Environmental Drivers for Cambial Reactivation of Qilian Junipers (*Juniperus przewalskii*) in a Semi-Arid Region of Northwestern China

Qiao Zeng [1,2,3]**, Sergio Rossi** [4,5]**, Bao Yang** [1,*]**, Chun Qin** [1,3] **and Gang Li** [6]

[1] Key Laboratory of Desert and Desertification, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China; zengqiao712@163.com (Q.Z.); qinchun@lzb.ac.cn (C.Q.)

[2] Key Lab of Guangdong for Utilization of Remote Sensing and Geographical Information System, Guangdong Open Laboratory of Geospatial Information Technology and Application, Guangzhou Institute of Geography, Guangzhou 510070, China

[3] University of Chinese Academy of Sciences, Beijing 100049, China

[4] Département des Sciences Fondamentales, Université du Québec à Chicoutimi, Chicoutimi, QC G7H2B1, Canada; sergio_rossi@uqac.ca

[5] Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

[6] Dongdashan Natural Reserve, Ganzhou District, Zhangye 734000, China; ligang1426@163.com

* Correspondence: yangbao@lzb.ac.cn

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Abstract: Although cambial reactivation is considered to be strongly dependent on temperature, the importance of water availability at the onset of xylogenesis in semi-arid regions still lacks sufficient evidences. In order to explore how environmental factors influence the initiation of cambial activity and wood formation, we monitored weekly cambial phenology in Qilian juniper (*Juniperus przewalskii*) from a semi-arid high-elevation region of northwestern China. We collected microcores from 12 trees at two elevations during the growing seasons in 2013 and 2014, testing the hypothesis that rainfall limits cambial reactivation in spring. Cambium was reactivated from late April to mid-May, and completed cell division from late July to early August, lasting 70–100 days. Both sites suffered from severe drought from January to April 2013, receiving < 1 mm of rain in April. In contrast, rainfall from January to April 2014 was 5–6 times higher than that in 2013. However, cambial reactivation in 2014 was delayed by 10 days. In spring, soil moisture gradually increased with warming temperatures, reaching 0.15 m³/m³ before the onset of xylogenesis, which may have ensured water availability for tree growth during the rainless period. We were unable to confirm the hypothesis that rainfall is a limiting factor of cambial reactivation. Our results highlight the importance of soil moisture in semi-arid regions, which better describe the environmental conditions that are favorable for cambial reactivation in water-limited ecosystems.

Keywords: cambial activity; *Juniperus przewalskii*; rainfall; temperature; soil moisture; xylogenesis

1. Introduction

In temperate and boreal ecosystems, cambium experiences periodic cycles of dormancy and growth, according to the seasonal variation of climate [1–3]. The sequential phenological events of xylogenesis, i.e., cell division, enlargement and cell wall formation, result in the annual growth rings. Cambial phenology is the critical event for tree growth, because it defines the reactivation and ending

of cell production in spring and summer, respectively, thus indicating the favorable periods for xylem formation [4,5]. In the context of climate change, the projected warming associated with the increased intensity and frequency of extreme events raises the uncertainty and risk of the survival of some forest ecosystems, mainly those subjected to extreme climatic events [6]. Therefore, it is important to investigate the environmental drivers and physiological mechanisms that regulate cambial phenology, and to explore how trees respond to extreme events.

It has been observed in the field, and confirmed under controlled experiments, that outside the tropics the cambial reactivation in spring is triggered by temperature [1,7–9]. Rossi et al. [10] found that conifer species at the alpine timberline started xylem formation at converging air temperature thresholds of 5.6–8.5 °C, thereby demonstrating temperature-dependent xylogenesis at high altitude. Swidrak et al. [11] studied *Pinus sylvestris* growing in a dry Alpine valley and revealed that early spring temperature was the main limiting factor for the onset of radial growth. Localized heating of the stem during winter and spring induced earlier cambial reactivation, confirming the role of temperature in the onset of cambial activity [7,12,13]. In the above studies, snowmelt or rainfall during early spring was sufficient to provide adequate water supply for the trees; however, other studies conducted in arid regions of the northeastern Tibetan Plateau and western United States demonstrated that moisture availability could be an important, although overlooked, factor triggering the onset of wood formation [14,15]. Water availability influences a number of physiological processes, such as cell expansion and division, by affecting the turgor pressure within cambial and derivative cells [16], which may alter the timing and duration of the cell enlargement phase as well as the final number and characteristics of tracheids [15,17]. These studies raise the issue of water availability for cambial reactivation, a question that remains unresolved because most studies have been performed in cold or humid areas.

