



# Critical temperature and precipitation thresholds for the onset of xylogenesis of *Juniperus przewalskii* in a semi-arid area of the north-eastern Tibetan Plateau

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1 Original Article

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

4

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26

1 **Abstract**

2 ● **Background and Aims** The onset of xylogenesis plays an important role in tree growth  
3 and carbon sequestration, and it is thus a key variable to model the responses of forest  
4 ecosystems to climate change. Temperature regulates the resumption of cambial activity,  
5 but little is known about the effect of water availability on the onset of xylogenesis in  
6 cold but semi-arid regions.

7 ● **Methods** We monitored the onset of xylogenesis during 2009–2014 by weekly  
8 microcoring *Juniperus przewalskii* trees at upper and lower treelines on the northeastern  
9 Tibetan Plateau. We used a logistic regression to calculate the probability of xylogenic  
10 activity at a given temperature and a two-dimensional reverse Gaussian model to fit the  
11 differences between the observed and estimated days of xylogenesis onset at given  
12 temperatures and precipitation within a certain time window.

13 ● **Key Results** The thermal thresholds at the beginning of the growing season were highly  
14 variable, suggesting that temperature was not the only factor initiating xylem growth  
15 under cold and dry climatic conditions. The onset of xylogenesis was predicted well for  
16 climatic thresholds characterized by a cumulative precipitation of  $17.0 \pm 5.6$  mm and an  
17 average minimum temperature of  $1.5 \pm 1.4$  °C for a period of 12 days.

18 ● **Conclusions** Xylogenesis in semi-arid regions with dry winters and springs can start  
19 when both critical temperature and precipitation thresholds reached. Such findings  
20 contribute to our knowledge of the environmental drivers of growth resumption that  
21 previously had been investigated mostly in cold regions without water shortages during  
22 early growing seasons. Models of the onset of xylogenesis should include water

1 availability to improve predictions of xylem phenology in dry areas. A mismatch of the  
2 thresholds of temperature and moisture for the onset of xylogenesis may increase forest  
3 vulnerability in semi-arid areas under forecasted warmer and drier conditions.

4

5 **Key words:** tree growth, temperature, precipitation, critical thresholds, xylogenesis,  
6 *Juniperus przewalskii*, xylem formation, drought, two-dimensional reverse Gaussian model,  
7 semi-arid area, Tibetan Plateau

8

## 1 INTRODUCTION

2 Interest in xylem phenology (xylogenesis) and its sensitivity to climate change is growing  
3 because wood is a major sink of carbon in terrestrial ecosystems (Chaffey, 2002; Cuny *et al.*,  
4 2015; Pérez-de-Lis *et al.*, 2017). Temperature is increasingly recognized as the primary driver  
5 of growth reactivation in cold climates (Rossi *et al.*, 2007, 2008). Both observations and  
6 controlled experiments have demonstrated that cambial activity is limited by low air  
7 temperatures in cold climates (Oribe *et al.*, 2001; Gricar *et al.*, 2006; Rossi *et al.*, 2008; Seo *et*  
8 *al.*, 2008; Gruber *et al.*, 2010; Begum *et al.*, 2013; Li *et al.*, 2013). In addition, the onset of  
9 xylem production is delayed at higher latitudes and altitudes, confirming the role of  
10 temperature for xylogenesis (Moser *et al.*, 2010; Oladi *et al.*, 2010; Huang *et al.*, 2011). In  
11 particular, Rossi *et al.* (2008) reported a critical daily minimum temperature for xylogenesis  
12 in conifers of 4–5 °C in cold climates. Shen *et al.* (2015), though, highlighted the impact of  
13 precipitation on the starting date of vegetation phenology (canopy greening) in cold and arid  
14 or semi-arid regions, indicating that cold and drought stress both affected the onset of growth.  
15 Ren *et al.* (2015) found a delay in the initiation of xylogenesis in Qilian junipers (*Juniperus*  
16 *przewalskii* Kom.) under extremely dry spring conditions in a cold and dry climate, which  
17 suggested a potential influence of water availability on the start of xylogenesis, i.e. on the  
18 onset of cambial reactivation after the cold dormant season (winter in the Northern  
19 Hemisphere).

20 The effect of precipitation on the growth dynamics of forest ecosystems needs to be  
21 quantified to better understand the adaptation of plants to a changing climate, which may be  
22 characterized by warmer and drier conditions (Allen *et al.*, 2015). In addition, climatic

1 thresholds for the resumption of xylem phenology may provide keys to better understand  
2 mechanisms of forest resilience (e.g. post-drought recovery) as the climate changes. Water  
3 acts on several important growth processes in plants. The expansion of xylem cells is  
4 turgor-driven, and depends on the uptake of cellular water and on solute accumulation.  
5 Drought stress affects the loss of turgor of differentiating cells (Kozłowski and Pallardy,  
6 2002), so shifts in the onset of xylogenesis might be affected by variation in moisture,  
7 especially in the arid and semi-arid regions of the world. The available literature, however, is  
8 limited to studies conducted in regions characterized by rains prior to the onset of xylogenesis  
9 (from winter to spring), such as the Mediterranean basin (Camarero *et al.*, 2010, 2015; Vieira  
10 *et al.*, 2013), or by abundant water released during snowmelt, such as alpine valleys (Gruber  
11 *et al.*, 2010; Eilmann *et al.*, 2011; Swidrak *et al.*, 2011). Soil moisture could be a less  
12 important limiting factor for the resumption of xylem formation at these sites than in arid or  
13 semi-arid areas. We investigated how cold and dry conditions could drive the onset of  
14 xylogenesis by determining the relative influence of these two climatic stressors.

