



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

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

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28

29 **Abstract**

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

41

42 **Keywords:** Cambial activity • critical minimum temperature • timberline • xylem • Vaganov-Shashkin  
43 model

44

## 45 **1 Introduction**

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

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

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

70 Our observations at the upper treeline of Smith fir (*Abies georgei* var. *smithii*) on the southeastern  
71 Tibetan Plateau, including a decade of uninterrupted *in situ* micrometeorological measurements and  
72 weekly collection of microcores containing cambium activity and wood formation during three  
73 consecutive growing seasons provide an opportunity to examine both gradual and threshold effects of  
74 temperature on xylogenesis at a natural alpine treeline. Specifically, we tested the potential for

75 thermal control of xylogenesis to be a mechanism underlying the growth limitation hypothesis by (1)  
76 identifying the timing and dynamics of xylogenesis in Smith fir growing at treeline as a function of  
77 climatic factors; and (2) detecting a plausible  $CT_{\min}$  for xylogenesis. Previous studies have found that  
78 the growth of Smith fir near treeline is constrained by the minimum temperature in summer [30, 31].  
79 The onset of bud swelling and needle unfolding in Smith fir is delayed by 3.5 days for each 100-m  
80 increase in elevation [32], indicating a thermal limitation of tree phenology. Therefore, we  
81 hypothesized that minimum temperature limits xylogenesis and that a threshold minimum temperature  
82 controls the timing of the onset and ending of xylogenesis.

83

## 84 **2 Materials and methods**

### 85 **2.1. Study sites and tree selection**

86 We studied the natural alpine treeline of Smith fir growing on the eastern side of the Sygera  
87 Mountains (29° 10' – 30° 15' N, 93° 12' – 95° 35' E) on the southeastern Tibetan Plateau [33]. The  
88 southeastern Tibetan Plateau is characterized by a cold and humid climate, and has the highest natural  
89 treeline (up to 4900 m a.s.l.) in the Northern Hemisphere [34]. Smith fir is a shade tolerant tree  
90 species and is one of the dominant treeline species in this region. The upper treeline position depends  
91 on topographic aspect and ranges from 4250 to 4400 m a.s.l. We studied two sites at open-canopy  
92 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  
93 southeast-facing slope. The sites were 200 m apart, on slopes < 15°. *Rhododendron aganniphum* var.  
94 *schizopeplum* dominated the understory. The coverage of Smith fir was < 20% and the podzolic soils  
95 had an average pH value of 4.5.

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

102

### 103 **2.2 Meteorological data**

104 An automatic weather station (Campbell Scientific, CR1000) was installed in November 2006 in an

105 open area above the treeline (29°39' N, 94°42'E, 4390 m a.s.l.) at a linear distance of  $\approx$ 150 m and 200  
106 m from sites 1 and 2, respectively. Measurements of air (3 m aboveground) and soil temperature (at  
107 10-, 20- and 40-cm depths), precipitation, snow fall, and soil water content (at 10-, 20-, and 40-cm  
108 depths) were collected at 30-minute intervals. These data were used to compute daily averages,  
109 minima, and maxima of each variable.

110

### 111 **2.3 Microcoring and histological analyses**

112 Xylem growth was studied from 2007 until 2010 at site 1 and from 2007 to 2009 at site 2. One  
113 microcore (15-mm long, 2-mm diameter) was collected from each tree weekly from May until  
114 October around the stem at breast height (1.3 m aboveground) using a Trephor tool. Immediately after  
115 removal from the trees, the microcores were fixed in a formalin-ethanol-acetic acid (FAA) solution.  
116 The microcores contained innermost phloem, cambium, developing xylem, and at least three previous  
117 xylem growth rings. In the laboratory, the microcores were dehydrated with successive immersions in  
118 a graded series of ethanol and *d*-limonene, then embedded in paraffin. Transverse sections (9–12  $\mu$ m  
119 in thickness) were cut from the samples with a Leica RM 2245 rotary microtome using Feather N35H  
120 knives (Osaka, Japan). Sections were stained with a mixture of safranin (0.5 % in 95 % ethanol) and  
121 astra blue (0.5 % in 95% ethanol) and observed with a Nikon Eclipse 800 light microscope under  
122 bright field and polarized light to identify the phases of differentiation of the developing xylem cells  
123 [35]. In cross-section, cambial cells were characterized by thin cell walls and small radial diameters  
124 [36, 37]. Newly-formed xylem cells in the phase of cell enlargement contained protoplasts, had thin  
125 primary walls, and a radial diameter at least twice the size of the cambial cells [38]. The onset of  
126 cell-wall thickening was determined by birefringence in the cell walls under polarized light. Mature  
127 cells had completely red-stained walls and empty lumen. For each sample, the total current xylem cell  
128 number was determined by counting the number of cells undergoing enlargement, cell-wall thickening,  
129 and the number of mature cells along three radial files.

130

### 131 **2.4 Data standardization and fitting of xylem growth**

132 The data were standardized to compensate for variation in the number of xylem cells along the tree  
133 circumference. The total cell number of the previous years was counted on three radial files per  
134 sample and used for standardization. The standardized number of cells  $nc_{ij}$  in the  $i^{\text{th}}$  phase of the  $j^{\text{th}}$

135 sample was calculated as:

$$136 \quad nc_{ij} = n_{ij} (a_m / a_j) \quad (1)$$

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

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

$$141 \quad y = A \exp[-e^{(\beta - kt)}] \quad (2)$$

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

146

## 147 **2.5 Estimation of the onset and ending of xylogenesis**

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

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

159

## 160 **2.6 Identifying CT<sub>min</sub>**

161 Logistic regression (LOGISTIC procedure in SPSS 16.0) was used to model the probability of  
162 xylogenesis as a function of air temperature. Xylogenesis was coded as zero (not occurring) or one  
163 (occurring). CT<sub>min</sub> was estimated as that temperature for which the probability of ongoing xylem  
164 growth equalled 0.5 [39]. For each tree and year, the model was fitted with three respective daily