In the semi-arid region of northwestern China, forest ecosystems generally experience long, cold and dry winters under the influence of the Mongolia anticyclone. On one hand, the low temperatures delay cambial activity in early spring: for example, Zhang et al. [18,19] investigated the cambial phenology in Qilian junipers (*Juniperus przewalskii*) along latitudinal and altitudinal gradients and confirmed the temperature-driven onset of wood formation in this region; based on a tree-ring growth model, Yang et al. [20] proposed that April-June minimum temperatures triggered the start of the growing season on the Tibetan Plateau. On the other hand, the extreme dry winters may prevent the rehydration of the tissues needed for cambial reactivation [21]. Ren et al. [22] demonstrated that precipitation controls the onset of xylem formation in Qilian junipers in the semi-arid area of northwestern China. Overall, diverging studies in the literature have reported conflicting results for the same species and area, indicating the complexity and uncertainty of cambial phenology in this climatically sensitive region [14,19,22]. The question of how extreme drought events influence the dynamics of growth reactivation in forest species is still unanswered.

Although the majority of dendrochronology researches have been carried out in the semi-arid region of northwestern China and helped to reconstruct climate change history based on tree-ring records at annual resolution [23–26], in situ field observations of cambial phenology are still insufficient because of the remote locations and harsh weather conditions. In order to investigate the climatic drivers of cambial phenology from an intra-annual perspective, the aim of this work is (1) to describe the timing and duration of xylogenesis in Qilian junipers in the semi-arid region of northwestern China, and (2) to assess the effect of environmental factors on the cambial activity during two consecutive growing seasons (2013–2014). Given the dry winter conditions at the study sites, we tested the hypothesis that rainfall is a limiting factor for cambial reactivation in spring.

2. Materials and Methods

2.1. Study Sites and Tree Selection

The study was conducted at the Sidalong Forestry Station in the Qilian Mountains National Natural Reserve. We chose two sites located on south-facing slopes in the central Qilian Mountains [27]: a higher altitude site (38°26.64′ N, 99°56.03′ E, 3550 m above sea level (a.s.l.)) named UL situated adjacent to a mountain top; and a lower altitude site (38°26.28′ N, 99°55.01′ E, 2865 m a.s.l.) named LL close to the lower timberline (Figure 1). Qilian juniper (*Juniperus przewalskii*) and Qinghai spruce (*Picea crassifolia*) are the dominant tree species in this region.
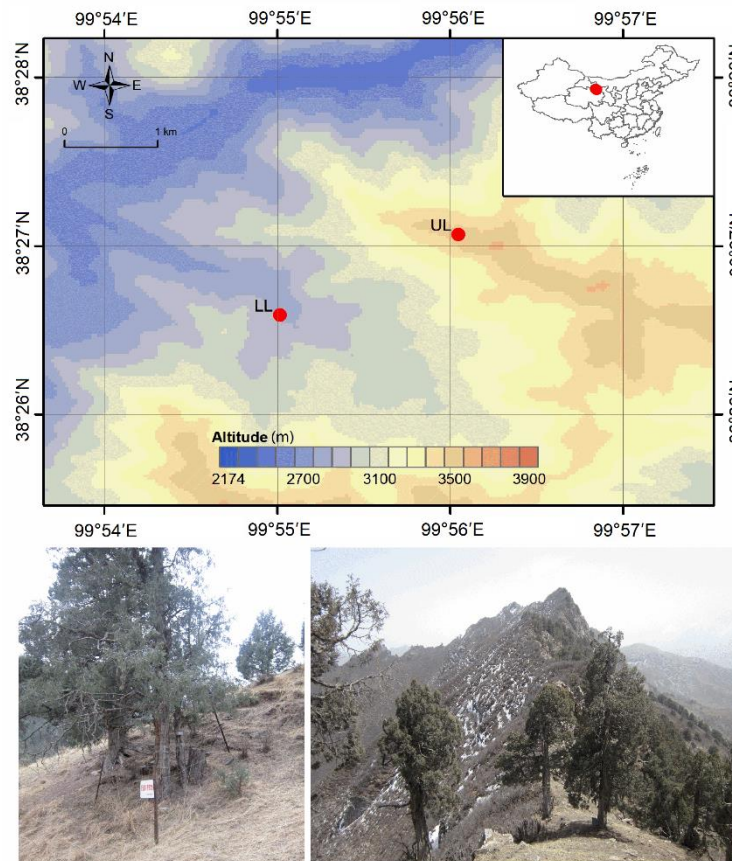

Figure 1. Locations and images of the study sites at Sidalong Forestry Station, a semi-arid area of northwestern China.