15 We selected a forested area on the northeastern Tibetan Plateau to test the effect of soil  
16 moisture on the onset of xylogenesis. The dry climate of this area is characterized by scarce  
17 winter precipitation, a very thin snowpack and the dependence of moisture availability for  
18 vegetation activity on the first rains of spring (Dai, 1990). The climate is described as cold  
19 and dry, with a mean annual temperature of 3.1 °C and a mean annual precipitation of ca. 200  
20 mm. Winter is extremely dry, and rain mainly falls from May to September (Dai, 1990). The  
21 Qilian juniper forests in this area are stressed by both drought and cold (Zheng *et al.*, 2008). A  
22 recent study reported that spring drought could delay the onset of xylogenesis in Qilian

1 juniper despite optimal thermal conditions (Ren *et al.*, 2015). In addition, warmer spring  
2 conditions on the plateau are increasing the vulnerability of forests to dry spells, indicated by  
3 a marked decrease in growth and an increase in the frequency of missing tree rings (Liang *et*  
4 *al.*, 2014, 2016). These findings suggested a potential interaction between precipitation and  
5 temperature in the onset of xylogenesis under cold and dry conditions.

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

11

## 12 **MATERIALS AND METHODS**

### 13 *Study site, field sampling and sample preparation*

14 The study was carried out in an undisturbed Qilian juniper forest near Dulan County on the  
15 northeastern Tibetan Plateau (36°00'N, 98°11'E). Two sites, at 3850 and 4210 m a.s.l. with  
16 slopes of 15°, were selected at the lower and upper treeline. Five trees were randomly selected  
17 at each site. The diameter at breast height was  $54 \pm 7$  cm and  $53 \pm 4$  cm at the lower and  
18 upper treeline sites, respectively, and the average height was 8 m. Microcores were extracted  
19 weekly from 2009 to 2014 from the stems at a height of 1.0-1.3 m using a Trephor microborer  
20 (Rossi *et al.*, 2006) and stored in a formalin–ethanol–acetic acid (FAA) solution. The  
21 microcores were prepared to obtain transverse sections (9-12  $\mu$ m in thickness) using a Leica  
22 RM 2245 rotary microtome (Leica Microsystems, Wetzlar, Germany), and the sections were

1 stained using a mixture of safranin, Astra Blue and ethanol and then permanently fixed. See  
2 [Ren et al. \(2015\)](#) for more details on sampling strategy and slide preparation.

3

#### 4 *Identification of the onset of xylogenesis*

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

14

#### 15 *Meteorological data*

16 Meteorological data were recorded at each site from October 2012 by automatic stations  
17 (HOBO; ONSET, Pocasset, USA). Air temperature and precipitation were measured every 30  
18 min and stored in data loggers. Minimum, mean, and maximum daily temperatures and daily  
19 precipitation were calculated for subsequent analyses. Data for January 2009 to September  
20 2012 were estimated using the measurements collected from a meteorological station in Dulan  
21 (36°18'N, 98°06'E; 3190 m a.s.l.), 32 km from the study sites. The consistency of the  
22 estimates was based on the high correlations ( $r > 0.92$ ) between the climatic data (temperature



1 and precipitation) at the two sites with those at the Dulan station (Supplementary data Fig.  
2 S1).

3

#### 4 *Statistical analyses to predict climatic thresholds of xylogenesis*

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

7 Logistic regression [LOGISTIC procedure in SAS 9.4 (SAS Institute Inc., Cary, USA)]  
8 was used to calculate the probability of xylogenic activity at a given temperature; responses  
9 were coded as non-active (value zero) or active (value 1). Temperature thresholds were  
10 calculated when the probability of xylogenesis being active was 0.5 (see Rossi *et al.* 2007,  
11 2008 for more details on the calculation of temperature thresholds and model verification).  
12 The model was fitted with the minimum, mean, and maximum temperatures for each tree, site  
13 and year. None of 180 models (2 sites  $\times$  6 years  $\times$  5 trees  $\times$  3 temperature series) applied was  
14 excluded because of a lack of fit (in all cases  $R^2 > 0.90$ ). Thermal thresholds were then  
15 compared between years using an ANOVA.

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

$$20 \quad Z_{xy} = Z_0 - Ae^{-\frac{1}{2}\left(\frac{x \cos \theta + y \sin \theta - x_0 \cos \theta - y_0 \sin \theta}{W_1}\right)^2 - \frac{1}{2}\left(\frac{-x \sin \theta + y \cos \theta + x_0 \sin \theta - y_0 \cos \theta}{W_2}\right)^2}$$

21 where  $Z_{xy}$  is the mean absolute difference between the observed day of onset of xylogenesis  
22 and the estimated day with a given average temperature  $x$  and cumulative precipitation  $y$

1 within the time window  $t$  across trees, sites, and years,  $Z_0$  is the distance from the edge of the  
2 surface to the plane  $z = 0$ ,  $A$  is the height of the trough,  $x_0$  and  $y_0$  are the coordinates defining  
3 the position of the center of the surface,  $W_1$  and  $W_2$  are the spreads of the surface on the  $x$ - and  
4  $y$ -axes, respectively, and  $\theta$  is the clockwise rotation angle of the surface (Supplementary data  
5 Fig. S2). The model was fitted with the corresponding temperature (minimum, mean and  
6 maximum air temperatures) and precipitation data from all sites and all years within different  
7 time windows. The coefficient of determination ( $R^2$ ) of the model was provided for evaluating  
8 the goodness of fits. The culmination of  $R^2$  was considered to correspond to the optimal time  
9 window  $t$ . The critical average temperature ( $x$ ) and cumulative precipitation ( $y$ ) were  
10 calculated when  $Z_{xy}$  was near 0 at the optimal time window  $t$ . Standardized residuals were  
11 calculated for model verification. Model validation was performed by comparing the  
12 observations (onset of xylogenesis) with the predicted values calculated using data for  
13 precipitation and temperature as predictors. Standardized regression coefficients were  
14 calculated by dividing a parameter estimate by the ratio of the sample standard deviation of  
15 the dependent variable to the sample standard deviation of the regressor (Bring, 1994).  
16 Standardized regression coefficients allow estimating the specific contribution of the  
17 independent variables (i.e. temperature and precipitation) on the dependent variable (onset of  
18 xylogenesis).

