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Cambial phenology and xylogenesis of *Juniperus przewalskii* over a climatic gradient is influenced by both temperature and drought

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ABSTRACT

While temperature is known to be an important factor determining cambial phenology in cold and humid climates, how it interacts with other factors in determining the onset and end of xylogenesis is still not fully understood. Here, we analyzed phenological traits related to observed cambial phenology and xylogenesis over the course of two extreme hydroclimatic years across six sites that span the spatial distribution of Qilian juniper (*Juniperus przewalskii* Kom.) in the northeastern Tibetan Plateau. Cambial phenology and xylogenesis were assessed weekly or biweekly from the microcores of 30 trees. We found that the onset of xylogenesis significantly correlated with annual mean and minimum temperatures, regardless of the moisture conditions, resulting in an advance of the onset of xylogenesis of 10.1 days $^{\circ}C^{-1}$. In contrast, the end of xylogenesis was related to both maximum temperatures and drought conditions. The contrast in drought conditions over the two growing seasons made the importance of the water balance on the end of xylogenesis quite clear. During the extremely dry conditions of 2013, xylogenesis ended up to 30 days earlier than during 2012, a wetter and cooler year. Our results indicate that strong shifts in water availability during the growing season are crucial to the rate of wood production. Also, the significant correlation between the total number of xylem cells and both the duration and rate of wood production, highlights how changes in the timing of xylogenetic processes and the growth rate can have a strong influence on the future growth and performance of *J. przewalskii*. Our findings indicate that while warming promotes an early growing season and, potentially, a longer growing season, warming and decreased moisture availability has a strong influence on tree growth and productivity in cold and arid regions.

1. Introduction

Climate change is increasing air temperatures globally and altering precipitation patterns in ways that impact the frequency, severity, and nature of drought (IPCC, 2013). These changes are significantly effecting natural and human systems around the world. In particular, trees are sensitive to changing environmental conditions, which can have both positive or negative on tree growth (McDowell et al., 2008; Körner and Basler, 2010; Keenan, 2015). A longer growing season, warmer temperatures, and increased levels of CO_2 may favor tree growth in certain environments (Salzer et al., 2009; Rossi et al., 2011). In other locations, tree mortality rates have increased due to increasing drought and heat stress (Allen et al., 2010; Phillips et al., 2010). Regional warming and drought-stress have also been linked to the reduction of tree growth, which may even lead to a reorganization of region's biomes (Zhou et al., 2013, 2014). Given the anticipated change in climate in the coming decades, further investigations of tree growth and its response to climate variability are needed to inform the conservation of forests and the ecosystem services they provide to society (Walther et al., 2002; Lindner et al., 2010).

Cambial phenology and xylogenesis in trees are fundamental processes to stem growth and carbon sequestration (Fonti et al., 2010; Deslauriers et al., 2017). These processes are dynamic and have been shown to be influenced by climate (Rossi et al., 2016; Deslauriers et al., 2017), species (Gruber et al., 2013; Antonucci et al., 2015), tree age (Rossi et al., 2008; Li et al., 2013), tree size (Mencuccini et al., 2005; Rathgeber et al., 2011), altitude (Moser et al., 2010), and latitude (Rossi et al., 2014). Investigating how these factors influence cambial phenology and xylogenesis is crucial to improve our understanding of tree response to changes in environmental conditions. Importantly, such work will shed light on the physiology of climate–growth interactions.

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Many studies on cambial phenology have stressed the importance of temperature on the onset of xylogenesis, both in cold humid (e.g., Körner, 2006; Körner and Basler, 2010; Rossi et al., 2011, 2014, 2016) and cold dry environments (e.g. Camarero et al., 2010; Moser et al., 2010). The most common hypothesis for what determines the onset of xylogenesis is that low temperatures control the initiation of new cells by meristems irrespective of the photoassimilate abundance (Körner, 1998; Piper et al., 2005; Alvarez-Uria and Körner, 2007; Rossi et al., 2016). Supporting this hypothesis, some studies have found a daily minimum temperature threshold for cambial activity of 3.7–5 °C in northern and alpine forests (Deslauriers et al., 2008; Rossi et al., 2007, 2011). We found consistent results where temperature played a pivotal role in the onset of xylogenesis in *J. przewalskii* along an altitudinal transect in the cold and arid northeastern Tibetan Plateau (NETP) (Zhang et al., 2018). In contrast to this hypothesis, however, precipitation was found to play a critical role in the onset of xylogenesis over the course of three years at one site in our study region (Ren et al., 2015). This indicates that further research regarding the onset of xylogenesis in response to climate in cold and arid regions over multiple sites and trees is still needed.

In contrast to xylogenesis onset, much less is understood about what factors lead to the end of xylogenesis. Over three continents and a range of ecosystems, Rossi et al. (2016) found that the end of xylogenesis was linearly related to mean annual temperature, confirming previous work in cold and humid Canada (Rossi et al., 2011, 2014). Studies in northern and alpine forests, however, have found little influence of temperature on the end of the growing season (Deslauriers et al., 2008; Moser et al., 2010; Duchesne et al., 2012). The discrepancy between studies suggests that more research is needed to better understand what drives the end of xylogenesis.