The climate in the study area is typically continental with wet and warm summers, but cold and dry winters (Figure 2). Long-term climate observations (1957–2012) from the national meteorological station at Qilian (38°11′ N, 100°15′ E, 2787 m a.s.l.), located at a linear distance of 40 km from the sites, show a long-term mean annual temperature of 1.1 °C, and annual precipitation of 404.8 mm. January and July are the coldest and warmest months, with mean temperatures of −13.1 and 13.1 °C, respectively. The mean maximum temperature of the warmest month and mean minimum temperature of the coldest month are 20.9 and −20.6 °C, respectively. The probable frost period (when absolute monthly minimum temperatures are below 0 °C) lasts from September to May, and the definite frost period (when mean monthly minimum temperatures are below 0 °C) lasts from November to March. Rainfall from May to September accounts for 90% of the annual total precipitation, indicating the humid period in this area [28].
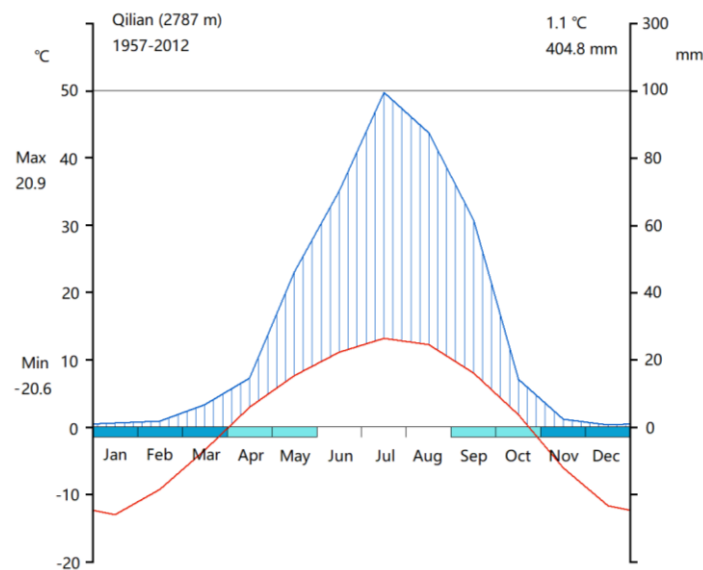
Figure 2. Walter and Lieth climatic diagram for Qilian meteorological station during 1957–2012. Mean monthly precipitation is plotted as the blue line and mean monthly air temperature as the red line. Humid periods are filled by vertical blue lines. The values of mean maximum temperature of the warmest month and mean minimum temperature of the coldest month are shown along the y-axis. Probable frost periods are shown by light blue boxes and definite frost periods are shown by dark blue boxes along the x-axis.

In total, twelve Qilian junipers were randomly selected for long-term observations. Eight trees in UL and four trees in LL were sampled, with ages of 319 ± 56 yr and 43 ± 6 yr, and diameters at breast height of 21 ± 6 cm and 11 ± 1 cm, respectively. Trees with partially dead crowns, polycormic stems, reaction wood, or obvious damage were avoided.

2.2. Meteorological Data

During 2013 and 2014, air temperature, rainfall, soil water content, and soil temperature were recorded at 30 min intervals with a 2 m high automatic meteorological station (HOBO U30) installed in a forest gap in each plot. Daily air and soil temperatures were calculated from the recorded time series.

2.3. Xylem Sampling and Observation

Xylem formation was monitored weekly from April to October during 2013 and 2014. At each sampling time, two microcores (15 mm in length, 2 mm in diameter) were collected from each tree at breast height (1.3 m) using a Trephor [29]. We collected > 1000 microcores, of which 700 were analyzed in the lab after excluding unsuitable samples. This procedure minimizes damage to the stem and enables long-term microcore samplings. The thick, dead outer bark was removed before sampling. Samples usually contained the previous 3–5 tree rings and the developing xylem with the cambial zone and adjacent phloem [30]. After sampling, the microcores were immediately placed in Eppendorf microtubes with ethanol (50% in water), and stored at 5 °C to protect against tissue deterioration.