19

## 20 **RESULTS**

### 21 *Spring meteorological conditions*

22 During the study period, the annual mean temperature at the upper and lower treeline sites

1 were  $-1.49$  and  $0.04$  °C, respectively. The years 2012 and 2013 were the coldest ( $-2.16$  and  
2  $-0.65$  °C at upper and lower treelines) and warmest ( $-1.14$  and  $0.39$  °C), respectively. Annual  
3 precipitation at the upper and lower treeline sites were  $433.1$  and  $364.0$  mm, respectively. The  
4 wettest ( $537.2$  and  $443.3$  mm) and driest ( $320.2$  and  $308.3$  mm) years occurred in 2010 and  
5 2013. The daily mean temperatures in March at the upper and lower treeline sites were  $-4.7$   
6 and  $-3.2$  °C, respectively, reaching  $1.8$  and  $3.4$  °C in May. Monthly precipitation, on average,  
7 increased tenfold, from  $5$ – $6$  mm in March to  $50$ – $60$  mm in May (Fig. 1).

8 Spring (March to May) conditions varied among years (Fig. 1). The warmest spring during  
9 the study was in 2009, with daily mean temperatures reaching  $1.4$  and  $-0.2$  °C at the lower  
10 and upper treeline sites, respectively. The coldest and driest springs were in 2014, with mean  
11 temperatures of  $-0.2$  and  $-1.8$  °C and total precipitation of  $25.8$  and  $31.0$  mm at the lower and  
12 upper treeline sites, respectively. Monthly precipitation in March 2014 ranged between  $17.4$   
13 and  $21.8$  mm, which represented the highest amount of spring rain during the study period.

14

#### 15 *Threshold temperatures*

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

1 between years ( $P < 0.001$ ). Thresholds were significantly higher in 2010 than the other years  
2 and were lower in 2014 for the daily minimum and mean temperatures and in 2012 and 2014  
3 for the maximum temperature.

#### 4 *Two-dimensional Gaussian models*

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

11 The minimal  $Z_{xy}$  was 2.21 days for a time window of 12 days. The critical cumulative  
12 precipitation was  $17.0 \pm 5.6$  mm and the average minimum temperature was  $1.5 \pm 1.4$  °C  
13 when  $Z_{xy}$  was  $< 2.5$  days (Fig. 3). The spreads of this trough on the  $x$ - and  $y$ -axes were 48.0  
14 mm and  $2.04$  °C, respectively, with a counter-clockwise rotation of  $4.73^\circ$ . In the model with  
15 the average mean temperature, the minimal  $Z_{xy}$  was 1.85 days. The critical precipitation and  
16 temperature were  $26.9 \pm 3.9$  mm and  $4.6 \pm 1.8$  °C, respectively when  $Z_{xy}$  was  $< 2$  days. The  
17 spreads of this trough on the  $x$ - and  $y$ -axes were 44.1 mm and  $1.94$  °C respectively, with a  
18 counter-clockwise rotation of  $8.22^\circ$ . The minimal  $Z_{xy}$  was 1.90 days in the model with the  
19 average maximum temperature. The critical precipitation and temperature were  $29.9 \pm 3.0$   
20 mm and  $8.5 \pm 1.8$  °C, respectively, when  $Z_{xy}$  was  $< 2$  days. The spreads of this trough on the  $x$ -  
21 and  $y$ -axes were 51.1 mm and  $2.39$  °C, respectively, with a counter-clockwise rotation of  
22  $9.52^\circ$ . Most of the standardized residuals of these three models converged from -2 to 2

1 (Supplementary data Fig. S3). The standardized regression coefficients revealed similar  
2 contributions of the independent variables for explaining the onset of xylogenesis, with  
3 temperature and precipitation accounting for 47% and 53% of the variability in the date of  
4 xylogenesis onset, respectively.

5 The absolute differences between the observed and predicted dates of onset of xylogenesis  
6 using average minimum temperature and cumulative precipitation in a time window of 12  
7 days were smaller than the sampling interval by averages of 5.9 and 4.6 days at the lower and  
8 upper treeline sites, respectively (Fig. 4). The largest divergence between observations and  
9 predictions was 16 days in 2014 at the lower treeline.

10

## 11 **DISCUSSION**

12 We challenged the general opinion that temperature was the only driver of growth reactivation  
13 at high elevations by analyzing the onset of xylogenesis of Qilian juniper subjected to cold  
14 and dry climatic conditions on the northeastern Tibetan Plateau. Published threshold  
15 temperatures for the onset of xylogenesis in trees for boreal forest or within a dry inner Alpine  
16 valley range from 2 to 3 °C (Rossi *et al.*, 2007, 2008; Swidrak *et al.*, 2011; Boulouf Lugo *et*  
17 *al.*, 2012), whereas on the southeastern Tibetan Plateau the critical minimum temperature  
18 occurred at  $0.7 \pm 0.4$  °C (Li *et al.*, 2017). The large range (5 °C) in the thermal thresholds for  
19 the onset of xylogenesis in Qilian juniper provides additional evidence that temperature was  
20 not the only factor initiating xylem growth under cold and dry climatic conditions (Table 1).  
21 More reliable predictions were attained when both thermal and precipitation thresholds for the  
22 onset of xylogenesis were included in the fitted models (Fig. 4). The interaction between

1 temperature and precipitation satisfactorily explained the day of onset of xylogenesis in 2010,  
2 which was delayed by ca. three weeks compared with 2009 and 2011, despite the warm  
3 conditions during that spring (Ren *et al.*, 2015). This finding suggests that spring precipitation  
4 is also an important factor in the resumption of xylem formation in Qilian juniper.

