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Primary Research Article

Title: Critical temperature and precipitation thresholds for the onset of xylogenesis of *Juniperus przewalskii* in a semi-arid area of the northeastern Tibetan Plateau

Running head: Thresholds for the onset of xylogenesis

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Abstract

The onset of xylogenesis plays an important role in tree growth and carbon sequestration at the level of ecosystems and is thus a key to modeling the responses of forest ecosystems to climate change. Temperature regulates the resumption of cambial activity, but little is known about the effect of water availability on the onset of xylogenesis. We monitored the onset of xylogenesis during 2009–2014 by weekly microcoring *Juniperus przewalskii* trees at the upper and lower altitudinal limits of the species on the northeastern Tibetan Plateau. A logistic regression was used to calculate the probability of xylogenic activity at a given temperature. A two-dimensional reversed Gaussian model was used to fit the differences between the observed date of onset of xylogenesis and days at given temperatures and precipitation within a certain time window. The thermal thresholds at the beginning of the growing season were highly variable, providing additional evidence that temperature was not the only factor initiating xylem growth under cold and dry climatic conditions. The onset of xylogenesis was predicted well for climatic thresholds characterized by a cumulative precipitation of 17.0 ± 5.6 mm and an average minimum temperature of 1.5 ± 1.4 °C for a period of 12 days. Xylogenesis in semi-arid regions with dry winters and springs can start when both critical temperature and precipitation thresholds are reached. Such findings contribute to our knowledge of the environmental drivers of growth resumption that were previously investigated only in regions with abundant snow accumulation in winter and frequent precipitation in spring. Models of the onset of xylogenesis should include water availability for more reliable predictions of xylem phenology in dry areas. A mismatch of the thresholds of temperature and moisture for the onset of xylogenesis may increase forest vulnerability in semi-arid areas under droughts due to global climate change.

Keywords: Phenology, xylem formation, Qilian juniper, two-dimensional Gaussian model, drought, rain, altitudinal gradient

Introduction

Interest in xylem phenology (xylogenesis) and its sensitivity to climate change is growing because wood is a major sink of carbon in terrestrial ecosystems (Babst *et al.*, 2014; Cuny *et al.*, 2015; Pérez-de-Lis *et al*., 2017). Temperature is increasingly recognized as the primary driver of growth reactivation in cold climates (Rossi *et al.*, 2007, 2008). Both observations and controlled experiments have demonstrated that cambial activity is limited by low air temperatures in cold climates (Oribe *et al.*, 2001; Gricar *et al.*, 2006; Rossi *et al.*, 2008; Seo *et al.*, 2008; Gruber *et al.*, 2010; Begum *et al.*, 2013; Li *et al.*, 2013). In addition, the onset of xylem production is delayed at higher latitudes and altitudes, confirming the role of temperature for xylogenesis (Moser *et al.*, 2010; Oladi *et al.*, 2010; Huang *et al.*, 2011). In particular, Rossi *et al.* (2008) reported a critical daily minimum temperature for xylogenesis in conifers of 4–5 °C in cold climates. Shen *et al.* (2015), though, highlighted the impact of precipitation on the starting date of vegetation phenology (canopy greening) in cold and arid or semi-arid regions, indicating that cold and drought stress both affected the onset of growth. Ren *et al.* (2015) found a delay in the initiation of xylogenesis in Qilian junipers (*Juniperus przewalskii* Kom.) under extremely dry spring conditions in a cold and dry climate, which suggested a potential influence of water availability on the start of xylogenesis, i.e. on the onset of cambial reactivation after the cold dormant season (winter in the Northern Hemisphere).

The effect of precipitation on the growth dynamics of forest ecosystems needs to be quantified to better understand the adaptation of plants to a changing climate, which may be characterized by warmer and drier conditions (Allen *et al.*, 2015). In addition, the climatic thresholds for the resumption of xylem phenology may provide keys to better understand mechanisms of forest resilience (e.g. post-drought recovery) and the potential for tipping points under global change. Water acts on several important growth processes in plants. The expansion of xylem cells is turgor-driven, depending on the uptake of cellular water and on solute accumulation. Drought stress affects the loss of turgor of differentiating cells (Kozlowski & Pallardy, 2002), so shifts in the onset of xylogenesis might be potentially affected by variation in moisture conditions, especially in the arid and semi-arid regions of the world. The available literature, however, is limited to studies conducted in regions characterized by rains prior to the onset of xylogenesis (from winter to spring), such as the Mediterranean basin (Camarero *et al.*, 2010, 2015; Vieira *et al.*, 2013), or by abundant water released during snowmelt, such as alpine valleys (Gruber *et al.*, 2010; Eilmann *et al.*, 2011; Swidrak *et al.*, 2011). Soil moisture could be a less important limiting factor for the resumption of xylem formation at these sites than in arid or semi-arid areas. We investigated how cold and dry conditions could drive the onset of xylogenesis by determining the relative influence of these two climatic stressors.