The microcores were dehydrated in different concentrations of ethanol and embedded in paraffin. Transverse sections (10–12 μm in thickness) were cut with a rotary microtome, stained with a 1% water solution of safranin and astra blue [31], and observed under bright field and polarized light at 200–400 × magnifications. The cambial and enlarging cells were only composed of thin cell primary walls which did not shine when observed under polarized light, unlike the secondary walls [30]. In spring, at least one horizontal row of cells observed in the enlarging phase indicated the onset of xylem formation. During the enlarging phase, the radial diameter of a cell was at least twice that of a cambial cell [32]. Because of the different arrangements of cellulose microfibrils from primary walls,

the developing secondary walls were observed to shine under polarized light. Lignification started from the cell corners and middle lamella and spread into the secondary walls, with the color of cell walls changing from blue to red [1,33]. In late summer, the totally red color of the cell walls and the empty lumen indicated the maturity of cells and the completion of xylem formation. We counted the number of cambial, enlarging, secondary wall thickening and mature cells along three radial rows for each samples to assess the dynamics of xylogenesis [34].

2.4. Statistical Analyses

The onset and end of the phenological phases were expressed in days of the year (DOY). Timings and duration of xylem differentiation and the final radial number of xylem cells were compared between sites and years using analysis of variance (ANOVA). The interactions between sites and years were also tested. All statistics were analyzed using SAS 9.4 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Weather during 2013 and 2014

At UL, the mean, maximum, and minimum annual temperatures in 2013 were higher than that in 2014 (Figure 3, Table 1). January (−11.2 °C) and August (9.9 °C) were the coldest and warmest months in 2013, while December (−11.6 °C) and July (10.0 °C) were the coldest and warmest months in 2014. During the growing season (from May to August), the monthly mean, maximum and minimum temperatures were also correspondingly higher than those in 2014. The daily variations in weather conditions were similar between the two sites (Figure 3). At LL, the daily air temperature showed larger fluctuations than that at UL. During the growing season, the mean monthly air temperatures were 10.5 °C (2013) and 9.6 °C (2014).
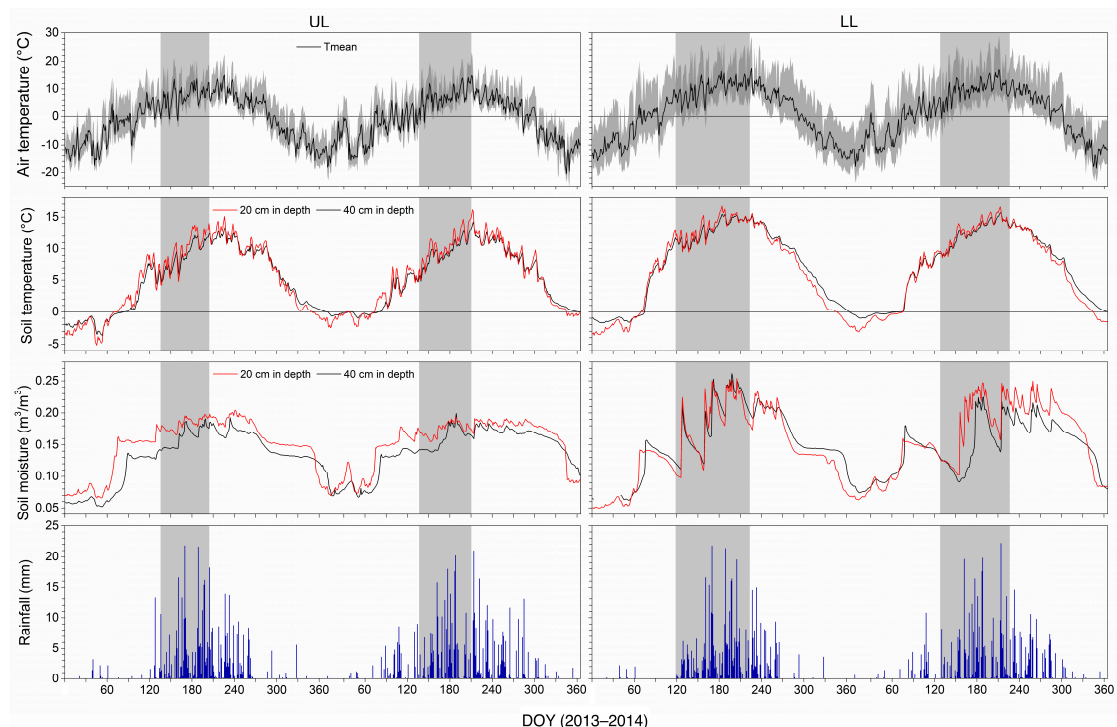

