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Article

Critical minimum temperature limits xylogenesis and maintains treelines on the southeastern Tibetan Plateau

Xiaoxia Li [a], Eryuan Liang [a,b,*], Jozica Gričar [c], Sergio Rossi [d,e], Katarina Čufar [f], Aaron M. Ellison [g]

[a] Key Laboratory of Alpine Ecology and Biodiversity, Key Laboratory of Tibetan Environment Changes and Land Surface Processes, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China
[b] CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China
[c] Slovenian Forestry Institute, Department of Yield and Silviculture, Vecna pot 2, SI-1000 Ljubljana, Slovenia
[d] University of Quebec in Chicoutimi, Département des Sciences Fondamentales, 555, Boulevard de l'Université, Chicoutimi (QC) G7H2B1, Canada
[e] Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[f] University of Ljubljana, Biotechnical Faculty, Department of Wood Science and Technology, Jamnikarjeva 101, SI-1000 Ljubljana, Slovenia
[g] Harvard Forest, Harvard University, 324 North Main St., Petersham, MA 01366, USA

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ABSTRACT

Physiological and ecological mechanisms that define treelines are still debated. It has been suggested that the absence of trees above the treeline is caused by low temperatures that limit growth. Thus, we hypothesized that there is a critical minimum temperature ($CT_{\min}$) preventing xylogenesis at treeline. We tested this hypothesis by examining weekly xylogenesis across three and four growing seasons in two natural Smith fir (*Abies georgei* var. *smithii*) treeline sites on the southeastern Tibetan Plateau. Despite differences in the timing of cell differentiation among years, minimum air temperature was the dominant climatic variable associated with xylem growth; the critical minimum temperature ($CT_{\min}$) for the onset and end of xylogenesis occurred at 0.7 ± 0.4 °C. A process-based modelling chronology of tree-ring formation using this $CT_{\min}$ was consistent with actual tree-ring data. This extremely low $CT_{\min}$ permits Smith fir growing at treeline to complete annual xylem production and maturation and provides both support and a mechanism for treeline formation.

1. Introduction

The explanations for treeline formation focus on limitations of available resources [1,2], establishment sites [3], or time available for growth [4], although these ecophysiological causes remain debated [5–8]. Based on notable similarities in temperatures at treelines [9], the growth limitation hypothesis proposed that low temperatures limit the time available for meristematic growth and cell division [4,10]. This hypothesis has been supported by phenomenological data. For example, treeline trees tend to have higher amounts of non-structural carbohydrates than trees growing at lower elevation, suggesting that treeline is limited more by growth processes than by photosynthesis and carbon assimilation [11–13]. In parallel, dendroclimatic studies have identified a signal of reduced growth during periods with low temperatures at treelines in cold and humid areas [14–17].

Physiological manifestations of the growth limitation hypothesis include a constraint on the production of new cells by meristems below a $CT_{\min}$ [4] and a trade-off between taking maximal advantage of the length of the growing season while avoiding cellular damage due to early (fall, winter) or late (winter, spring) freezing events [18,19]. Such a trade-off would suggest a narrow thermal window for the onset and cessation of xylogenesis at treeline and recent studies have described temporal dynamics in xylogenesis of various tree species at treeline [20–24]. Some studies reported that a gradual increase in temperature (heat sum) was associated with the onset of cambial activity [21,25], whereas others estimated a $CT_{\min}$ of 6–8 °C for xylogenesis at the altitudinal treeline in the Eastern Alps [20,26]. Separating gradual (heat-sum) and threshold ($CT_{\min}$) effects on xylogenesis at treeline has not yet been accomplished.

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* Corresponding author.
E-mail address: liangey@itpcas.ac.cn (E. Liang).

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A mechanistic model can provide a deeper understanding on the climatic control on tree growth dynamics. The process-based Vaganov-Shashkin (VS) model has been used to simulate climatic controls on conifer tree-ring growth [27–29]. In the VS model, the critical temperature for cambial activity is a key parameter for modelling tree growth, but there are limited data available to estimate this parameter.

Our observations at the upper treeline of Smith fir (*Abies georgei* var. *smithii*) on the southeastern Tibetan Plateau, including a decade of uninterrupted *in situ* micrometeorological measurements and weekly collection of microcores containing cambium activity and wood formation during three consecutive growing seasons provide an opportunity to examine both gradual and threshold effects of temperature on xylogenesis at a natural alpine treeline. Specifically, we tested the potential for thermal control of xylogenesis to be a mechanism underlying the growth limitation hypothesis by (1) identifying the timing and dynamics of xylogenesis in Smith fir growing at treeline as a function of climatic factors; and (2) detecting a plausible $CT_{\min}$ for xylogenesis. Previous studies have found that the growth of Smith fir near treeline is constrained by the minimum temperature in summer [30,31]. The onset of bud swelling and needle unfolding in Smith fir is delayed by 3.5 days for each 100-m increase in elevation [32], indicating a thermal limitation of tree phenology. Therefore, we hypothesized that minimum temperature limits xylogenesis and that a threshold minimum temperature controls the timing of the onset and ending of xylogenesis.

