



# Moisture mediates temperature-growth couplings of high-elevation shrubs in the Tibetan plateau

Yang Han<sup>1</sup> · Yafeng Wang<sup>1</sup> · Bo Liu<sup>2</sup> · Ru Huang<sup>3</sup> · J. Julio Camarero<sup>4</sup>

Received: 16 April 2021 / Accepted: 19 August 2021 / Published online: 7 September 2021  
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

## Abstract

**Key message** Radial growth of high-elevation shrubs shows the high sensitivity to climate in dry regions, providing new evidence for drought-mediated dynamics of alpine woody plants.

**Abstract** In mountains, shrubs forming their uppermost distributional limits (shrubline) are highly sensitive to increasing cold limitations upwards. However, the constraints imposed by a shorter growing season due to lower temperatures upslope could interact with drought stress in mountainous regions. Here, we aim to investigate that question by comparing radial growth patterns of shrubs in wet (forest region of Nangqian County, BZ hereafter) vs. dry (forest region of Leiwuqi County, LWQ hereafter) regions located on the eastern Tibetan plateau. Considering the climate trend in this area towards warmer and drier conditions, we hypothesize that growth of high-elevation shrubs will be mainly limited by low summer temperatures under sufficient soil moisture. To test this hypothesis, we collected ring-width data from 123 alpine shrubs (*Salix oritrepha* Schneid.) along an altitudinal gradient from 4200 to 4600 m a.s.l. Dendroecological analyses showed that shrub growth was positively related to mean June or July temperature during the past decades in both wet (BZ) and dry (LWQ) regions regardless of site elevation. By contrast, correlations between shrub growth and seasonal precipitation were not significant. Shrub growth trends were positive before 2010 but turned negative afterwards. Overall, radial growth of shrubs along the altitudinal gradients up to the shrubline could shift from being temperature to moisture limited if warming-induced drought stress intensifies.

**Keywords** Alpine shrub · Climate change · Dendroecology · Drought · Secondary growth

## Introduction

Shrublands account for a considerable part of terrestrial vegetation cover across the globe (Peng et al. 2021). Shrublands are widely distributed in harsh treeless sites

as at high latitudes and high elevations, in particular, they are the unique woody species above the treeline (Liang et al. 2012). There is growing evidence that shrublands play a key role in the carbon sink, nutrient cycling, hydrological regulation and biodiversity maintenance in treeless biomes (Knapp et al. 2008; Myers-Smith et al. 2011; Pearson et al. 2013). Growth dynamics of shrubs under climate change are closely linked to the ecological services provided by arctic and alpine shrublands (Ding et al. 2021). Thus, understanding how shrub growth responds to climate change is highly relevant for ecological monitoring and conservation as well as bush management in the arctic and alpine regions (Gazol and Camarero 2012).

Climate warming had a significant impact on high-latitude biomes and already triggered substantial changes in the growth of arctic shrubs (Au and Tardif 2007; Post et al. 2009; Martin et al. 2017). Based on the analyses of annual ring-width series of shrubs, it was found that summer temperature was the main growth-limiting factor for deciduous

---

Communicated by Arthur Gessler.

✉ Yafeng Wang  
wangyf@njfu.edu.cn

- <sup>1</sup> College of Biology and the Environment, Nanjing Forestry University, Nanjing 210037, China
- <sup>2</sup> College of Urban and Environmental Sciences, Northwest University, Xi'an 710127, China
- <sup>3</sup> State Key Laboratory of Tibetan Plateau Earth System, Resources and Environment (TPESRE), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China
- <sup>4</sup> Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50080 Zaragoza, Spain

(e.g., *Betula nana* and *Salix pulchra*) and evergreen shrubs (e.g., *Juniperus communis* subsp. *nana*) across large parts of the circumpolar north tundra (Hallinger et al. 2010; Blok et al. 2011). In some arid areas, shrub growth appeared to be constrained by soil moisture through either direct moisture limitation of photosynthesis or indirect effects on active layer depth (Elmendorf et al. 2012; Ackerman et al. 2017; Gamm et al. 2018). Besides, snow condition was found to exert opposing influences on the growth of deciduous shrubs in northeastern Greenland and the growth of evergreen shrubs in Canadian low arctic tundra (Schmidt et al. 2010; Christiansen et al. 2018). There has also been a report of diverging growth of coexisting trees and shrubs near the treeline in Russian Polar Urals (Pellizzari et al. 2017). Given this background, shrub-ring based studies should explicitly consider how regional warming and non-thermal variables (e.g., moisture) drive shrub growth dynamics, particularly in alpine regions where microclimate conditions rapidly change depending on elevation and topography (Barry 2008).

Alpine regions such as the Tibetan Plateau host some of the highest treelines and shrublines in the world representing the uppermost limits of the existence of woody plants (Miehe et al. 2007; Wang et al. 2015; Lu et al. 2021). Therefore, they provide an excellent opportunity for studying growth dynamics of woody plant communities along extreme altitudinal gradients. Dendroecological studies have shown that radial growth of alpine deciduous shrubs (e.g., *Hippophae rhamnoides*) sampled near the treeline was temperature sensitive on the northeastern Tibetan Plateau (Xiao et al. 2007). By contrast, due to the intense evaporation, pre-monsoon moisture condition was the main climatic variables constraining the radial growth of evergreen shrubs (*Juniperus pingii* var. *wilsonii*) above the treeline on the central Tibetan Plateau (Liang et al. 2012). The radial growth of evergreen shrubs (*Rhododendron campanulatum*) was mainly controlled by winter minimum temperature at the treeline in the central Himalaya (Panthi et al. 2021). Another study indicated that the radial growth of evergreen shrubs (*Rhododendron nivale*) and trees reaching the treeline (*Abies georgei* var. *smithii*) reflected the signal of mean July temperature on the southeastern Tibetan Plateau, where humid conditions dominate (Liang and Eckstein 2009; Liang et al. 2009). However, it remains unclear whether the climate-growth relationships for deciduous shrubs along the altitudinal gradients from subalpine shrublands to alpine shrubline would be consistent on the eastern Tibetan Plateau. The alpine willow *Salix oritrepha* Schneid. is a widespread deciduous shrub forming the upper shrubline across the eastern Tibetan Plateau and could be a model species for investigating variations of radial growth of deciduous shrubs along the altitudinal gradients up to the shrubline.

