

Contents lists available at [ScienceDirect](http://www.sciencedirect.com/science/journal/01681923)

## Agricultural and Forest Meteorology

journal homepage: [www.elsevier.com/locate/agrformet](https://www.elsevier.com/locate/agrformet)

Short communication

# Growth response of alpine treeline forests to a warmer and drier climate on the southeastern Tibetan Plateau



Chunming Shi $^{\rm a, *},$  $^{\rm a, *},$  $^{\rm a, *},$  M[ia](#page-0-0)ogen Shen $^{\rm b}$  $^{\rm b}$  $^{\rm b}$ , Xiu[c](#page-0-3)hen Wu $^{\rm c, *},$  Xiao Cheng $^{\rm a}$ , Xiaoyan Li $^{\rm c}$ , Tianyi Fan $^{\rm a}$ , Zongshan Li $^{\tt d}$  $^{\tt d}$  $^{\tt d}$ , Y[ua](#page-0-0)ndong Zhang $^{\tt e}$  $^{\tt e}$  $^{\tt e}$ , Zexin Fan $^{\tt f}$  $^{\tt f}$  $^{\tt f}$ , Fangzhong Shi $^{\tt c}$  $^{\tt c}$  $^{\tt c}$ , Guocan Wu $^{\tt a}$ 

<span id="page-0-2"></span><span id="page-0-0"></span><sup>a</sup> *Joint Center for Global Change Studies (JCGCS), College of Global Change and Earth System Science, Beijing Normal University, Beijing 100875, China* <sup>b</sup> *Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China*

<span id="page-0-3"></span>c *State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China*

<span id="page-0-4"></span><sup>d</sup> *State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China*

<span id="page-0-5"></span><sup>e</sup>*Key Laboratory of Forest Ecology and Environment, State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry,*

*Beijing 100091, China*

<span id="page-0-6"></span>f *Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China*

#### ARTICLE INFO

*Keywords:* Alpine treeline Divergence problem Climate response Tibetan Plateau Tree ring

#### ABSTRACT

Forest growth at high altitudes and latitudes is sensitive to climate warming. However, warming-induced drought stress has decreased forest growth and survival rates, and constitutes a key uncertainty in projections of forest ecosystem dynamics. A fast warming rate has occurred over the Tibetan Plateau (TP), and the response pattern of alpine forest growth on the TP to a warmer and possibly drier climate is still unknown. By compiling tree-ring width records from ten alpine treeline ecotones (ATEs), we developed an index of regional tree growth in ATEs (RTGA) on the southeastern TP, which is a major forested region of the TP. Our results showed a stable and clear coherence between RTGA and the regional summer (June-August) minimum temperature during the studied period (1950–2012,  $R^2 = 0.59$ ,  $P < 0.001$ ), despite a prominent drying trend since the 1990s. We conclude that warming-induced drought stress has not limited ATE forest growth on the moist southeastern TP.

## **1. Introduction**

Warming rates that are faster than the global mean have been observed at high elevations and latitudes ([Brohan et al., 2006](#page-5-0); [Pepin et al.,](#page-6-0) [2015\)](#page-6-0). Forest growth at the upper altitudinal and high latitudinal limits is generally limited by low temperatures; therefore, the growth of these forests has been considered to be particularly sensitive to climate warming [\(Korner and Paulsen, 2004;](#page-6-1) [Rossi et al., 2007](#page-6-2)). However, growing evidence of decreased tree growth rates and increased drought sensitivity in the northern high latitudes has been reported ([Briffa et al.,](#page-5-1) [1998;](#page-5-1) [Driscoll et al., 2005](#page-6-3); [Hellmann et al., 2016;](#page-6-4) [Porter and Pisaric,](#page-6-5) [2011;](#page-6-5) [Wilmking et al., 2004\)](#page-6-6). This phenomenon, known as the divergence problem (DP), has been mainly attributed to drought stress aggravated by warming and has caused a high degree of uncertainty in tree-ring-based climate reconstructions and forest growth projections ([D'Arrigo et al., 2008](#page-6-7); [Hellmann et al., 2016](#page-6-4)). The DP has mainly been observed in northern high latitudes; however, it has seldom been tested in regions with high elevations, such as the Tibetan Plateau (TP).

In recent decades, the rate of warming on the TP has been faster

than that recorded across the Northern Hemisphere and that in other regions at the same latitude [\(Liu and Chen, 2000;](#page-6-8) [Kang et al., 2010](#page-6-9)). In association with a fast rate of warming, precipitation has been reported to limit forest growth at the alpine treeline ecotone (ATE) in the dry regions of the TP, such as in the northeast [\(Liang et al., 2016a](#page-6-10); [Liu et al.,](#page-6-11) [2006;](#page-6-11) [Yang et al., 2013](#page-6-12)) and on the northern slope of the Himalayas ([Liang et al., 2014\)](#page-6-13), since the 1950s. Drought stress induced by fast warming is responsible for ATE forest growth limitation in both regions ([Liang et al., 2016a](#page-6-10); [Schwab et al., 2018\)](#page-6-14).