165 temperature series (mean, minimum, and maximum). Therefore, the  $CT_{\min}$  represents the critical night  
166 temperature for xylogenesis. Model verification included the likelihood-ratio  $\chi^2$ , Wald's  $\chi^2$  for  
167 regression parameter and goodness of fit, and Hosmer-Lemeshow  $\hat{C}$  for possible lack of fit. None of  
168 the models were excluded because of a lack of fit.  $CT_{\min}$  values were compared between sites and  
169 years using analysis of variance (ANOVA) models. Model validation was performed by comparing  
170 the observed and predicted  $CT_{\min}$  values. Degree-day sum (DD) is an index representing a measure of  
171 accumulated heat. In spring, accumulation of DD began when daily air average temperature  $\geq 5^\circ\text{C}$  for  
172 five consecutive days. The temperature  $5^\circ\text{C}$  is a commonly used standard in calculating the effective  
173 heat sum in agriculture and forestry [40].

174

## 175 **2.7 Climate-growth relationships**

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

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

191

## 192 **2.8 Tree-ring modeling**

193 We used the Vaganov-Shashkin (VS) model to simulate tree-ring growth at the Smith fir treelines in



194 the Sygera Mountains. The VS model estimates xylem growth and its internal characteristics based on  
195 equations relating daily temperature, precipitation, and sunlight to the kinetics of xylem development  
196 [43]. It assumes that climatic influences are directly but nonlinearly related to tree-ring characteristics  
197 through controls on the rates of cambial activity processes. To date, it has been successfully used to  
198 simulate and evaluate the relationships between climate and tree-ring formation under a variety of  
199 environmental conditions in many different regions [28, 29, 44-47]. Values from field observations  
200 were used for input parameters needed by the VS model: soil moisture, depth of root system,  
201 temperature sum for initiation of growth, soil water drainage rate, and maximum daily precipitation  
202 infiltrating into soil. We used our estimates of  $CT_{\min}$  as the starting value for the minimum  
203 temperature parameter. Model fit was evaluated against an actual tree-ring width chronology from  
204 Smith fir treeline in the Sygera Mts., which had been developed and used for paleoclimatic  
205 reconstructions in this region [31]. The best estimate of physiological  $CT_{\min}$  was found by iteration  
206 and comparison between simulated and observed chronologies (1960 – 2006).

207 Finally, a single simulated tree-ring width chronology was created for the Smith fir treeline in the  
208 Sygera Mts. based on daily climate data from the Nyingchi meteorological station (3,000 m a.s.l.). To  
209 account for the altitude differences between Nyingchi and the study sites, we extended the time series  
210 of daily temperatures at the treeline back to 1960 based on a linear regression of the Nyingchi data  
211 and our own micrometeorological data ( $r \geq 0.89$ , 2007–2010, Supporting Information Fig. S1).

212

### 213 **3 Results**

#### 214 **3.1 Micrometeorological conditions at the upper treeline**

215 The sampling sites at the upper treeline were cold and humid. Despite a difference of 110 m in  
216 elevation and different topographical aspects of the two treeline sites, they had similar temperatures  
217 (Supporting Information Fig. S2). Annual average temperatures (2007 – 2010) ranged from 0.1 to 0.9  
218 °C, while growing-season (June-September) temperatures ranged from 6.4 to 7.1 °C (Fig. 1). On  
219 average, annual precipitation was 951 mm, of which 62 % fell during the monsoon season (June to  
220 September). Snowfall occurred mainly from November to May. Because of snowmelt and increased  
221 precipitation, soil moisture content increased rapidly from the beginning of April and remained above  
222 30% from early May until November, and finally decreased to near zero in late November and early  
223 December. The year 2008 was characterized by heavy spring snowfall and had the latest snowmelt

224 and soil thawing during the four studied years (Fig. 1).

225

### 226 **3.2 Xylogenesis**

227 The onset of xylogenesis occurred from late May to early June and differed significantly among years  
228 ( $F = 15.73$ ,  $P < 0.001$ ). The onset of xylogenesis was observed 4 – 9 days later in 2008 than in the  
229 other years, at both sites (Fig. 2 a). No difference was found in onset of xylogenesis between sites ( $F$   
230  $= 2.31$ ,  $P > 0.05$ ). Xylogenesis ended between the beginning and the end of September and differed  
231 significantly among years ( $F = 10.42$ ,  $P < 0.005$ ), and occurred 1–2 weeks later in 2010 at site 1 (Fig.  
232 2 b).

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

238

### 239 **3.3 Relationship between climate and xylem growth**

240 Weekly cumulative xylem production was fit well by the Gompertz function ( $0.96 \leq r^2 \leq 0.98$ ;  
241 Supporting Information Table S1 and Fig. S3). Intra-annual xylem cell production was significantly  
242 and positively correlated with daily minimum and mean air temperatures and GDD  $> 5$  °C at both  
243 sites (Fig. 3 a, b). However, only minimum temperature was significantly correlated with growth  
244 indices after removing the growth trends (Figs. 3 c, d). At site 1, positive correlations between growth  
245 indices and minimum temperatures were found for time lags of 0 – 3 days ( $r = 0.34$ ,  $P < 0.05$ ),  
246 whereas the corresponding time lags were 7 – 10 days at site 2 ( $r = 0.42$ ,  $P < 0.05$ ). No significant  
247 correlations were found between xylem cell production or growth index and precipitation from P0 to  
248 P10.