5 Water availability is an important determinant of xylem formation. Before the start of  
6 xylem phenology, trees must compensate for the water lost during winter and spring to  
7 recover an adequate water balance, because turgor is an important requisite for xylem cell  
8 growth (Sevanto *et al.*, 2006). Rehydration time in spring can exceed six weeks, and stems are  
9 fully rehydrated one month before the onset of radial growth (Turcotte *et al.*, 2009). Both cell  
10 division and expansion in the xylem are sensitive to changes in water potential (Abe and  
11 Nakai, 1999; Savidge, 2001). The water potential in the cambium regulates mitosis and  
12 influences cell extension and the deposition of wall polymers (Abe and Nakai, 1999;  
13 Cosgrove, 2005; Arend and Fromm, 2007). Springs were rainy or water was abundantly  
14 supplied by snowmelt in the cold regions of previous studies, so the initiation of xylem  
15 growth was not limited by rehydration, and trees responded more to temperature rather than  
16 precipitation (Turcotte *et al.*, 2009). Warmer springs in such areas can substantially advance  
17 xylem phenology (Rossi *et al.*, 2011). The response to seasonal changes, including both  
18 initiation and cessation of growth, also can be controlled by photoperiod in many trees of the  
19 boreal and temperate regions (Körner and Basler, 2010; Maurya and Bhalerao, 2017). Winter  
20 and spring similarly are often wet in cold and drought-prone regions such as continental  
21 Mediterranean forests, and moisture is not considered the only factor in the resumption of  
22 xylem formation (Camarero *et al.*, 2010). With scarce snow, winter is extremely dry in our

1 study area; consequently water availability is low before growth reactivation. Moreover,  
2 drought stress would be higher under drier and warmer conditions, which would thus slow the  
3 onset of xylogenesis, as observed in spring 2010. Soil moisture occasionally can be increased  
4 by snowfall, such as the snowfall in 2014, as also occurs in boreal forests (Vaganov *et al.*,  
5 1999). The amount of water available during the snowmelt in our study increased soil  
6 moisture and possibly advanced the onset of xylogenesis, likely explaining the difference of  
7 16 days between observations and predictions in 2014 at the lower treeline. This research  
8 found that the onset of xylogenesis in Qilian juniper should meet the prerequisite for both  
9 critical temperature and precipitation.

10 This study is the first statistical attempt to demonstrate that the onset of xylogenesis is  
11 driven by an interaction between thermal and precipitation thresholds. The selected time  
12 window of 12 days agrees with the period required for tracheid expansion and differentiation  
13 (Vaganov *et al.*, 2006; Cuny *et al.*, 2015). Temperature is a well-recognized factor controlling  
14 the onset of xylem formation, but our findings provide new insights into the climatic forcing  
15 of growth. The critical temperatures and precipitation provide keys for modelling the response  
16 of forest ecosystems subjected to cold and dry constraints in response to climate change and  
17 could help our understanding of the regime shifts in these ecosystems (Scheffer *et al.*, 2001;  
18 Zhu *et al.*, 2014). In addition, temperature and precipitation were more efficient for modelling  
19 the onset of xylogenesis than the Standardized Precipitation Evapotranspiration Index (SPEI)  
20 (Ren *et al.*, 2015). The data of daily temperature and precipitation are absolute values  
21 obtained by direct measurement, while the SPEI drought index is quantified as monthly  
22 values and is estimated based on climatic data (Vicente-Serrano *et al.*, 2010). Our findings

1 also support the constraint of growth by drought stress in high-elevation forests or near the  
2 alpine treeline, as indicated by previous studies (Liang *et al.*, 2014; Piper *et al.*, 2016).

3 On the other hand, our predictions differed from observations when winter prior to tree  
4 growth was extremely cold or dry. For example, the mean temperature from March to April in  
5 2012 at the lower treeline was very low ( $-2.2^{\circ}\text{C}$ ), allowing for long-term storage of water as  
6 snow. Snowmelt combined with increasing temperature in spring can yield sufficient soil  
7 moisture for the onset of xylogenesis. A similar situation happened in 2014 at the lower  
8 treeline. However, at the upper treeline, a deeper snowpack in spring may delay the onset of  
9 xylogenesis by reflecting radiation and reducing the heat received by plants. In 2013, less  
10 snow (1.4 mm in precipitation) in March at the upper treeline was linked to an earlier onset of  
11 xylogenesis.