Nevertheless, forest growth has showed substantial spatial incoherence in different regions of the TP due to diverse hydrothermal conditions [\(Brauning and Mantwill, 2004](#page-5-2)). A comprehensive understanding of the climate response patterns of ATE tree growth is essential for predicting alpine forest growth on the TP. On the southeastern TP, where the highest alpine treeline in the world is located [\(Miehe et al.,](#page-6-15) [2007\)](#page-6-15), increased ATE forest growth has been reported in site-specific studies. However, whether the growth stimulation is due to increased CO2 concentration or increased growing season temperature is still unclear ([Huang et al., 2017](#page-6-16); [Li et al., 2017\)](#page-6-17). Moreover, attribution of

<span id="page-0-1"></span>⁎ Corresponding authors. *E-mail addresses:* [chunming.shi@bnu.edu.cn](mailto:chunming.shi@bnu.edu.cn) (C. Shi), [xiuchen.wu@bnu.edu.cn](mailto:xiuchen.wu@bnu.edu.cn) (X. Wu).

<https://doi.org/10.1016/j.agrformet.2018.10.002>

Received 2 May 2018; Received in revised form 30 September 2018; Accepted 2 October 2018 0168-1923/ © 2018 Elsevier B.V. All rights reserved.

<span id="page-1-0"></span>

**Fig. 1.** Sampling sites (blue circles) and meteorological stations (black triangles). The top left insert shows the TP (grey shading depicting elevation 3000 m a.s.l.), with a black rectangle delimiting the region shown in the main figure. The top right insert is the 1950–2012 CRU TS4.01 dataset monthly mean temperature (black curve) and precipitation (grey bars) in the study region (28–33 °N, 98.5–103.5 °E). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

<span id="page-1-1"></span>

ю л n	
-------------	--

Latitude (Lat.), longitude (Long.), mean elevation (Elev.) of trees, tree species, and number of trees (No. tree) sampled at each site and the time span of each TRW chronology with an expressed population signal (EPS) value greater than 0.85.



alpine forest growth variability could be biased by non-climatic factors at the local scale, including inter- and intra-species competition [\(Liang](#page-6-18) [et al., 2016b;](#page-6-18) [Qi et al., 2015;](#page-6-19) [Wang et al., 2016](#page-6-20)), soil nutrient availability [\(McNown and Sullivan, 2013](#page-6-21); [Sullivan et al., 2015](#page-6-22)), and topography ([Liu et al., 2016](#page-6-23); [Salzer et al., 2014](#page-6-24); [Wang et al., 2017](#page-6-25)). Therefore, a better understanding of the climate response of ATE tree growth at the regional scale could improve our ability to predict regional alpine forest growth.

In this study, we addressed the question of whether the DP exists for forest growth in ATEs on the southeastern TP through a regional treering chronology network and gridded climate data. Specifically, we aimed to understand the following: 1) the relative importance of different climate variables in controlling local and regional ATE forest growth and 2) the temporal stability of the climate response of regional ATE forest growth.

<span id="page-2-0"></span>

**Fig. 2.** Tree-ring width chronologies standardized by Z-score (thin black lines) and the corresponding sampling replications (number of trees, grey shading). The thick red lines show the 30-year LOESS smoothing of each chronology. The thick black lines are linear regressions of each chronology. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

<span id="page-2-1"></span>

**Fig. 3.** Correlation coefficients between TRW chronologies and the 1950–2012 monthly CRU TS4.01 climate data of the corresponding grid. a) Minimum temperature; b) mean temperature; and c) precipitation. This analysis was conducted for each month from January to December of the current year and for the current summer (June-August) mean (indicated by grey dashed lines). The results for each chronology are shown in blocks separated by grey dashed lines. The yellow, blue, red and green shading represents species from the genera *Abies, Picea, Larix* and *Sabina*, respectively. Black and red stars indicate coefficients significant at the 95% and 99% levels, respectively. The summer (JJA) season was highlighted with black rectangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

