregular rings, such a method is better than BAI calculation based on ring width (e.g., Biondi and Qeadan, 2008).

The RW and BAI series were detrended and standardized by using the ARSTAN program (Cook and Krusic, 2005). A negative exponential function or a straight line was fitted to each individual RW or BAI series, and the resulting indices were averaged for all individuals using a biweight robust mean to obtain standard RW and BAI chronologies.

Serial Sectioning

To detect the presence of missing rings along the sampled shoots, we selected three individuals (B1, B2, and B3) to apply the serial-sectioning method following Kolishchuk (1990) and Wilmking et al. (2012). Cross sections were collected at 20-cm intervals along the main shoot. The rings were cross-dated among the cross sections and then the RW were measured along three radii (every 120°) per section. There was only one missing ring in 2013 at the base of one cross section.

Data Analysis

We calculated several statistics to describe the raw measurement and standardized chronologies: standard deviation (SD), first-order autocorrelation (AC), mean sensitivity (MS), mean series intercorrelation (R_{bar}), and expressed population signal

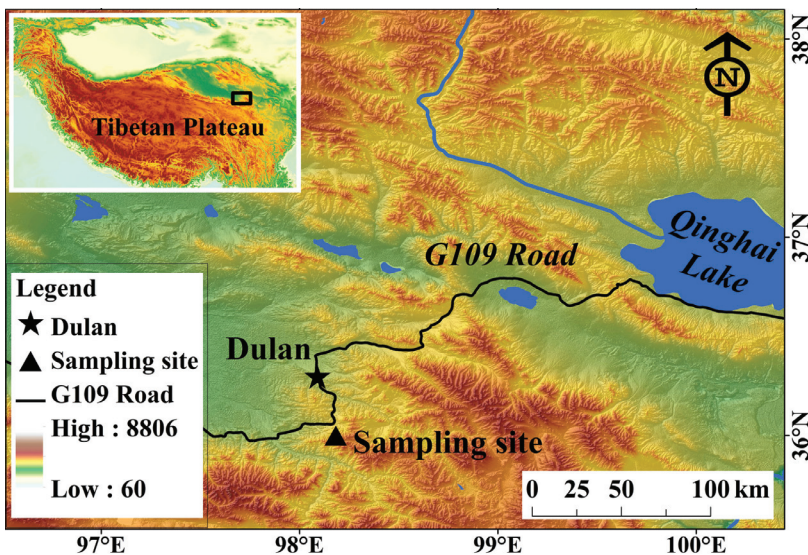


FIGURE 2. The study area and the sampling site located on the Tibetan Plateau (inset).

(EPS). The AC measures the persistence in growth, whereas the MS quantifies the relative changes between years of RW or BAI (Fritts, 2001). The R_{bar} allows characterizing the strength of the common growth signal over a period (Briffa and Jones, 1990). The EPS evaluates the degree to which the chronology represents a hypothetical chronology of an infinite number of cores, that is, how well replicated a chronology is; an $\text{EPS} \geq 0.85$ is usually accepted to identify the reliable part of a ring width chronology (Wigley et al., 1984).

To determine which climatic factors were more strongly related to *Salix* growth, Pearson correlation coefficients were calculated between monthly climatic variables and RW and BAI standard chronologies from 1980–2014 in which $\text{EPS} \geq 0.85$. The monthly climatic variables were monthly mean minimum and maximum temperatures, and total precipitation. As the relative air humidity is a fundamental indicator of hydroclimate conditions (Lendzion and Leuschner, 2008; Liang et al., 2016),

it was also employed for our analysis. The temporal window for the analysis encompassed from May of the previous year to current September (i.e., corresponding to the year of tree-ring formation). In addition to monthly variables, summer means or totals (July to August) were also used, as we assumed that maximum growth rates occurred in that period.

RESULTS

As shown by the serial sectioning method, the growth rings throughout each shoot were obviously formed at the same time. The mean series of intercorrelation coefficients from the 21 cross sections of B1, B2, and B3 shoots was 0.64 ($P < 0.001$) (see an example for the B1 shoot in Fig. 3). Therefore, we concluded that cross sections taken close to the soil level contain the maximum possible number of growth rings and can be used for dendrochronological research.