In this study, we aimed to fill this knowledge gap by comparing climate-growth relationships of *S. oritrepha* forming

the shrubline along two elevational transects (4200–4600 m) located in the dry and wet regions on the eastern Tibetan Plateau. Our objectives were: (1) to characterize the growth patterns of the alpine willow shrubs in recent decades; (2) to compare the growth-limiting factor for willow shrubs along two elevational transects. Due to similarly cold climates on the eastern Tibetan Plateau, we hypothesize that the growth of shrubs along the altitudinal gradients will be temperature limited when seasonal moisture is sufficient, but will be moisture limited under warmer and drier climate conditions.

## Materials and methods

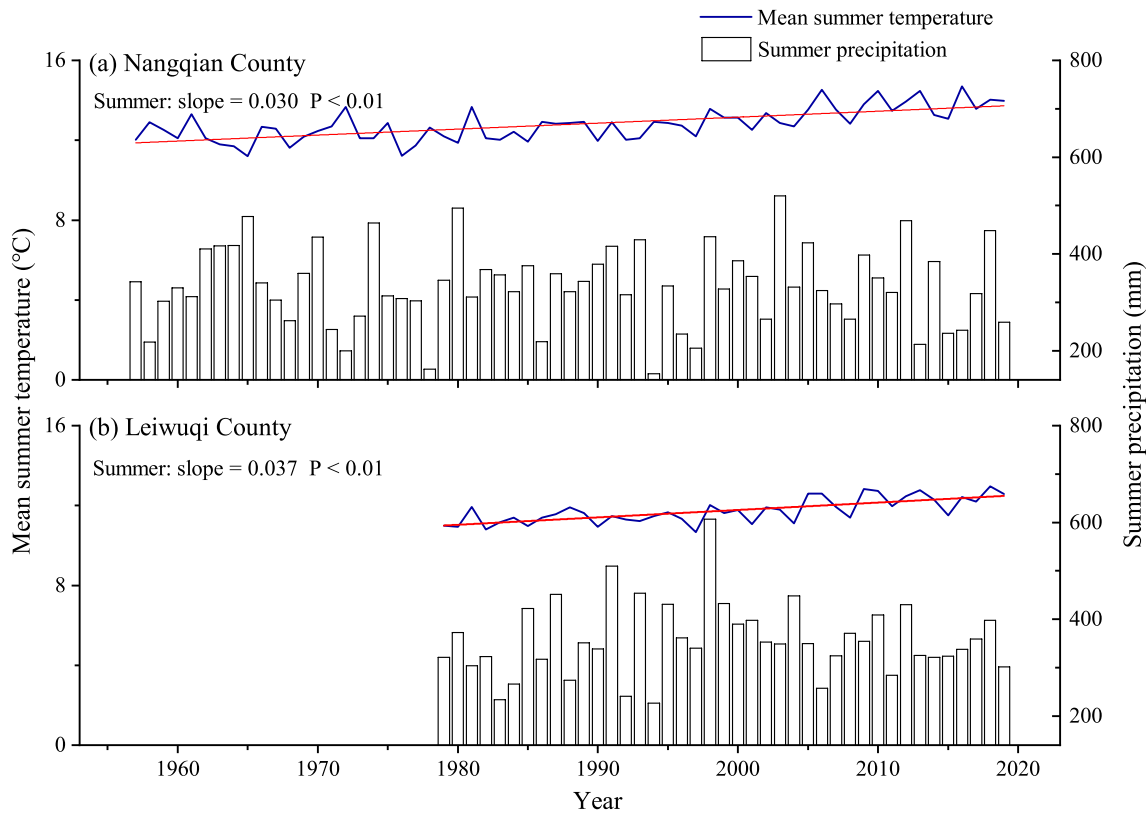
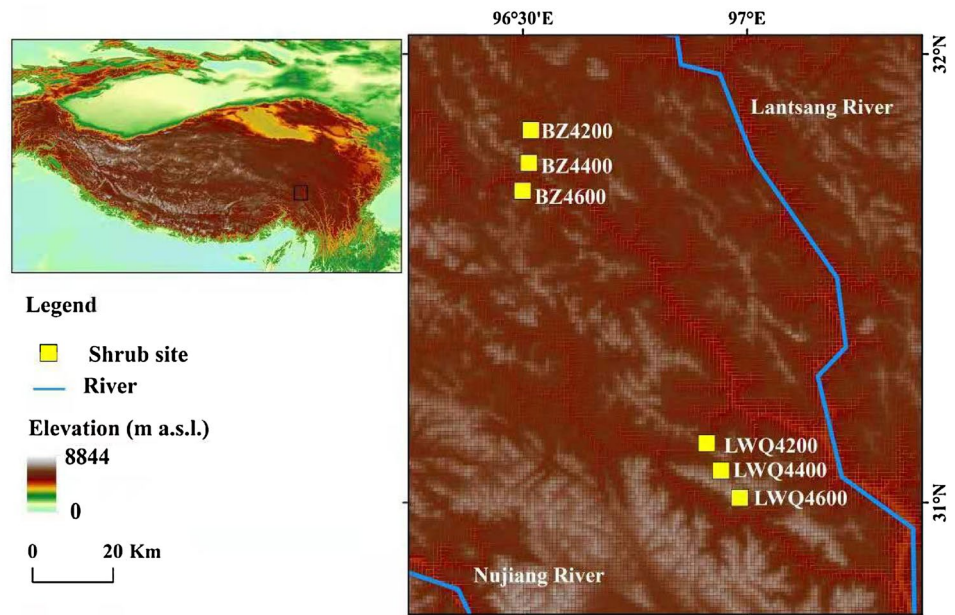
### Study area and climate