We selected a forested area on the northeastern Tibetan Plateau to test the effect of soil moisture on the onset of xylogenesis. The dry climate of this area is characterized by scarce winter precipitation, a very thin snowpack and the dependence of moisture availability for vegetation activity on the first rains of spring (Dai, 1990). The climate is described as cold and dry, with a mean annual temperature of 3.1 °C and a mean annual precipitation of ca. 200 mm. Winter is extremely dry, and rain mainly falls from May to September (Dai, 1990). The Qilian juniper forests in this area are stressed by both drought and cold (Zheng *et al.*, 2008). A recent study reported that spring drought could delay the onset of xylogenesis in Qilian juniper despite optimal thermal conditions (Ren *et al.*, 2015). In addition, warmer spring conditions on the plateau are increasing the vulnerability of forests to dry spells, indicated by a marked decrease in growth and an increase in the frequency of missing tree rings (Liang *et al.*, 2014, 2016). These findings suggested a potential interaction between precipitation and temperature in the onset of xylogenesis under cold and dry conditions.

The objective of this study was to use Qilian juniper as a model species to investigate the onset of xylogenesis at the upper and lower altitudinal boundaries of its distribution during six growing seasons (2009-2014) and to identify the thresholds of temperature and precipitation controlling the onset of xylogenesis. We hypothesized that the onset of xylogenesis in Qilian juniper was constrained more by water deficit than by low temperatures.

Materials and Methods

Study site, field sampling and sample preparation

The study was carried out in an undisturbed Qilian juniper forest near Dulan County on the northeastern Tibetan Plateau (36°00'N, 98°11'E). Two sites, at 3850 and 4210 m a.s.l. with slopes of 15°, were selected at the lower and upper timberline limits of the altitudinal distribution of the species. Five trees were randomly selected at each site. The average diameter at breast height was 50–60 cm, and the average height was 8 m. Microcores were extracted weekly from 2009 to 2014 from the stems at a height of 1.0-1.3 m using a Trephor microborer (Rossi *et al.*, 2006) and stored in a formalin–ethanol–acetic acid solution. The microcores were prepared to obtain transverse sections (9-12 μm in thickness) using a Leica RM 2245 rotary microtome (Leica Microsystems, Wetzlar, Germany), and the sections were stained using a mixture of safranine, Astra Blue and ethanol and then permanently fixed. See Ren *et al*. (2015) for more details on sampling strategy and slide preparation.

Identification of the onset of xylogenesis

The xylem sections were observed under a microscope at a magnification of 100× with visible and polarized light to distinguish the differentiating xylem cells. We concentrated on the radial-enlargement phase, which indicates the beginning of xylem growth (Antonova & Stasova, 1993). Tracheids in the radial-enlarging phase contained a protoplast enclosed in thin primary cell walls, and their radial diameters were at least twice that of a cambial cell (Rossi *et al*., 2006). The tracheids had light-blue walls under normal light during this phase but were not visible under polarized light due to the lack of a secondary wall. Xylogenesis was considered to have begun for each tree when at least one radial file of enlarging cells was observed in spring.

Meteorological data

Meteorological data were recorded at each site from October 2012 by automatic stations (HOBO; ONSET, Pocasset, USA). Air temperature and precipitation were measured every 30 min and stored in data loggers. Minimum, mean, and maximum daily temperatures and daily precipitation were calculated for subsequent analyses. Data for January 2009 to September 2012 were estimated using the measurements collected from a meteorological station in Dulan (36°18'N, 98°06'E; 3190 m a.s.l.), 32 km from the study sites. The consistency of the estimates was based on the high correlations (r >0.92) between the climatic data (temperature and precipitation) at the two sites with those at the Dulan station (Supporting Information, Fig. S1).

Statistical analyses to predict climatic thresholds of xylogenesis

Based on previous research (Ren *et al*., 2015), air temperature and precipitation were selected as potential climatic drivers of the beginning of xylogenesis.

Logistic regression was used to calculate the probability of xylogenic activity at a given temperature using the LOGISTIC procedure in the SAS 9.4 statistical package [SAS Institute Inc., Cary, USA]). See Rossi *et al*. (2007, 2008) for more details on the calculation of temperature thresholds and model verification. The model was fitted with the minimum, mean, and maximum temperatures for each tree, site and year. None of 180 models applied was excluded because of a lack of fit (in all cases R^2 >0.90). Thermal thresholds were then compared between years using an ANOVA.

Two-dimensional reversed Gaussian models were used to calculate the difference between the onset of xylogenesis and the day with a given temperature and precipitation within a certain time window. The Gaussian model generates a funnel-surface plot, with a circular-to-elliptical cross-section with the general form:

$$Z_{xy} = Z_0 - A exp(-\frac{1}{2}(\frac{xcos\theta + ysin\theta - x_c cos\theta - y_c sin\theta}{W_1})^2 - \frac{1}{2}(\frac{-xsin\theta + ycos\theta + x_c sin\theta - y_c cos\theta}{W_2})^2)$$

where Z_{xy} is the mean absolute difference between the day of onset of xylogenesis and the estimated day with a given average temperature x and cumulative precipitation y within the time window t across trees, sites and years, Z_0 is the distance from the edge of the surface to the plane $z = 0$, A is the height of the trough, x_0 and y_0 are the coordinates defining the position of the center of the surface, W_1 and W_2 are the spreads of the surface on the x- and y-axes, respectively, and θ is the clockwise rotation angle of the surface (see Supporting Information, Fig. S2). The model was fitted with the corresponding temperature (minimum, mean and maximum air temperatures) and precipitation series for each time window. The culmination of the coefficient of determination (R^2) of the model was considered to correspond to the optimal time window t. The critical average temperature (x) and cumulative precipitation (y) were calculated when Z_{xy} was near 0 at the optimal time window t. Standardized residuals were calculated for model verification. Model validation was performed by comparing the observations (onset of xylogenesis) with the predicted values calculated using data for precipitation and temperature as predictors.