<span id="page-3-0"></span>

**Fig. 4.** Index of regional tree growth in alpine treeline ecotones (RTGA, black line) and regional 1950–2012 CRU summer minimum temperature (MinT, red line). The thick lines represent 30-year LOESS smoothing (a); the blue line is the 30-year moving correlation coefficient of the regional RTGA and the summer MinT, and the green line is same as the blue line but using the RTGA and summer MinT detrended by their 30-year LOESS smoothing (b). Horizontal black solid and dashed lines in panel b are 0.001 and 0.01 significance levels for the moving correlation analysis using both raw and detrended data (blue and green lines, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### **2. Materials and methods**

### *2.1. Study area and climate data*

Our study region included the western Sichuan and northwestern Yunnan Provinces, which are located on the southeastern TP. Monthly temperature, precipitation, and self-calibrating Palmer Drought Severity Index (scPDSI) data spanning the period from 1901 to 2012 were extracted from the Climate Research Unit (CRU) TS 4.01 dataset with a spatial resolution of 0.5°. Monthly relative humidity data were obtained from ten meteorological stations of the China Meteorology Administration (black triangles in [Fig. 1](#page-1-0)). The Monsoon Asia Drought Atlas (MADA) reconstruction was downloaded fro[mhttps://www.ncdc.](https://www.ncdc.noaa.gov/paleo-search/study/10435) [noaa.gov/paleo-search/study/10435](https://www.ncdc.noaa.gov/paleo-search/study/10435) ([Cook et al., 2010\)](#page-5-3). The CRU dataset is an interpolation of nearby station data. As extensive meteorological observations did not start until the 1950s over the TP, the CRU data for the TP before the 1950s are less reliable. The annual mean temperature and annual total precipitation for the study region (defined as 28–32 °N, 98.5–103.5 °E) provided by the 1950–2012 CRU dataset were 5.58 °C and 753 mm, respectively, according to our own calculations. Approximately 57% of the precipitation falls in the summer (June-August), which is the main growing season for ATE trees on the southeastern TP.

#### *2.2. Tree ring sampling, processing and chronology construction*

Tree cores were extracted from trees in ten ATEs at nine sites on the southeastern TP ([Fig. 1\)](#page-1-0). For site MYL, two ATEs with different tree species were sampled ([Table 1](#page-1-1)**)**. In general, 26–57 trees of the following species were sampled in each ATE: *Abies squamata*, *Abies faxoniana*, *Sabina saltuaria*, *Picea asperata* and *Larix potaninii* [\(Table 1\)](#page-1-1).

The selected trees had open canopies, straight stems and no signs of damage or internal rot. Two cores per tree were bored at breast height with an increment borer (inner diameter of 5.14 mm). The cores were polished, and tree-ring width (TRW) was measured and cross-dated according to standard dendrochronology procedures. The cross-dated TRW series were quality-checked using COFECHA 2002 software ([Holmes, 1998\)](#page-6-26). Then, the TRWs of the cores from the same tree were averaged. To preserve the climate signals and avoid the effects of trend distortion, the TRWs of the same species within each ATE were detrended and combined into a standard chronology with Climatic Research Unit Standardisation of Tree-ring data (CRUST) software using signal-free regional curve standardization (sf-RCS) ([Melvin and Briffa,](#page-6-27) [2014a,](#page-6-27)[b](#page-6-28)).

The portions of the chronology at both ends with an expressed population signal (EPS) value less than 0.85 were truncated. All the standard chronologies were normalized by Z-score for further analysis. The leading principal component (PC1) of the normalized chronologies was calculated to test the common signals among these chronologies.

## *2.3. Calibration with climate data and response stability test*

To determine the key climate factors dominating ATE forest growth, correlations and response functions were calculated with DendroClim 2002 software between the chronologies and the 1950–2012 CRU data of the corresponding grid point, including minimum temperature, mean temperature and precipitation [\(Biondi and Waikul, 2004](#page-5-4)). This analysis was conducted for each month from January to December of the current year and for June-August (JJA). Then, the ten chronologies were averaged into one chronology to represent the regional tree growth in ATEs (RTGA), which was calibrated to the 1950–2012 regional climate index exhibiting the highest correlation and response coefficients with the chronologies. The stability of the forest growth response to the climate was tested using a 30-year moving correlation analysis, with 14 and 15 years before and after the year of interest. To eliminate a possible trend effect on the moving correlation result, the same analysis was conducted using the time series detrended by the 30-year locally weighted scatterplot smoothing (LOESS) trends.

#### **3. Results**

All TRW chronologies normalized by Z-score are shown in [Fig. 2](#page-2-0), with a 30-year LOESS smoothing. In the post-1900 period, eight out of ten chronologies showed a statically increasing trend (*P < 0.001*), while the other two chronologies depicted insignificant (*P > 0.05*) decreasing trends (MYL\_Sab and DF\_Abi). PC1 explained 41% of the total variance, suggesting a strong common signal embedded in these chronologies.