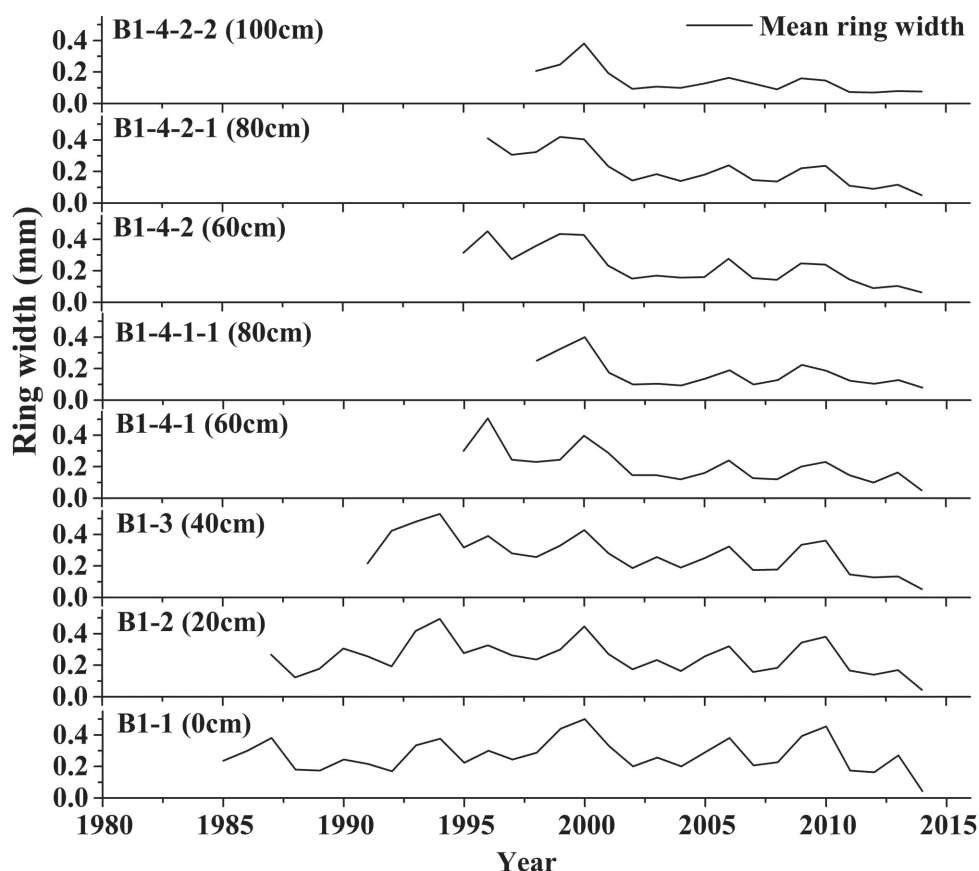


FIGURE 3. Serial sections of *Salix oritrepha* individual B1 showing a consistent year-to-year variability in the radial width between sections and within the same shoot. The codes indicate the name of each section. The numbers between brackets indicate the height above the ground of the sampled wood sections.

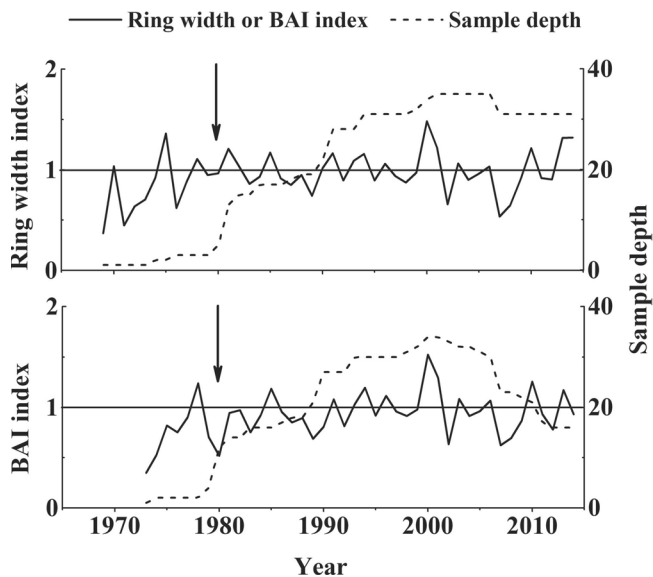


FIGURE 4. Standard chronologies of ring width (RW) and basal area increment (BAI). The first year, when the chronology is considered well replicated (Expressed Population Signal ≥ 0.85), is indicated with a vertical arrow.