Figure 3. Daily time series of mean air temperature (minimum and maximum values are shown in dark gray), mean soil temperature and soil moisture of the upper (20 cm depth) and lower (40 cm depth) soil layers, and total rainfall at UL and LL during 2013 and 2014. Periods of cambial activity are shown by light gray shading.

Table 1. Annual climate records at UL and LL during 2013 and 2014. Values in parentheses are related to the growing season (May–August).

		Air Temperature (°C)			Soil Temperature (°C)		Soil Moisture (m³/m³)		
Year	Site	Mean	Maximum	Minimum	At 20 cm	At 40 cm	At 20 cm	At 40 cm	Rainfall (mm)
2013	UL	−0.3 (7.6)	6.1 (13.2)	−4.5 (3.7)	5.3 (10.4)	5.0 (9.5)	0.15 (0.18)	0.13 (0.16)	500.4 (420.2)
2014		−0.9 (6.5)	5.3 (12.3)	−5.2 (2.5)	5.5 (10.5)	5.3 (9.6)	0.15 (0.18)	0.14 (0.16)	584.8 (411.8)
2013	LL	1.5 (10.5)	10.9 (18.5)	−4.8 (4.6)	7.0 (13.6)	7.4 (13.2)	0.14 (0.19)	0.16 (0.19)	505.3 (431.8)
2014		1.0 (9.6)	10.2 (17.9)	−5.2 (3.4)	6.8 (13.0)	7.2 (12.6)	0.16 (0.18)	0.14 (0.16)	549.6 (388.0)

The mean annual soil temperature was similar in both years, and showed lower daily amplitudes than that of air temperature. During winter, mean daily soil temperature was colder in the upper layer compared to the lower layer, and both declined after rainfall events > 2 mm. During the growing season, the monthly mean soil temperature was higher in the upper layer.

At UL, the annual rainfall in 2013 (500.4 mm) was lower than that in 2014 (584.8 mm); the main differences where from April to August, and in October. April rainfall in 2013 was only 1.0 mm, compared with 40.6 mm in 2014. In addition, the rainfall during the growing season was higher in 2013 (420.2 mm) than in 2014 (411.8 mm). At LL, the annual rainfall was higher in 2014 (549.6 mm) than in 2013 (505.3 mm); however, the growing period in 2013 (431.8 mm) received more rainfall than that in 2014 (388.0 mm).

Soil moisture at 20 and 40 cm depth was lowest during winter, increasing rapidly after complete snowmelt in late spring. Soil moisture at LL fluctuated more sharply than at UL, despite the similar annual averages. In early spring, soil moisture in the upper layer increased markedly when the daily mean air temperature rose above 0 °C; this was earlier than that in the lower layer, which increased with the warmer soil temperature, in spite of the total March–April rainfall in 2013 being less than 5 mm at both sites.