The monthly correlation analysis of the TRW chronology and local climate data showed the following: (1) all chronologies were significantly ( $P < 0.05$ ) and positively correlated with the summer (JJA) minimum temperature [\(Fig. 3](#page-2-1)a); (2) six out of ten chronologies were significantly ( $P < 0.05$ ) and positively correlated with the summer mean temperature, with lower correlation coefficients than those for the minimum temperature ([Fig. 3](#page-2-1)b); and (3) correlations between the chronologies and precipitation were insignificant for all months ([Fig. 3c](#page-2-1)).

The response function analysis demonstrated that eight and five

TRW chronologies exhibited significant ( $P < 0.05$ ) positive responses to the local summer minimum and mean temperatures, respectively (Appendix [Fig. A1a](#page-4-0) and b). No significant response was found to summer precipitation (Appendix [Fig. A1](#page-4-0)c).

Calibration showed that 59% of the variance in the 1950–2012 regional CRU summer minimum temperature can be explained by the RTGA index (the averaged chronology) [\(Fig. 4](#page-3-0)a). The coherence of the RTGA index and the CRU summer minimum temperature is highly stable over the period from 1950 to 2012, with significant (*P* < 0.001) moving correlation coefficients for the raw data (blue line in [Fig. 4](#page-3-0)b) and the detrended time series  $(P < 0.01$ , green line in [Fig. 4b](#page-3-0)).

## **4. Discussion and conclusion**

Similar to the DP observed at the northern high latitudes, increased temperature insensitivity and drought-limited forest growth have been frequently reported in ATEs in subtropical and mid-latitude mountains ([Gonzalez De Andres et al., 2015;](#page-6-29) [Morales et al., 2004\)](#page-6-30), especially in dry ATEs, such as the Mediterranean Basin ([Diego Galvan et al., 2015](#page-6-31)), the northeast TP [\(Liang et al., 2016a](#page-6-10); [Zhang and Wilmking, 2010](#page-6-32)), and the north slope of the Himalayas, which has a significant rain shadow effect [\(Dawadi et al., 2013;](#page-6-33) [Liang et al., 2014\)](#page-6-13). For ATEs with sufficient moisture availability, the DP was not detected, and forest growth was mainly controlled by the growing season temperature [\(Buentgen et al.,](#page-5-5) [2008;](#page-5-5) [Salzer et al., 2009](#page-6-34)).

Alpine trees start or cease growing when the air temperature is above or below a certain limit [\(Moser et al., 2010;](#page-6-35) [Rossi et al., 2007](#page-6-2); [Ziaco et al., 2016\)](#page-6-36). The summer minimum temperature was shown to be a good approximation of the growing season length and was well calibrated with the annual radial growth of ATE forests on the southeastern TP [\(Li et al., 2017](#page-6-17); [Liang et al., 2010\)](#page-6-37). Our study region, with an

## **Appendix A**

<span id="page-4-0"></span>

annual precipitation ranging between 500 and 800 mm, is among the wettest regions north of the Himalayas on the TP (Appendix [Fig. A2](#page-5-6)).

The summer warming of the study region has been most prominent since the 1980s (Appendix [Fig. A3a](#page-5-7)) and has been accompanied by a drying trend with decreased PDSI, precipitation and relative humidity since the 1990s (Appendix [Fig. A3b](#page-5-7)–d). However, this drying trend has not yet reached a threshold beyond which ATE tree growth has started to be limited by drought because the RTGA index showed a close and stable coherence with the summer minimum temperature in the studied period. Therefore, we conclude that the DP does not yet exist for the ATE forests on the southeastern TP.

However, little is known about when ATE forest growth will reach the point of moisture limitation. The TP is expected to continue to warm, according to all future projections, except in the most optimistic scenario (i.e., RCP 2.6, and even under this scenario temperatures will continue to rise until the mid-century) (Chapter 14 in IPCC AR5, WG1, 2013). Predicting alpine treeline growth responses to future climate change is inherently complex and depends on many variables including climate, soils and local adaptation [\(Cavin and Jump, 2017;](#page-5-8) [McCullough](#page-6-38) [et al., 2017](#page-6-38); [Monson and Grant, 1989](#page-6-39)), but our study demonstrates that warming summer temperature, not precipitation, is the dominant driver of tree growth in the TP. Thus, the divergence problem has not yet been observed.

#### **Acknowledgements**

This study was supported by the National Key Research and Development Plan (2017YFD0600106), the National Natural Science Foundation of China (31600354, 31770490 and 31570645), and the Fundamental Research Funds for the Central Universities.