Results

Spring meteorological conditions

The daily mean temperatures in March at the upper and lower sites were -4.7 and

-3.2 °C, respectively, reaching 1.8 and 3.4 °C in May. Monthly precipitation, on average, increased tenfold, from 5–6 mm in March to 50–60 mm in May (Supporting Information, Fig. S3).

Spring (March to May) conditions varied between years (Fig. S3). The warmest spring during the study was in 2009, with daily mean temperatures reaching 1.4 and -0.2 °C at the lower and upper sites, respectively. The coldest and driest springs were in 2014, with mean temperatures of -0.2 and -1.8 °C and total precipitation of 25.8 and 31.0 mm at the lower and upper sites, respectively. Monthly precipitation in March 2014 ranged between 17.4 and 21.8 mm, which represented the highest amount of spring rain during the study period.

Threshold temperatures

The threshold temperature with a probability of 0.5 for active xylogenesis was calculated as an average for each year and site (Table 1). Thermal thresholds at the lower site varied within large ranges, 0-5, 4-9 and 10-14 °C for the daily minimum, mean and maximum temperatures, respectively. Thresholds were significantly higher in 2010 than in other years and were lowest in 2014 (P<0.001). The thermal thresholds were lower at the upper site, but also with large ranges, 0–5, 3–8 and 8–12 °C for the daily minimum, mean and maximum temperatures, respectively. The thresholds at the upper site also differed significantly between years (P<0.001). Thresholds were significantly higher in 2010 than the other years and were lower in 2014 for the daily minimum and mean temperatures and in 2012 and 2014 for the maximum temperature.

Table 1 Threshold minimum, mean and maximum temperatures corresponding to 95% probability of active xylogenesis in *Juniperus przewalskii* estimated during 2009-2014 at the lower and upper study sites. Results from an ANOVA are reported as *F* and *P*. Different letters within a row indicate significant differences at *P*<0.05.

Site	Temperature (°C)	2009	2010	2011	2012	2013	2014	F	P
Lower	Minimum	2.5 ± 0.4[a]	5.0 ± 0.7[b]	2.4 ± 0.7[a]	1.8 ± 0.4[a]	2.0 ± 0.9[a]	0.0 ± 0.7[c]	29.93	<0.001
	Mean	7.2 ± 0.4[a]	9.3 ± 0.8[b]	7.5 ± 0.7[a]	6.0 ± 0.4[a]	6.3 ± 0.9[a]	4.5 ± 0.7[c]	26.33	<0.001
	Maximum	12.0 ± 0.5[a]	14.2 ± 0.9[b]	12.0 ± 1.0[a]	10.0 ± 0.4[c]	11.3 ± 0.9[a,c]	9.8 ± 0.8[c]	21.80	<0.001
Upper	Minimum	1.9 ± 0.2[a,b]	4.5 ± 0.3[c]	2.4 ± 0.4[a]	1.0 ± 0.6[b]	1.2 ± 0.9[b]	-0.5 ± 0.4[d]	53.83	<0.001
	Mean	5.9 ± 0.2[a,b]	8.0 ± 0.3[c]	6.4 ± 0.3[a]	4.5 ± 0.6[d]	5.0 ± 0.9[b,d]	3.4 ± 0.4[e]	52.06	<0.001
	Maximum	10.1 ± 0.2[a,b]	12.2 ± 0.3[c]	10.8 ± 0.5[a]	7.9 ± 0.6[d]	9.4 ± 0.9[b]	8.1 ± 0.4[d]	51.31	<0.001

Two-dimensional Gaussian models

R^2 of the Gaussian models varied with the length of the time window (Fig. 1). R^2 increased for longer time windows, culminating with a time window of 12 days when R^2 reached 0.97, 0.99 and 0.94 for the minimum, mean and maximum temperatures, respectively. R^2 decreased slightly (minimum and mean temperature) or substantially (maximum temperature) for time windows longer than 12 days.

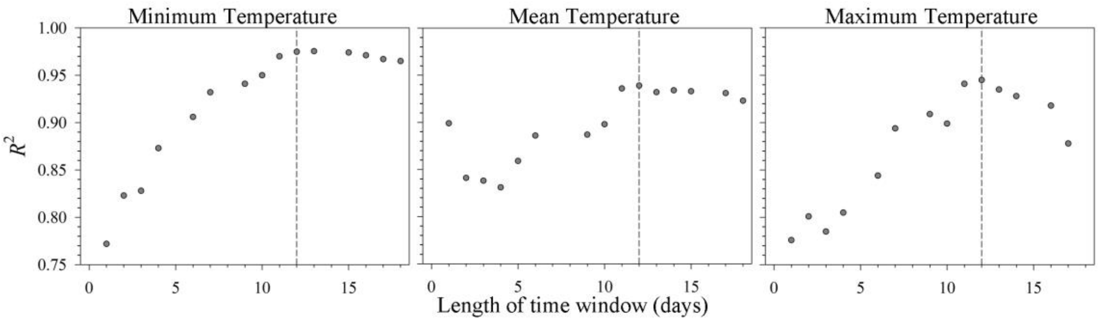

Fig. 1 Coefficient of determination (R^2) for the two-dimensional Gaussian models within the time window from 1 to 18 days. Dotted lines indicate the time windows (in days) corresponding to maximum R^2.