2. Materials and methods

2.1. Study sites and tree selection

We studied the natural alpine treeline of Smith fir growing on the eastern side of the Sygera Mountains (29°10′–30°15′N, 93°12′–95°35′E) on the southeastern Tibetan Plateau [33]. The southeastern Tibetan Plateau is characterized by a cold and humid climate, and has the highest natural treeline (up to 4900 m a.s.l.) in the Northern Hemisphere [34]. Smith fir is a shade tolerant tree species and is one of the dominant treeline species in this region. The upper treeline position depends on topographic aspect and ranges from 4250 to 4400 m a.s.l. We studied two sites at open-canopy treelines: site 1 was at 4360 m a.s.l. on an east-facing slope, and site 2 was at 4250 m a.s.l. on a southeast-facing slope. The sites were 200 m apart, on slopes <15°. *Rhododendron aganniphum* var. *schizopeplum* dominated the understory. The coverage of Smith fir was <20% and the podzolic soils had an average pH value of 4.5.

At each site, five dominant trees were selected in April 2007. These trees had a mean age of 201 ± 24 and 117 ± 14 years, and mean diameters at 1.3 m aboveground of 34 ± 4 and 44 ± 7 cm in sites 1 and 2, respectively. Because repeated sampling could cause severe wounding that could modify xylogenesis, another five trees per site with similar diameters at breast height were chosen for samplings in 2009 and 2010. Trees with polycormic stems, partially dead crowns, reaction wood, or other evident damage were avoided.

2.2. Meteorological data

An automatic weather station (Campbell Scientific, CR1000) was installed in November 2006 in an open area above the treeline (29°39′N, 94°42′E, 4390 m a.s.l.) at a linear distance of ≈150 m and 200 m from sites 1 and 2, respectively. Measurements of air (3 m aboveground) and soil temperature (at 10-, 20- and 40-cm depths), precipitation, snow fall, and soil water content (at 10-, 20-, and 40-cm depths) were collected at 30-min intervals. These data were used to compute daily averages, minima, and maxima of each variable.

2.3. Microcoring and histological analyses

Xylem growth was studied from 2007 until 2010 at site 1 and from 2007 to 2009 at site 2. One microcore (15-mm long, 2-mm diameter) was collected from each tree weekly from May until October around the stem at breast height (1.3 m aboveground) using a Trephor tool. Immediately after removal from the trees, the microcores were fixed in a formalin-ethanol-acetic acid (FAA) solution. The microcores contained innermost phloem, cambium, developing xylem, and at least three previous xylem growth rings. In the laboratory, the microcores were dehydrated with successive immersions in a graded series of ethanol and *d*-limonene, then embedded in paraffin. Transverse sections (9–12 μm in thickness) were cut from the samples with a Leica RM 2245 rotary microtome using Feather N35H knives (Osaka, Japan). Sections were stained with a mixture of safranin (0.5% in 95% ethanol) and astra blue (0.5% in 95% ethanol) and observed with a Nikon Eclipse 800 light microscope under bright field and polarized light to identify the phases of differentiation of the developing xylem cells [35]. In cross-section, cambial cells were characterized by thin cell walls and small radial diameters [36,37]. Newly-formed xylem cells in the phase of cell enlargement contained protoplasts, had thin primary walls, and a radial diameter at least twice the size of the cambial cells [38]. The onset of cell-wall thickening was determined by birefringence in the cell walls under polarized light. Mature cells had completely red-stained walls and empty lumen. For each sample, the total current xylem cell number was determined by counting the number of cells undergoing enlargement, cell-wall thickening, and the number of mature cells along three radial files.

2.4. Data standardization and fitting of xylem growth

The data were standardized to compensate for variation in the number of xylem cells along the tree circumference. The total cell number of the previous years was counted on three radial files per sample and used for standardization. The standardized number of cells nc_{ij} in the ith phase of the jth sample was calculated as:

$$nc_{ij} = n_{ij}(a_m/a_j), \tag{1}$$

where n_{ij} is the number of cells in the current year, a_m is the mean number of cells of the previous ring of all j-samples, and a_j is the mean number of cells of the previous ring in each j-sample.

We modelled the dynamics of xylem growth by fitting a Gompertz function to the number of xylem cells that were produced through time:

$$y = A\exp[-e^{(\beta-\kappa t)}], \tag{2}$$

where y is the weekly cumulative sum of tracheids, t is the time of the year computed as day of the year, A is an asymptote (constant), and β and k are constants reflecting the x-intercept placement and rate of change, respectively. Model parameters were estimated using the Origin software package (Version 8.5, OriginLab Corporation, Northampton, MA, USA).

2.5. Estimation of the onset and ending of xylogenesis

We used observations of cell differentiation to identify the onset, ending, and duration of xylogenesis from counts of the number of cells in three radial files per tree. In spring, xylogenesis was considered to have started when at least one tangential row of cells was observed in the enlarging phase. Because of the weekly resolution of the monitoring, we used the occurrence of 1–2 enlarging xylem cells along any of the checked three radial files as an indicator the xylogenesis had begun [35]. In late summer, when cells were no longer observed in the wall thickening and lignification phase, xylogenesis was considered to have ended. The duration of xylogenesis was estimated as the number of days between the dates of onset and ending of xylogenesis.

Comparisons between sites in onset, duration, and ending of differentiation in the developing xylem ring were done with generalized linear models (GLM). Homoscedasticity was checked using Shapiro-Wilk and Levene tests.