3.2. Cambial Activity

In autumn and winter, the dormant cambium of Qilian junipers was composed of 3–4 cells at UL and 5–6 cells at LL (Figure 4). In late spring, the cambial cells started to divide, indicating the onset of cambial activity. At UL, the earliest cambial reactivation was observed in early May 2013 (DOY 126). Cambium was still dormant on 15 May 2014 (DOY 135). As the number of cambial cells decreased in mid-July, cambial activity gradually reduced and returned to the dormancy stage. Cambial activity terminated at the end of July in both years. At LL, cambial activity in 2014 showed similar but delayed annual dynamics when compared to 2013: cambial activity started in late April 2013, 10 days earlier than in 2014, and ended in early August (DOY 223–226) in both years.
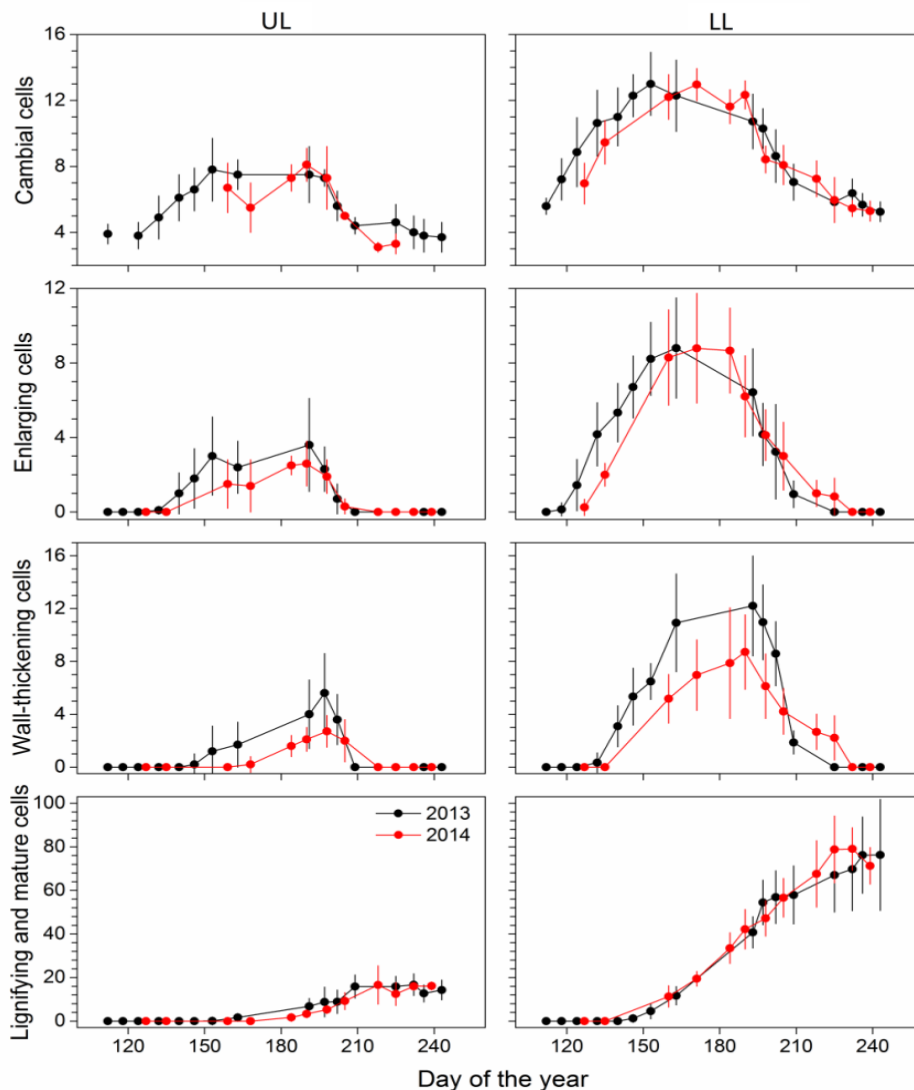
Figure 4. Number of cells during different xylogenesis phases at UL and LL during 2013 and 2014. Error bars indicate standard deviations for sampling trees per sampling date.