The minimal Z_{xy} was 2.21 days for a time window of 12 days. The critical cumulative precipitation was 17.0 ± 5.6 mm and the average minimum temperature was 1.5 ± 1.4 °C when Z_{xy} was <2.5 days (Fig. 2). The spreads of this trough on the *x*- and *y*-axes were 48.0 mm and 2.04 °C, respectively, with a counter-clockwise rotation of 4.73°. In the model with the average mean temperature, the minimal Z_{xy} was 1.85 days. The critical precipitation and temperature were 26.9 ± 3.9 mm and 4.6 ± 1.8 °C, respectively when Z_{xy} was <2 days. The spreads of this trough on the *x*- and *y*-axes were 44.1 mm and 1.94 °C respectively, with a counter-clockwise rotation of 8.22°. The minimal Z_{xy} was 1.90 days in the model with the average maximum temperature. The critical precipitation and temperature were 29.9 ± 3.0 mm and 8.5 ± 1.8 °C, respectively, when Z_{xy} was <2 days. The spreads of this trough on the *x*- and *y*-axes were 51.1 mm and 2.39 °C, respectively, with a counter-clockwise rotation of 9.52°. Most of the standardized residuals of these three models converged from -2 to 2 (Supporting Information, Fig. S4).

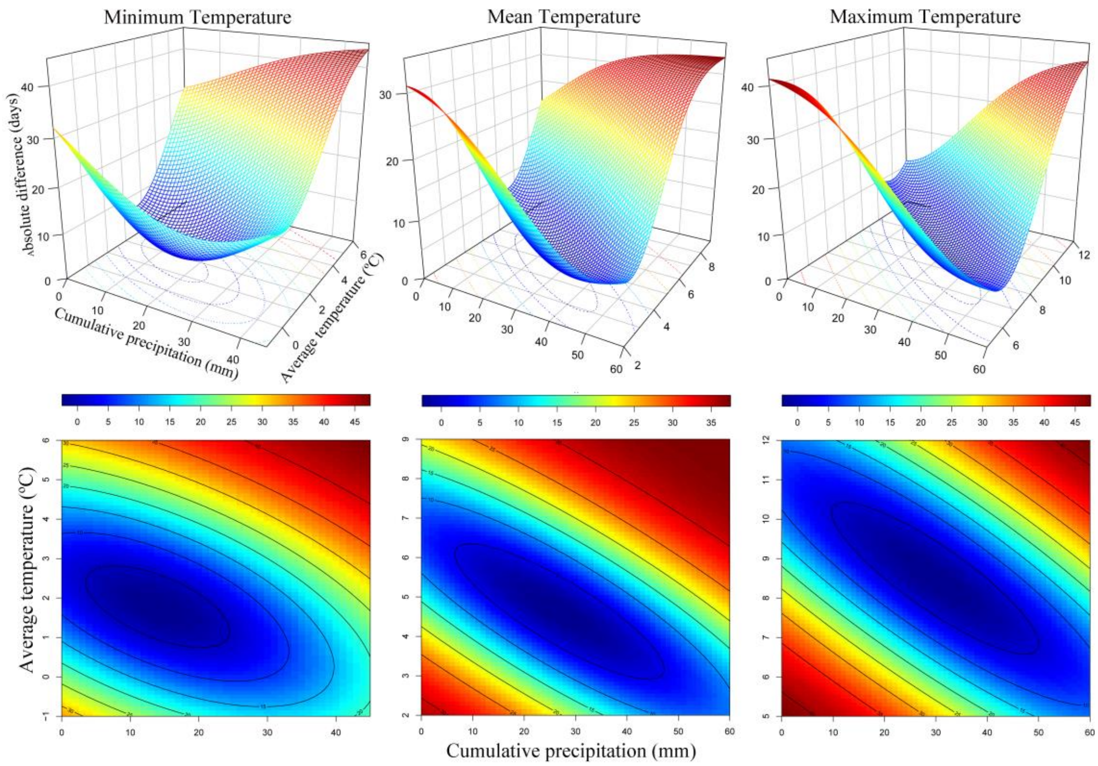

Fig. 2 Surface plots and the corresponding level sets showing the two-dimensional Gaussian distribution of the absolute difference between the day of onset of xylogenesis and the estimated day with a given average temperature and cumulative precipitation in the time window of 12 days. Note that the axes have different scales.

The absolute differences between the observed and predicted dates of onset of xylogenesis using average minimum temperature and cumulative precipitation in a time window of 12 days were smaller than the sampling interval by averages of 5.9 and 4.6 days at the lower and upper sites, respectively (Fig. 3). The predictions for 2009, 2011 and 2013 were the most reliable. The divergences between observations and predictions (16 days) were largest in 2014 at the lower site.