2.6. Identifying CT_{min}

Logistic regression (LOGISTIC procedure in SPSS 16.0) was used to model the probability of xylogenesis as a function of air temperature. Xylogenesis was coded as zero (not occurring) or one (occurring). CT_{min} was estimated as that temperature for which the probability of ongoing xylem growth equalled 0.5 [39]. For each tree and year, the model was fitted with three respective daily temperature series (mean, minimum, and maximum). Therefore, the CT_{min} represents the critical night temperature for xylogenesis. Model verification included the likelihood-ratio χ^2, Wald's χ^2 for regression parameter and goodness of fit, and Hosmer-Lemeshow $\hat{C}$ for possible lack of fit. None of the models were excluded because of a lack of fit. CT_{min} values were compared between sites and years using analysis of variance (ANOVA) models. Model validation was performed by comparing the observed and predicted CT_{min} values. Degree-day sum (*DD*) is an index representing a measure of accumulated heat. In spring, accumulation of *DD* began when daily air average temperature ≥ 5 °C for five consecutive days. The temperature 5 °C is a commonly used standard in calculating the effective heat sum in agriculture and forestry [40].

2.7. Climate-growth relationships

We used two approaches to identify relationships between intra-annual xylem growth and climatic variables during four growing seasons. One approach consisted of computation of Pearson's correlation coefficients between xylem cell production and weather data for weekly intervals. Weather data here include daily mean, daily absolute minimum, daily absolute maximum temperatures, growing degree-days (GDD) > 5 °C, and sums of precipitation.

Intra-annual xylem growth may be controlled both by endogenous (e.g., hormonal regulation) and exogenous factors (e.g., climate). To analyse the climatic effect, a common approach was used to remove the endogenous growth trend by fitting a growth curve, and to estimate the growth departure, calculated as the dimensionless ratio between observed and expected growth [41]. This ratio (hereafter called the 'growth index') was calculated as the number of tracheids produced during the week divided by the expected values estimated using the Gompertz function [42]. To account for possible effects of time-lags, daily weather data were averaged (temperature) or summed (precipitation) weekly from 1 to 10 d prior to each sampling date (referred to as P1–P10). To minimize the effects of temporal autocorrelation, correlation coefficients were calculated on first-order differences for both datasets.

2.8. Tree-ring modelling

We used the Vaganov-Shashkin (VS) model to simulate tree-ring growth at the Smith fir treelines in the Sygera Mountains. The VS model estimates xylem growth and its internal characteristics based on equations relating daily temperature, precipitation, and sunlight to the kinetics of xylem development [43]. It assumes that climatic influences are directly but nonlinearly related to tree-ring characteristics through controls on the rates of cambial activity processes. To date, it has been successfully used to simulate and evaluate the relationships between climate and tree-ring formation under a variety of environmental conditions in many different regions [28,29,44–47]. Values from field observations were used for input parameters needed by the VS model: soil moisture, depth of root system, temperature sum for initiation of growth, soil water drainage rate, and maximum daily precipitation infiltrating into soil. We used our estimates of CT_{min} as the starting value for the minimum temperature parameter. Model fit was evaluated against an actual tree-ring width chronology from Smith fir treeline in the Sygera Mts., which had been developed and used for paleoclimatic reconstructions in this region [31]. The best estimate of physiological CT_{min} was found by iteration and comparison between simulated and observed chronologies (1960–2006).

Finally, a single simulated tree-ring width chronology was created for the Smith fir treeline in the Sygera Mts. based on daily climate data from the Nyingchi meteorological station (3000 m a.s.l.). To account for the altitude differences between Nyingchi and the study sites, we extended the time series of daily temperatures at the treeline back to 1960 based on a linear regression of the Nyingchi data and our own micrometeorological data ($r \geq 0.89$, 2007–2010, Supporting Information Fig. S1).

3. Results

3.1. Micrometeorological conditions at the upper treeline

The sampling sites at the upper treeline were cold and humid. Despite a difference of 110 m in elevation and different topographical aspects of the two treeline sites, they had similar temperatures (Supporting Information Fig. S2). Annual average temperatures (2007–2010) ranged from 0.1 to 0.9 °C, while growing-season (June–September) temperatures ranged from 6.4 to 7.1 °C (Fig. 1). On average, annual precipitation was 951 mm, of which 62% fell during the monsoon season (June–September). Snowfall occurred mainly from November to May. Because of snowmelt and increased precipitation, soil moisture content increased rapidly from the beginning of April and remained above 30% from early May until November, and finally decreased to near zero in late November and early December. The year 2008 was characterized by heavy spring snowfall and had the latest snowmelt and soil thawing during the four studied years (Fig. 1).