After successful cross-dating, we were able to develop a 42-year-long (1973–2014) BAI standard chronology and a 46-year-long (1969–2014) RW standard chronology (Fig. 4). The mean age of the individuals sampled was 27 years old. Their mean BAI and RW were 5.83 mm² and 0.25 mm, respectively. The AC was relatively low, whereas the MS values of RWI and BAI *Salix* standard chronologies were moderate (0.26–0.29) (Table 1). The correlation between RW and BAI standard chronologies for the 1980–2014 period was high and significant ($r = 0.82$, $P < 0.05$).

July temperatures were positively correlated to RWI and BAI standard chronologies (in both cases: $r > 0.40$, $p < 0.05$; Fig. 5). The temperature in August also presented a significantly positive effect on the BAI standard chronology. The BAI standard chro-

nology showed higher correlation strength with July temperatures than that of RW standard chronology. Furthermore, the BAI was most responsive to the mean temperatures of July and August. Elevated January minimum temperatures were also positively related to *Salix* growth. Besides the summer and winter temperatures, summer moisture, particularly the July relative humidity, showed negative associations with *Salix* growth (in both cases: $r < -0.40$, $p < 0.05$; Fig. 5).

DISCUSSION

The mean *Salix* RW is similar to that observed for *J. przewalskii* (0.28 mm) growing on the same slope (Zheng et al., 2008), but around three times lower than that of erect willows (*S. alaxensis*) in the western Canadian Arctic (Zalatan and Gajewski, 2006). The MS values are lower than those observed in most prostrate and erect willows growing in the Arctic (Woodcock and Bradley, 1994; Schmidt et al., 2010; Forbes et al., 2010; Blok et al., 2011; Buchwal et al., 2013). The R_{bar} of RW and BAI standard chronologies indicate a high common growth signal, probably relating to climate factors, which is confirmed by the EPS reaching values above the threshold of 0.85 since 1980.

July temperature is a dominant climatic factor in controlling the growth of *Salix* shrubs. This is in accordance with findings reported for nearby *J. przewalskii* forming the juniper treeline (Zheng et al., 2008; Zhu et al., 2008), and also for other alpine shrub species found across the TP (Liang and Eckstein, 2009; Li et al., 2013; Lu et al., 2015). This finding is also in agreement with what has been found for some shrub willows and other woody species growing in the Arctic (Forbes et al., 2010; Hallinger et al., 2010; Weijers et al., 2010; Blok et al., 2011; Buchwal et al., 2013; Jørgensen et al., 2015). The high temperature in July may enhance the rate of carbon uptake and use for build-

TABLE 1

Statistics of the raw measurement and standard chronologies of ring width (RW) or basal area increment (BAI).

Variable	No. stems / no. radii	Time span	Raw measurements		Standard chronologies	
			Mean \pm SD (mm or mm ²)	AC	MS	R_{bar}
RW	35/105	1969–2014	0.25 \pm 0.13	0.55	0.29	0.32
BAI	—	1973–2014	5.83 \pm 2.93	0.53	0.26	0.38

Abbreviations: SD, standard deviation; AC, first-order autocorrelation; MS, mean sensitivity; R_{bar} , mean correlation between individual series.