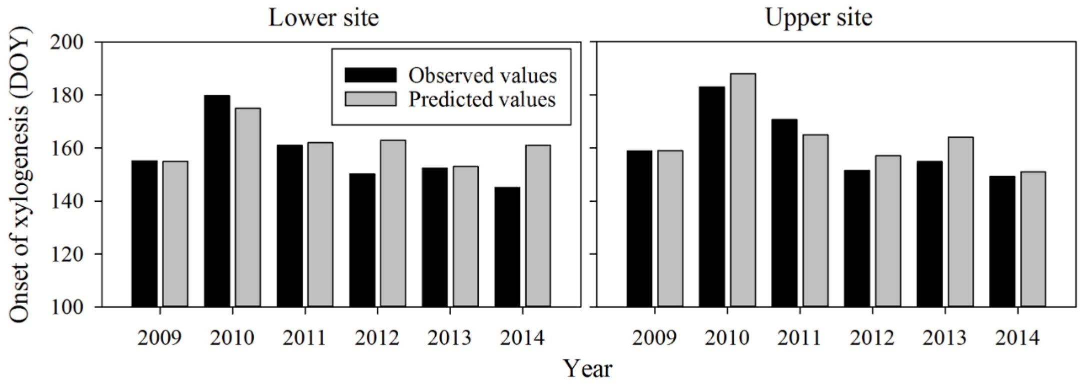

Fig. 3 Observed and predicted days of onset of xylogenesis (DOY, day of the year) in *Juniperus przewalskii* during 2009-2014 at the lower and upper study sites. Predictions were obtained using the threshold average minimum temperature and cumulative precipitation calculated by the models.

Discussion

We challenged the general opinion that temperature was the only driver of growth reactivation at high elevations by analyzing the onset of xylogenesis of Qilian juniper subjected to cold and dry climatic conditions on the northeastern Tibetan Plateau. Published threshold temperatures for the onset of xylogenesis in trees range from 2 to 3 °C (Rossi *et al.*, 2007, 2008; Swidrak *et al.*, 2011; Boulouf Lugo *et al.*, 2012). The range in the thermal thresholds of 5 °C for the onset of xylogenesis in Qilian juniper provides additional evidence that temperature was not the only factor initiating xylem growth under cold and dry climatic conditions. More reliable predictions were attained when both thermal and precipitation thresholds for the onset of xylogenesis were included in the fitted models. The interaction between temperature and precipitation satisfactorily explained the day of onset of xylogenesis in 2010, which was delayed by ca. three weeks compared with 2009 and 2011, despite the warm conditions during that spring (Ren *et al.*, 2015). This finding suggests that spring precipitation is also an important factor in the resumption of xylem formation in Qilian juniper.

Water availability is an important determinant of xylem formation. Before the start of xylem phenology, trees must compensate for the water lost during winter and spring to recover an adequate water balance, because turgor is an important requisite for xylem cell growth (Sevanto *et al.*, 2006). Rehydration in spring can exceed six weeks, and stems are fully rehydrated one month before the onset of radial growth (Turcotte *et al.*, 2009). Both cell division and expansion in the xylem are sensitive to changes in water potential (Abe & Nakai, 1999; Savidge, 2001). The water potential in the cambium regulates mitosis and influences cell extension and the deposition of wall polymers (Abe & Nakai, 1999; Cosgrove, 2005; Arend & Fromm, 2007). Springs were rainy or water was abundantly supplied by snowmelt in the cold regions of previous studies, so the initiation of xylem growth was not limited by rehydration, and trees responded essentially to temperature rather than precipitation (Turcotte *et al.*, 2009). Warmer springs in such areas can substantially advance xylem phenology (Rossi *et al.*, 2011). Winter and spring are similarly often wet in cold and drought-prone regions such as continental Mediterranean forests, and moisture is not considered the only factor in the resumption of xylem formation (Camarero *et al.*, 2010). Winter is extremely dry in our study area, with scarce snow, and water availability is consequently low before growth reactivation. Moreover, drought stress would be higher under drier and warmer conditions, which would thus slow the onset of xylogenesis, as observed in spring 2010. Soil moisture occasionally can be increased by snowfall, such as the snowfall in 2014, as also occurs in boreal forests (Vaganov *et al.*, 1999). The amount of water available during the snowmelt in our study increased soil moisture and possibly advanced the onset of xylogenesis, likely explaining the difference of 16 days between observations and predictions in 2014 at the lower site. This research found that the onset of xylogenesis in Qilian juniper should meet the prerequisite for both critical temperature and precipitation.

This study is the first to demonstrate that the onset of xylogenesis is driven by an interaction between thermal and precipitation thresholds. The selected time window of 12 days agrees with the period required for tracheid expansion and differentiation (Vaganov *et al.*, 2006; Cuny *et al.*, 2015). Temperature is a well-recognized factor controlling the onset of xylem formation, but our findings provide new insights on the climatic forcing of growth. The critical temperatures and precipitation provide keys for modelling the response of forest ecosystems subjected to cold and dry constraints in response to climate change and would help our understanding of the regime shifts in these ecosystems (Scheffer *et al.*, 2001; Zhu *et al.*, 2014). Our findings also support the constraint of growth by drought stress in high-elevation forests or near the alpine treeline, as indicated by previous studies (Liang *et al.*, 2014; Piper *et al.*, 2016).

