

Drought limits wood production of *Juniperus przewalskii* even as growing seasons lengthens in a cold and arid environment



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ABSTRACT

Studies of xylogenesis can provide mechanistic understandings of the influence of climate on wood production and carbon sequestration at the cellular level. It is not yet clear how trees will respond to increasing temperature and precipitation variability and other extreme meteorological events that are expected to occur as climate continues to change. Here, we analyzed cambial phenology and xylogenesis of *Juniperus przewalskii* Kom. weekly (2011–2014) or biweekly (2015–2016) over six years on the northeastern Tibetan Plateau. We found that temperature plays a decisive role in the onset of xylogenesis and a daily mean temperature of 6.1 °C appears to be the threshold that determines growth onset. Additionally, we observed the end of xylogenesis is related to summer drought conditions. During the course of our observations, the onset of xylogenesis advanced nearly twice as much as the end of xylogenesis (3.1 vs 1.8 days decade⁻¹, respectively), indicating a slight lengthening of the growing season. However, an increase in the duration of the growing season did not necessarily result in a greater level of wood production. In fact, we found that water availability affects the growth rate and early summer precipitation appears to be a key factor of wood production over the northeastern Tibetan Plateau. Our study provides new evidence of the malleable nature of tree growth and reveals potential mechanisms of how tree growth adjusts to climatic variations in cold and arid region.

1. Introduction

Forests account for almost half of the annual carbon uptake (Bonan, 2008) and sequester nearly 30% of anthropogenic emissions (Le Quere et al., 2016; Pan et al., 2011), making them a key component to the global carbon balance. Wood is the main terrestrial biotic reservoir for long-term carbon sequestration (Pan et al., 2011). Xylem growth continuously adds carbon to this pool and hence impacts the carbon balances of terrestrial ecosystems (Duveneck et al., 2017). However, increasing air temperatures and shifting precipitation regimes threaten the ability of forest to sequester carbon through myriad physiological processes (IPCC, 2013), such as reducing photosynthesis (Dusenge et al., 2019), hydraulic failure (Adams et al., 2017; Allen et al., 2010), decreasing growth rates (Balducci et al., 2016), and shifts in key intra-

annual phenology such as leaf out (Fernandez-de-Una et al., 2017) or cambial activation and xylem growth (Deslauriers et al., 2017). Given the projected changes in climate for the coming decades, long-term *in situ* observations are required to better identify and quantify the intra-annual dynamics of processes controlling wood production and carbon sequestration.

Wood formation (xylogenesis), a complex process influenced by many biological events, results in the growth and differentiation of the vascular cambium (Deslauriers et al., 2017). Xylogenesis studies allow us to identify the uncertainties at the cellular level that can have profound implications for the mechanistic understanding of how climate influences wood production and carbon sequestration. In this sense, the kinetics of wood production, its timing, duration, and rate, are crucial because they are the main parameters that determine total wood

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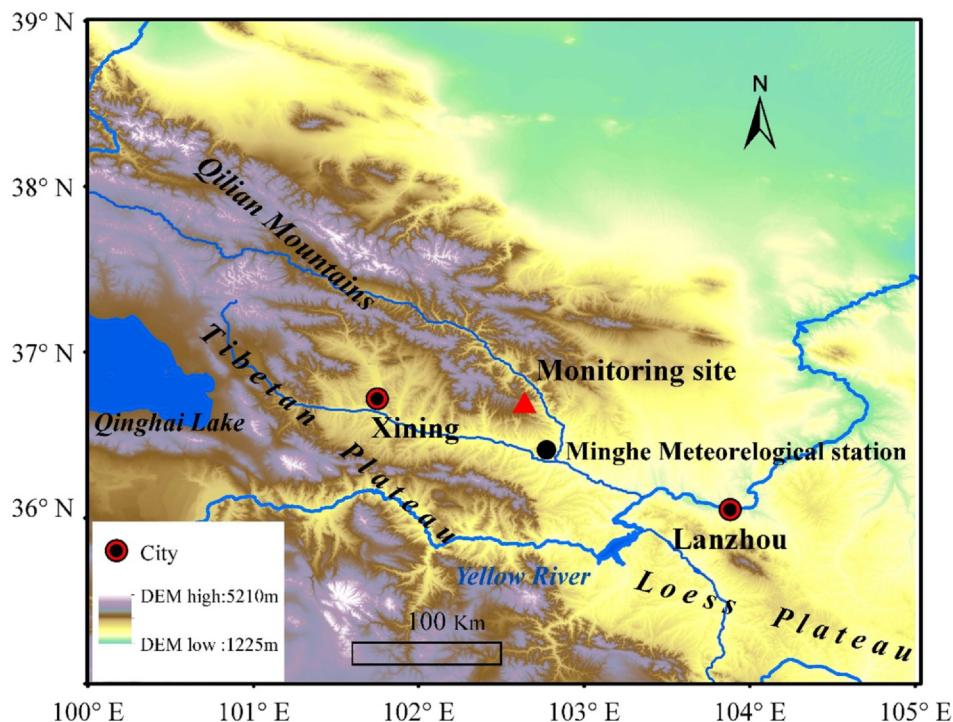


Fig. 1. Map of the monitoring site. The study area forms the boundary region between the Loess Plateau (southeastern) and the Tibetan Plateau (southwestern).

production (Cuny et al., 2014; Deslauriers et al., 2017). However, relative impact of kinetics to wood production varies with local and regional climatology and can result in different radial growth strategies of trees. In dry regions, variability in wood production is more driven by growth rate than growth duration (Cuny et al., 2012; Rathgeber et al., 2011; Ren et al., 2019; Vieira et al. 2020; Zhang et al., 2018a; Ziaoc et al., 2018). Under wet conditions, however, the importance of growth duration seems to be even higher than the growth rate (Rossi et al., 2014). Therefore, it is crucial to identify the kinetics of xylogenesis and their impacts at the cellular level across many different environments.

The duration of cell production is determined by both the timing of onset and end of xylogenesis. Many studies on cambial phenology from observations and controlled experiments have demonstrated the crucial role of temperature on the onset of cambial growth (e.g., Deslauriers et al., 2008; Körner, 2006; Körner and Basler, 2010; Rossi et al., 2011). In temperate and boreal forests, a daily mean temperature threshold of 6–8 °C has been demonstrated to spur the onset of cambial activity (Deslauriers et al., 2008; Rossi et al., 2007, 2008). In more xeric conditions, the onset of xylogenesis is related to temperature (Vieira et al., 2014), although it can be delayed at higher latitudes and altitudes by cooler temperatures (Zhang et al., 2018a,b) and lower spring precipitation (Ren et al., 2015, 2018). The end of xylogenesis is even less well understood. Though in cold regions and alpine forests temperature can be a primary constraint on end of seasonal growth (Rossi et al., 2016), summer drought conditions play an important role in environments with drier growing seasons, such as the Mediterranean region (Vieira et al., 2014). Of the few studies in cold and arid ecoregions, drought appears influence the end of xylogenesis (Zhang et al., 2018a). New research, however, indicates that the end of xylogenesis could be more complex in the context of climate change. Similar as Mediterranean, late-season warming supported by elevated rainfall may lead to an extension of the growing season in cold and dry environment, potentially for a month longer than expected (Zhang, 2018). In this light, further research is needed to investigate the timing and duration of tree growth in response to changing climate in cold and arid regions.