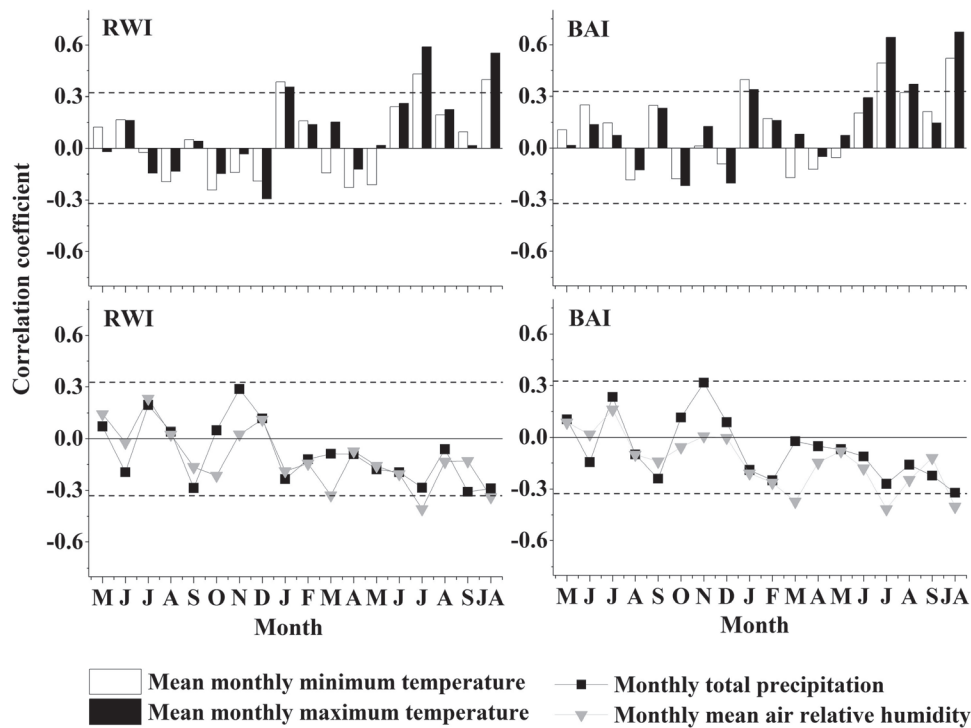


FIGURE 5. Correlations (Pearson coefficients) calculated between the standard chronologies of ring width (RW) and basal area increment (BAI) indices and monthly climatic data (mean maximum and minimum temperatures; total precipitation, mean air relative humidity). The temporal window includes months of the previous (May to December) and current (January to September) years; that is, they are prior and concurrent to ring formation. The last code (JA) in axis *x* indicates the mean or summed values of July and August. The horizontal dashed lines show the 0.05 significance levels.

ring new woody tissue (Rossi et al., 2008). The remarkable highest correlation between BAI and mean temperatures in July and August suggests that summer temperature is the main growth-limiting factor. The significant positive effect of August temperatures on the BAI standard chronology could be explained by a longer xylogenesis phase of cell enlargement during the late growing season (Ren et al., 2015). In addition, higher January minimum temperature could also enhance the *Salix* growth, possibly implying that very low winter temperature may threaten the survival of this species above the treeline. Low winter temperature can kill the fine roots and buds of alpine shrubs through direct frost damage or freeze-thaw related cavitation (Field and Brodribb, 2001), albeit the redundant narrow vessels should provide hydraulic safety to these species. In any case, our findings indicate that cold winters may limit the growth of shrub species above the alpine treeline.

The negative effect of July relative humidity on shrub growth suggests that low summer precipitation does not constrain the radial growth of alpine shrub willows. Conversely, abundant summer rain-

fall is accompanied by the thick cloud cover that reduces air temperature, thereby negatively affecting shrub growth (Buchwal et al., 2013; Stine and Huybers, 2015). In addition, we found significant negative correlations between relative humidity and July mean temperatures, providing additional evidence for this idea. A significant negative relationship between the BAI and relative air humidity in March could be related to a delayed start of shrub xylogenesis due to wet and cloudy spring conditions.

Eccentric or discontinuous rings occur frequently in shrub species (Bär et al., 2006; Au and Tardif, 2007). In comparison with RW, a direct measurement of growth and conducting area such as BAI better captures the irregular geometry of radial growth in shrubs (Latte et al., 2015). Thus, it could be better using BAI to describe alpine shrub growth dynamics than RW, as the correlation analyses between BAI/RW and climate show.

As one of the most widely distributed alpine deciduous shrubs in the northeastern TP (Fang et al., 2011), *S. oritrepha* is an indicator species in alpine ecosystem. This study is the first survey of growth

trends with *S. oritrepha* as a model deciduous shrub species in the TP. In spite of the short time span of the chronology compared with other shrub dendrochronological studies performed in the TP (Liang and Eckstein, 2009; Liang et al., 2012; Li et al., 2013; Lu et al., 2015), it still provides valuable information on climatic drivers of alpine ecosystems.

CONCLUSIONS

The growth of the alpine shrub *Salix oritrepha* is limited by cold summer temperature on the Tibetan Plateau, which is a similar climate-growth response as observed in the nearby junipers (*Juniperus przewalskii*) forming the treeline. The BAI standard chronology captures a stronger summer temperature signal than the RW standard chronology. Climatic warming could enhance the radial growth of these alpine shrub willows, thus contributing to a potential upslope shift and promoting shrub encroachment in treeless areas of the TP.

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