The study area is located on the eastern Tibetan Plateau (Fig. 1). Due to its complexity of geological structure and special atmospheric circulation, this area is highly sensitive to climate change (Zhao et al. 2015). The study area includes the wet forest region of Nangqian County (BZ hereafter) and the dry forest region of Leiwuqi County (LWQ hereafter) on the eastern Tibetan Plateau (Fig. 1). Based on the meteorological data in Nangqian County (96.28°E, 32.12°N, 3644 m), the mean annual precipitation is 535.8 mm and the mean annual temperature is 4.4 °C, July and January were the warmest (mean temperature of 13.2 °C) and coldest months (− 5.9 °C), respectively. According to the meteorological record in Leiwuqi County (96.36°E, 31.13°N, 3810 m), the mean annual precipitation is 606.7 mm and the mean annual temperature is 3.3 °C, the warmest and coldest months were July (mean temperature of 12.4 °C) and January (− 6.8 °C), respectively. The mean temperature during summer showed significant positive trends in these two regions during the past decades ( $p < 0.01$ ). The warming rate of summer during the past decades in Leiwuqi County was slightly higher than that of Nangqian County (Fig. 2). The average summer and annual 3-month SPEI (Standardized Precipitation Evapotranspiration Index; cf. Vicente-Serrano et al. 2010) values in Leiwuqi County (mean  $\pm$  SD; summer:  $-0.01 \pm 0.85$ ; annual:  $0.013 \pm 0.63$ ) were lower than in Nangqian County (summer:  $0.043 \pm 0.81$ ; annual:  $0.025 \pm 0.61$ ) between 1960 and 2019 (Fig. S1).

### Study species

In BZ and LWQ, Balfour spruce (*P. likiangensis* var. *balfouriana*) is the dominant tree species between 3800 and 4300 m on the north-facing slopes, whereas *S. oritrepha* grows from 4200 to 4600 m and dominates the woody plant communities above the treeline (here located at 4300 m). *S. oritrepha* is one of the most widespread alpine shrub species on the eastern Tibetan Plateau (Fang et al. 2011). Previous

**Fig. 1** Locations of the shrub study sites (yellow squares) along two altitudinal transects (from 4200 to 4600 m) situated on the eastern Tibetan Plateau. Abbreviations: *BZ* (wet Nangqian County), *LWQ* (dry Leiwuqi County)



**Fig. 2** Changes in mean summer temperature and precipitation in Nangqian County (a BZ region) and Leiwuqi County (b LWQ region)

studies confirmed that *S. oritrepha* can be used to conduct the dendrochronological studies in light of its clearly visible ring boundaries (Lu et al. 2016).

**Field sampling and chronology development**

In the field, 123 stem discs of *S. oritrepha* were randomly selected along the elevational gradients in the BZ and LWQ

**Table 1** Descriptive information of BAI chronologies for the alpine shrub (*S. oritrepha*)

Forest region	Elevation (m)	Time span	No. individuals (No. radii)	Ring width (mm)	BAI (mm <sup>2</sup> )	$R_{bar}$	MS	EPS > 0.85 since	AR1
BZ	4600	1981–2018	22 (44)	0.26 ± 0.05	4.63 ± 2.68	0.21	0.27	1984	0.027
	4400	1983–2018	22 (44)	0.29 ± 0.08	4.89 ± 3.75	0.33	0.27	1990	0.085
	4200	1991–2018	20 (40)	0.33 ± 0.10	5.47 ± 3.99	0.46	0.29	1991	0.016
LWQ	4600	1978–2018	21 (42)	0.26 ± 0.07	4.58 ± 2.79	0.32	0.25	1982	0.053
	4400	1989–2018	18 (36)	0.27 ± 0.07	4.70 ± 2.02	0.22	0.29	1991	0.084
	4200	1993–2018	20 (40)	0.36 ± 0.07	5.95 ± 2.75	0.32	0.24	1993	0.209

$R_{bar}$  mean interseries correlation, MS mean sensitivity, EPS expressed population signal, AR1 first-order autocorrelation

Values are denoted by means with standard deviations

regions (Table 1). Shrub individuals were cut from the major stems at the root collar close to the soil to acquire older samples (Lu et al. 2019). Previous studies via a serial-sectioning method corroborated that *S. oritrepha* basal stems contain the utmost of rings (Lu et al. 2016). Wood samples were air-dried and were sanded with gradually finer sandpapers to distinguish annual rings. Rings were measured with TSAP-LINTAB 6 system (accuracy: 0.001 mm). The wood samples cross-dating was then checked using the COFECHA software (Holmes 1983).

To retain potentially important low-frequency signal, we converted ring widths into basal area increment (BAI) given the concentric radial growth of *S. oritrepha* shrub. We then removed the biological growth trend in individual BAI series with a negative exponential curve and calculated the mean, detrended BAI site series using bi-weight robust means in ARSTAN programme (Cook 1985). In this way, standard BAI chronologies were developed at each study site. Then, we calculated the commonly used dendrochronological statistics (see details in Table 1) on standard BAI series to measure the internal coherence of BAI series within each site. An EPS threshold above 0.85 was defined to assess the reliability of the established chronologies for the common period (Cook and Kairiukstis 2013). Meanwhile, the standard chronologies of ring-width indices (RWI) were also built in the same way for further comparison.