The relatively dry and cool northeastern Tibetan Plateau is an important area for studying the impacts of climate change because it not

only encompasses the highest altitude in the world, but also is characterized by a wide range of climatic conditions (Yao et al., 2012). The northeastern Tibetan Plateau has experienced continuous warming and a significant increase in the frequency of extreme climate events (Liu and Chen, 2000). Mean annual temperatures have increased at a rate of 0.37 °C decade⁻¹ while winter to spring temperatures have increased at an even faster rate of 0.56 °C decade⁻¹ (Song et al., 2016). It is uncertain whether contemporary trees in a cold and arid region are capable of adapting to rapidly changing weather conditions such as those that are expected to occur with future climate change. Therefore, the northeastern Tibetan Plateau is an important area to improve our understanding of the impacts of climatic change on forests in dry and cool environments.

In this study, we conducted high-resolution monitoring of the cambial phenology and xylogenesis of *Juniperus przewalskii* from 2011 to 2016 within the northeastern Tibetan Plateau. Climate varied substantially throughout the monitoring period, including an extreme drought in 2013, cold and wet conditions in 2012, and a dry spell followed by a period of consistent rainfall warming in mid-August of 2016. The transient drought and subsequent deluge of precipitation could be a harbinger of future climate change. The purpose of our study was to (i) investigate the dynamic processes of cambial phenology and xylogenesis and (ii) highlight the relationships between climatic variation and the timing, duration, and rate of wood production. As growth onset has been observed to be driven by temperature in previous studies in this region (Zhang et al., 2018a,b), we hypothesize that (i) there is a daily mean temperature threshold for the onset of xylogenesis and (ii) a warmer climate will lead to a longer growing season, resulting in greater wood production. Given that we can observe the impact of synchronous meteorological factors on stem growth over the course of six years, we expect to gain insight into the patterns of timing and duration of xylogenesis while also assessing and quantifying the impacts of changing climate on tree growth in cold and arid region.

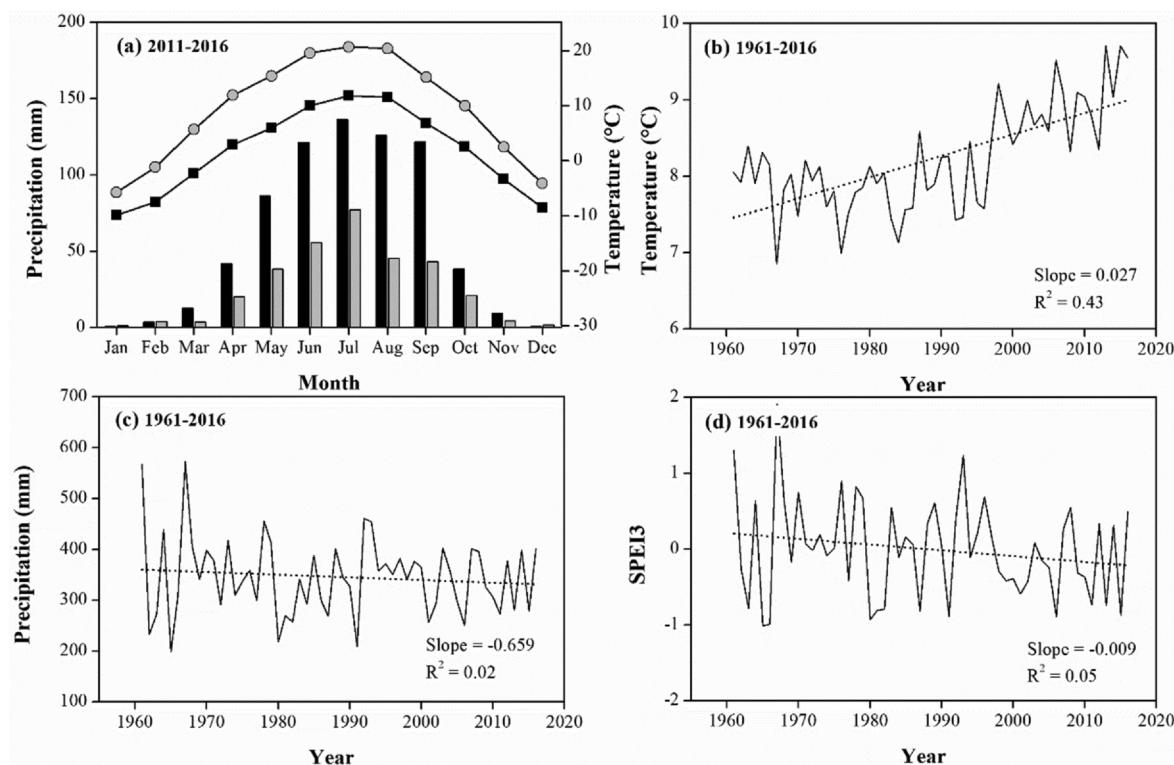


Fig. 2. Distribution of the monthly mean temperature (symbol-line) and precipitation (bar) during the period of 2011–2016 from the on-site meteorological station of the monitoring site (black) and Minhe meteorological station near our study site (grey) (a). Long-term series of annual mean temperature (b), precipitation (c), and 3-month standardized precipitation evapotranspiration index (SPEI3, d) and their trends (dashed lines) recorded by Minhe meteorological station for the period of 1961–2016.

2. Materials and methods

2.1. Study site

Our study site was located in the Tulugou National Forest Park ($36^{\circ}43'21''\text{N}$, $103^{\circ}37'59''\text{E}$) of the northeastern corner of the Tibetan Plateau (Fig. 1). This area forms the boundary region between the Loess Plateau and the Tibetan Plateau, where the climate is cold and semiarid (Fig. 2a). The study area represented a mountainous virgin forest with abundant vegetation that exhibited a typical vertical distribution. *J. przewalskii* is primarily distributed on dry, infertile, and south-facing slopes between 2600 m and 3300 m above sea level (asl) in this region, is located along the easternmost boundary of the distribution of this tree species. The trees we monitored grow at 3100 m asl. Since the examined forests are open (having < 20% coverage of the landscape), we expected tree-to-tree interactions to be minimal, and the main impacts on tree growth to be abiotic (i.e. climate driven). Most trees in the monitoring site were 6–9 m in height and 15–30 cm in diameter at breast height (DBH).