> **Fig. A1.** Response coefficients between TRW chronologies and the 1950–2012 monthly CRU TS4.01 climate data of the corresponding grid. a) Minimum temperature; b) mean temperature; and c) precipitation. This analysis was conducted for each month from January to December of the current year and for the current summer (June-August) mean (indicated by grey dashed lines). The results for each chronology are shown in blocks separated by grey dashed lines. The yellow, blue, red and green shading represent species of the genera *Abies, Picea, Larix* and *Sabina*, respectively. Black and red stars indicate coefficients significant at the 95% and 99% levels, respectively. The summer (JJA) season was highlighted with black rectangle.

<span id="page-5-6"></span>

<span id="page-5-7"></span>**Fig. A2.** 1950–2012 annual total precipitation (CRU TS4.01 dataset) for the Tibetan Plateau and the surrounding region. Filled black circles indicate the sampling sites.



**Fig. A3.** Summer (JJA) climate variability over the study region, including the CRU mean and minimum temperature (a); the CRU self-calibrating PDSI and the Monsoon Asia Drought Atlas (MADA) reconstruction by [Cook et al., 2010](#page-5-3) (b); total precipitation documented by the CRU datasets and meteorological stations (c); and relative humidity (d). The thick lines are the 30-year LOESS smoothing.

## **References**

- <span id="page-5-4"></span>Biondi, F., Waikul, K., 2004. Dendroclim 2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput. Geosci. 30 (3), 303–311. [https://doi.org/10.1016/j.cageo.2003.11.004.](https://doi.org/10.1016/j.cageo.2003.11.004)
- <span id="page-5-2"></span>Brauning, A., Mantwill, B., 2004. Summer temperature and summer monsoon history on the Tibetan Plateau during the last 400 years recorded by tree rings. Geophys. Res. Lett. 31 (L24205). [https://doi.org/10.1029/2004gl020793.](https://doi.org/10.1029/2004gl020793)
- <span id="page-5-1"></span>Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G., Vaganov, E.A., 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391 (6668). [https://doi.org/10.1038/35596.](https://doi.org/10.1038/35596)
- <span id="page-5-0"></span>Brohan, P., Kennedy, J.J., Harris, I., Tett, S.F.B., Jones, P.D., 2006. Uncertainty estimates in regional and global observed temperature changes: a new data set from 1850. J. Geophys. Res.—Atmos. 111 (D12106D12). <https://doi.org/10.1029/2005jd006548>.
- <span id="page-5-5"></span>Buentgen, U., Frank, D., Wilson, R., Carrer, M., Urbinati, C., 2008. Testing for tree-ring divergence in the European Alps. Glob. Change Biol. 14 (10), 2443–2453. [https://doi.](https://doi.org/10.1111/j.1365-2486.2008.01640.x) [org/10.1111/j.1365-2486.2008.01640.x.](https://doi.org/10.1111/j.1365-2486.2008.01640.x)
- <span id="page-5-8"></span>Cavin, L., Jump, A.S., 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. Glob. Change Biol. 23 (1), 362–379. [https://doi.org/10.1111/gcb.13366.](https://doi.org/10.1111/gcb.13366)
- <span id="page-5-3"></span>Cook, E.R., Anchukaitis, K.J., Buckley, B.M., D'Arrigo, R.D., Jacoby, G.C., Wright, W.E., 2010. Asian monsoon failure and megadrought during the last millennium. Nature 5977 (328), 486–489. <https://doi.org/10.1126/science.1185188>.