## Data analyses

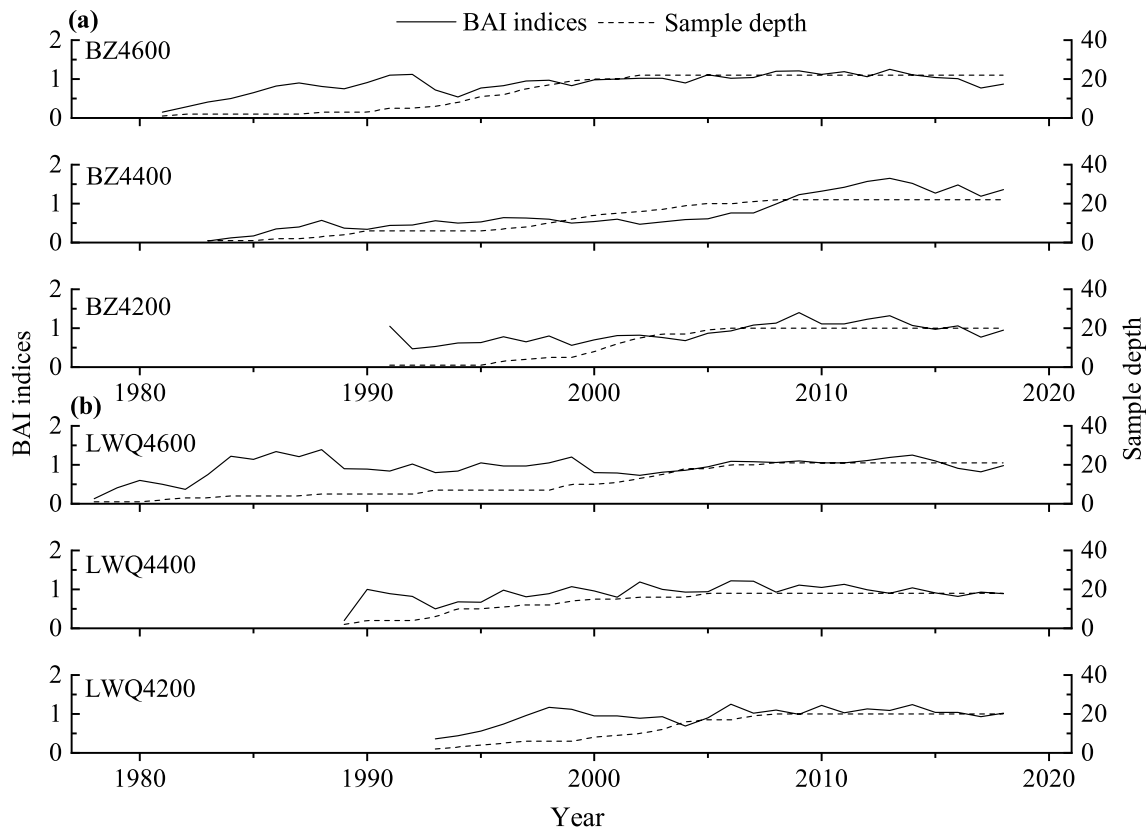
To calculate climate-growth correlations, monthly climate data (temperature, precipitation) from local meteorological station were used for succeeding analyses. First, standard BAI site chronologies of shrubs were related to monthly variables (mean temperature, mean maximum and minimum temperatures, total precipitation) considering regional climate data. Relationships were assessed from September of the previous year to September of the current year using Pearson correlations. We considered the periods when EPS

was above the 0.85 threshold within each site (Table 1). Among the monthly temperature variables, only the most significant temperature variable was shown in the results. Second, linear mixed-effects models (LMEs) were applied to quantify the best climatic predictor of shrub growth at each site. Climatic factors were set as fixed effects in the LMEs, whilst years and individuals were set as random effects to explain the nonindependence of data within years and individuals (Crawley 2007). The models with the fewest explanatory variables and the minimum Akaike Information Criterion (AIC) were selected (Wagenmakers 2003). We ran the LMEs using the nlme package and R software (Pinheiro et al. 2020).

## Results

### Chronology development and growth pattern

Six shrub standard BAI and RWI chronologies were established along two elevational gradients encompassing the shrubline and the treeline. No missing rings were found (Table 1, Fig. 3). The longest (41 years) and shortest (26 years) *S. oritrepha* chronologies were built in sites LWQ4600 and LWQ4200, respectively. Along the altitudinal transect in BZ, the mean ring-width of study shrub varied from 0.26 to 0.33 mm, whilst the average BAI ranged from 4.63 mm<sup>2</sup> to 5.47 mm<sup>2</sup> (Table 1). Similarly, along the altitudinal transect in LWQ, the mean shrub-ring width ranged between 0.26 and 0.36 mm, whilst the BAI varied from 4.58 mm<sup>2</sup> to 5.95 mm<sup>2</sup> (Table 1). In general, all shrub BAI chronologies showed significant increasing trend in the past decades ( $p < 0.01$ ), with higher mean values in the wet BZ region (0.35 mm<sup>2</sup> yr<sup>-1</sup>) than in the dry LWQ region (0.28 mm<sup>2</sup> yr<sup>-1</sup>). However, shrub growth declined since 2011 for both regions with only three sites reaching the significant level ( $p < 0.05$ ) (Table 2).



**Fig. 3** Standard shrub BAI chronologies along two altitudinal transects for the wet BZ (a) and dry LWQ (b) regions. Solid and dashed lines correspond to the BAI indices and the sample depth, respectively

**Table 2** The growth trends of shrub BAI chronologies since 2011 and their correlations with mean July SPEI (\* $p < 0.05$ )

Forest region	Change rate of July SPEI	Shrub site	Change rate of BAI	CCs
BZ	− 0.26	BZ4600	− 0.053*	0.38
		BZ4400	− 0.036	0.64
		BZ4200	− 0.049*	0.59
LWQ	− 0.13	LWQ4600	− 0.035	0.12
		LWQ4400	− 0.028*	0.20
		LWQ4200	− 0.016	0.25