2.2. Meteorological data

An on-site meteorological station (HOBO U30, Onset, USA) was installed in 2011, and the data were recorded at 10-min intervals across an open and relatively flat area within 50 m of the studied trees. Observed meteorological data included air temperature, precipitation, relative humidity, soil temperature (10 cm depth), and soil water content (10 cm depth). To quantify drought severity, the three-month standardized precipitation evapotranspiration index (SPEI3) was calculated using the monthly difference between precipitation and potential evapotranspiration for the period of 2011–2016 (Vicente-Serrano et al., 2010). The positive and negative SPEI values represent wet and drought periods, respectively.

To identify long-term trends of climate change in the study region, we used temperature, precipitation, and SPEI3 values for the Minhe meteorological station ($36^{\circ}19'48''\text{N}$, $102^{\circ}51'06''\text{E}$, 1814 m asl) for 1961–2016 close to our study site (Fig. 1). According to these records, our study area is characterized by a typical arid climate with an average of 335 mm in annual precipitation during 2011–2016 (Fig. 2a). The mean annual temperatures increased significantly from 1961 to 2015 at the rate of $0.27\text{ }^{\circ}\text{C decade}^{-1}$. However, total precipitation decreased at a rate of $6.5\text{ mm decade}^{-1}$, resulting in a decrease of SPEI values (Fig. 2b–d).

2.3. Microcore sampling and preparation

In 2011, five upright trees without substantial stem or crown damage or anomalies were selected for microcoring. To avoid the influence of long-term microcoring on tree growth, we replaced two trees in 2014 and another three trees in 2015. The study trees were 64 ± 7 (mean \pm SD) years old, 6.3 ± 0.5 m in height, and 24.2 ± 3.0 cm in DBH. Microcores were taken weekly (2011–2014) or biweekly (2015–2016) from mid-April to the end of September from 2011 to 2016 at breast height (1.3 m) using a Trehor tool (Rossi et al., 2006a). To avoid lateral influence of wound reactions on adjacent sampling positions, samples were taken on the slope-parallel side of the stem at breast height (1.3 m) and followed a spiral trajectory with 30 mm both in tangential and longitudinal directions over the course of each field season. Microcores were placed in centrifuge tube with formalin-alcohol-acetic acid solution (mixing ratio: 5:90:5) immediately after collection. Slide preparation for anatomical investigation followed standard methods (Rossi et al., 2006a; Zhang et al., 2013). Microcores were softened in 70% alcohol and glycerin solution (mixing ratio: 1:1), dehydrated in different concentrations of ethanol (70, 85, 95, and 100%), cleaned in dimethylbenzene, and embedded in paraffin. The samples were cut in transverse sections of $12\text{ }\mu\text{m}$ thick using a rotary

microtome (RM 2245, Leica, Germany). The sections were stained with a 1% water solution of safranin and 0.5% ethanol solution of fast green, photographed under an optical microscope at 100–400 of magnification (bright field and polarized light).

2.4. Determination of cambial activity and wood formation

Cells of the cambial zone had rectangular shape, small radial diameters and thin primary walls. Cells in the enlargement phase were at least two times larger than cambial cells and had thin walls that were not birefringent under polarized light. Because secondary wall formation and lignification processes largely overlap, they were not discriminated, but were regrouped under the term “wall-thickening” (Cuny et al., 2015). We distinguished wall-thickening cells by the birefringence of the secondary walls under polarized light because cellulose microfibrils are deposited according to a particular orientation in the secondary wall that makes them shining under polarized light (Abe et al., 1997). Mature cells had lignified walls without protoplasts, and the walls were completely stained red by saffron and fast green counterstaining (Zhang et al., 2013). Cell enlargement, cell wall-thickening, or mature cells was generally considered to have begun when at least one cell was observed in the enlarging phase, wall-thickening phase, or mature cells, respectively (Rossi et al. 2006b). When no other cell was observed in cell enlarging, the cell production was considered complete; when no other cell was observed in wall-thickening and lignification, xylem formation was considered complete, indicating the end of cell wall lignification (Rossi et al. 2006b).

Cambial phenology was assessed and calculated in day of the year (DOY) corresponding to the dates of (i) first enlarging cell, (ii) first wall-thickening cell, (iii) first mature cell, (iv) end of cell enlargement, and (v) end of cell wall lignification. The duration of cell production was identified as the period between the onset of cell enlargement and end of cell enlargement. The duration of xylogenesis was defined as the period from the onset of cell enlargement to the end of cell wall lignification (Rossi et al., 2014).

2.5. Data analysis and statistics

The number of cambial, enlargement, wall-thickening, and mature cells along three radial rows for each tree were distinguished and counted. The total current number of xylem cells was determined by totaling the number of cells undergoing enlargement, wall-thickening, and mature cells. The number of xylem cells was standardized based on the previous ring width (Gruber et al., 2009):

$$nc_i = ncm_i \times rw_m / rw_s$$

where nc_i is the standardized number of xylem cells, ncm_i is the measured number of xylem cells, rw_m is the mean ring width of previous rings for all samples, and rw_s is the ring width of previous rings for each sample. For each stage, differences observed across different monitoring years were compared using analysis of variance (ANOVA) and Tukey's tests (Quinn and Keough, 2002).

The increase in the number of xylem cells for each tree was modeled with Gompertz function using the nonlinear regression tool available through the Origin software package (OriginLab Corporation, USA):

$$Y = Ae^{-e^{(\beta - \kappa t)}}$$

where Y is the cumulative sum of xylem cells, t is the date expressed as DOY, β is the x-axis placement parameter, A is the upper asymptote, and κ is the rate of change parameter. The total number of xylem cells (N_{cell}) were estimated by A . The maximum rate of cell production (R_{max}), the corresponding date of the inflection point (t_p), and the mean rate of cell production (R_{mean}) were calculated as (Rathgeber et al., 2011):

$$R_{max} = \kappa A / e$$

$$t_p = \beta / \kappa$$

$$R_{mean} \approx 9/40eR_{max}$$

The relationship between the duration of cell production (Δt_E), R_{mean} , and N_{cell} was calculated using simple linear regressions. We propose expressing N_{cell} as a function of R_{mean} and Δt_E :

$$N_{cell} = f(R_{mean} \times \Delta t_E)$$

The contribution of R_{mean} and Δt_E to N_{cell} was determined by sensitivity analysis, which consisted of computing the impact of the relative variations of the input variables (based on their standard deviations) on the results of the model (Cariboni et al., 2007; Rathgeber et al., 2011). All the above parameters were calculated for each tree at each monitoring year. To compare the wood production among different years, Δt_E , N_{cell} , t_p , and R_{mean} were assessed by ANOVA and Tukey's test.