12 Tree growth in semi-arid areas generally is limited by drought stress resulting from lower  
13 precipitation and high evapotranspiration caused by warm temperature in the early growing  
14 season (Allen *et al.*, 2015). A similar constraint has been reported for the Tibetan Plateau and  
15 other Asian mountains (Shao *et al.*, 2005; Liang *et al.*, 2006, 2016; Liu *et al.*, 2006; Gou *et al.*,  
16 2014; Pederson *et al.*, 2014; Yang *et al.*, 2014; Zhang *et al.*, 2015). Warming-induced drought  
17 stress has been decreasing generalized tree growth and increasing mortality in semi-arid areas  
18 across Asia (Dulamsuren *et al.*, 2010; Liu *et al.*, 2013; Allen *et al.*, 2015; Liang *et al.*, 2016).  
19 In particular, the failure to produce stem wood in a particular year (missing rings) is a  
20 response to dry and warm spring conditions, and an increasing frequency of missing tree rings  
21 also is evident in response to the warming in recent decades (Liang *et al.*, 2014, 2016).  
22 Moreover, the frequency of missing rings has been strongly linked to tree mortality (Liang *et*



1 *al.*, 2016). We hypothesize that a failure to reach critical water availability for growth  
2 reactivation or a delay in cambial resumption in response to increasing drought stress could be  
3 primary factors in the failure to form a complete ring and portend lower growth and forest  
4 dieback. A mismatch between critical temperatures and amounts of moisture for the onset of  
5 xylogenesis under the drought conditions of global climate change and the acceleration of  
6 dryland expansion (Peñuelas *et al.*, 2007; Allen *et al.*, 2015; Huang *et al.*, 2015) will reduce  
7 forest resilience and risk regime shifts in vulnerable semi-arid forests. Reyer *et al.* (2015)  
8 proposed the assessment of forest resilience and potential tipping points at various levels,  
9 from leaf to biosphere, and our study has stressed that climatic thresholds for the onset of  
10 xylogenesis might be key indicators of forest resilience and tipping points under changing  
11 climates.

12

### 13 **SUPPLEMENTARY DATA**

14 [Supplementary data](#) are available online at [www.aob.oxfordjournals.org](http://www.aob.oxfordjournals.org) and consist of the  
15 following. [Table S1](#): Mean  $\pm$  SD of onset of xylogenesis (DOY, day of the year) during  
16 2009-2014 at the lower and upper treeline sites. [Figure S1](#): Correlations between the daily  
17 minimum, mean and maximum temperatures recorded at the Dulan meteorological station and  
18 the corresponding temperatures recorded during 2012-2014 at the lower and upper study  
19 treeline sites. [Figure S2](#): Sample surface plot and the corresponding level sets of a  
20 two-dimensional Gaussian model. [Figure S3](#): The distribution of standardized residuals in the  
21 time window of 12 days as a function of minimum, mean and maximum temperatures.

22

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1 **Tables**

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

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

1 **Figure legends**

2 **FIG. 1** Daily air temperature (lines) and precipitation (bars) during the 2009-2014  
3 period at the lower and upper study treeline sites.

4

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

8

9 **FIG. 3** Surface plots and the corresponding level sets showing the two-dimensional  
10 Gaussian distribution of the absolute difference between the observed day of onset of  
11 xylogenesis and the estimated day with a given average temperature and cumulative  
12 precipitation in the time window of 12 days. Note that the axes have different scales.

13

14 **FIG. 4** Observed and predicted days of onset of xylogenesis (DOY, day of the year) in  
15 *Juniperus przewalskii* during 2009-2014 at the lower and upper study treeline sites.  
16 Predictions were obtained using the threshold average minimum temperature and  
17 cumulative precipitation calculated by the models in the time window of 12 days.

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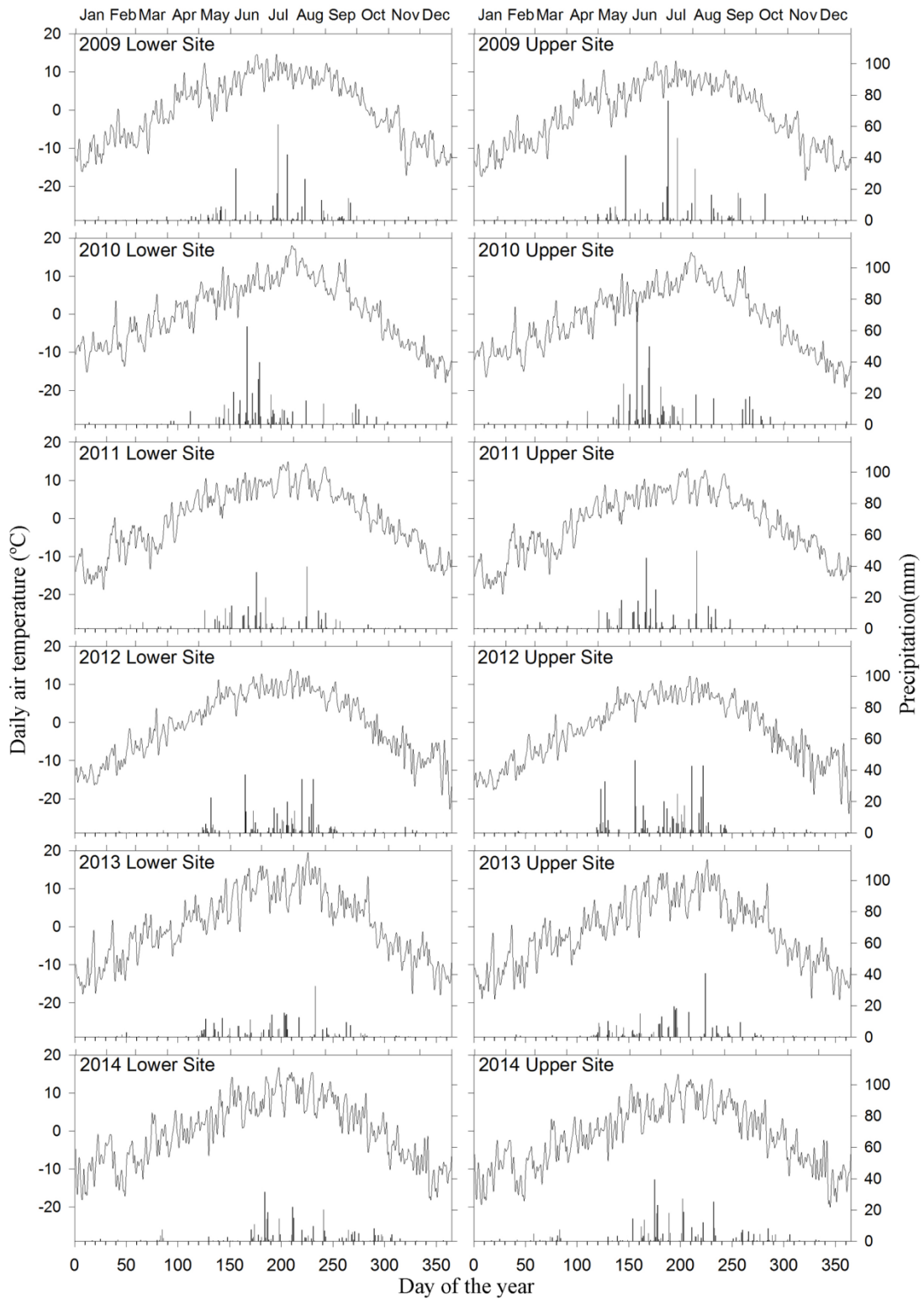
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Fig.1