249

### 250 **3.4 CT<sub>min</sub>**

251 The critical minimum air temperature (CT<sub>min</sub>) at which there was a 0.5 probability that xylem  
252 formation was ongoing is shown in Fig. 4 and Table 1 for site 1 (2007 – 2010) and site 2 (2007 –  
253 2009). The values for minimum, mean, and maximum temperatures of 0.6, 4.0, and 9.3 °C were

254 estimated for the onset of xylogenesis, whereas the corresponding values for the ending of xylem  
255 differentiation were 0.7, 3.9, and 9.0 °C. There were no differences among critical temperatures for  
256 the onset and ending of xylogenesis (ANOVA,  $P > 0.05$ ), with values of  $0.7 \pm 0.4$ ,  $3.9 \pm 0.5$ , and  $9.1 \pm$   
257  $0.6$  °C for the minimum, mean, and maximum temperatures, respectively. No significant differences  
258 were found between the two sites in terms of the estimated air temperature thresholds for the onset  
259 and ending of xylogenesis (ANOVA,  $P > 0.05$ ). The mean air temperature during the period of xylem  
260 formation at both sites was  $6.8 \pm 0.4$  °C.

261 Among years, degree-day sum until the onset of xylogenesis at site 1 ranged from 8–41 DD,  
262 whereas corresponding temperature sums ranged from 12–34DD at site 2 (Table 2). Accumulated heat  
263 sum from 1 January until onset of xylem growth varied strongly between study years at both sites ( $F=$   
264  $17.6$ ,  $P < 0.01$ ).

265

### 266 **3.5 Tree-ring modelling**

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

272

## 273 **4 Discussion**

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

281

### 282 **4.1 Effects of climate on xylem growth**

283 As predicted, minimum air temperature strongly limited xylem growth of Smith fir at the upper

284 treeline on the southeastern Tibetan Plateau. This finding agrees with those from dendroclimatological  
285 analysis in the same study area [31] and wood formation studies at high latitudes and altitudes [22,  
286 37]. The importance of minimum air temperature may be related to the timing of cell differentiation,  
287 which may occur mainly during the night when the temperature is lower [53, 54]. Controlled  
288 experiments also showed that night temperatures could directly influence xylem cell expansion of  
289 *Podocarpus latifolius* [55]. According to Körner [7], cell doubling time, which is highest and fairly  
290 constant at temperatures of 10–25°C, approaches infinity at 1–2°C, suggesting a minimum  
291 temperature limit on cell division. The simulated ring-width chronologies produced by the VS model  
292 of tree-ring formation also exhibit similar positive correlations with the minimum temperature during  
293 summer (Supporting Information Fig. S4,  $P < 0.01$ ).  $CT_{\min}$  is thus expected to limit xylogenesis of  
294 Smith fir at the treeline.

295

#### 296 **4.2 Critical temperatures for xylogenesis**

297 Our results suggest that threshold effects, not heat sum effects, play a key role in the onset of  
298 xylogenesis at Smith fir treeline. Despite the variance in timing and duration of xylogenesis during  
299 our four years of observations, minimum, average, and maximum temperatures for the onset and  
300 ending of xylogenesis were narrowly bounded with average values of 0.7, 3.9, and 9.1 °C,  
301 respectively.

302 Most studies to date have indicated that xylogenesis in conifers growing in cold climates can take  
303 place when the daily minimum temperatures  $\geq 4\text{--}5$  °C [39, 56]. However, based on the presented  
304 4-year observations of xylogenesis and uninterrupted *in situ* micrometeorological measurements  
305 directly at the treeline, we found that the  $CT_{\min}$  for xylogenesis in Smith fir is as low as 0.7 °C. In  
306 particular, based on this  $CT_{\min}$ , the modelled chronology produced by VS model is consistent with  
307 actual tree-ring data, suggesting that minimum temperature could be considered as a significant driver  
308 of xylem growth. Such a low  $CT_{\min}$  may have evolved to provide sufficient time to complete  
309 xylogenesis at alpine treelines. The length of the growing season for stem growth diminishes with  
310 altitude and reaches a minimum at the alpine treeline. According to some authors [10, 39], a tree can  
311 only survive when the growing seasons are at least 3 months long and the mean air temperature during  
312 the growing season is 6.4 °C; each of these constraints critically limit the growth and development of  
313 trees. At Smith fir treelines in southeastern Tibet, the duration of xylem growth of 115 days provided

314 by a  $CT_{\min} < 1$  °C and a mean air temperature of 6.8 °C during the growing season extended by this  
315 low  $CT_{\min}$  together meet these prerequisites for tree growth and development.

316 The dates of snow melting and soil thawing also are thought to be critical for the onset of  
317 xylogenesis and could therefore determine the annual xylem production [27]. At our treeline sites, the  
318 onset of xylem growth occurred 4-46 days after snow melting and 4-29 days after soil thawing in  
319 spring, which coincided with the surpassing of  $CT_{\min}$  (Table 2). This temporal lag also suggests that  
320 threshold effects exist for the onset of xylogenesis at Smith treeline.

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

329

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338

339 **Conflict of interest** The authors declare that they have no conflict of interest.

340

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486 **Table 1** Mean ( $\pm$  standard deviation) of the threshold daily maximum (MaxT), mean (MeanT)  
 487 and minimum (MinT) temperatures for the onset and ending of xylogenesis.