Trees in semi-arid areas are generally limited by drought and high temperature at the beginning of the growing season, which increase rates of evapotranspiration (Allen *et al.*, 2015), and a similar constraint has been reported for the Tibetan Plateau and other Asian mountains (Shao *et al.*, 2005; Liang *et al.*, 2006, 2016; Liu *et al.*, 2006; Gou *et al.*, 2014; Pederson *et al.*, 2014; Yang *et al.*, 2014; Zhang *et al.*, 2015). Warming-induced drought stress has been decreasing generalized tree growth and increasing mortality in semi-arid areas across Asia (Dulamsuren *et al.*, 2010; Liu *et al.*, 2013; Liang *et al.*, 2016; Allen *et al.*, 2015). In particular, the failure to produce stem wood in a particular year (missing rings) is a response to dry and warm spring conditions, and an increasing frequency of missing tree rings is also evident in response to the warming in recent decades (Liang *et al.*, 2014, 2016). Moreover, the frequency of missing rings has been strongly linked to tree mortality (Liang *et al.*, 2016). We hypothesize that a failure to reach critical water availability for growth reactivation or a delay in cambial resumption in response to increasing drought stress could be primary factors in the failure to form a complete ring and portend lower growth and forest dieback. A mismatch between critical temperatures and amounts of moisture for the onset of xylogenesis under the drought conditions of global climate change and the acceleration of dryland expansion (Peñuelas *et al.*, 2007; Allen *et al.*, 2015; Huang *et al.*, 2015) will reduce forest resilience and risk regime shifts in vulnerable semi-arid forests. Reyer *et al.* (2015) proposed the assessment of forest resilience and potential tipping points at various levels, from leaf to biosphere, and our study has stressed that climatic thresholds for the onset of xylogenesis can be key indicators of forest resilience and tipping points under changing climates.

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Supporting Information captions

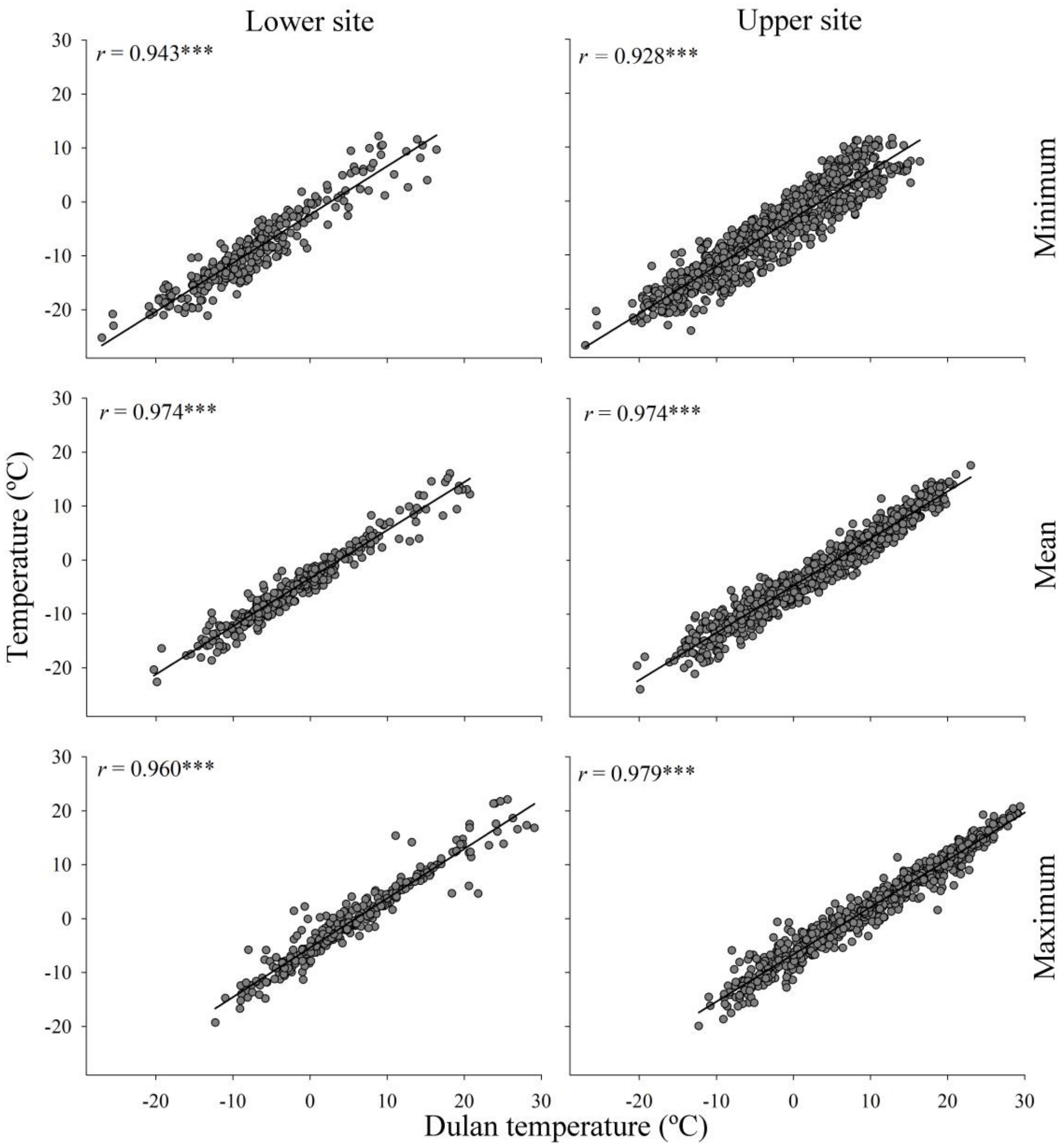
Fig. S1 Correlations between the daily minimum, mean and maximum temperatures recorded at the Dulan meteorological station and the corresponding temperatures recorded during 2012-2014 at the lower and upper study sites. ***, correlation coefficients (*r*) at $P<0.001$.

