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Article

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

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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.

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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.

A mechanistic model can provide a deeper understanding on the climatic control on tree growth dynamics. The process-based

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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 *i*th phase of the *j*th sample was calculated as:

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

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:

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

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

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