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Site	Year	Onset of xylogenesis			Ending of xylogenesis		
		MinT(°C)	MeanT(°C)	MaxT(°C)	MinT(°C)	MeanT(°C)	MaxT(°C)
1	2007	0.6 $\pm$ 0.2	4.3 $\pm$ 0.1	9.7 $\pm$ 0.4	0.8 $\pm$ 0.3	3.9 $\pm$ 0.3	9.0 $\pm$ 0.4
	2008	0.8 $\pm$ 0.2	3.7 $\pm$ 0.3	8.9 $\pm$ 0.4	0.6 $\pm$ 0.2	3.5 $\pm$ 0.2	8.7 $\pm$ 0.1
	2009	0.8 $\pm$ 0.3	4.4 $\pm$ 0.1	9.8 $\pm$ 0.2	1.1 $\pm$ 0.1	4.7 $\pm$ 0.1	9.9 $\pm$ 0.1
	2010	0.3 $\pm$ 0.1	3.4 $\pm$ 0.2	9.1 $\pm$ 0.3	0.4 $\pm$ 0.1	2.9 $\pm$ 0.3	8.0 $\pm$ 0.2
2	2007	0.5 $\pm$ 0.3	4.3 $\pm$ 0.2	9.4 $\pm$ 0.5	0.9 $\pm$ 0.4	4.1 $\pm$ 0.5	9.3 $\pm$ 0.6
	2008	1.0 $\pm$ 0.3	3.9 $\pm$ 0.3	8.7 $\pm$ 0.4	0.7 $\pm$ 0.3	3.6 $\pm$ 0.2	8.7 $\pm$ 0.1
	2009	0.8 $\pm$ 0.3	4.4 $\pm$ 0.4	9.8 $\pm$ 0.2	1.1 $\pm$ 0.3	4.5 $\pm$ 0.4	9.8 $\pm$ 0.3

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502 **Table 2** Mean ( $\pm$ standard deviation) of degree-day sums ( $\geq 5^{\circ}\text{C}$ ) at onset of xylogenesis,  
 503 number of days from the date of snow melting ( $\text{Date}_{\text{snow}}$ ) and soil thawing ( $\text{Date}_{\text{soil}}$ ) to the  
 504 onset date of xylogenesis ( $\text{Date}_{\text{xylogenesis}}$ ).

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

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517 **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 ( $^{\circ}C$ )	0.9
$T_{\text{opt1}}$	Lower end of range of optimal temperatures ( $^{\circ}C$ )	5.9
$T_{\text{opt2}}$	Upper end of range of optimal temperatures	9.3
$T_{\max}$	Maximum temperature for tree growth ( $^{\circ}C$ )	19.9
$W_{\min}$	Minimum soil moisture for tree growth (v/v)	0.06
$W_{\text{opt1}}$	Lower end of range of optimal soil moisture (v/v)	0.18
$W_{\text{opt2}}$	Upper end of range of optimal soil moisture (v/v)	0.22
$W_{\max}$	Maximum soil moisture for tree growth (v/v)	0.50
$T_{\text{beg}}$	Temperature sum for initiation of growth ( $^{\circ}C$ )	30
$D_{\text{root}}$	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 ( $1/^{\circ}C$ )	0.175
$K_r$	Coefficient for water infiltration from soil (dimensionless)	0.006

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520 **Figure captions:**

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

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

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531 **Fig. 3** Lagged (0–10 days) Pearson correlation coefficients between xylem cell production (a,  
532 b), growth index (c, d), and corresponding climatic variables. P0 represents the weekly  
533 climatic mean for the exact period between two sampling dates. P1 to P10 represent the  
534 weekly means lagged 1–10 days before the sampling date. Dotted horizontal lines show the  
535 95% confidence limits. *Abbreviations:* MaxT = maximum temperature, MeanT= mean  
536 temperature, MinT= minimum temperature, P = precipitation, and GGD = growing degree  
537 days above 5°C.

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539 **Fig. 4** Critical minimum (black dots), mean (white dots), and maximum (grey dots) air  
540 temperatures at sites 1 and 2, corresponding with the 0.5-probability of the onset and ending

541 of xylem formation according to xylogenesis observations in Smith fir. Error bars indicate the  
542 standard deviation among trees.

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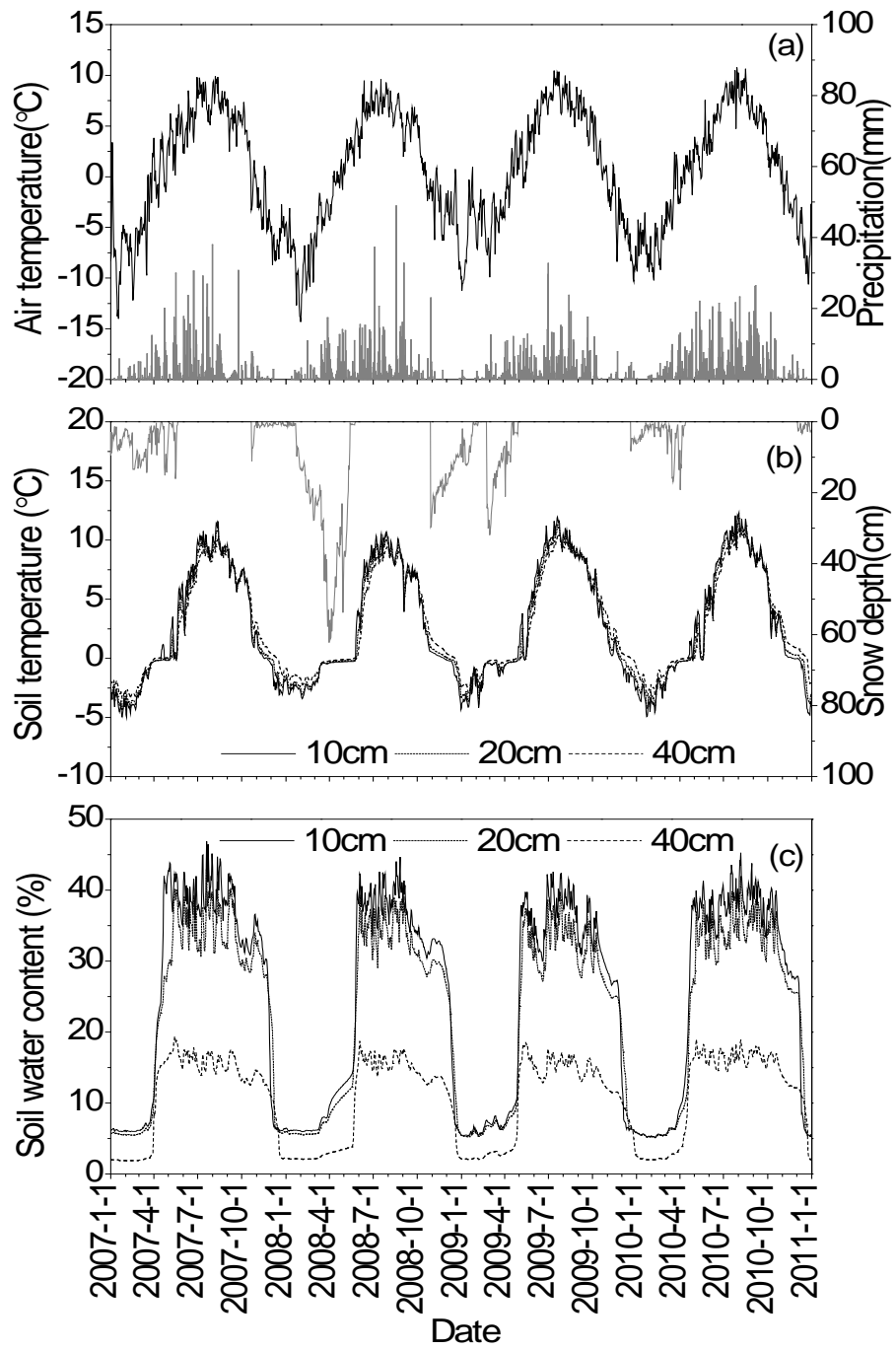
544 **Fig. 5** Observed (solid line) and simulated (dashed line) tree-ring width indices at Smith fir  
545 treeline in the Sygera Mts. on the southeastern Tibetan Plateau, 1960–2006.