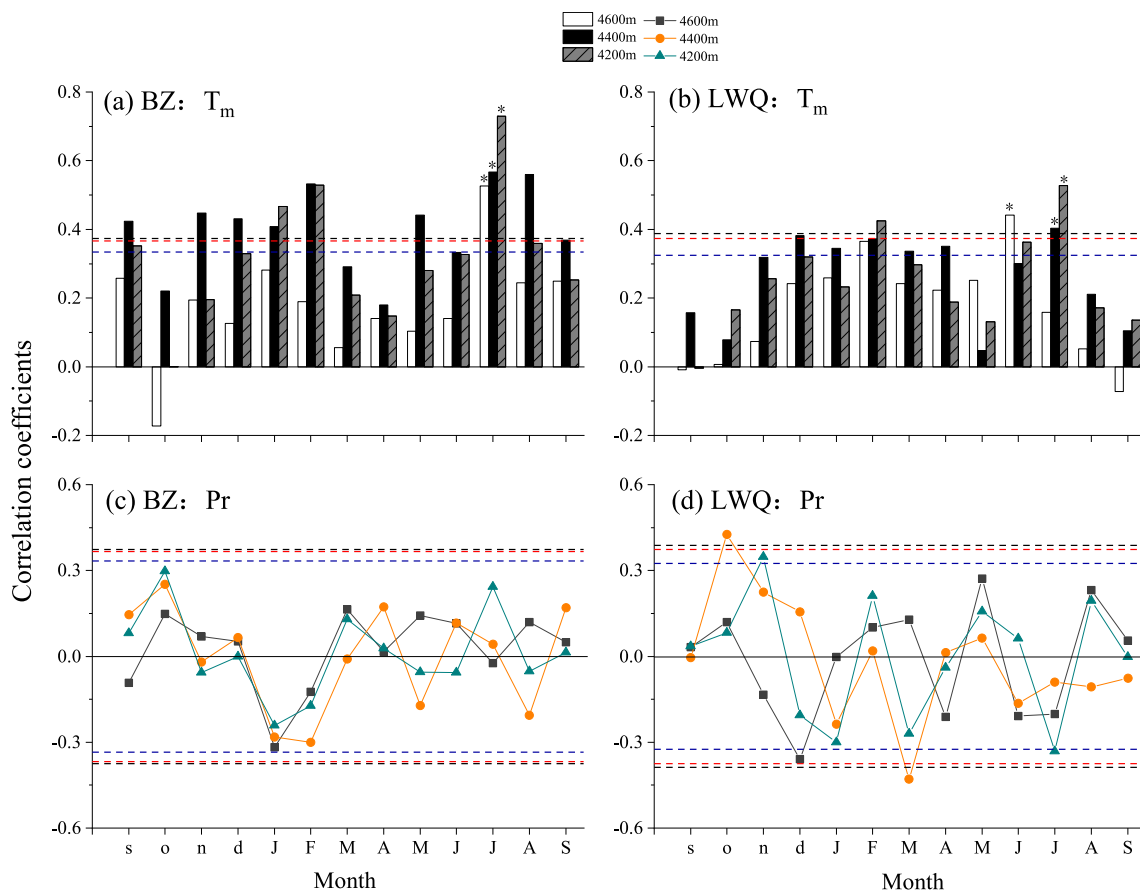
CCs denote the correlation coefficients between BAI series and July SPEI data in the last decade

**Climate-growth relationships**

Both BAI and RWI chronologies were significantly and positively correlated with mean June or July temperature in the two study regions (Fig. 4; Fig. S2). The BAI chronologies were more responsive to growing-season temperatures than the RWI chronologies. Therefore, we used

shrubs BAI chronologies for further analyses. In BZ, all *S. oritrepha* BAI chronologies showed significantly positive responses to mean July temperature ( $p < 0.01$ ) regardless of the elevation (Fig. 4a). However, no significant precipitation-growth correlations were detected in this region (Fig. 4c). In LWQ, shrub BAI chronologies were significantly and positively associated with mean July temperature in two elevational sites (LWQ4200,  $p < 0.01$ ; LWQ4400,  $p < 0.05$ ), whereas another elevational site (LWQ4600) responded positively and significantly to mean June temperature ( $p < 0.05$ ) (Fig. 4b). At site LWQ4600, shrub growth was significantly and negatively associated with precipitation of previous December ( $p < 0.05$ ). At site LWQ4400, it responded positively and significantly to precipitation of previous October and negatively with March precipitation ( $p < 0.05$ ) (Fig. 4d). Specifically, five out of six sites showed significant positive responses to mean summer temperature before 2011 (Table 3). In the period 2011–2018, correlations between growth and summer temperature were not significant observed (Table 3).

As shown by the LMEs, mean July temperature was the best predictor of shrub growth at three elevational sites (BZ4200, BZ4400, BZ4600) in BZ (Table 4). In LWQ, the



**Fig. 4** Correlation coefficients calculated between the shrub BAI chronologies and climatic variables (mean monthly temperature and monthly precipitation from September of the prior year (lowercase letters: s, o, n, d) to September of the current year (uppercase letters: J, F, M, etc.)) at different elevations in the wet BZ (a, c) and

dry LWQ regions (b, d).  $T_m$  mean monthly temperature,  $Pr$  monthly precipitation. The dashed lines indicate significant levels of  $p < 0.05$  (black, red and blue dashed lines correspond to the sites at elevations of 4200, 4400 and 4600 m, respectively). The highest correlation for each site is indicated by an asterisk

**Table 3** Correlation coefficients calculated between the shrub BAI chronologies and climatic variables (mean summer temperature and summer total precipitation) during the two sub-periods (pre-2011 and 2011–2018)

Sub-period		Pre-2011		2011–2018	
Study region	Elevation (time span)	$T_{sum}$	$P_{sum}$	$T_{sum}$	$P_{sum}$
BZ	4600 (1984–2018)	0.43*	0.35	0.06	-0.34
	4400 (1990–2018)	0.62**	-0.02	0.42	0.04
	4200 (1991–2018)	0.62**	0.14	0.43	-0.06
LWQ	4600 (1982–2018)	0.32	-0.01	-0.01	-0.19
	4400 (1991–2018)	0.57**	-0.18	-0.32	-0.33
	4200 (1993–2018)	0.47*	0.08	0.13	-0.02

$T_{sum}$  denotes mean summer temperature;  $P_{sum}$  denotes summer total precipitation. Significance levels: \* $p < 0.05$ ; \*\* $p < 0.01$

**Table 4** Summary of the best-fitted linear mixed-effects models (LMEs) fitted to growth data at six shrub sites (\* $p < 0.05$ ; \*\* $p < 0.01$ )

Study region	Shrub site	Climate variable of best-fit model	Temperature variable (REAR1)	$\Delta AIC$
BZ	BZ4600	$T_7$	0.11** (0.04*)	1.93
	BZ4400	$T_7$	0.27** (0.04*)	10.81
	BZ4200	$T_7$	0.17** (0.09**)	13.43
LWQ	LWQ4600	$T_6$	0.11** (0.06*)	2.89
	LWQ4400	$T_7$	0.06* (0.09*)	2.58
	LWQ4200	$T_7$	0.11** (0.06*)	1.35

$T_6$  mean June temperature,  $T_7$  mean July temperature  
 $\Delta AIC$  means the difference in AIC values between the null model and the best-fit model. REAR1 denotes the LMEs results considering the first-order autocorrelation

best predictor of shrub growth was July (sites LWQ4200 and LWQ4400) or June temperature (site LWQ4600) (Table 4).