Fig. S2 Sample surface plot and the corresponding level sets of a two-dimensional Gaussian model. In the upper plot, Z_0 is the distance from the edge of the surface to the plane ($z = 0$), and A is the height of the trough. In the lower plot, x_0 and y_0 are the coordinates defining the position of the center of the surface, and θ is the clockwise rotation angle of the surface.

Fig. S3 Daily air temperature (lines) and precipitation (bars) during 2009-2014 at the lower and upper study sites.

Fig. S4 The distribution of standardized residuals in the time window of 12 days as a function of minimum, mean and maximum temperatures.

Supporting Information



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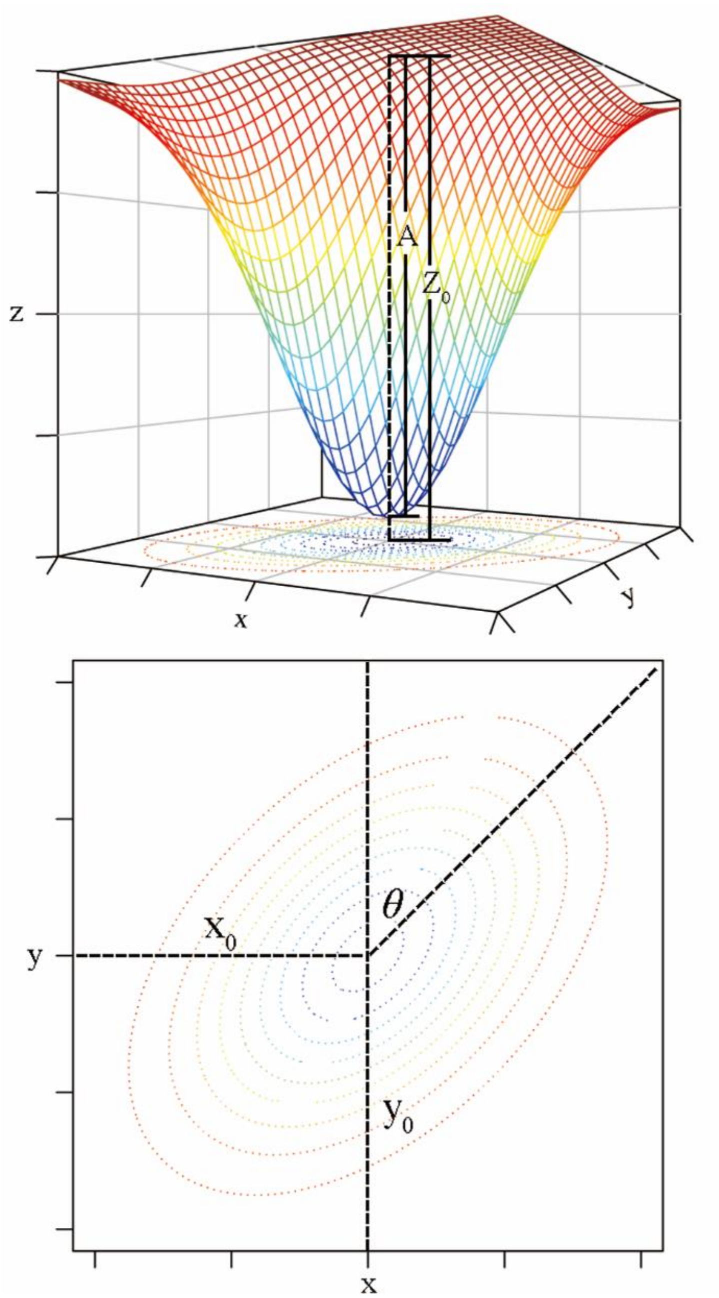