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

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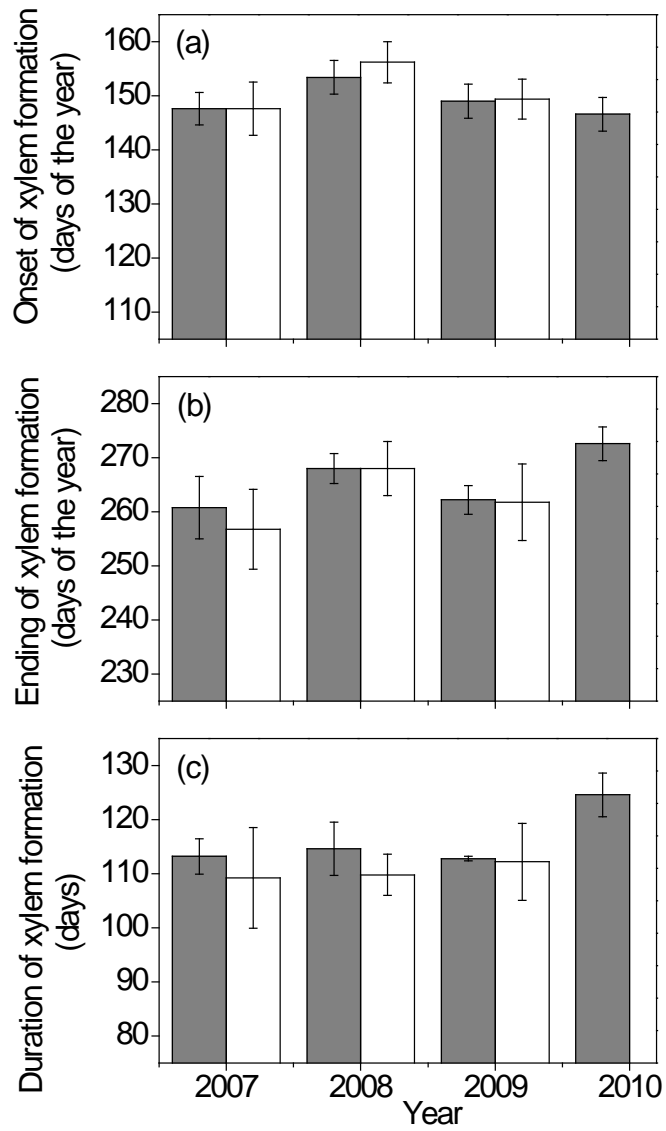