3.2. Xylogenesis

The onset of xylogenesis occurred from late May to early June and differed significantly among years ($F = 15.73$, $P < 0.001$). The onset of xylogenesis was observed 4–9 days later in 2008 than in the other years, at both sites (Fig. 2a). No difference was found in onset of xylogenesis between sites ($F = 2.31$, $P > 0.05$). Xylogenesis ended between the beginning and the end of September and

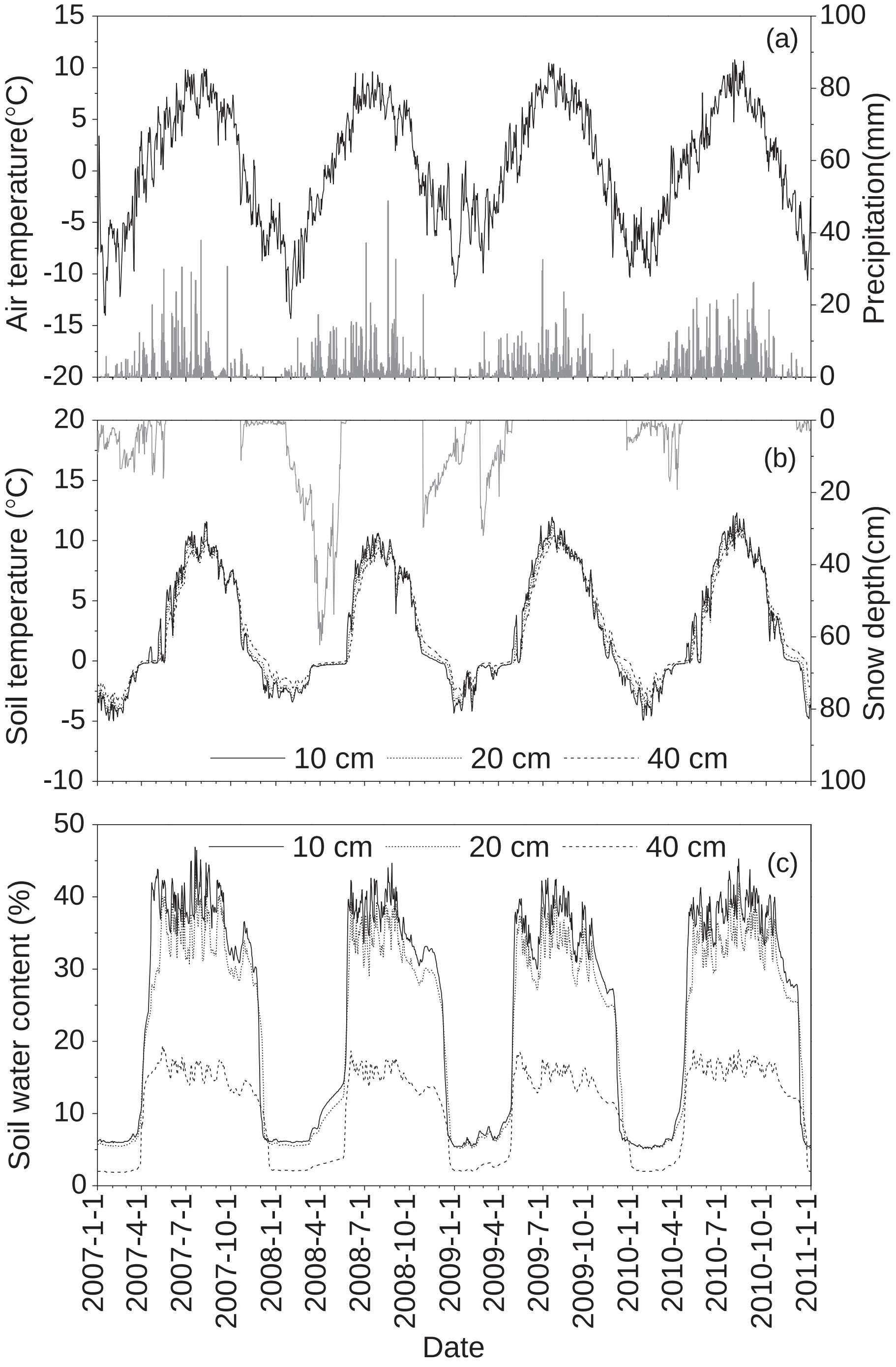

Fig. 1. Micrometeorological conditions (2007–2010) at the upper treeline in the Sygera Mts., southeastern Tibetan Plateau, showing (a) daily mean air temperature and daily total precipitation, (b) daily soil temperature (at depths of 10, 20 and 40 cm) and snow depth, and (c) daily mean soil volumetric moisture contents (at depths of 10, 20 and 40 cm).

differed significantly among years ($F = 10.42$, $P < 0.005$), and occurred 1–2 weeks later in 2010 at site 1 (Fig. 2b).

Overall, the duration of xylogenesis lasted from 109 to 125 days (Fig. 2c), with no significant differences detected between sites ($F = 3.80$, $P > 0.05$). Conversely, there were significant variations among years ($F = 4.71$, $P < 0.05$). From 2007 to 2009, the average period between the onset and ending of xylogenesis was 113 days, whereas the average of 125 days was required to complete xylogenesis in 2010.

3.3. Relationship between climate and xylem growth

Weekly cumulative xylem production was fit well by the Gompertz function ($0.96 \leq r^2 \leq 0.98$; Supporting Information Table S1 and Fig. S3). Intra-annual xylem cell production was significantly and positively correlated with daily minimum and mean air temperatures and GDD > 5 °C at both sites (Fig. 3a, b). However, only minimum temperature was significantly correlated with growth indices after removing the growth trends (Fig. 3c, d). At site