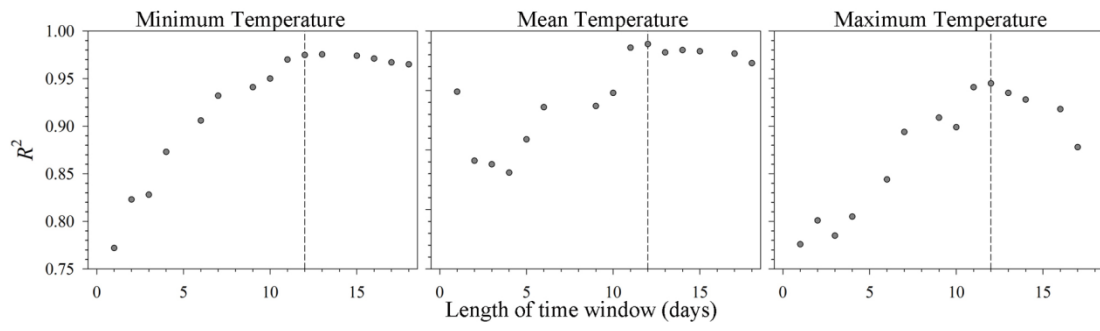
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Fig. 2

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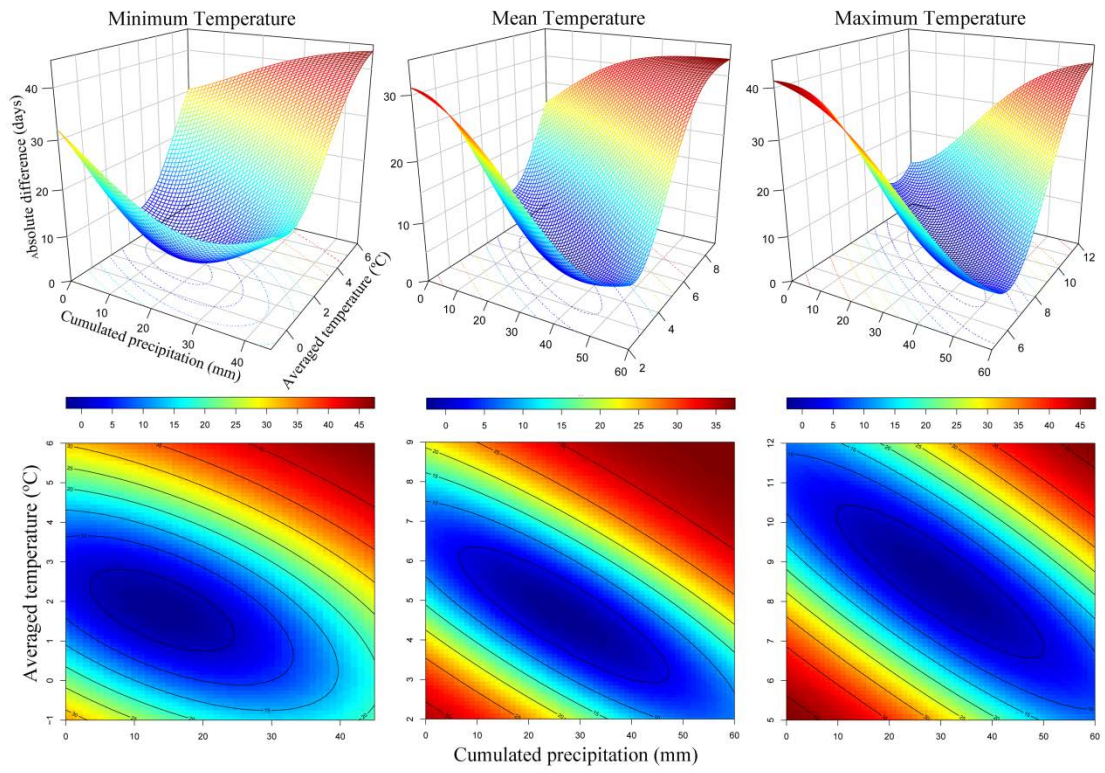
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4 Fig. 3