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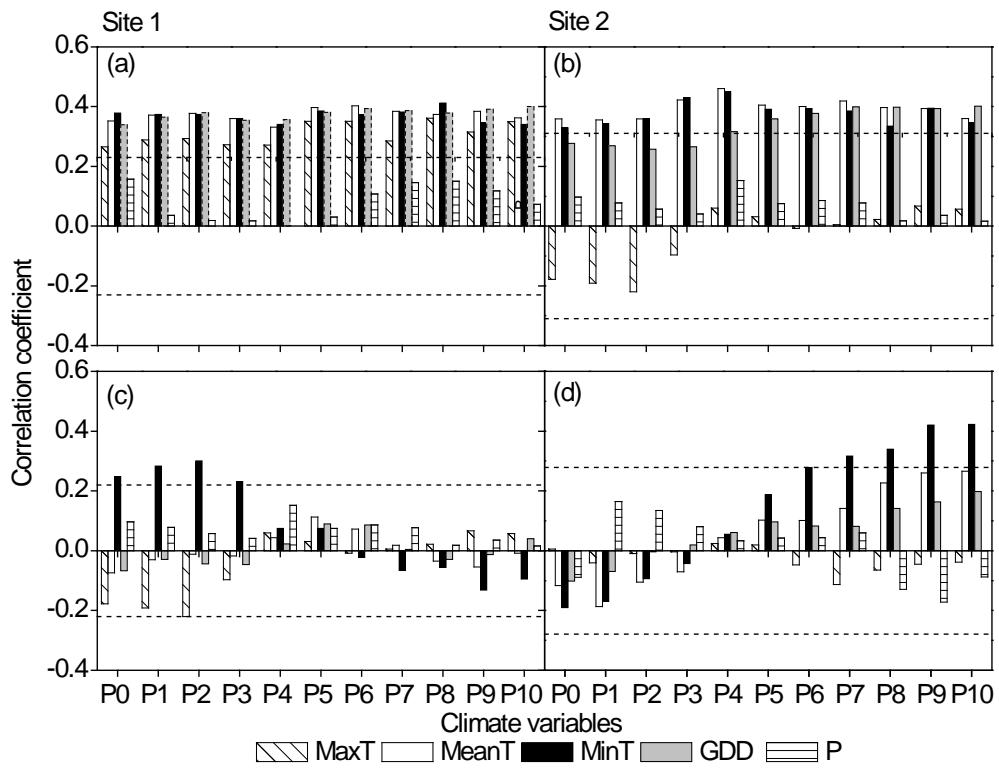
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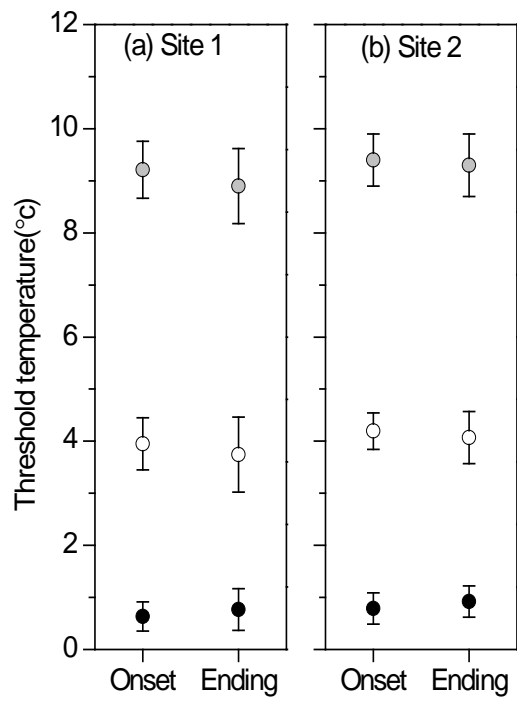
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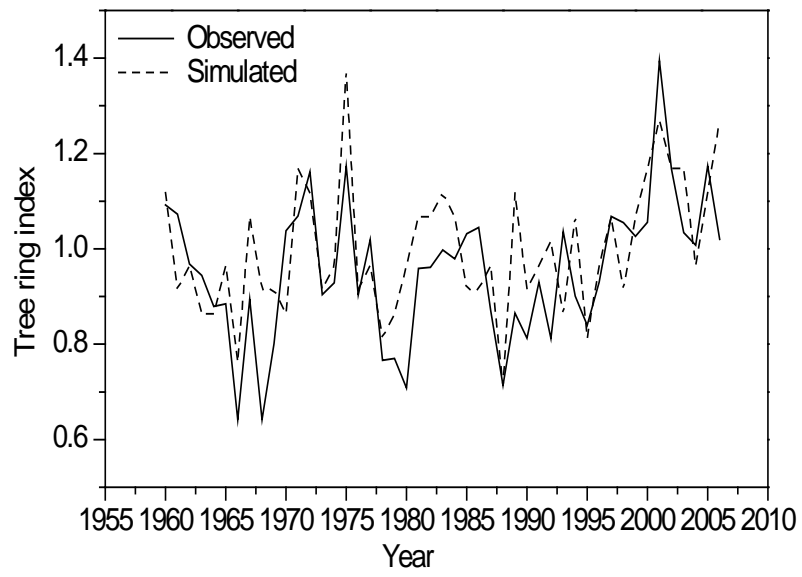
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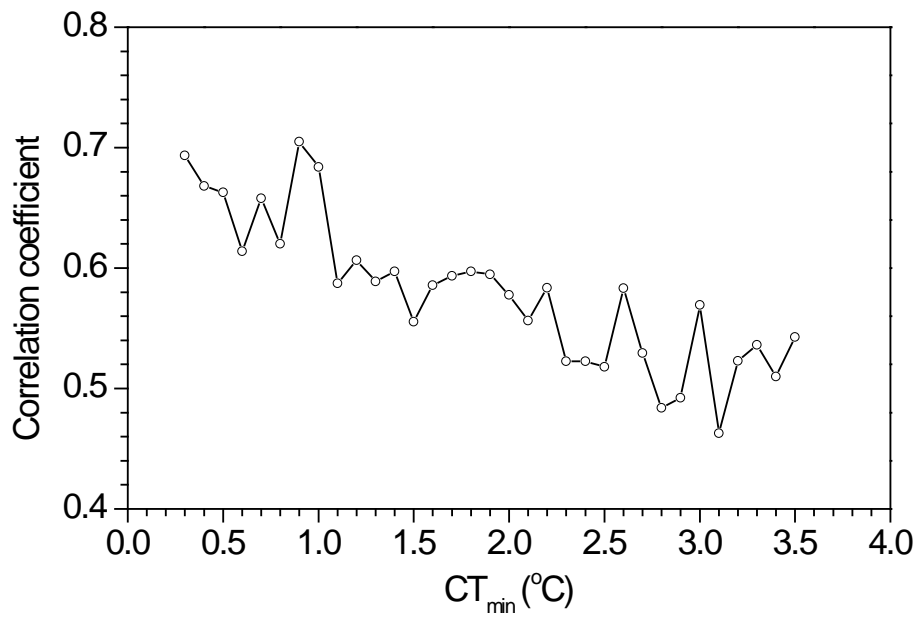
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610 Fig. 6

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1 **Supplementary content**

2 **Table S1** Parameters of the Gompertz function ( $A$ ,  $\beta$ ,  $K$ ),  $R^2$  and day of the inflection  
3 point (tp) for Smith fir growing at two treeline sites, 2007 – 2010.