Logistic regressions were used to assess the probability of cambium being active at a given temperature (Rossi et al., 2008). Binary responses were coded as active (value 1) or non-active (value 0):

$$\text{Logit}(\pi_x) = \ln\left(\frac{\pi_x}{1 - \pi_x}\right) = \beta_0 + \beta_1 x_j$$

where π_x is the probability of cambium being active, x_j is the temperature on a given day j , and β_0 and β_1 are the intercept and slope of the logistic regression, respectively (Quinn and Keough, 2002). Temperature thresholds (x) were calculated when the probability of xylogenesis being active was 0.5, i.e., when $\text{Logit}(\pi_x) = \beta_0 + \beta_1 x_j = 0$ and $x = -\beta_0 / \beta_1$. Therefore, for a temperature exceeding x , a cambial cell was more likely to be active than non-active. Model verification included χ^2 of the likelihood ratio, Wald's χ^2 for regression parameter and goodness of fit and Hosmer-Lemeshow's \hat{C} for possible lack of fit (Quinn and Keough, 2002). For each tree and each monitoring year, the model was fit to the mean, minimum, and maximum temperatures for an interval of 30 days before and after cambial activity. All 90 models (6 years \times 5 trees \times 3 temperature series) were applied. Differences in temperature thresholds between monitoring years were compared by an ANOVA.

The relationships between climate and the timing, duration and rate of wood production were assessed by correlation analysis. Annual temperatures, precipitation, and soil water content for the previous October to the following September were used. Considering that tree growth as discerned by tree-ring analysis in this region was negatively correlated with May temperature and positively with May precipitation (Gou et al., 2015), we also used temperature and precipitation in May for further analysis. All tests were assessed for significance at the $P = 0.05$ unless otherwise noted.

3. Results

3.1. Meteorology records

Mean annual temperature from 2011 to 2016 was 1.7 °C and ranged from a mean of −9.9 °C in January to a mean of 11.8 °C in July (Fig. 2a). Average total annual precipitation was 699 mm for this same period. Precipitation was distributed unevenly throughout the year. Precipitation from May to September accounted for 80% of annual precipitation (Fig. 2a).

We found 2012 to be a cold and wet year during our observation period (Fig. 3, Table 1), having the lowest mean temperature (0.6 °C), the highest precipitation (746 mm), and the highest SPEI3 value (0.99). In contrast, 2013 and 2015 were warm and dry years, with relatively higher mean temperatures (2.0 and 2.1 °C, respectively), less precipitation (640 and 663 mm, respectively), and lower SPEI3 values (−0.86 and −0.34, respectively). We found 2016 to be the warmest year. There was no measurable precipitation for 16 days from July 29 to

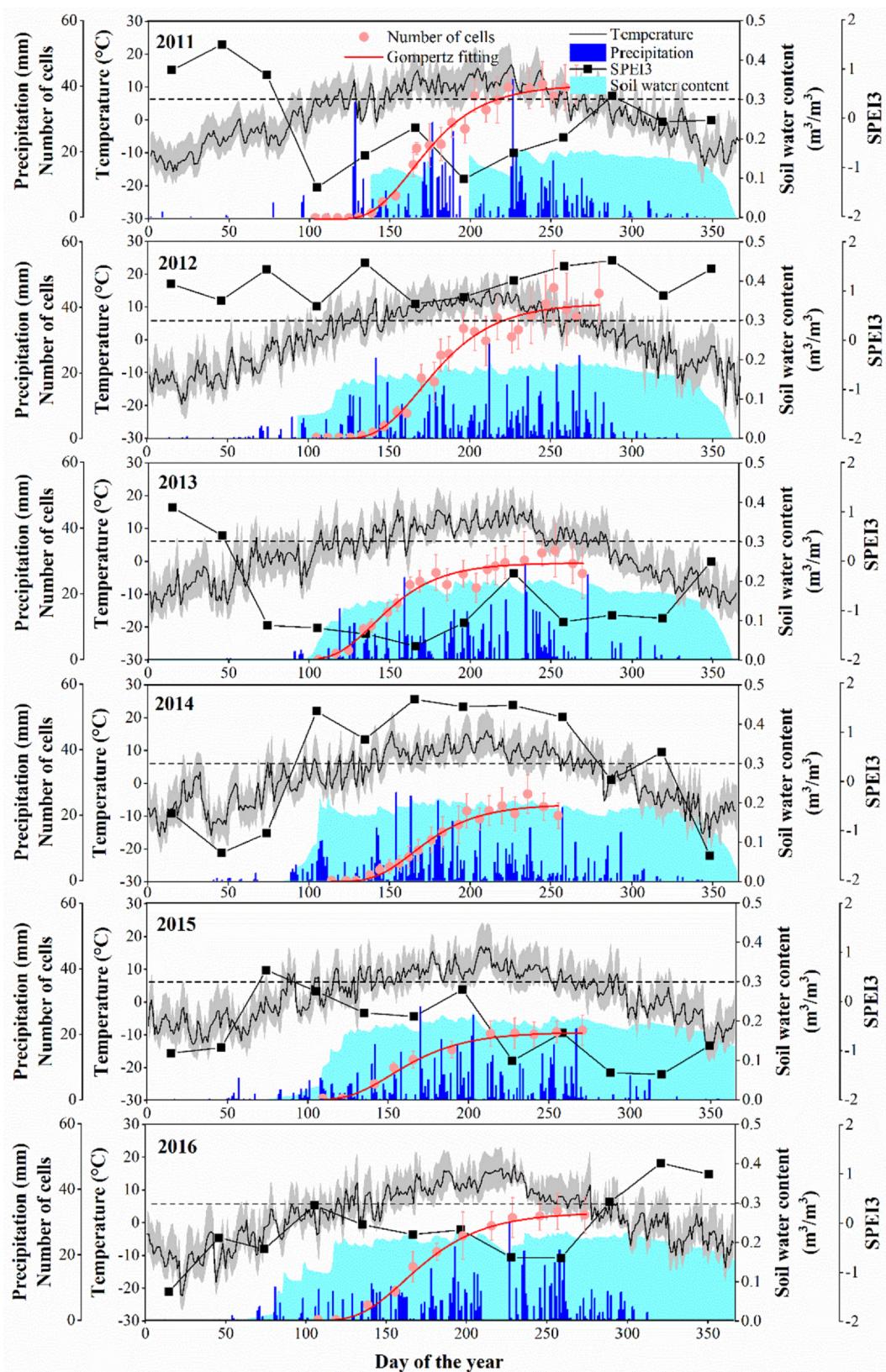


Fig. 3. Daily mean temperature (black line), maximum and minimum temperature (grey shaded area), precipitation (blue bar), soil water content (light blue shaded area), and 3-month standardized precipitation evapotranspiration index (SPEI3, black squares) during 2011–2016, plotted together with number of xylem cells (enlargement cell + wall-thickening cells + mature cells; light red circles) formed throughout the season (error bars indicate mean \pm SE) and their Gompertz fitting curves (red line). The dash line indicates 6.1 °C of the mean air temperature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Climatic characteristics observed from the monitoring site from 2011 to 2016