- <span id="page-6-33"></span>Dawadi, B., Liang, E., Tian, L., Devkota, L.P., Yao, T., 2013. Pre-monsoon precipitation signal in tree rings of timberline *Betula utilis* in the central Himalayas. Quat. Int. 283, 72–77. <https://doi.org/10.1016/j.quaint.2012.05.039>.
- <span id="page-6-7"></span>D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'Divergence Problem' in Northern Forests: a review of the tree-ring evidence and possible causes. Glob. Planet. Change 60 (3–4), 289–305. <https://doi.org/10.1016/j.gloplacha.2007.03.004>.
- <span id="page-6-31"></span>Diego Galvan, J., Buentgen, U., Ginzler, C., Grudd, H., Gutierrez, E., Labuhn, I., Julio Camarero, J., 2015. Drought-induced weakening of growth-temperature associations in high-elevation Iberian pines. Glob. Planet. Change 124, 95–106. [https://doi.org/](https://doi.org/10.1016/j.gloplacha.2014.11.011) [10.1016/j.gloplacha.2014.11.011.](https://doi.org/10.1016/j.gloplacha.2014.11.011)
- <span id="page-6-3"></span>Driscoll, W.W., Wiles, G.C., D'Arrigo, R.D., Wilmking, M., 2005. Divergent tree growth response to recent climatic warming, Lake Clark National Park and Preserve Alaska. Geophys. Res. Lett. 32 (L2070320). [https://doi.org/10.1029/2005gl024258.](https://doi.org/10.1029/2005gl024258)
- <span id="page-6-29"></span>Gonzalez De Andres, E., Julio Camarero, J., Buentgen, U., 2015. Complex climate constraints of upper treeline formation in the Pyrenees. Trees—Struct. Funct. 29 (3), 941–952. <https://doi.org/10.1007/s00468-015-1176-5>.
- <span id="page-6-4"></span>Hellmann, L., Agafonov, L., Ljungqvist, F.C., Churakova Sidorova, O., Duethorn, E., Esper, J., Hulsmann, L., Kirdyanov, A.V., Moiseev, P., Myglan, V.S., Nikolaev, A.N., Reinig, F., Schweingruber, F.H., Solomina, O., Tegel, W., Buntgen, U., 2016. Diverse growth trends and climate responses across Eurasia's boreal forest. Environ. Res. Lett. 11 (0740217). [https://doi.org/10.1088/1748-9326/11/7/074021.](https://doi.org/10.1088/1748-9326/11/7/074021)
- <span id="page-6-26"></span>[Holmes, R.L., 1998. Computer-assisted quality control in tree-ring dating and measure](http://refhub.elsevier.com/S0168-1923(18)30320-4/sbref0070)[ment. Tree—Ring Bull. 43, 69–78.](http://refhub.elsevier.com/S0168-1923(18)30320-4/sbref0070)
- <span id="page-6-16"></span>Huang, R., Zhu, H., Liu, X., Liang, E., Griessinger, J., Wu, G., Li, X., Brauning, A., 2017. Does increasing intrinsic water use efficiency (iWUE) stimulate tree growth at natural alpine timberline on the southeastern Tibetan Plateau? Glob. Planet. Change 148, 217–226. [https://doi.org/10.1016/j.gloplacha.2016.11.017.](https://doi.org/10.1016/j.gloplacha.2016.11.017)
- <span id="page-6-9"></span>Kang, S., Xu, Y., You, Q., Fluegel, W., Pepin, N., Yao, T., 2010. Review of climate and cryospheric change in the Tibetan Plateau. Environ. Res. Lett. 5 (0151011). [https://](https://doi.org/10.1088/1748-9326/5/1/015101) [doi.org/10.1088/1748-9326/5/1/015101](https://doi.org/10.1088/1748-9326/5/1/015101).
- <span id="page-6-1"></span>Korner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31 (5), 713–732. [https://doi.org/10.1111/j.1365-2699.2003.01043.x.](https://doi.org/10.1111/j.1365-2699.2003.01043.x)
- <span id="page-6-17"></span>Li, X., Liang, E., Gricar, J., Rossi, S., Cufar, K., Ellison, A.M., 2017. Critical minimum temperature limits xylogenesis and maintains treelines on the southeastern Tibetan Plateau. Sci. Bull. 62 (11), 804–812. [https://doi.org/10.1016/j.scib.2017.04.025.](https://doi.org/10.1016/j.scib.2017.04.025)
- <span id="page-6-37"></span>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—Struct. Funct. 24 (2), 363–373. [https://doi.org/10.1007/s00468-](https://doi.org/10.1007/s00468-009-0406-0) [009-0406-0](https://doi.org/10.1007/s00468-009-0406-0).
- <span id="page-6-13"></span>Liang, E., Dawadi, B., Pederson, N., Eckstein, D., 2014. Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? Ecology 95 (9), 2453–2465. <https://doi.org/10.1890/13-1904.1>.
- <span id="page-6-10"></span>Liang, E., Leuschner, C., Dulamsuren, C., Wagner, B., Hauck, M., 2016a. Global warmingrelated tree growth decline and mortality on the north-eastern Tibetan Plateau. Clim. Change 134 (1-2), 163–176. <https://doi.org/10.1007/s10584-015-1531-y>.