	Year	A	$\beta$	$K(10^{-2})$	tp	$R^2$
Site 1	2007	23.95	5.48	3.25	170.59	0.98
	2008	22.97	5.97	3.32	179.32	0.96
	2009	25.68	7.07	4.08	174.50	0.96
	2010	21.08	5.67	3.25	176.67	0.99
Site 2	2007	24.79	5.03	2.85	176.56	0.98
	2008	21.22	6.97	3.87	178.13	0.98
	2009	23.62	5.70	3.02	188.53	0.98

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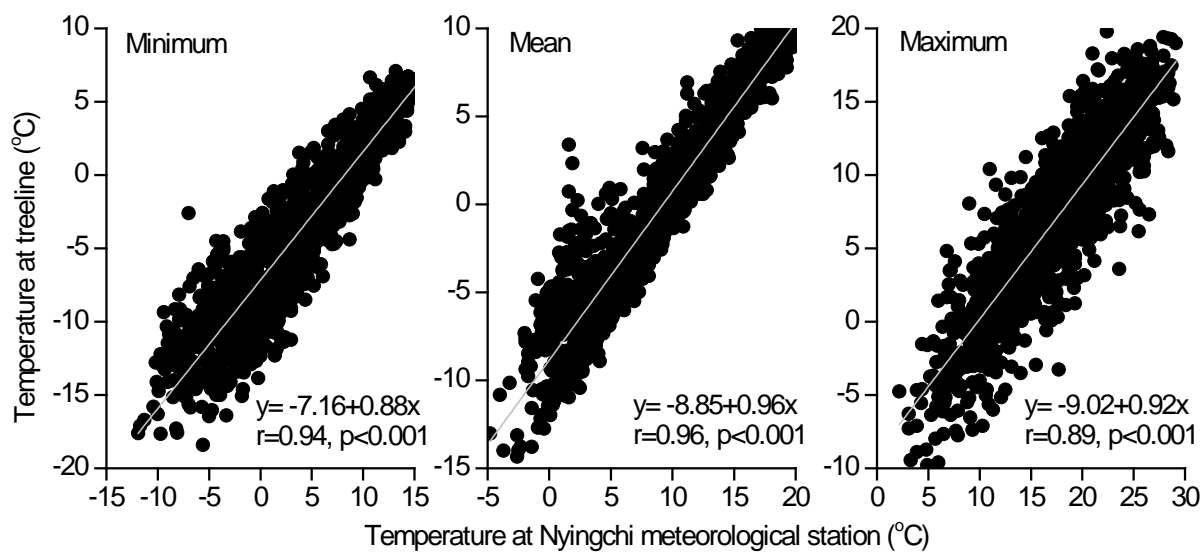
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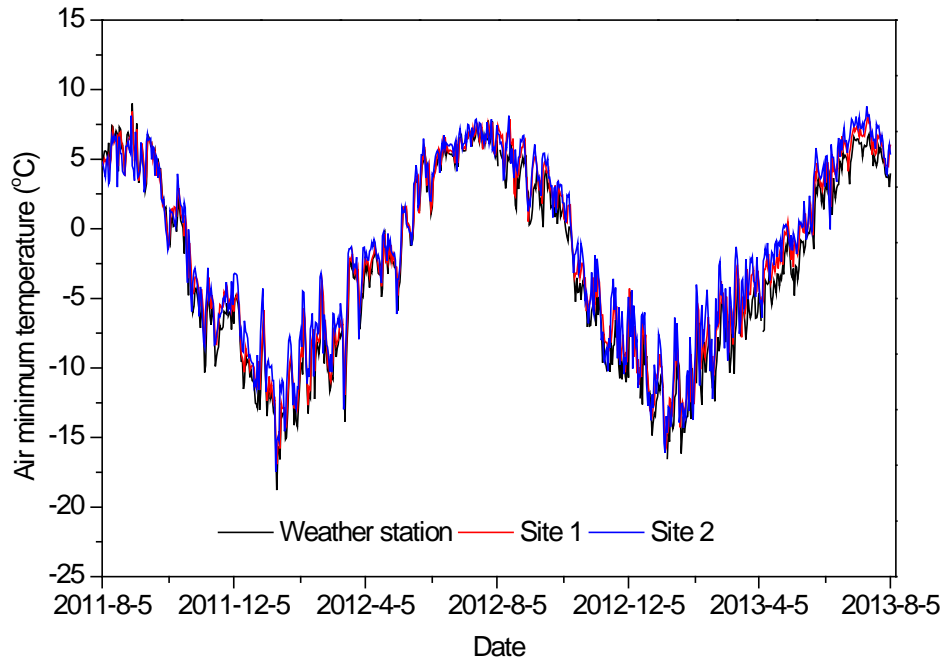
16 **Fig. S1.** Plots of the daily minimum, mean, and maximum temperature from automatic

17 weather stations at treeline in the Sygera Mountains and at the Nyingchi meteorological

18 station from January 1, 2007 to December 31, 2010.