Year	Annual Mean temperature (°C)	Annual maximum temperature (°C)	Annual minimum temperature (°C)	July temperature (°C)	January temperature (°C)	Annual Precipitation (mm)	May Precipitation (mm)	Annual mean SPEI3
2011	1.7	7.4	-2.6	11.6	-12.5	690	98	-0.38
2012	0.6	6.3	-3.8	12.0	-12.7	746	123	0.99
2013	2.0	8.1	-2.5	11.5	-9.0	640	82	-0.86
2014	1.3	7.2	-3.0	11.7	-7.3	721	75	0.40
2015	2.1	8.0	-2.5	11.1	-7.0	663	72	-0.34
2016	2.2	8.1	-2.3	12.8	-10.8	732	76	0.18
Mean	1.7	7.5	-2.8	11.8	-9.9	699	88	-

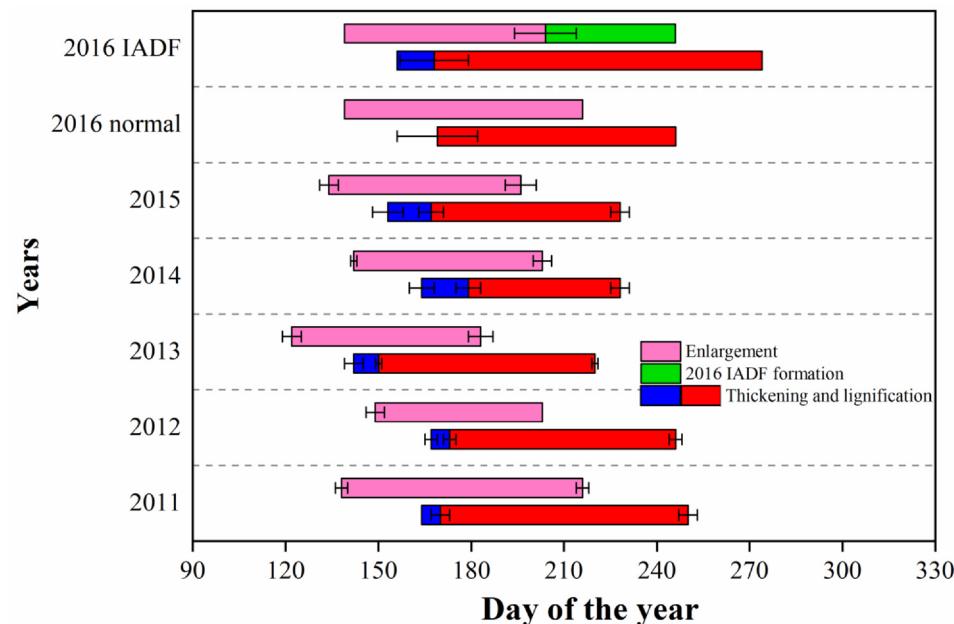


Fig. 4. Cambial phenology of *J. przewalskii* during 2011–2016 growing season. The beginning and end of pink horizontal bars indicate the timing of onset and end of cell enlargement, respectively; The beginning of blue horizontal bars indicate the date of first wall-thickening cell, and the beginning of red horizontal bars indicate the date of first mature cell, the end of red horizontal bars indicate the end of cell wall lignification; Note the Intra-annual density fluctuation (IADF) formation in the end of 2016 growing season (green horizontal bar). Error bars indicate mean \pm SE.

August 13, 2016. This drought period was twice as long as three other dry spells observed in previous years from April through September: July 14–22, 2011; April 21–28, 2012; and August 12–19, 2013 (Fig. 3).

3.2. Timing of xylogenesis

The timing of xylogenesis varied significantly during the period of monitoring (Fig. 4, Table S1). The first enlarging cell (corresponding to the onset of cell production and the onset of the growing season), first wall-thickening cell, and first mature cell occurred earliest during the warm year of 2013. The latest dates of first enlarging cell and wall-thickening cell observed in 2012 among 2011–2016 whereas the latest date of first mature cell observed in 2014. The dates of first enlarging cell, first wall-thickening cell, and first mature cell during the warmer year (2013) occurred 27 days, 25 days, and 23 days earlier than the coldest year (2012), respectively.

The end of cell enlargement (corresponding to the end of cell production) and cell wall lignification (corresponding to the end of xylogenesis or the end of growing season) occurred significantly earlier during 2013 than in other years (Fig. 4, Table S1). In 2016, we observed interrupted stem wood formation (intra-annual density fluctuation) and then an extended growing season in three of the five studied trees (see Zhang, 2018 for detail). Due to this interruption, the end of cell enlargement (DOY 233) and cell wall lignification (DOY 263) in 2016 occurred 17–50 days, and 13–43 days later respectively than during the previous five years (2011–2015).

The duration of cell production (corresponding to the period of cell enlargement phase) and the duration of xylogenesis (the length of the growing season) differed among observation years (Figs. 4 and 5, Table

S1). We observed that 2012 had the shortest period of cell production (55 days), and 2014 had the shortest period of xylogenesis (87 days). We also identified 2016 as the year in which both the duration of cell production (95 days) and xylogenesis (125 days) were the longest, which, again, appears to be related to the extra-month growth.

We found strong negative trends between annual, and May temperatures and the onset of cell enlargement, wall-thickening, and mature cell, indicating that phenological traits of stem growth consistently emerged earlier in warmer years than in colder years (Figs. 6 and S1). That is, as annual mean temperature increased, the dates of first cell enlargement, wall-thickening, and maturation occurred earlier by 11.3, 11.4, and 8.9 days $^{\circ}\text{C}^{-1}$, respectively. We also found significantly positive correlations between precipitation and the onset of cell enlargement, wall-thickening, and mature cell (i.e., trees delay the onset of the growing season when more precipitation occurs). However, no significant relationships were found between soil water content and the onset of cell enlargement, wall-thickening, or mature cell.

No significant relationships were found between temperature and the end of cell enlargement and cell wall lignification (Figs. 6 and S1). However, the end of these phenological phases was positively correlated with both precipitation and soil water content, indicating that the end of xylogenesis occurred earlier when it was drier. The end of cell enlargement and cell wall lignification can be delayed by both 2.7 days for every 10 mm increase in annual precipitation, respectively.

The duration of cell production and xylogenesis both showed significant relationships with temperature and soil water content (Figs. 6 and S2). With each 1 $^{\circ}\text{C}$ increase in annual mean temperature, the duration of cell production increased by 14.3 days.