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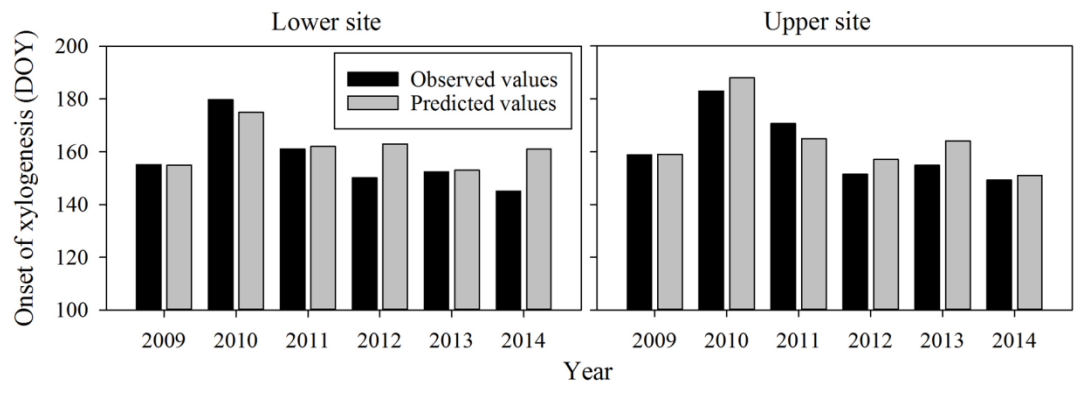
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4 Fig. 4

## SUPPLEMENTARY DATA

**Table S1** Mean  $\pm$  s.d. of onset of xylogenesis (DOY, day of the year) during 2009-2014 at the lower and upper site.

Site	Year					
	2009	2010	2011	2012	2013	2014
Lower	155 $\pm$ 4	180 $\pm$ 7	162 $\pm$ 8	150 $\pm$ 4	152 $\pm$ 7	145 $\pm$ 6
Upper	159 $\pm$ 2	183 $\pm$ 3	171 $\pm$ 4	151 $\pm$ 6	155 $\pm$ 7	149 $\pm$ 3



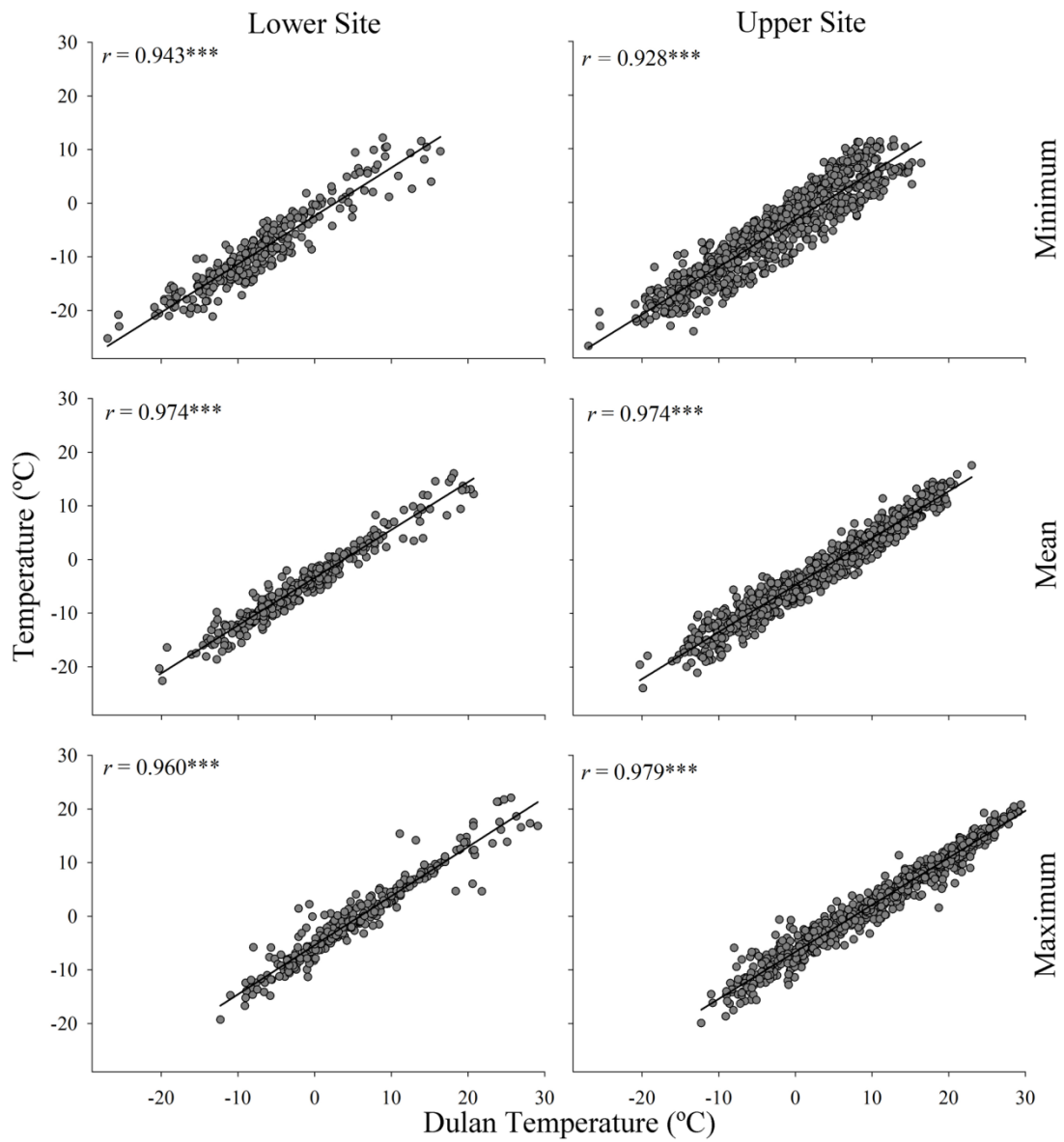


Figure S1: Correlations between the daily minimum, mean and maximum temperatures recorded at the Dulan meteorological station and the corresponding temperatures recorded during 2012-2014 at the lower and upper study treeline sites.