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22 **Fig. S2.** Minimum air temperatures recorded by the automatic weather station (black line)

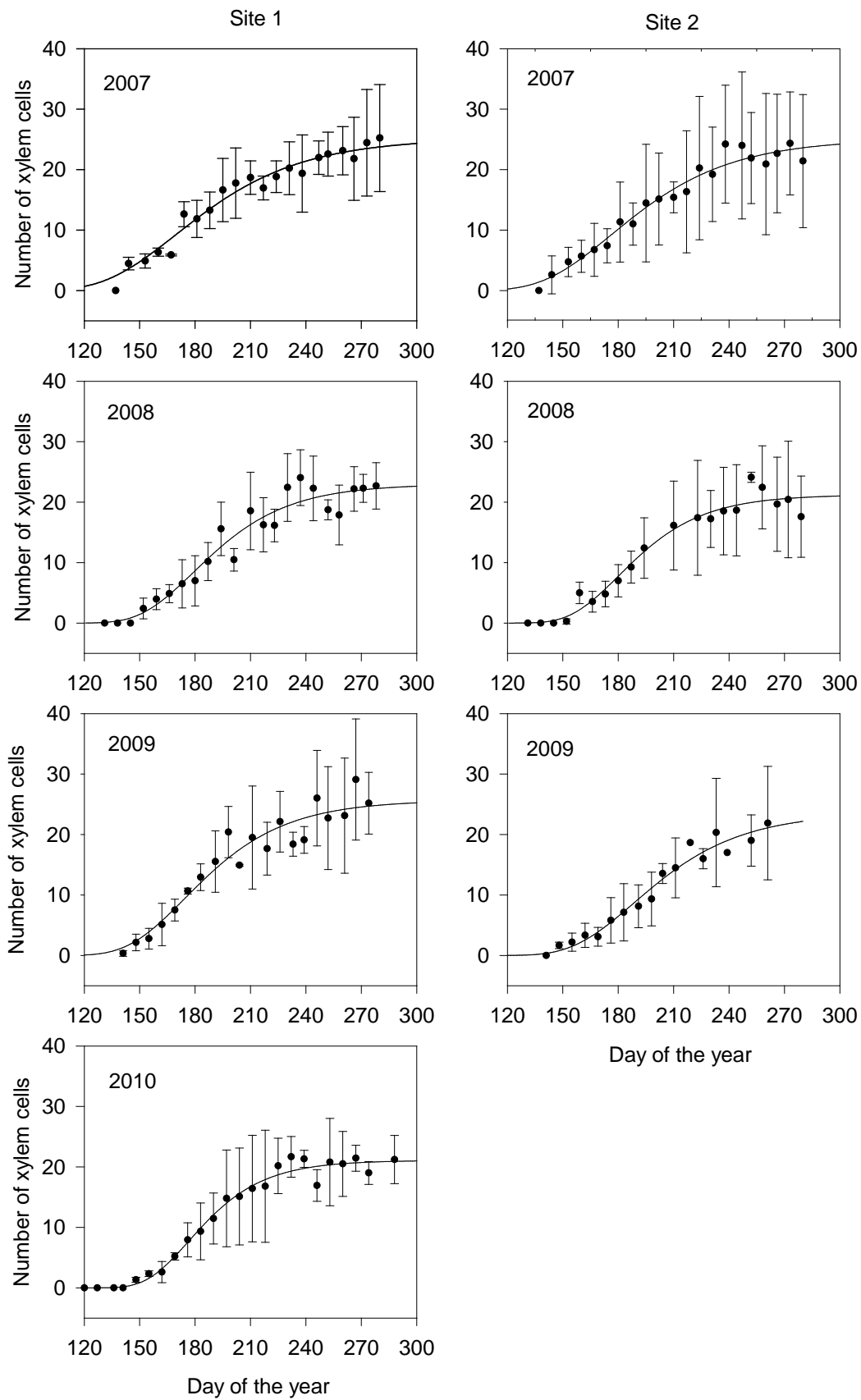
23 and temperature data logger (TidbiT v2 Temp UTBI-001, Onset Computer Corporation,

24 Bourne, MA, USA) at site 1 (red line) and site 2 (blue line) from August 5, 2011 to August 5,

25 2013.

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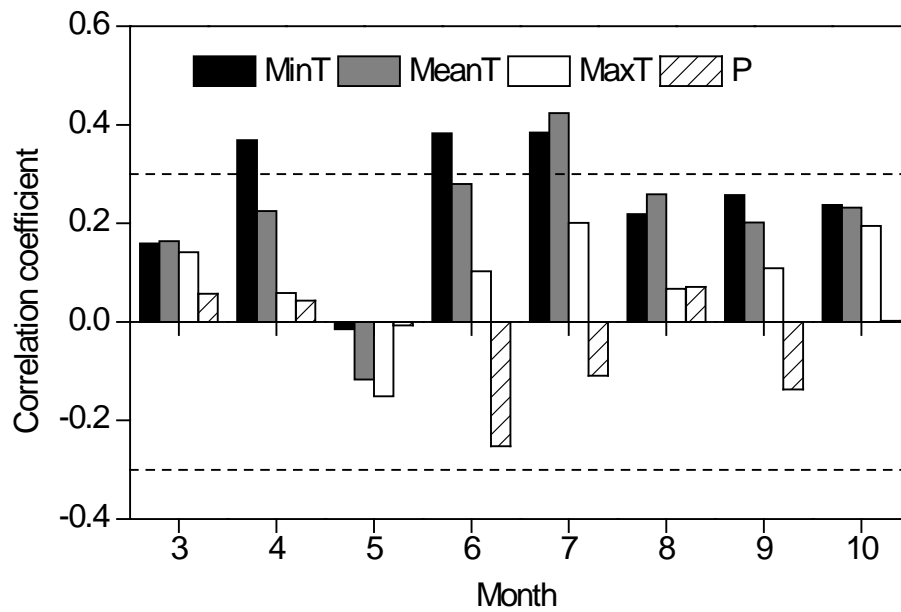


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28 **Fig. S3.** Dynamics of xylem growth (including enlarging, wall thickening, and mature xylem

29 cells) at two Smith fir treelines as modeled using a Gompertz function.

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33 **Fig. S4.** Correlations between the simulated tree ring chronology and monthly temperature

34 and precipitation at Smith fir treeline in the Sygera Mountains on the southeastern Tibetan

35 Plateau. Dotted horizontal lines show the 95% confidence limits. *Abbreviations:* MaxT =

36 maximum temperature, MeanT= mean temperature, MinT= minimum temperature and P =

37 precipitation.

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