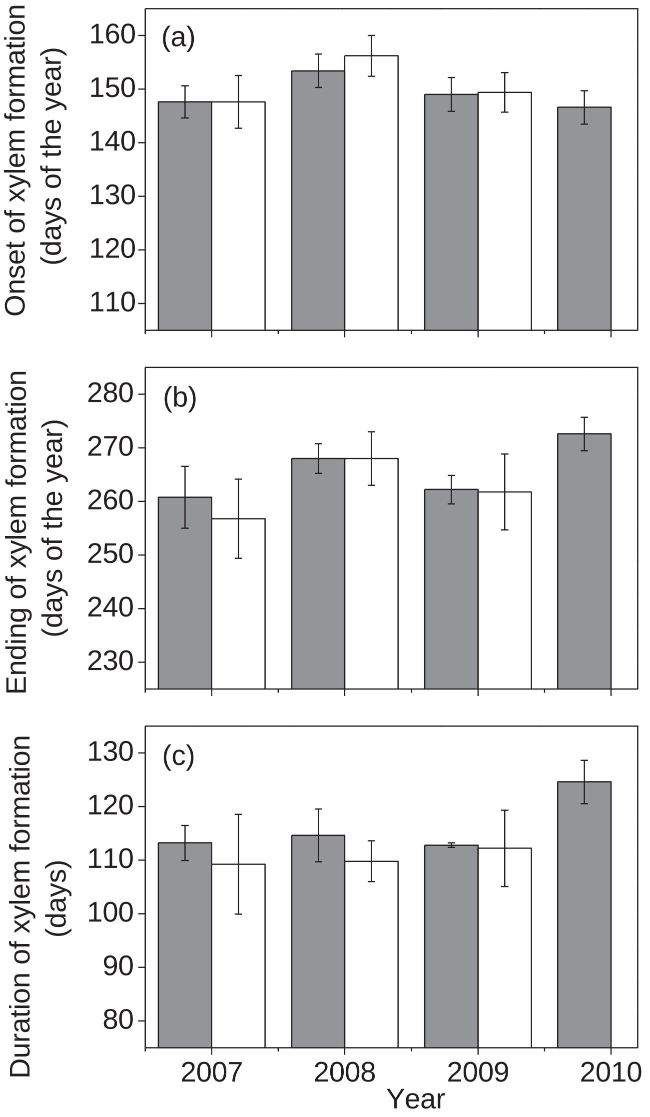

Fig. 2. Onset (a), ending (b), and duration (c) of xylem formation of Smith fir (*Abies georgei* var. *smithii)* based on weekly xylogenesis observations at site 1 (4360 m a.s.l.) (grey columns) and site 2 (4250 m a.s.l.) (white columns). Error bars indicate standard deviations among trees.

1, positive correlations between growth indices and minimum temperatures were found for time lags of 0–3 days ($r = 0.34$, $P < 0.05$), whereas the corresponding time lags were 7–10 days at site 2 ($r = 0.42$, $P < 0.05$). No significant correlations were found between xylem cell production or growth index and precipitation from P0 to P10.

3.4. CT_{min}

CT_{min} at which there was a 0.5 probability that xylem formation was ongoing is shown in Fig. 4 and Table 1 for site 1 (2007–2010) and site 2 (2007–2009). The values for minimum, mean, and maximum temperatures of 0.6, 4.0, and 9.3 °C were estimated for the onset of xylogenesis, whereas the corresponding values for the ending of xylem differentiation were 0.7, 3.9, and 9.0 °C. There were no differences among critical temperatures for the onset and ending of xylogenesis (ANOVA, $P > 0.05$), with values of 0.7 ± 0.4, 3.9 ± 0.5, and 9.1 ± 0.6 °C for the minimum, mean, and maximum temperatures, respectively. No significant differences were found between the two sites in terms of the estimated air temperature thresholds for the onset and ending of xylogenesis (ANOVA, $P > 0.05$). The mean air temperature during the period of xylem formation at both sites was 6.8 ± 0.4 °C.

Among years, degree-day sum until the onset of xylogenesis at site 1 ranged from 8 to 41 *DD*, whereas corresponding temperature sums ranged from 12 to 34 *DD* at site 2 (Table 2). Accumulated heat sum from 1 January until onset of xylem growth varied strongly between study years at both sites ($F = 17.6$, $P < 0.01$).

3.5. Tree-ring modelling

Initializing the Vaganov-Shashkin (VS) model with an estimated $CT_{\mathrm{min}} = 0.7$ °C yielded a best-fit estimate of physiological $CT_{\mathrm{min}} = 0.9$ °C (Table 3, Fig. 5). The correlation between observations and predictions varied slightly for CT_{min} of 0.3–1.0 °C, whereas it decreased rapidly for $CT_{\mathrm{min}} > 1$ °C (Fig. 6). Overall, significant, positive correlations were found between the modelled and measured chronologies when CT_{min} varied within the range of 0.7 ± 0.4 °C ($r = 0.62$, $P < 0.01$).

4. Discussion

The importance of temperature for xylogenesis during and after its onset has been demonstrated repeatedly [25,37,48–51]. These and other data suggest that air temperature, not soil temperature, directly limits xylogenesis at high latitudes and altitudes [20,24,52]. Minimum temperature is assumed to be an important driver of tree species range limits [7,19], and so a CT_{min} with narrow bounds should exist for the onset and ending of xylogenesis. However, long-term monitoring of xylem growth at natural treelines is limited, which has precluded assessment of CT_{min} for xylogenesis by direct observations.