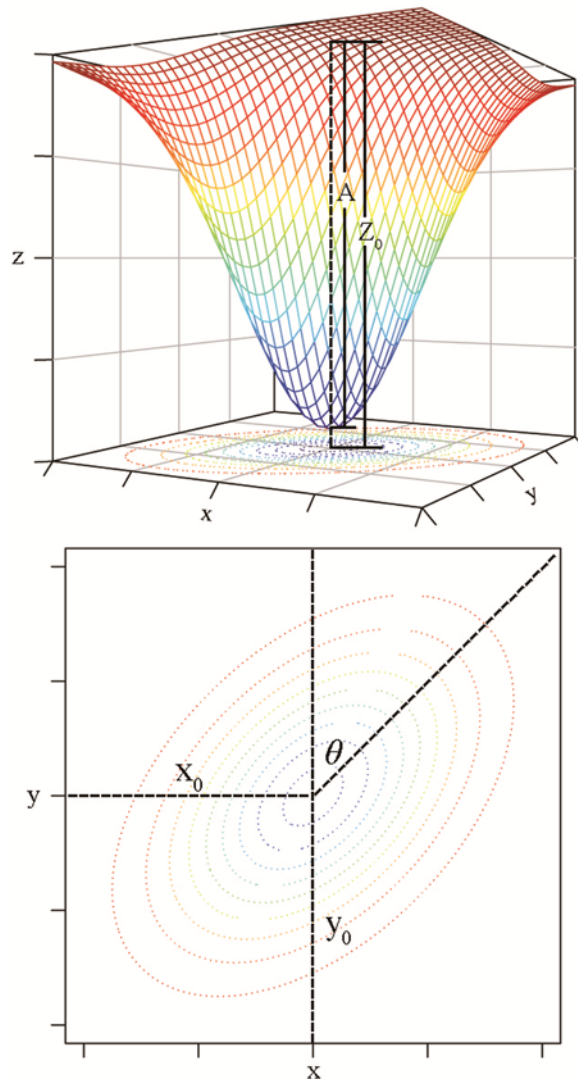


Figure S2: Sample surface plot and the corresponding level sets of a two-dimensional Gaussian model.

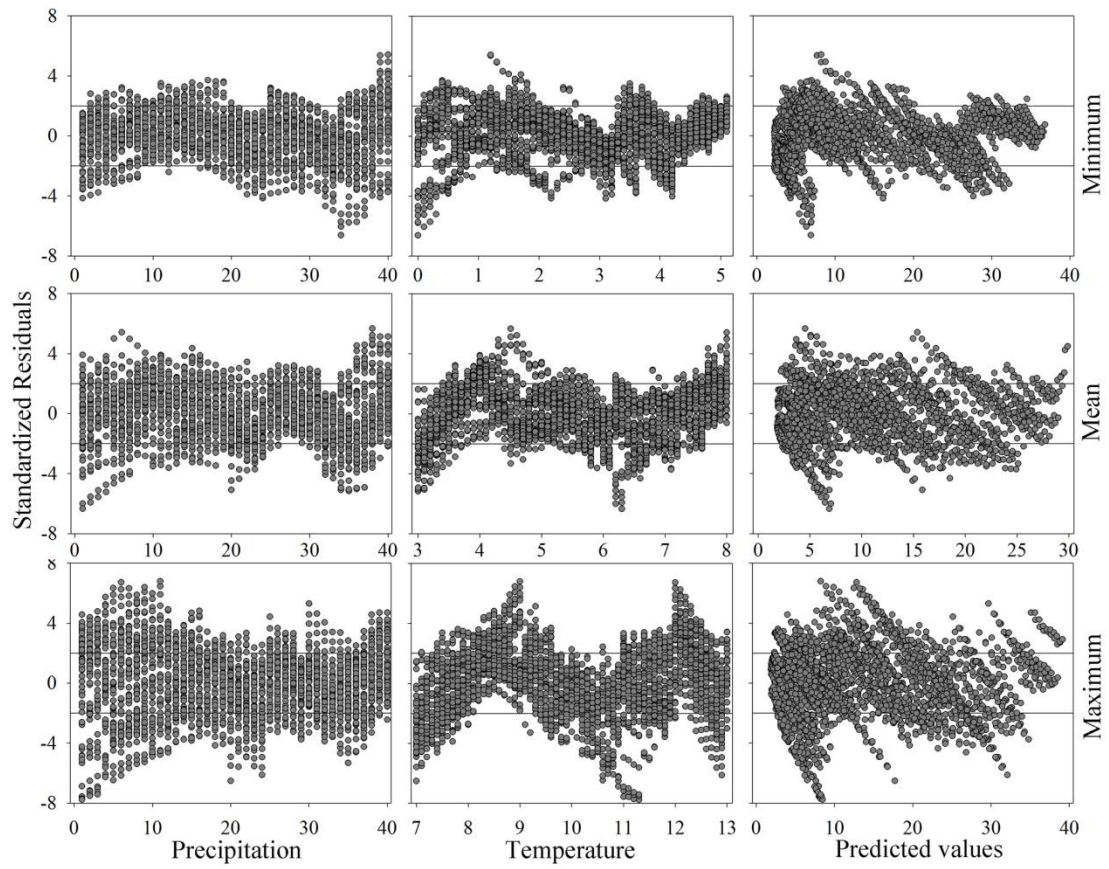


Figure S3: The distribution of standardized residuals in the time window of 12 days as a function of minimum, mean and maximum temperatures.