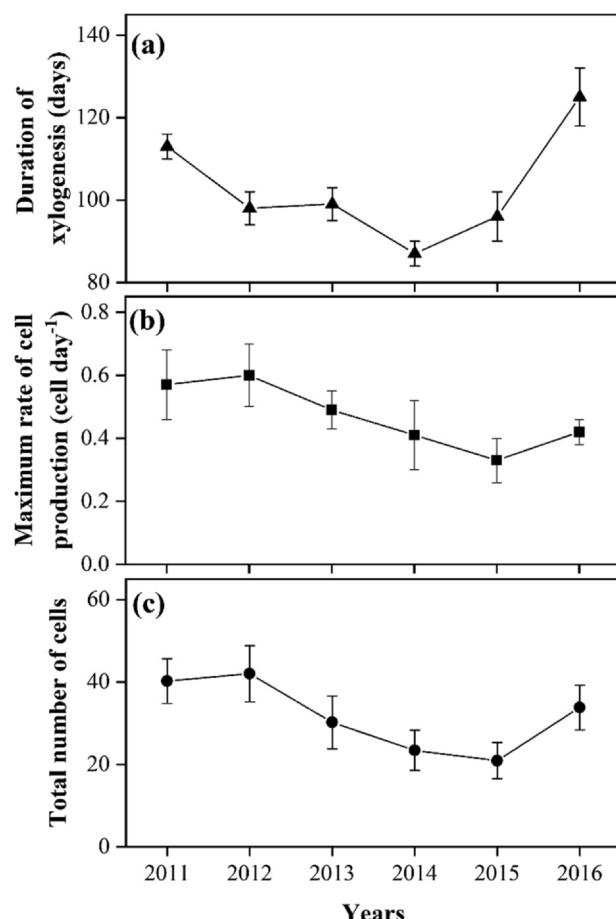


Fig. 5. Duration of xylogenesis (a), maximum growth rate (b), and total number of xylem cells (c) of *J. przewalskii* during 2011–2016 growing season. Error bars indicate mean \pm SE.

3.3. Threshold temperature for the onset of xylogenesis

Threshold temperatures with a probability of 0.5 for the onset of xylogenesis were calculated for each year and site (Table 2). There were

no significant differences in threshold temperatures between the six monitoring years ($P > 0.05$), indicating that critical temperatures initiating xylogenesis in *J. przewalskii* occurred uniformly across our study site. The mean threshold of the daily mean temperature initiating xylogenesis was found to be 6.1 °C and was found to range from 5.2 to 6.7 °C during the course of our observations. The mean threshold for the daily maximum temperature was 11.7 °C and found to range between 11.0 and 12.4 °C between years. For the daily minimum temperature, the mean threshold was 1.7 °C and was found to range from 1.2 to 2.3 °C across years.

3.4. Growth rate and wood production

The Gompertz models accounted for 75–99% of the variation in the number of xylem cells produced each year (Table S2). Although differences in growth rate among years were not significant ($P = 0.057$), they varied considerably among years (Table S1, Fig. 5). The maximum growth rate in 2011 and 2012 was 0.67 and 0.60 cells day⁻¹, respectively, which were approximately double the value observed in the warm dry year of 2015 (0.33 cells day⁻¹). Similarly, differences in total number of xylem cells were not significant among years ($P = 0.073$) while the mean value of xylem cells changed considerably across years (Table S1, Fig. 5). The mean number of xylem cells for 2012 reached 42 cells, which is approximately twice the value for 2015, which registered only 21 cells.

The total number of xylem cells was mainly attributable to rate and duration of cell production ($R^2 = 0.68$, $P < 0.001$, $n = 30$, Fig. 7a). When the growth rate was kept constant to its mean value and the duration of cell production was allowed to vary within two standard deviations from the mean, we observed a range of variation of 3.7 cells (29.9 to 33.6 cells). However, when the growth duration was kept constant at its mean value and growth rate was allowed to vary within two standard deviations from the mean, the total number of xylem cells varied from 20.8 to 42.6 cells (i.e., a range of variation of 21.8 cells). Therefore, the sensitivity analysis estimated the effects of rate and duration of cell production as 85.5 and 14.5%, respectively (Fig. 7b).

Although no significant relationships were found between growth rate, the total number of xylem cells, and annual climatic factors (Figs. 6 and S2), both growth rate and total wood production were found to be significantly correlated with precipitation in May (Figs. 6 and S3).

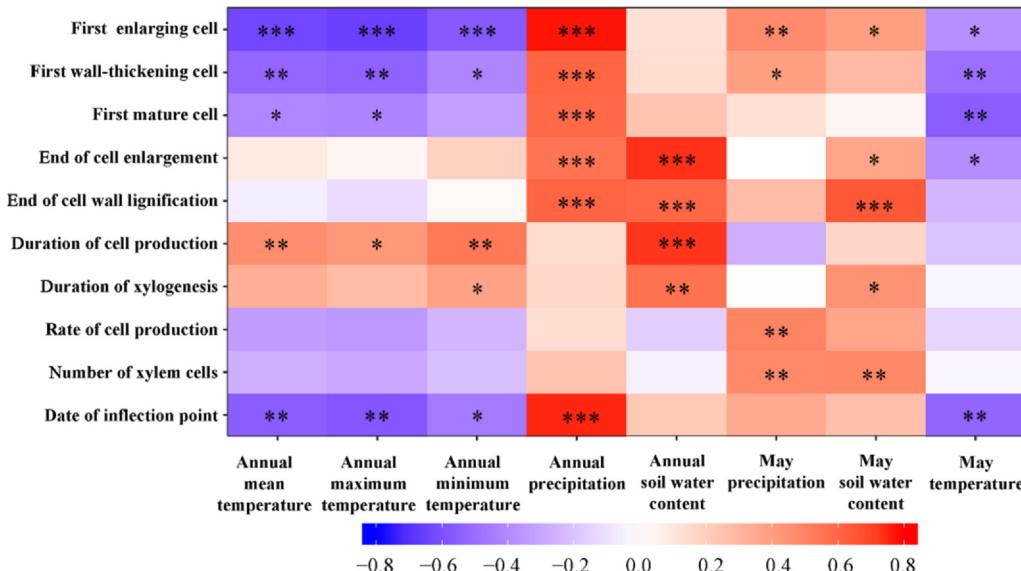


Fig. 6. Pearson's linear correlations between cambial phenology and associated climatic factors. Significant correlations of $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***) are displayed.

Table 2

Threshold mean, maximum, and minimum temperatures (mean \pm SD) corresponding to a 95% probability of xylogenesis onset in *J. przewalskii* estimated for 2011–2016 tested by Logistic regressions for a temperature interval of 30 days before and after cambial activity. Results of a one-way ANOVA are reported as *F* and *P* statistics.