4.1. Effects of climate on xylem growth

As predicted, minimum air temperature strongly limited xylem growth of Smith fir at the upper treeline on the southeastern Tibetan Plateau. This finding agrees with those from dendroclimatological analysis in the same study area [31] and wood formation studies at high latitudes and altitudes [22,37]. The importance of minimum air temperature may be related to the timing of cell differentiation, which may occur mainly during the night when the temperature is lower [53,54]. Controlled experiments also showed that night temperatures could directly influence xylem cell expansion of *Podocarpus latifolius* [55]. According to Körner [7], cell doubling time, which is highest and fairly constant at temperatures of 10–25 °C, approaches infinity at 1–2 °C, suggesting a minimum temperature limit on cell division. The simulated ring-width chronologies produced by the VS model of tree-ring formation also exhibit similar positive correlations with the minimum temperature during summer (Supporting Information Fig. S4, $P < 0.01$). CT_{min} is thus expected to limit xylogenesis of Smith fir at the treeline.

4.2. Critical temperatures for xylogenesis

Our results suggest that threshold effects, not heat sum effects, play a key role in the onset of xylogenesis at Smith fir treeline. Despite the variance in timing and duration of xylogenesis during

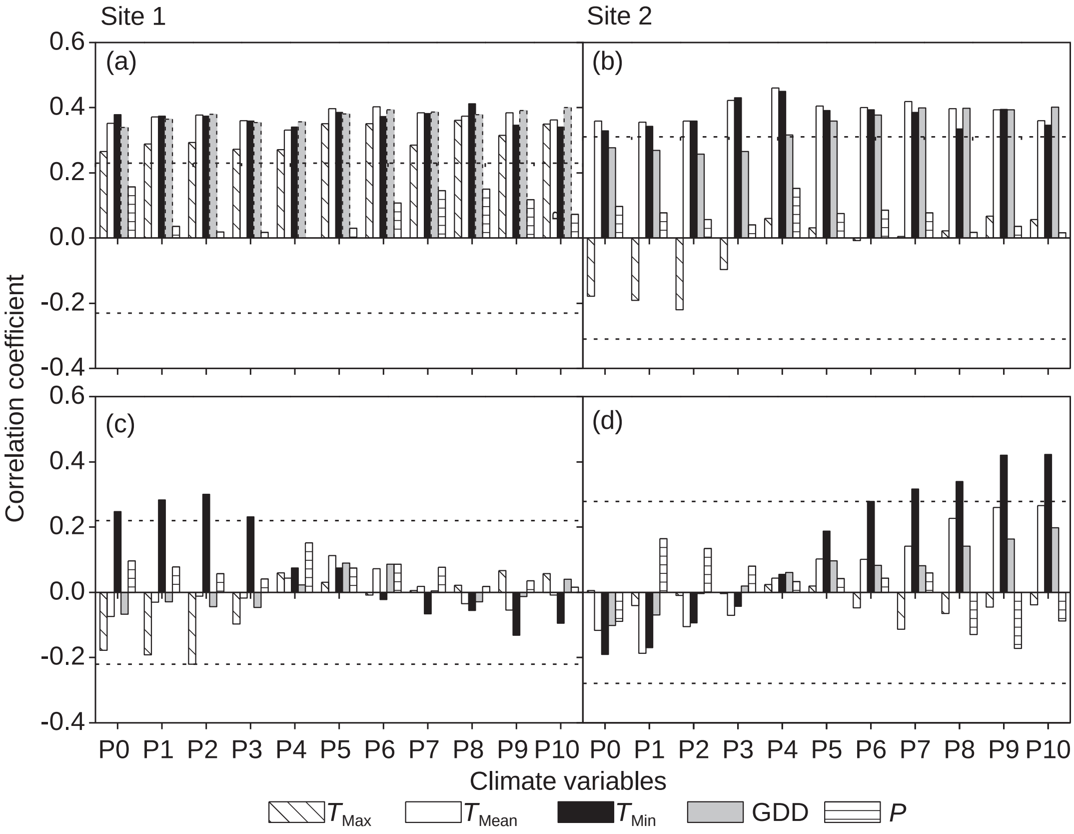

Fig. 3. Lagged (0–10 days) Pearson correlation coefficients between xylem cell production (a, b), growth index (c, d), and corresponding climatic variables. P0 represents the weekly climatic mean for the exact period between two sampling dates. P1–P10 represent the weekly means lagged 1–10 days before the sampling date. Dotted horizontal lines show the 95% confidence limits. *Abbreviations*: T_{Max} = maximum temperature, T_{Mean} = mean temperature, T_{Min} = minimum temperature, P = precipitation, and GDD = growing degree days above 5 °C.