- <span id="page-6-18"></span>Liang, E., Wang, Y., Piao, S., Lu, X., Julio Camarero, J., Zhu, H., Zhu, L., Ellison, A.M., Ciais, P., Penuelas, J., 2016b. Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. Proc. Natl. Acad. Sci. U. S. A. 113 (16), 4380–4385. [https://doi.org/10.1073/pnas.1520582113.](https://doi.org/10.1073/pnas.1520582113)
- <span id="page-6-8"></span>Liu, X.D., Chen, B.D., 2000. Climatic warming in the Tibetan Plateau during recent decades. Int. J. Climatol. 20, 1729–1742. [https://doi.org/10.1002/1097-](https://doi.org/10.1002/1097-0088(20001130)20:14<1729::aid-joc556>3.0.co;2-y) [0088\(20001130\)20:14<1729::aid-joc556>3.0.co;2-y](https://doi.org/10.1002/1097-0088(20001130)20:14<1729::aid-joc556>3.0.co;2-y).
- <span id="page-6-11"></span>Liu, L.S., Shao, X.M., Liang, E.Y., 2006. Climate signals from tree ring chronologies of the upper and lower treelines in the Dulan region of the Northeastern Qinghai-Tibetan Plateau. J. Integr. Plant Biol. 48 (3), 278–285. [https://doi.org/10.1111/j.1744-7909.](https://doi.org/10.1111/j.1744-7909.2006.00158.x) 2006.00158 x
- <span id="page-6-23"></span>Liu, B., Wang, Y., Zhu, H., Liang, E., Camarero, J.J., 2016. Topography and age mediate the growth responses of Smith fir to climate warming in the southeastern Tibetan Plateau. Int. J. Biometeorol. 60 (10), 1577–1587. [https://doi.org/10.1007/s00484-](https://doi.org/10.1007/s00484-016-1148-5) [016-1148-5](https://doi.org/10.1007/s00484-016-1148-5).
- <span id="page-6-38"></span>McCullough, I.M., Davis, F.W., Williams, A.P., 2017. A range of possibilities: assessing geographic variation in climate sensitivity of ponderosa pine using tree rings. For. Ecol. Manag. 402 (15), 223–233. [https://doi.org/10.1016/j.foreco.2017.07.025.](https://doi.org/10.1016/j.foreco.2017.07.025)
- <span id="page-6-21"></span>McNown, R.W., Sullivan, P.F., 2013. Low photosynthesis of treeline white spruce is associated with limited soil nitrogen availability in the Western Brooks Range, Alaska. Funct. Ecol. 27 (3SI), 672–683. <https://doi.org/10.1111/1365-2435.12082>.
- <span id="page-6-27"></span>Melvin, T.M., Briffa, K.R., 2014a. CRUST: software for the implementation of regional chronology standardisation: part 1. Signal-free RCS. Dendrochronologia 32 (1), 7–20. [https://doi.org/10.1016/j.dendro.2013.06.002.](https://doi.org/10.1016/j.dendro.2013.06.002)
- <span id="page-6-28"></span>Melvin, T.M., Briffa, K.R., 2014b. CRUST: software for the implementation of regional chronology standardisation: part 2. Further RCS options and recommendations. Dendrochronologia 32 (4), 343–356. [https://doi.org/10.1016/j.dendro.2014.07.008.](https://doi.org/10.1016/j.dendro.2014.07.008)
- <span id="page-6-15"></span>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 (2), 169–173. [https://doi.org/](https://doi.org/10.1659/mrd.0792) [10.1659/mrd.0792.](https://doi.org/10.1659/mrd.0792)
- <span id="page-6-39"></span>Monson, R.K., Grant, M.C., 1989. Experimental studies of *Ponderosa Pine*. III. Differences in photosynthesis, stomatal conductance, and water-use efficiency between two genetic lines. Am. J. Bot. 76 (7), 1041–1047. [https://doi.org/10.2307/2444526.](https://doi.org/10.2307/2444526)
- <span id="page-6-30"></span>Morales, M.S., Villalba, R., Grau, H.R., Paolini, L., 2004. Rainfall-controlled tree growth in high-elevation subtropical treelines. Ecology 85 (11), 3080–3089. [https://doi.org/](https://doi.org/10.1890/04-0139) [10.1890/04-0139.](https://doi.org/10.1890/04-0139)
- <span id="page-6-35"></span>Moser, L., Fonti, P., Buentgen, U., Esper, J., Luterbacher, J., Franzen, J., Frank, D., 2010. Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. Tree Physiol. 30 (2), 225–233. [https://doi.org/10.1093/treephys/](https://doi.org/10.1093/treephys/tpp108) [tpp108.](https://doi.org/10.1093/treephys/tpp108)
- <span id="page-6-0"></span>Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schoener, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N., Yang, D.Q., 2015. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Change 5 (5), 424–430. [https://doi.org/10.1038/](https://doi.org/10.1038/nclimate2563) [nclimate2563](https://doi.org/10.1038/nclimate2563).