## Discussion

We showed that suitable shrub-ring width and BAI series are sensitive proxies of climatic impacts on mountainous woody plant communities encompassing the shrubline. Specifically, the series of the deciduous alpine willow shrub *S. oritrepha* can be used to quantify climate-growth relationships in treeless mountain regions.

Along two elevational gradients, the radial growth of *S. oritrepha* decreased with increasing elevation as temperature decreased. This result was in line with previous studies on evergreen shrubs of eastern Tibetan Plateau and deciduous shrubs in central Alps (Rixen et al. 2010; Lu et al. 2015; Boscutti et al. 2018). The result was also similar to the findings on tree growth along the altitudinal gradients from wet regions in Asia, Europe and South America (Di Filippo et al. 2007; Massaccesi et al. 2008; Liang et al. 2010), confirming the dominant role of thermal factors in those sites with abundant moisture. Generally, altitudinal gradients in high-elevation forest regions are mainly characterized by colder climates upwards, which limit the physiological activities (e.g., photosynthesis and respiration rates as well as the cambial activity) of alpine woody plants (Körner 2007; Gaire et al. 2020). Besides, decreased soil nutrient availability due to the reduction of soil temperature (Körner 2003) may also result in the decline of radial growth observed in the uppermost shrubs, which were not the youngest populations.

The results of correlation analyses indicated that mean June or July temperature was the main climatic factor constraining the radial growth of *S. oritrepha* along two altitudinal transects up to the shrubline on the eastern Tibetan Plateau. Despite the distinct regional climatic conditions, the shrubs of the two forest regions showed similar growth responses. These results could be explained by the fact that June and July are the warmest months of the year in these regions and drive photosynthesis rates, cambial activity and the radial growth of alpine woody plants (Liang and Eckstein 2009; Li et al. 2013, 2016). All the shrub BAI series showed the significant increasing trends during the past decades, implying that climatic warming (particularly summer warming) would enhance shrub growth when moisture regime is sufficient. Interestingly, the correlation between July temperature and shrub growth decreased upwards in the two regions, suggesting that moisture regime could also be a relevant driver of shrub growth there. However, all precipitation-growth correlations were not significant in six shrub sites during the growing season. Given that the climatic sensitivity of woody plant growth is largely age-dependent (Rozas et al. 2009), the mean length of shrub chronology

increased with increasing elevation in the two study regions suggesting that shrub age could mediate the growth-temperature relationships. In addition, shrub growth might be influenced by local factors such as microenvironmental conditions. For instance, microtopography, soil nutrition availability and biotic interactions could create site-specific microhabitats which impact on growth-temperature associations (HilleRisLambers et al. 2013; Ellison et al. 2019; Mu et al. 2021).

Shrub BAI chronologies in the two regions declined over the last decade. They were positively associated with main growing-season SPEI suggesting that post-2010 shrub growth could be moisture limited. The shrub growth responses to summer temperature showed a non-significant trend in recent decade. The growth decline under warm-dry climatic conditions was also observed in Tibetan juniper (*Juniperus tibetica* Kom) on the eastern Tibetan Plateau (Mou et al. 2019). However, we did not detect significant shrub growth-SPEI correlations, which could be attributed to the short time span of their ring-width series. Significant decreasing growth trends since 2011 only occurred at three shrub sites, possibly indicating the impacts of local-site conditions (e.g., microtopography, soil nutrients and microclimate) (Mu et al. 2021). In particular, shrub meristems are more coupled to soil microclimate conditions than tall tree meristems which usually react quickly to changes in atmospheric climate conditions (Körner 2003). Further monitoring of shrub growth is necessary to test if the hotter and drier climate in the near future can lead to the shift in limiting factors for alpine shrubs (Wu et al. 2019; Buchwal et al. 2020). Collectively, shrub growth would benefit from climate warming when the moisture content is high enough, whereas shrub growth could be suppressed if the warmer and drier climate conditions prevail, thus supporting our hypothesis.

## Conclusions

This study is one of the first comparing climate-growth relationships of shrubs along the altitudinal gradients encompassing the uppermost shrubline on the eastern Tibetan Plateau. The radial growth of shrubs was enhanced by warmer June or July conditions in the wet BZ region and the relatively dry LWQ region regardless of site elevation. Overall, the growth of shrubs will benefit from climate warming when seasonal moisture is relatively sufficient, but the increasing trend in shrub growth would be reversed due to the warming-induced drought stress. This study provides useful information for understanding climate-growth relationships of shrubs along wide altitudinal gradients in mountain treeless ecosystems. Further measurements of in situ microclimate conditions (soil moisture and temperature)

combined with key plant functional traits are needed to clarify the mechanisms for temperature-growth couplings of high-elevation shrubs.

**Author contribution statement** YW and JJC designed the research; YW and YH did the field work; YH did the shrub-ring experiment; YH, YW, BL, RH and JJC analysed the data and wrote the paper.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00468-021-02204-w>.

**Funding** This study was funded by the National Natural Science Foundation of China (41771222), and the Second Tibetan Plateau Scientific Expedition and Research Programme (2019QZKK0301).