	2011	2012	2013	2014	2015	2016	<i>F</i>	<i>P</i>
Mean temperature (°C)	6.1 \pm 1.3	6.7 \pm 1.1	5.2 \pm 1.0	6.3 \pm 0.5	6.0 \pm 0.9	6.5 \pm 0.0	1.59	0.201
Maximum temperature (°C)	11.9 \pm 1.2	12.4 \pm 0.6	11.0 \pm 1.0	11.6 \pm 0.5	11.4 \pm 0.9	12.2 \pm 0.0	2.19	0.088
Minimum temperature (°C)	2.3 \pm 0.9	2.2 \pm 0.9	1.3 \pm 0.4	1.9 \pm 0.5	1.2 \pm 1.1	1.7 \pm 0.0	2.22	0.086

4. Discussion

Using six years of data collected via high-resolution microcoring and from an on-site meteorological station, we found that the timing, duration, rate, and total wood production varies considerably with climatic variation in a cold and dry region. Importantly, we infer water availability is key to wood production in this cold and arid region. While the onset of growth is directly related to warming, the end of the growing season and wood production appears to be primarily driven by precipitation and water availability. In this way, warming could have symmetrical impacts on the advancement and duration of the potential growing season, but water availability could result in an asymmetrical impact on the realized growing season. That is, while the potential growing season could be extended equally in the spring and fall, the actual growth of trees in cool, dry regions might not follow suit and terminate much earlier than temperatures would permit due to increasing drought conditions during late summer.

4.1. Temperature threshold of growth onset

We found that temperature played an important role in the onset of xylogenesis. We observed significant negative trends between the onset of growth and annual air temperatures. These findings reveal that temperature is the major trigger of the growth initiation in *J. przewalskii* in the cold northeastern portion of the Tibetan Plateau. Our observed connection between temperature and growth initiation supports previous studies conducted over shorter periods within the region (Zhang et al., 2018a,b). Our findings also fall in line with many studies that report the importance of temperature to the onset of xylogenesis both in experimental (Gričar et al., 2006, 2007; Oribe et al., 2003) and natural conditions (Körner and Basler, 2010; Moser et al., 2010; Rossi et al., 2008, 2016). Although our study region is relatively dry, we found no relationships between soil water content and the onset of xylogenesis. To illustrate this, there was no delay in the onset of xylogenesis during the relatively strong drought of early 2013 and yet there was a 30-day delay in the onset during the very wet 2012 season when cool temperatures prevailed. Although significant positive correlations between

precipitation and the onset of xylogenesis were found, we do not think that trees delay the onset of the growing season when more precipitation occurs. This pattern is likely related due to the relationship between temperatures and precipitation during 2011–2016 (Fig. S4). Therefore, temperature remains the main factor drive the onset of xylogenesis in cold region, regardless of water stress.

Supporting our hypothesis, there is a threshold temperature for the onset of xylogenesis. The daily mean, maximum, and minimum threshold temperatures found in this study (6.1, 11.7, and 1.7 °C, respectively) are consistent with studies at treeline in the eastern Italian Alps (5.6–8.5, 10.9–13.3, 1.7–5.5 °C, respectively) (Deslauriers et al., 2008; Rossi et al., 2007). Studies have shown that mean threshold temperatures of 6–8 °C may determine treeline distributions worldwide (Hoch and Körner, 2012; Körner, 2003). Experimental findings suggested that a mean air temperature of 6 °C was suitable for cellular division (Gričar et al., 2006). Critical mean temperatures of 6–8 °C have also been shown to spur cell division in other parts of trees, such as shoots extension (James et al., 1994) and root growth (Alvarez-Uria and Körner, 2007). Our data adds more weight to the body of evidence that mean air temperature of 6–8 °C is the primary driver of growth reactivation in cold environments.

The estimated mean temperatures of 6–8 °C seem to constitute the threshold for limiting demand for photo-assimilates through metabolic processes involved in cell growth (Hoch et al., 2003). Supporting this hypothesis, seasonal photosynthesis monitoring results show that the net photosynthetic rate in *J. przewalskii* increased rapidly in early May when daily mean temperatures exceeded 6 °C, coinciding with radial growth onset (Su et al., 2011; Zhang et al., 2016). Temperature may also influence the enzymatic activities and auxin levels during cambial cell division (Hughes and Dunn, 1996; Love et al., 2009). Low temperatures may inhibit enzyme activity and affect cell division in cold environments (Buker, 1995).

The variability in temperature observed over the six monitoring years allowed us to estimate the potential advancement of tree growth with future climate change. We found the onset of xylogenesis in *J. przewalskii* to be advanced only 11.3 days °C⁻¹. This value is much lower than a prediction based on a “space-for-time” over an altitudinal

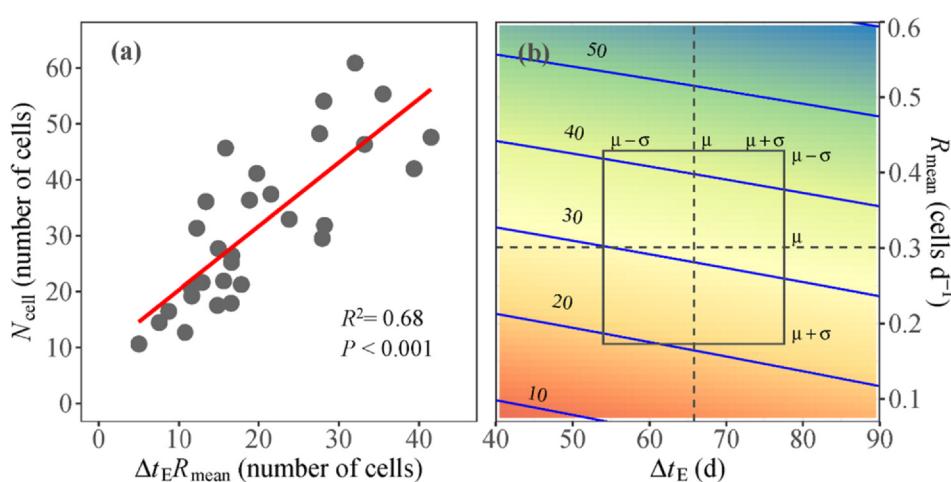


Fig. 7. (a) The simple physical model of the total number of xylem cells (N_{cell}) and the duration (Δt_E) and rate (R_{mean}) of cell production. The red line represents the regression. (b) Sensitivity analysis of the physical model. Dashed lines represent mean values and the square delimits the area of the mean \pm SD; blue lines denote the number of cells. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

gradient that suggested it would be 14.1 days $^{\circ}\text{C}^{-1}$ (Zhang et al., 2018b). If this holds for other settings and species, it indicates that “space-for-time” substitutions may overestimate the impact of climate change on tree growth, a finding in line with prior work (Elmendorf et al., 2015; Roitberg and Shoshany, 2017). According to our predictions from the data in this study, if temperatures continue to rise at the same rate in the study region ($0.27\ ^{\circ}\text{C decade}^{-1}$), the onset of xylogenesis in *J. przewalskii* might occur approximately 3.1 days earlier per decade.

4.2. Effects of drought on end of xylogenesis

In contrast to our finding that temperature regulated the onset of xylogenesis, no significant relationships between temperature and the end of xylogenesis were found. Research across latitudes indicated that drought conditions may determine the end of the growing season in *J. przewalskii* (Zhang et al., 2018a). That relationship remained consistent as we increased the amount of stem growth data over more years. Our study supports previous work indicating that cambial cell division in a dry environment is closely related to water potential (Balducci et al., 2016; Vieira et al., 2014; Ziaoc et al., 2018). We believe that water deficit may lead to a decrease of cell turgor, resulting in a termination in cell division and enlargement in end of the growing season (Steppe et al., 2015).