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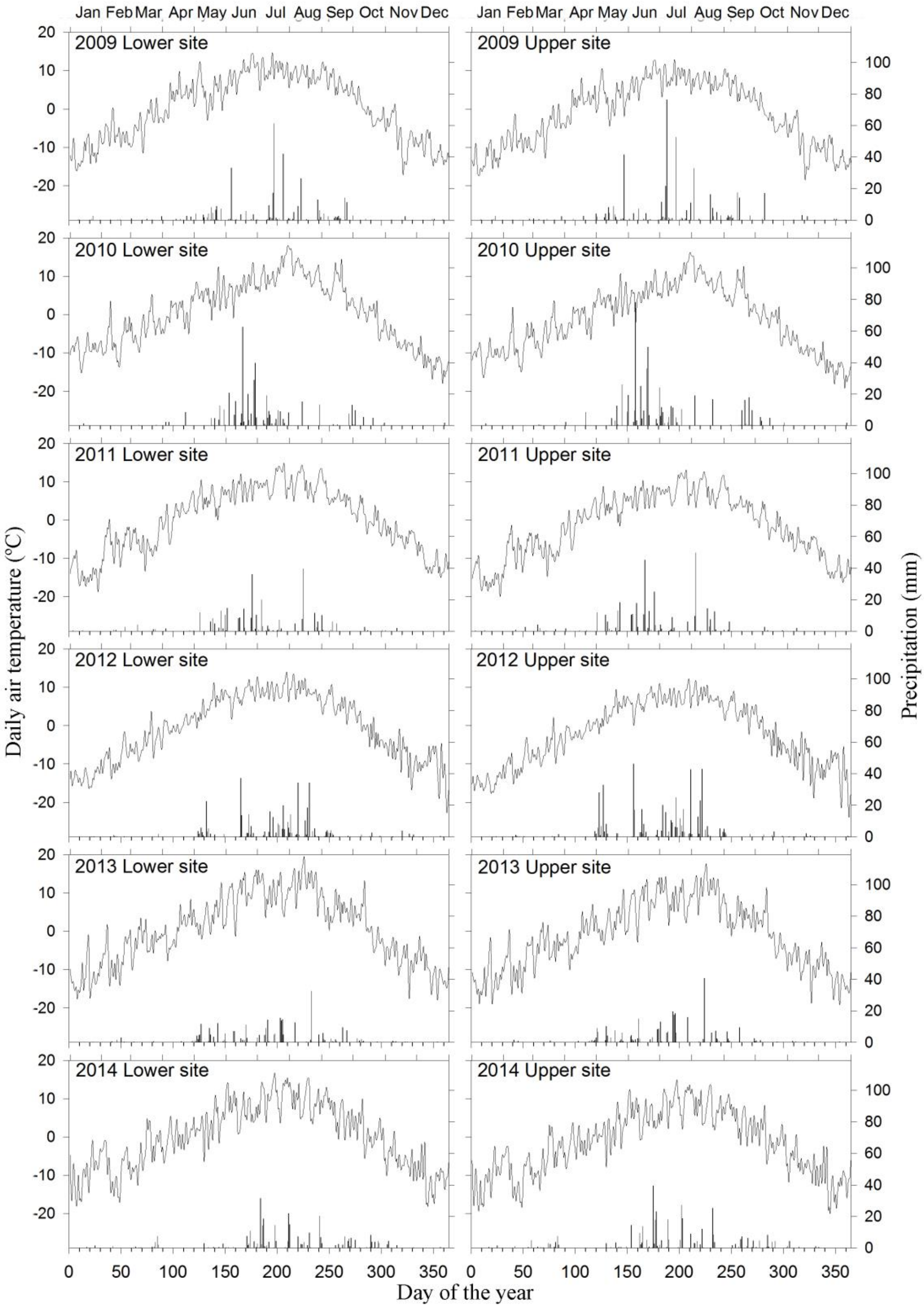

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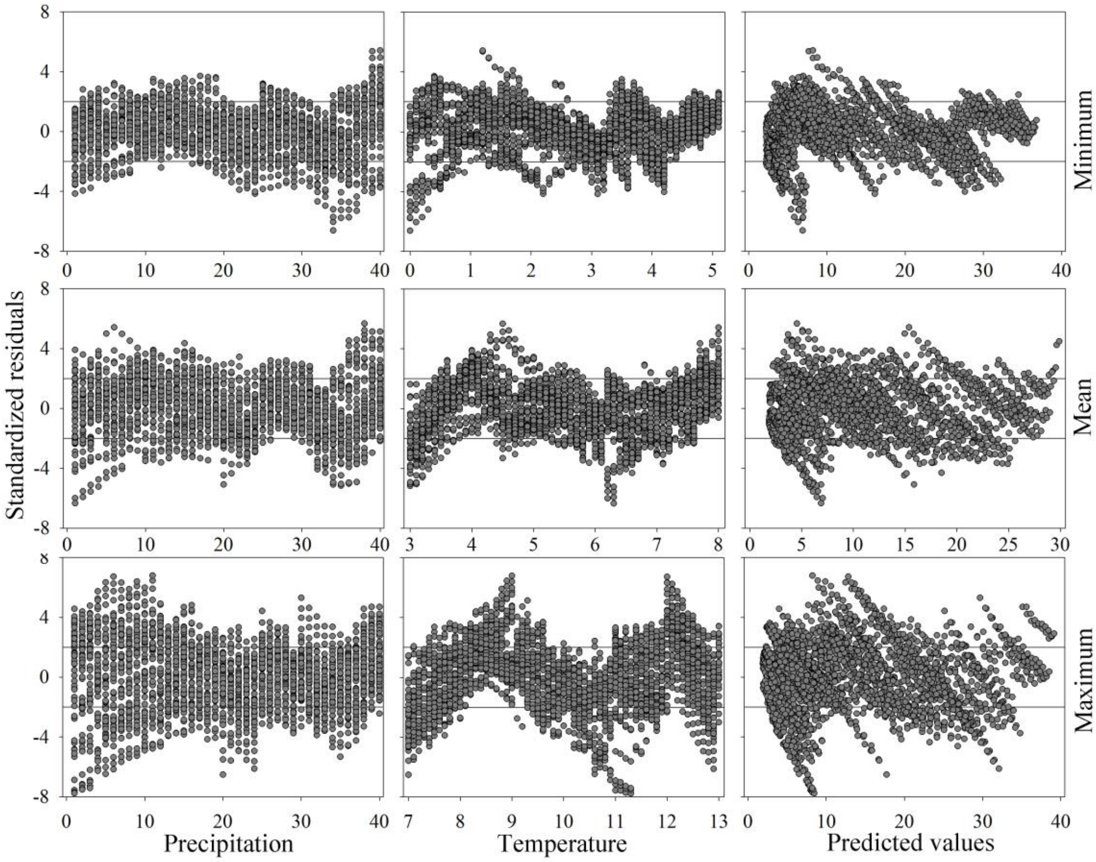

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