**Data availability** All the data analysed was included in our paper.

**Code availability** This paper did not include codes.

## Declarations

**Conflict of interest** All the authors declare no competing interest.

## References

- Ackerman D, Griffin D, Hobbie SE, Finlay JC (2017) Arctic shrub growth trajectories differ across soil moisture levels. *Glob Change Biol* 23:4294–4302. <https://doi.org/10.1111/gcb.13677>
- Au R, Tardif JC (2007) Allometric relationships and dendroecology of the dwarf shrub *Dryas integrifolia* near Churchill, subarctic Manitoba. *Can J Bot* 85:585–597. <https://doi.org/10.1139/b07-055>
- Barry R (2008) Mountain weather and climate, 3rd edn. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511754753>
- Blok D, Sass-Klaassen U, Schaepman-Strub G, Heijmans MMPD, Sauren P, Berendse F (2011) What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* 8:1169–1179. <https://doi.org/10.5194/bg-8-1169-2011>
- Boscutti F, Casolo V, Beraldo P, Braidot E, Zancani M, Rixen C (2018) Shrub growth and plant diversity along an elevation gradient: Evidence of indirect effects of climate on alpine ecosystems. *PLoS ONE* 13:e0196653. <https://doi.org/10.1371/journal.pone.0196653>
- Buchwal A, Sullivan PF, Macias-Fauria M (2020) Divergence of Arctic shrub growth associated with sea ice decline. *PNAS* 117:33334–33344. <https://doi.org/10.1073/pnas.2013311117>
- Christiansen CT, Lafreniere MJ, Henry GHR, Grogan P (2018) Long-term deepened snow promotes tundra evergreen shrub growth and summertime ecosystem net CO<sub>2</sub> gain but reduces soil carbon and nutrient pools. *Glob Change Biol* 24:3508–3525. <https://doi.org/10.1111/gcb.14084>
- Cook ER (1985) A time-series analysis approach to tree ring standardization. Ph.D. Thesis, University of Arizona, Tucson
- Cook ER, Kairiukstis LA (2013) Methods of dendrochronology: applications in the environmental sciences. Springer Science & Business Media, Berlin
- Crawley MJ (2007) The R book. John Wiley and Sons, Chichester, UK
- Di Filippo A, Biondi F, Čufar K, De Luis M, Grabner M, Maugeri M, Presutti Saba E, Schirone B, Piovesan G (2007) Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. *J Biogeogr* 34:1873–1892. <https://doi.org/10.1111/j.1365-2699.2007.01747.x>
- Ding A, Xiao S, Peng X, Tian Q, Han C (2021) Shrub-rings used to reconstruct drought history of the central Alxa desert, northwest China. *Int J Climatol*. <https://doi.org/10.1002/joc.7108>
- Ellison SBZ, Sullivan PF, Cahoon SMP, Hewitt RE (2019) Poor nutrition as a potential cause of divergent tree growth near the Arctic treeline in northern Alaska. *Ecology* 100:e02878. <https://doi.org/10.1002/ecy.2878>
- Elmendorf SC, Henry GHR, Hollister RD et al (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat Clim Change* 2:453–457. <https://doi.org/10.1038/nclimate1465>
- Fang J, Wang Z, Tang Z (2011) Atlas of woody plants in China: distribution and climate. Springer, Berlin
- Gaire NP, Fan ZX, Brauning A, Panthi S, Rana P, Shrestha A, Bhuj DR (2020) *Abies spectabilis* shows stable growth relations to temperature, but changing response to moisture conditions along an elevation gradient in the central Himalaya. *Dendrochronologia* 60:12. <https://doi.org/10.1016/j.dendro.2020.125675>
- Gamm CM, Sullivan PF, Buchwal A, Dial RJ, Young AB, Watts DA, Cahoon SMP, Welker JM, Post E (2018) Declining growth of deciduous shrubs in the warming climate of continental western Greenland. *J Ecol* 106:640–654. <https://doi.org/10.1111/1365-2745.12882>
- Gazol A, Camarero JJ (2012) Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. *Plant Ecol* 213:1687–1698. <https://doi.org/10.1007/s11258-012-0124-3>
- Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol* 186:890–899. <https://doi.org/10.1111/j.1469-8137.2010.03223.x>
- HilleRisLambers J, Harsch MA, Ettinger AK, Ford KR, Theobald EJ (2013) How will biotic interactions influence climate change-induced range shifts? *Ann NY Acad Sci* 1297:112–125. <https://doi.org/10.1111/nyas.12182>
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* 43:69–75
- Knapp AK, Briggs JM, Collins SL, Archer SR, Bret-Harte MS, Ewers BE, Peters DP, Young DR, Shaver GR, Pendall E, Cleary MB (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Glob Change Biol* 14:615–623. <https://doi.org/10.1111/j.1365-2486.2007.01512.x>
- Körner C (2003) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin
- Körner C (2007) The use of “altitude” in ecological research. *Trends Ecol Evol* 22:569–574. <https://doi.org/10.1016/j.tree.2007.09.006>
- Li X, Rossi S, Liang E, Camarero JJ (2016) Temperature thresholds for the onset of xylogenesis in alpine shrubs on the Tibetan Plateau. *Trees* 30:2091–2099. <https://doi.org/10.1007/s00468-016-1436-z>
- Li Z, Liu G, Fu B, Zhang Q, Ma K, Pederson N (2013) The growth-ring variations of alpine shrub *Rhododendron przewalskii* reflect regional climate signals in the alpine environment of Miyaluo Town in Western Sichuan Province, China. *Acta Ecol Sin* 33:23–31. <https://doi.org/10.1016/j.chnaes.2012.12.004>
- Liang E, Eckstein D (2009) Dendrochronological potential of the alpine shrub *Rhododendron nivale* on the south-eastern Tibetan Plateau. *Ann Bot* 104:665–670. <https://doi.org/10.1093/aob/mcp158>
- Liang E, Lu X, Ren P, Li X, Zhu L, Eckstein D (2012) Annual increments of juniper dwarf shrubs above the treeline on the central Tibetan Plateau: a useful climatic proxy. *Ann Bot* 109:721–728. <https://doi.org/10.1093/aob/mcr315>