3.3. Xylem Differentiation and Cell Production

The trends in xylem differentiation in Qilian junipers were similar, but the timings and duration of xylogenesis differed significantly between sites (P < 0.0001) (Figures 4 and 5, Table 2). At UL, the enlarging phase started in mid-May (DOY 136–137) in both years, while at LL, the enlarging cells occurred from late April to early May (DOY 119–128) (Figure 5, Table 2). On average, the onset of cell enlargement was earlier in 2013 than in 2014 (F = 4.96, P < 0.05), while the enlarging phase terminated from late July to early August without a significant difference between years (F = 3.99, P > 0.05). The duration of cell production was similar in 2013 and 2014 (F = 0.39, P > 0.05), on average lasting 69 d at UL and 98-104 d at LL. Furthermore, the duration of xylogenesis (which corresponded to the time from the onset of cell enlargement to the end of lignification) was similar between years (F = 0.11, P > 0.05) but varied significantly between sites (F = 68.20, P < 0.0001), lasting 72–73 d at UL and 102–105 d at LL. Trees at a given site produced similar numbers of radial cells at the end of the two growing seasons (F = 0.01, P > 0.05), with 15–16 cells at UL and 81–83 cells at LL. We also tested the interaction effects between sites and years (Table 2); the results showed that the interaction effects were not statistically significant (P > 0.05), indicating that the two sites responded in the same way in both years.
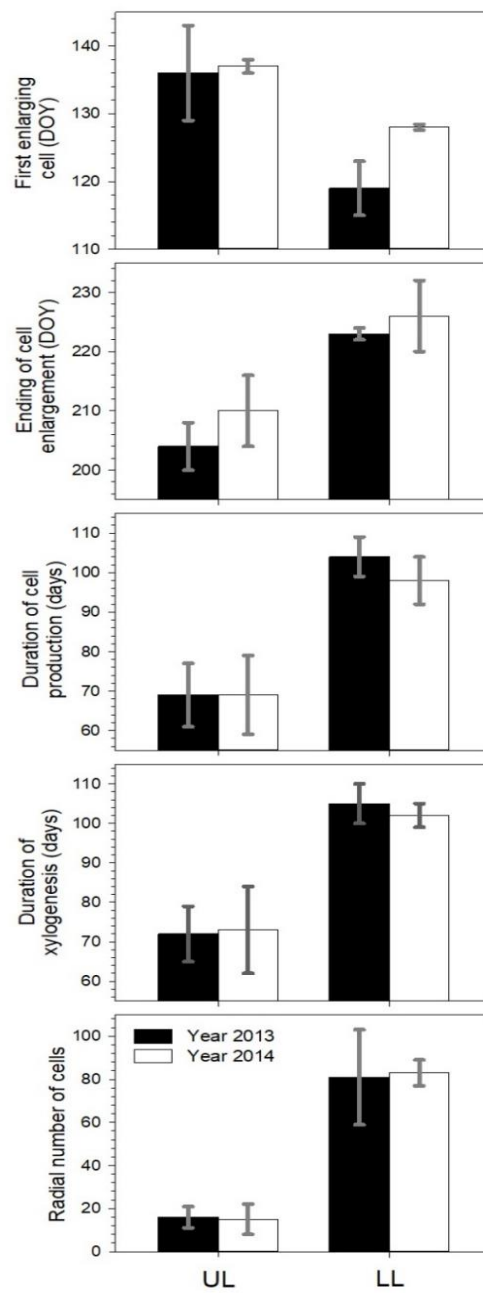
Figure 5. Timings and duration of xylem formation and cell production observed at UL and LL during 2013 and 2014. Error bars indicate standard deviations among trees.

Table 2. ANOVA results comparing timings and duration of xylogenesis and cell production between sites, years, and their interaction.

	Site		Year		Site × Year	
	F	P	F	P	F	P
First enlarging cell	34.10	<0.0001	4.96	0.038	2.98	0.100
Ending of enlargement	56.95	<0.0001	3.99	0.060	0.31	0.585
Duration of cell production	67.00	<0.0001	0.39	0.539	0.62	0.441
Duration of xylogenesis	68.20	<0.0001	0.11	0.739	0.22	0.641
Radial number of cells	170.37	<0.0001	0.01	0.916	0.21	0.655

4. Discussion

4.1. Impact of Climatic Factors on Cambial Reactivation

Cambial phenology, especially the timing of the initiation of cambial activity, has a significant impact on xylem formation as well as on a tree's ability to adapt to its environment [5,35]. Before the growth initiation in spring, trees recover from the winter dehydration and, uptake the required amount of water in preparation for cell extension [36–38]. Thus, water availability is crucial for cambial reactivation, particularly in semi-arid and arid regions where trees are more susceptible to water stress. Ren et al. [22] proposed that precipitation can limit cambial reactivation in spring even if temperature is favorable for tree growth in drought-prone areas. Accordingly, given the contrasting patterns of spring rainfall between 2013 and 2014 in our study sites, we expected that the onset of cambial activity in Qilian junipers in the semi-arid region of northwestern China would have been delayed because of the lack of rainfall in early spring. Surprisingly, in 2013 our results showed that both sites experienced a very dry period from January to April, with precipitation totals of only 11.2 and 7.0 mm at UL and LL, respectively. In particular, there were 58 days without rainfall before cambial reactivation at LL, and only 1 mm precipitation was received in April at UL. However, the onset of cambial activity was on average 10 days earlier in 2013 when compared to 2014. Based on this result, we reject the initial hypothesis that rainfall is the main factor driving cambial reactivation in spring.