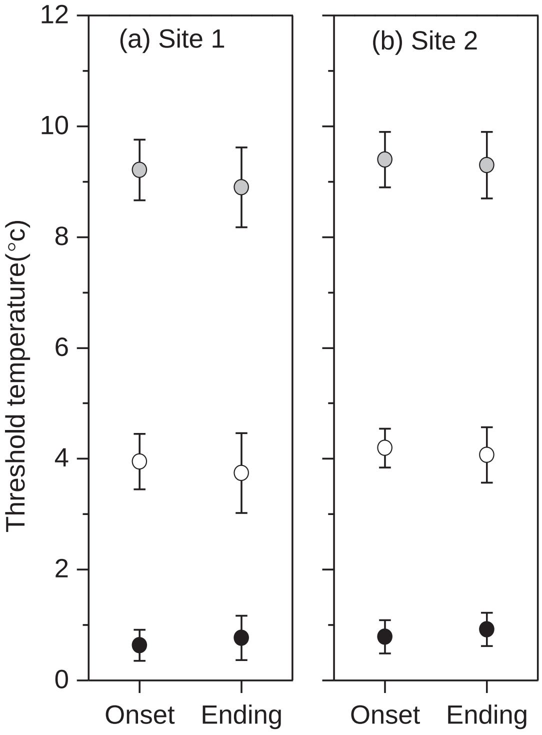

Fig. 4. Critical minimum (black dots), mean (white dots), and maximum (grey dots) air temperatures at sites 1 and 2, corresponding with the 0.5-probability of the onset and ending of xylem formation according to xylogenesis observations in Smith fir. Error bars indicate the standard deviation among trees.

our four years of observations, minimum, average, and maximum temperatures for the onset and ending of xylogenesis were narrowly bounded with average values of 0.7, 3.9, and 9.1 °C, respectively.

Most studies to date have indicated that xylogenesis in conifers growing in cold climates can take place when the daily minimum temperatures ≥4–5 °C [39,56]. However, based on the presented 4-year observations of xylogenesis and uninterrupted *in situ* micrometeorological measurements directly at the treeline, we found that the CT_{min} for xylogenesis in Smith fir is as low as 0.7 °C. In particular, based on this CT_{min}, the modelled chronology produced by VS model is consistent with actual tree-ring data, suggesting that minimum temperature could be considered as a significant driver of xylem growth. Such a low CT_{min} may have evolved to provide sufficient time to complete xylogenesis at alpine treelines. The length of the growing season for stem growth diminishes with altitude and reaches a minimum at the alpine treeline. According to some authors [10,39], a tree can only survive when the growing seasons are at least 3 months long and the mean air temperature during the growing season is 6.4 °C; each of these constraints critically limit the growth and development of trees. At Smith fir treelines in southeastern Tibet, the duration of xylem growth of 115 days provided by a $CT_{min} < 1$ °C and a mean air temperature of 6.8 °C during the growing season extended by this low CT_{min} together meet these prerequisites for tree growth and development.

The dates of snow melting and soil thawing also are thought to be critical for the onset of xylogenesis and could therefore determine the annual xylem production [27]. At our treeline sites, the onset of xylem growth occurred 4–46 days after snow melting and 4–29 days after soil thawing in spring, which coincided with

Table 1
Mean (±standard deviation) of the threshold daily maximum (T_{Max}), mean (T_{Mean}) and minimum (T_{Min}) temperatures for the onset and ending of xylogenesis.

Site	Year	Onset of xylogenesis			Ending of xylogenesis		
		T_{Min} (°C)	T_{Mean}(°C)	T_{Max}(°C)	T_{Min}(°C)	T_{Mean} (°C)	T_{Max} (°C)
1	2007	0.6 ± 0.2	4.3 ± 0.1	9.7 ± 0.4	0.8 ± 0.3	3.9 ± 0.3	9.0 ± 0.4
	2008	0.8 ± 0.2	3.7 ± 0.3	8.9 ± 0.4	0.6 ± 0.2	3.5 ± 0.2	8.7 ± 0.1
	2009	0.8 ± 0.3	4.4 ± 0.1	9.8 ± 0.2	1.1 ± 0.1	4.7 ± 0.1	9.9 ± 0.1
	2010	0.3 ± 0.1	3.4 ± 0.2	9.1 ± 0.3	0.4 ± 0.1	2.9 ± 0.3	8.0 ± 0.2
2	2007	0.5 ± 0.3	4.3 ± 0.2	9.4 ± 0.5	0.9 ± 0.4	4.1 ± 0.5	9.3 ± 0.6
	2008	1.0 ± 0.3	3.9 ± 0.3	8.7 ± 0.4	0.7 ± 0.3	3.6 ± 0.2	8.7 ± 0.1
	2009	0.8 ± 0.3	4.4 ± 0.4	9.8 ± 0.2	1.1 ± 0.3	4.5 ± 0.4	9.8 ± 0.3

Table 2
Mean (±standard deviation) of degree-day sums (≥5 °C) at onset of xylogenesis, number of days from the date of snow melting ($Date_{snow}$) and soil thawing ($Date_{soil}$) to the onset date of xylogenesis ($Date_{xylem}$).

	Year	Degree-day sum at onset of xylogenesis (DD)	Number of days between $Date_{snow}$ and $Date_{xylem}$ (days)	Number of days between $Date_{soil}$ and $Date_{xylem}$ (days)
Site 1	2007	41 ± 13	4 ± 5	4 ± 3
	2008	11 ± 0	18 ± 3	6 ± 3
	2009	8 ± 2	29 ± 3	11 ± 3
	2010	8 ± 3	46 ± 3	29 ± 5
Site 2	2007	34 ± 20	6 ± 5	6 ± 3
	2008	13 ± 12	21 ± 4	9 ± 5
	2009	12 ± 7	29 ± 3	11 ± 3

Table 3
The best-fit parameter estimates for the VS model used in this study.