- Liang E, Shao X, Xu Y (2009) Tree-ring evidence of recent abnormal warming on the southeast Tibetan Plateau. *Theor Appl Climatol* 98:9–18. <https://doi.org/10.1007/s00704-008-0085-6>
- Liang E, Wang Y, Xu Y, Liu B, Shao X (2010) Growth variation in *Abies georgei* var. *smithii* along altitudinal gradients in the Sygera Mountains, southeastern Tibetan Plateau. *Trees* 24:363–373. <https://doi.org/10.1007/s00468-009-0406-0>
- Lu X, Camarero JJ, Wang Y, Liang E, Eckstein D (2015) Up to 400-year-old *Rhododendron* shrubs on the southeastern Tibetan Plateau: prospects for shrub-based dendrochronology. *Boreas* 44:760–768. <https://doi.org/10.1111/bor.12122>
- Lu X, Huang R, Wang Y, Sigdel SR, Dawadi B, Liang E, Camarero JJ (2016) Summer temperature drives radial growth of alpine shrub willows on the northeastern Tibetan Plateau. *Arct Antarct Alp Res* 48:461–468. <https://doi.org/10.1657/aaar0015-069>
- Lu X, Liang E, Camarero JJ, Ellison AM (2021) An unusually high shrubline on the Tibetan Plateau. *Ecology*. <https://doi.org/10.1002/ecy.3310>
- Lu X, Sigdel SR, Dawadi B, Wang Y (2019) Climate response of *Salix oritrepha* growth along a latitudinal gradient on the northeastern Tibetan Plateau. *Dendrobiology* 81:14–21. <https://doi.org/10.12657/denbio.081.002>
- Martin AC, Jeffers ES, Petrokofsky G, Myers-Smith I, Macias-Fauria M (2017) Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach. *Environ Res Lett* 12:085007. <https://doi.org/10.1088/1748-9326/aa7989>
- Massaccesi G, Roig FA, Pastur GJM, Barrera MD (2008) Growth patterns of *Nothofagus pumilio* trees along altitudinal gradients in Tierra del Fuego, Argentina. *Trees* 22:245–255. <https://doi.org/10.1007/s00468-007-0181-8>
- Miehe G, Miehe S, Vogel J, Co S, Duo L (2007) Highest treeline in the northern hemisphere found in southern Tibet. *Mt Res Dev* 27:169–173. <https://doi.org/10.1659/mrd.0792>
- Mou Y, Fang O, Cheng X, Qiu H (2019) Recent tree growth decline unprecedented over the last four centuries in a Tibetan juniper forest. *J for Res* 30:1429–1436. <https://doi.org/10.1007/s11676-018-0856-6>
- Mu Y, Zhang Q, Fang O, Lyu L, Cherubini P (2021) Pervasive tree-growth reduction in Tibetan juniper forests. *For Ecol Manag* 480:6. <https://doi.org/10.1016/j.foreco.2020.118642>
- Myers-Smith IH, Forbes BC, Wilmking M et al (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6:15. <https://doi.org/10.1088/1748-9326/6/4/045509>
- Panhi S, Fan ZX, Brauning A (2021) Ring widths of *Rhododendron* shrubs reveal a persistent winter warming in the central Himalaya. *Dendrochronologia* 65:11. <https://doi.org/10.1016/j.dendro.2020.125799>
- Pearson RG, Phillips SJ, Loranty MM, Beck PSA, Damoulas T, Knight SJ, Goetz SJ (2013) Shifts in Arctic vegetation and associated feedbacks under climate change. *Nat Clim Change* 3:673–677. <https://doi.org/10.1038/nclimate1858>
- Pellizzari E, Camarero JJ, Gazol A, Granda E, Shetti R, Wilmking M, Moiseev P, Pividori M, Carrer M (2017) Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. *Glob Change Biol* 23:3169–3180. <https://doi.org/10.1111/gcb.13577>
- Peng D, Wang Y, Xian G, Huete AR, Huang W, Shen M, Wang F, Yu L, Liu L, Xie Q (2021) Investigation of land surface phenology detections in shrublands using multiple scale satellite data. *Remote Sens Environ* 252:112133. <https://doi.org/10.1016/j.rse.2020.112133>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S R (2020) R Core Team\_nlm: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-151
- Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Høye TT (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358. <https://doi.org/10.1126/science.1173113>
- Rixen C, Schwoerer C, Wipf S (2010) Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. *Polar Res* 29:85–94. <https://doi.org/10.1111/j.1751-8369.2010.00155.x>
- Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytol* 182:687–697. <https://doi.org/10.1111/j.1469-8137.2009.02770.x>
- Schmidt NM, Baittinger C, Kollmann J, Forchhammer MC (2010) Consistent dendrochronological response of the dioecious *Salix arctica* to variation in local snow precipitation across gender and vegetation types. *Arct Antarct Alp Res* 42:471–475. <https://doi.org/10.1657/1938-4246-42.4.471>
- Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multi-scalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J Clim* 23:1696–1718. <https://doi.org/10.1175/2009jcli2909.1>
- Wagenmakers EJ (2003) Model selection and multimodel inference: a practical information-theoretic approach. *J Math Psychol* 47:580–586. [https://doi.org/10.1016/s0022-2496\(03\)00064-6](https://doi.org/10.1016/s0022-2496(03)00064-6)
- Wang Y, Liang E, Ellison AM, Lu X, Camarero JJ (2015) Facilitation stabilizes moisture-controlled alpine juniper shrublines in the central Tibetan Plateau. *Glob Planet Change* 132:20–30. <https://doi.org/10.1016/j.gloplacha.2015.06.007>
- Wu X, Guo W, Liu H, Li X, Peng C, Allen CD, Zhang C, Wang P, Pei T, Ma Y, Tian Y, Song Z, Zhu W, Wang Y, Li Z, Chen D (2019) Exposures to temperature beyond threshold disproportionately reduce vegetation growth in the northern hemisphere. *Natl Sci Rev* 6:786–795. <https://doi.org/10.1093/nsr/nwy158>
- Xiao S, Xiao H, Kobayashi O, Liu P (2007) Dendroclimatological investigations of sea buckthorn (*Hippophae rhamnoides*) and reconstruction of the equilibrium line altitude of the July first glacier in the Western Qilian mountains, northwestern China. *Tree-Ring Res* 63:15–26. <https://doi.org/10.3959/1536-1098-63.1.15>
- Zhao X, Wang Y, Zhang Q, Luo L (2015) Climatic characteristics of heavy precipitation events during summer half year over the Eastern Tibetan Plateau in recent 50 years. *Arid Land Geogr* 38:675–683. <https://doi.org/10.13826/j.cnki.cn65-1103/x.2015.04.004>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.