As part of Earth's third pole, the NETP is an important area to study climate change impacts. This region not only encompasses the highest altitude and most complex terrain in the world, but it also possesses a wide range of climatic conditions, including high evaporation, low precipitation, and cold temperature (Yao et al., 2012). Notably, the NETP has experienced continuous warming and changes in the frequency of precipitation and extreme events (Liu and Chen, 2000). Despite being a region expected to experience significant environmental change, little is known about the impact that these changes can cause on the region's ecosystems, especially at the level of stem growth and carbon sequestration. Therefore, assessing cambial phenology in this region will also improve our overall understanding of the impact of climatic change on trees in cold and arid environments.

Juniperus przewalskii is a widely distributed and endemic tree species in the NETP. This species plays a key role in maintaining soil stability, conserving water, and mitigating regional droughts and floods (Gao et al., 2013). Due to its great longevity, drought and cold tolerance, and its ubiquitous nature, *J. przewalskii* has previously been used to reconstruct past climate (e.g. Zhang et al., 2003; Shao et al., 2010; Yang et al., 2014; Gou et al., 2015). These reconstructions generally provide information on the inter-annual to multi-centennial time scale, but they cannot provide information with enough resolution to understand intra-annual radial growth processes occurring in the tree. While a few studies have explored the cambial phenology and intra-annual growth dynamics in *J. przewalskii* (e.g. Ren et al., 2015; He et al., 2016; Zhang et al., 2018), most have used a limited number of trees or sites. To better understand what drives *J. przewalkii* growth and how it could respond to environmental change, it is essential to study the cambial phenology and xylogenesis of *J. przewalskii* with a much greater spatial and tree replication. Such a study will allow us to draw general patterns and ecological consequences.

We performed a high-resolution monitoring of the xylogenesis of *J. przewalksii* across its distribution on the NETP to investigate the relationship between cambial phenology and climate. Our study network covered a large gradient of moisture and temperature conditions. We test two hypotheses derived from our previous work on *J. przewalskii* over an altitudinal gradient (Zhang et al., 2018). Our first hypothesis is that temperature is the main driver for the onset of cambial phenology. Support for this hypothesis would leads us to expect that warming will advance the onset of growing season and thus increase its length on the cold NETP. Our second hypothesis is that drought also influences cambial phenology and xylogenesis regardless of altitude and latitude. Specifically, we found that moisture availability constrained the end of phenology and xylogenesis regardless of altitude (Zhang et al., 2018). Consequently, we expect lower growth rates and reduced cell production during drought conditions. We hope for our network to become a source of long-term information on the study of intra-annual stem growth processes that will help elucidate the many remaining questions regarding stem xylogenesis and contribute to test the hypotheses of prior research.

2. Materials and methods

2.1. Study area

The study area is located in the Qilian Mountains of the NETP in northwest China. The Qilian Mountains are surrounded by the Badain Jaran Desert and the Tengger Desert to the north, the Qaidam Basin to the south, the Taklimakan Desert and the Tarim Basin to the west and the Loess Plateau to the east (Fig. 1). This region is characterized by a typical arid climate with more precipitation falling in summer than winter. Vegetation is sparse, and the ecological environment is fragile (Tian et al., 2007). *J. przewalskii* is widely distributed on dry and infertile sunny slopes between 2600 and 4300 m a.s.l. across the whole Qilian Mountains (Shao et al., 2010). In this study, six permanent monitoring sites (LCG, DLH1, DLH2, QYG, YHLG, TLG) were established in mature *J. przewalskii* forests. These sites are located along altitudinal and latitudinal gradients that cover most of *J. przewalskii*'s spatial distribution on the Qilian Mountains (Table 1 and Fig. 1). Because the forests are open (canopy coverage is < 10%), tree-to-tree interactions between adult individuals is expected to be minimal, and the main factors determining tree growth are expected to be abiotic.

2.2. Climate

Two weather stations were installed in forest gaps at TLG and YHLG to measure air temperature and precipitation at 10 min intervals. Daily values were then calculated with the time series obtained from the 144 measurements collected each day. For the remaining monitoring sites (DLH, QYG and LCG) we used data from the nearest national weather stations, which are in all cases closer than 50 km away. We used daily mean, maximum and minimum temperatures, and total precipitation recorded by the Delingha (10 km from DLH), Qilian (15 km from QYG), and Jiuquan (50 km from LCG) meteorological stations (Fig. 2). These meteorological observations cover from 1961 to 2015. Missing daily temperature data were linearly interpolated and missing daily precipitation data were set to zero. Because the lower elevation of the meteorological stations compared to our sites, we used a lapse rate of 0.65 °C for each 100 m increase in elevation. No interpolation was performed on the precipitation data. To quantify the drought severity, the 3-month standardized precipitation evapotranspiration index (SPEI3) was calculated for each site using the monthly difference between precipitation and potential evapotranspiration for the same 1961–2015 period (Vicente-Serrano et al., 2010).

From 1961–2015, the mean annual temperature varied between -2.5 and 1.7 °C among monitoring sites. Temperatures changed according to latitude and altitude, with the sites located at lower altitudes and latitudes being the least cold in winter and warmest in summer (Table S1). Precipitation is distributed unevenly throughout the year, with May to September accounting for 79–90% of the annual precipitation (Fig. 2). In comparison to the long-term record, our study sites showed relatively cold and wet conditions in 2012 and warm and