- <span id="page-6-5"></span>Porter, T.J., Pisaric, M.F.J., 2011. Temperature-growth divergence in white spruce forests of Old Crow Flats, Yukon Territory, and adjacent regions of northwestern North America. Glob. Change Biol. 17 (11), 3418–3430. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2011.02507.x) [2486.2011.02507.x.](https://doi.org/10.1111/j.1365-2486.2011.02507.x)
- <span id="page-6-19"></span>Qi, Z., Liu, H., Wu, X., Hao, Q., 2015. Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains, Northwestern China. Glob. Change Biol. 21 (2), 816–826. [https://doi.org/10.1111/gcb.12703.](https://doi.org/10.1111/gcb.12703)
- <span id="page-6-2"></span>Rossi, S., Deslauriers, A., Anfodillo, T., Carraro, V., 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia 152 (1), 1–12. [https://doi.org/10.1007/s00442-006-0625-7.](https://doi.org/10.1007/s00442-006-0625-7)
- <span id="page-6-34"></span>Salzer, M.W., Hughes, M.K., Bunn, A.G., Kipfmueller, K.F., 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proc. Natl. Acad. Sci. U. S. A. 106 (48), 20348–20353. [https://doi.org/10.1073/pnas.](https://doi.org/10.1073/pnas.0903029106) [0903029106](https://doi.org/10.1073/pnas.0903029106).
- <span id="page-6-24"></span>Salzer, M.W., Larson, E.R., Bunn, A.G., Hughes, M.K., 2014. Changing climate response in near-treeline bristlecone pine with elevation and aspect. Environ. Res. Lett. 9 (11400711). <https://doi.org/10.1088/1748-9326/9/11/114007>.
- <span id="page-6-14"></span>Schwab, N., Kaczka, R.J., Janecka, K., Boehner, J., Chaudhary, R.P., Scholten, T., Schickhoff, U., 2018. Climate change-induced shift of tree growth sensitivity at a central Himalayan treeline ecotone. Forests 9 (5), 267. [https://doi.org/10.3390/](https://doi.org/10.3390/f9050267) [f9050267.](https://doi.org/10.3390/f9050267)
- <span id="page-6-22"></span>Sullivan, P.F., Ellison, S.B.Z., McNown, R.W., Brownlee, A.H., Sveinbjoernsson, B., 2015. Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. Ecology 96 (3), 716–727. [https://doi.org/10.1890/14-](https://doi.org/10.1890/14-0626.1) [0626.1](https://doi.org/10.1890/14-0626.1).
- <span id="page-6-20"></span>Wang, Y., Pederson, N., Ellison, A.M., Buckley, H.L., Case, B.S., Iang, E.L., Camarero, J.J., 2016. Increased stem density and competition may diminish the positive effects of warming at alpine treeline. Ecology 97 (7), 1668–1679. [https://doi.org/10.1890/15-](https://doi.org/10.1890/15-1264.1) [1264.1](https://doi.org/10.1890/15-1264.1).
- <span id="page-6-25"></span>Wang, Y., Liang, E., Sigdel, S.R., Liu, B., Camarero, J.J., 2017. The coupling of treeline elevation and temperature is mediated by non-thermal factors on the Tibetan Plateau. Forests 8 (1094). <https://doi.org/10.3390/f8040109>.
- <span id="page-6-6"></span>Wilmking, M., Juday, G.P., Barber, V.A., Zald, H., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Glob. Change Biol. 10 (10), 1724–1736. [https://doi.org/10.](https://doi.org/10.1111/j.1365-2486.2004.00826.x) [1111/j.1365-2486.2004.00826.x](https://doi.org/10.1111/j.1365-2486.2004.00826.x).
- <span id="page-6-12"></span>Yang, B., He, M., Melvin, T.M., Zhao, Y., Briffa, K.R., 2013. Climate control on tree growth at the upper and lower treelines: a case study in the Qilian Mountains, Tibetan Plateau. PLoS One 8 (e690657). [https://doi.org/10.1371/journal.pone.](https://doi.org/10.1371/journal.pone.0069065) [0069065.](https://doi.org/10.1371/journal.pone.0069065)
- <span id="page-6-32"></span>Zhang, Y., Wilmking, M., 2010. Divergent growth responses and increasing temperature limitation of Qinghai spruce growth along an elevation gradient at the northeast Tibet Plateau. For. Ecol. Manag. 260 (6), 1076–1082. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.foreco.2010.06.034) [foreco.2010.06.034.](https://doi.org/10.1016/j.foreco.2010.06.034)
- <span id="page-6-36"></span>Ziaco, E., Biondi, F., Rossi, S., Deslauriers, A., 2016. Environmental drivers of cambial phenology in Great Basin bristlecone pine. Tree Physiol. 36 (7), 818–831. [https://doi.](https://doi.org/10.1093/treephys/tpw006) [org/10.1093/treephys/tpw006](https://doi.org/10.1093/treephys/tpw006).