Model parameter	Description (unit)	Value
CT_{min}	Minimum temperature for tree growth (°C)	0.9
T_{opt1}	Lower end of range of optimal temperatures (°C)	5.9
T_{opt2}	Upper end of range of optimal temperatures	9.3
T_{max}	Maximum temperature for tree growth (°C)	19.9
W_{min}	Minimum soil moisture for tree growth (v/v)	0.06
W_{opt1}	Lower end of range of optimal soil moisture (v/v)	0.18
W_{opt2}	Upper end of range of optimal soil moisture (v/v)	0.22
W_{max}	Maximum soil moisture for tree growth (v/v)	0.50
T_{beg}	Temperature sum for initiation of growth (°C)	30
D_{root}	Depth of root system (mm)	50
P_{max}	Maximum daily precipitation for saturated soil (mm)	20
K_1	Fraction of precipitation penetrating soil (dimensionless)	0.86
K_2	First coefficient for calculation of transpiration (mm/day)	0.12
K_3	Second coefficient for calculation of transpiration (1/ °C)	0.175
K_r	Coefficient for water infiltration from soil (dimensionless)	0.006

the surpassing of CT_{min} (Table 2). This temporal lag also suggests that threshold effects exist for the onset of xylogenesis at Smith treeline.

The growth limitation hypothesis predicts that the absence of trees above the treeline is attributable to critical minimum temperature for growth [4]. Treeline trees often have slower growth rates and higher non-structural carbohydrate levels than trees at lower altitudes [11–13], suggesting a carbon sink rather than carbon gain limitation [57]. However, some authors have argued that tree populations with the highest non-structural carbohydrate concentrations may be the most carbon limited in terms of growth [58,59]. Although our observations of xylogenesis cannot differentiate between carbon limitation and a carbon sink in Smith fir, the significant effect of a narrowly bounded CT_{min} on xylem growth provides a physiological mechanism for the growth limitation hypothesis.

Conflict of interest

The authors declare that they have no conflict of interest.

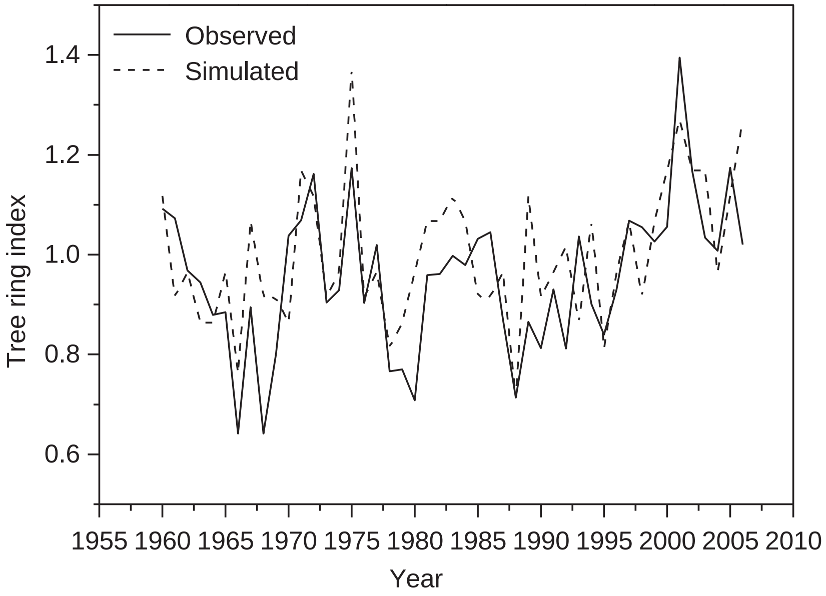

Fig. 5. Observed (solid line) and simulated (dashed line) tree-ring width indices at Smith fir treeline in the Sygera Mts. on the southeastern Tibetan Plateau, 1960–2006.

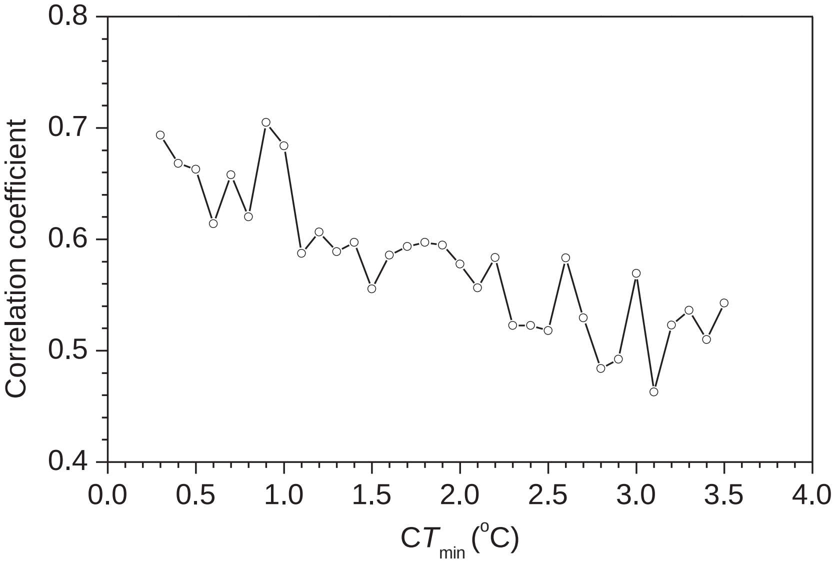

Fig. 6. Pearson correlation coefficients between the observed and estimated values of tree-ring width for different estimates of CT_{min}.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.scib.2017.04.025.

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