Demonstrating further the importance of water to the end of xylogenesis in our system is the water-growth dynamics we observed in 2016. The first end of cell production in 2016 occurred during a 16-day period without any measurable precipitation. After the 16-day dryspell, the occurrence of rather frequent and relatively large rainfall events over the following 38 days made September 2016 the wettest month of the year. This distribution of rainfall is unusual compared to the prior five years of monitoring. Concurrent with the 38 days of rather frequent and relatively large rainfall events, new earlywood-like cells were produced. We cannot ignore the role of temperature on the cambial reactivity we observed. Daily mean temperatures did not drop below $6.1\ ^{\circ}\text{C}$ until September 19, which is also unusual compared to the previous five years. It seems the trees with intra-annual density fluctuation formation would have ceased wood production if temperatures had decreased in mid-August and stayed below $6.1\ ^{\circ}\text{C}$. In combination with continued rainfall, the elevated warmth during August and early-September 2016 likely allowed for these trees to use the available moisture for a month longer than what had been previously observed. Therefore, we infer that the combination of extreme meteorological events—16 consecutive rainless days, the deluge on August 14, the resumption of frequent rainfall, and the warm conditions—likely played important roles in the interruption and then extension of stem growth. To the best of our knowledge, this kind of post-growing season growth has only been observed in the Mediterranean region where the resumption of rainfall in the autumn can produce these types of growth phenologies (Battipaglia et al., 2016; Camarero et al., 2010), making this potentially the first identification and intensive study of post-growing season cambial growth in a cool, dry, and continental environment. Observations from 2016 illustrate the seemingly tight coupling between water and the end of growing season.

Our study quantified how changes in precipitation late in the growing season leverage the end of xylogenesis in *J. przewalskii* over the northeastern Tibetan Plateau. We found that xylogenesis can be extended by 2.7 days for every increase of 10 mm in annual precipitation. If precipitation continues to decline at the same rate in the future ($6.5\ \text{mm decade}^{-1}$), the end of xylogenesis in *J. przewalskii* might occur approximately 1.8 days earlier per decade. However, as we observed in 2016, a late-summer and early-fall wetting trend could hypothetically reverse that potential trend, even if there is an increase of flash droughts during summer.

4.3. Impacts of climate on duration, rate, and wood production

It is no surprise that both temperature and soil water content were found to show positive relationships with the duration of xylogenesis, since the onset of growth was determined by temperature while the termination of growth was triggered by water availability. However, the response of the onset and termination of tree growth to changing climatic conditions are not the same, indicating that further warming could result in a net increase in the length of the growing season. These results are consistent with previous reports showing that the net growing season will extend in the future according to monitoring results for multiple sites across the Qilian Mountains (Zhang et al., 2018a). Although our data support the hypothesis that a warmer climate leads to a longer growing season, the negative effect of water availability on the duration of xylogenesis should not be underestimated in arid environment.

An increase in the duration of the growing season, however, does not always result in a higher level of wood production. Sensitivity analysis showed that the growth rate had a strong effect (85.5%) on wood production than growth duration. This result is further supported by multi-site and multi-elevation microcore study results for the Qilian Mountains (Zhang et al., 2018a,b) and the surrounding region (Ren et al., 2019). Our findings also echoes the results reported for other dry regions (Cuny et al., 2012; Rathgeber et al., 2011). Therefore, we conclude that wood production mainly depends on radial growth rate in arid regions.

We found that both the growth rate and total xylem cells showed a significant relationship with precipitation in May, indicating that water availability before the monsoon played a key role in growth rate and a determinant of wood production. Simulation studies in *J. przewalskii* showed same results that soil water content in May and early June played a crucial role in growth rates and tree ring widths, while temperature has no effects on wood production (Gou et al., 2013; Zhang et al., 2016). Consistently, intra-annual (He et al., 2016; Ren et al., 2015) and inter-annual (Gou et al., 2015; Liang et al., 2009; Shao et al., 2010) tree-ring growth have found to be positively correlated with early summer precipitation and drought conditions over the northeastern Tibetan Plateau. These results indicated that water availability is favoured exclusively to growth rate and wood production in arid environment, both in intra- and inter-annual levels.

May through early June is the main period of radial growth for *J. przewalskii* and accounts for more than two thirds of xylem cell formation. As dividing cambium and differentiating xylem cells are sinks of energy and require particularly high levels of sucrose for photosynthesis (Hansen and Beck, 1994; Oribe et al., 2003), we believe that drought conditions may influence the rate of cell division and enlargement via modulating the photosynthetic rate and assimilated carbohydrates. If a good conditions of water availability exist at the beginning of the growing period, *J. przewalskii* will maintain a high photosynthetic rate and produce a high level of carbohydrates to maintain a high division and enlargement rate of cambial cells, resulting in a high level of wood production. In support of these findings, studies have found that the photosynthetic rate of *J. przewalskii* had a significant correlation with moisture availability in the late spring and early summer (Zhang et al., 2016). However, when drought occurs in this period, although the photosynthetic rate in *J. przewalskii* still to be higher (Zhang et al., 2016), it appears that cell division in the stem is more sensitive to drought and is impacted earlier than photosynthesis and metabolism under drought stress (Muller et al., 2011). Therefore, the occurrence of drought stress in the early summer caused a direct decline in the water potential of cambial cells, creating unfavorable conditions for cell enlargement and decreasing growth rate and wood production. Our findings provide a specific mechanism on the decline in growth of *J. przewalskii* in recent three decades in the region (Gou et al., 2015).

5. Conclusion

We found a threshold daily mean temperature of 6.1 °C to determine the onset of xylogenesis in trees over the northeastern Tibetan Plateau, regardless of initial moisture conditions at the beginning of the growing season. We found that warmer temperatures likely result in an earlier initiation while drought results in an earlier end of the growing season, suggesting an advance and extension in the full growing season. Although our data supports the hypothesis that a warmer climate leads to a longer growing season, prolonged wood production is favored by water availability in this cold and arid environment. This conclusion is supported by observations that drought conditions in the early growing season result in a lower rate of wood production, a substantial reduction in cell production, and in a potential decline in radial growth under global warming conditions. Considering extreme weather conditions observed in our study region, with 2016 as the prime example here, trees may adapt their growing season and wood production patterns in response to more frequent extreme events in the future. Our findings highlight the resiliency of trees to the ongoing global change and provide the mechanistic understanding of how climate influence wood production at the cellular level in cold and arid region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

XG and JZ designed the project. JZ, JX, FW, and ZM performed field-based microcores. JZ, FZ, and JX performed lab-based experiments and data analysis. JZ drafted the manuscript, and MRA and NP contributed to the final version. All authors reviewed the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2020.104936>.

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