Bernal et al. [39] monitored the appearance of new stems of *Erica multiflora* in the Mediterranean basin, and detected an earlier onset of growth in plants under experimental drought in spring. They considered that drought increased stomatal closure and decreased the cooling effect of transpiration; therefore, plants under drought conditions experienced higher temperatures than those of the control, which advanced the growth of the warming-sensitive *Erica multiflora* [40]. According to the climatic records at our study sites, 2014 was characterized by a cold and wet spring, especially in April, with mean air temperatures 1.12 and 0.63 °C lower in 2014 at UL and LL, respectively, compared to 2013. Thus, the cold spring in 2014 led to a delayed initiation of cambial activity in Qilian junipers, consequently delaying the onset of cell differentiation. Based on a series of temperature and moisture gradients, Zhang et al. [19] studied the cambial phenology of Qilian juniper and confirmed the significant effect of temperature on cambial reactivation in spite of the extreme drought in 2013 in northwestern China. Therefore, we conclude that the warmer spring induced an earlier initiation of cambial activity, which is in agreement with the previous studies [1,10,13,41,42].

It is well-known that in ecosystems where radial growth is controlled by temperature, growth reactivation occurs after snowmelt and the thawing of the upper soil layer [2,10,43]. Rossi et al. [10] considered that cold soil conditions limit root activity and water uptake ability, thereby delaying the enlarging phase of stem cells that depend on positive turgor pressure. In this work, we found that, even with little rainfall before the growing season in 2013, soil moisture had substantially recovered by March to a level close to that observed during the growing season ($0.15 \text{ m}^3/\text{m}^3$) (Figure 3, Table 1). We suggest that the low temperatures and low evaporation during winter and early spring in the semi-arid region of northwestern China aid the retention of soil moisture inputs from snow melt and water vapor condensation. As the air temperature gradually warms up in spring, thawing of the remaining snow cover and frozen soil water releases moisture for uptake by trees [44]. Thus, we assume that the soil moisture was adequate for cambial reactivation at the beginning of the growing season in 2013. Moreover, we propose the hypothesis that soil moisture is a necessary but not sufficient condition for growth reactivation, because of its interaction with spring warming. Thus, as observed in spring 2014, when air temperature is low the soil moisture alone is unable to trigger an earlier onset of cambial activity. Our findings highlight the importance of measuring soil moisture in semi-arid regions to gain deeper insights into the environmental conditions of tree growth in water-limited ecosystems.

4.2. Phenology and Cell Production

Although the onset of the enlarging phase differed significantly between 2013 and 2014, our results showed no corresponding difference in the duration of cell production or final number of radial cells in Qilian juniper; therefore, the earlier onset of cambial activity in spring did not appear to prolong the growing season or increase final cell production. Zhang et al. [19] proposed that relatively higher water availability could enhance the rate of cell production in summer, while drought stress could inhibit wood formation at the end of xylogenesis in a drought-prone environment. In our case, during the second half of July, radial growth gradually slowed down and approached to the end of cambial activity in all the sampling trees. However, the amount of rainfall in the second half of July was three times higher in 2013 than in 2014, which resulted in a relatively lower air temperature during this period, thereby delaying the highest temperature of 2013 until mid-August. While continuous rain events brought abundant water during the last stage of wood formation, we consider that these did not help to prolong the growing season. Overall, due to the inconclusive evidence concerning driving factors of the end of xylogenesis, especially in this cold and arid environment, long-term in situ observations will be needed to discover how cambial phenology responds to different climatic conditions.

5. Conclusions

The present study has demonstrated that, for the initiation of cambial reactivation in this semi-arid region of northwestern China, rainfall is not a critical factor per se. Water is important for spring rehydration of cambium and phloem, but water availability originating from other sources can play an important role during the rain-free period. During two consecutive years with contrasting rainfall patterns, abundant rainfall in early spring decreased the simultaneous air temperature, in turn delaying the onset of xylogenesis in 2014, while the warmer spring in 2013 provided favorable heat conditions and advanced the start of the growing season. In 2013, little rainfall was received during winter and early spring; however, the increase in soil moisture following the snowmelt represented an important source of water for spring rehydration in Qilian junipers. Under ongoing global climate change, spring warming may cause an earlier onset of cambial reactivation in Qilian junipers in the semi-arid region of northwestern China, if snow cover and its associated input to spring soil moisture remain similar to those of present-day conditions.

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