

Article

Intra-Annual Growth and Its Response to Climatic Factors of Two *Salix* Species under Warm Temperate Environment

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Abstract: Monitoring cambial activity and intra-annual growth dynamics is an effective method for identifying tree growth response to climate change. However, there have been few pieces of research on intra-annual wood formation of diffuse-porous species under monsoonal warm temperate environment. Here, we monitored weekly the cambial activity and xylem differentiation of *Salix babylonica* and *Salix matsudana* by collecting microcores during the 2018 growing season. Two willow species exhibited similar cambial activity and xylem differentiation processes, of which the onset and cessation of xylem growth was from middle/late March to early/middle November. The onset and cessation of cambial activity were slightly earlier for *Salix matsudana* (19 March and 12 October) than for *Salix babylonica* (26 March and 17 October), which peaked on 2 June and 31 May, respectively. *Salix babylonica* showed wider xylem increment and higher growth rate than that of *Salix matsudana*, of which the intra-annual xylem width was $8525 \pm 1201 \mu\text{m}$ and $7603 \pm 826 \mu\text{m}$, respectively, fitted by Gompertz function. Moreover, the maximum growth rate of *Salix babylonica* and *Salix matsudana* was $79.75 \mu\text{m day}^{-1}$ and $66 \mu\text{m day}^{-1}$, respectively, occurring on 4 June (DOY155) and 26 May (DOY146). Both temperature and water availability were important factors influenced the xylem growth for two species, which *Salix matsudana* had a stronger response to temperature but not to water availability than *Salix babylonica*. These results suggested that *Salix babylonica* seem to grow better under moist warm temperate environment due to it being a more conservative response to the climate than *Salix babylonica*. These observed species-specific differences at the intra-annual scale may help researchers more accurately anticipate the species suitability in temperate forests.



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Keywords: microcore; cambium; radial growth; temperature; water availability

1. Introduction

Forests represent a large carbon sink and their woody tissues account for 15% of annual anthropogenic CO₂ emissions [1]. However, their capacity to uptake carbon as woody tissues depends on how their radial growth responds to the climate. Therefore, understanding how wood formation and radial growth occur and respond to climate at inter- and intra-annual scales is necessary for assessing the climate change potential of forests [2–4].

Both biotic and abiotic factors, including fire, drought, and insect outbreaks, can influence forest ecosystem and their regulating services [5–7], where climatic variability has a direct effect on tree growth [8]. Analytic wood and increment borer are traditional methods to study trees inter-annual growth and their relationship with climatic factors [9]. However, trees have seasonal growth pattern, thus the drivers of wood (i.e., xylem) formation and cambial dynamics at intra-annual scale may shift. Previous studies demonstrated that the rate and timing of xylem growth (xylogenesis) vary in space and time because cambial processes are predominantly controlled by temperature, moisture, or their interaction [10,11], which reflect local climatic conditions [12,13]. In cold boreal and mountainous regions, xylem growth is closely related to the seasonal course of temperature and usually exhibits

a peak of growth rates around the summer solstice [14]. In semi-arid alpine forests, low spring precipitation may delay the onset of the growing season [15]. In the Mediterranean forests, due to the dry summer, growth is divided into the warm, wet spring and autumn seasons [16], and precipitation is the main driving factor that influences the tree growth [17], which leads to bimodal or even multimodal patterns in xylem growth [18]. Therefore, the level of seasonal xylem growth in response to climatic conditions may differ between different sites.

Moreover, recent research showed that, besides the site conditions, seasonal growth dynamics may also differ between forest ecosystems with different forest types (broadleaved, coniferous) [19]. In Europe and North America, intensive studies have focused on the seasonal dynamics of xylem growth, not only discussing the conifers [20] but also involving the diffuse-porous trees (birch, maple, beech, or poplar) [21,22] and ring-porous species (oak, chestnut, or ash) [23]. Michelot et al., (2012) observed clear longer growth duration for Scots pine (*Pinus sylvestris*), compared with that of European beech (*Fagus sylvatica*) and Sessile oak (*Quercus petraea*) under the same climatic conditions [24]. As a result, a significantly larger ring width was found for pine, which was influenced by longer growth duration. Species-specific wood anatomy structural properties (e.g., tracheid and vessel xylem) and stomata sensitivity (e.g., anisohydric and isohydric) could result in between-species different responses to climatic factors [25]. In China, most previous studies on cambial phenology were conducted in the Qinghai–Tibet Plateau [26,27], arid/semiarid region [28,29], and subtropical region [30], which referred to mainly on conifers species (e.g., *Juniperus przewalskii*, *Picea crassifolia*, *Pinus massoniana*) but fewer focus on broadleaf species [31]. For many species, therefore, the impacts of climate warming on xylem growth and development remain poorly understood.

Weeping willow (*Salix babylonica*) and Hankow willow (*Salix matsudana*) are deciduous broadleaved trees, and both are native willow species in China, which are currently dominant in temperate broadleaved and mixed forests of China and Europe [32,33]. The distribution ranges of these two species are almost similar, and all of them are common species used for afforestation and greening in northern China, due to its rapid growth. *Salix babylonica* often grows in wet areas, which are adjacent to rivers or drains, whereas *Salix matsudana* is more drought resistant [34,35]. At present, research of these two willows mainly focus on the cultivation technology [36]; drought tolerance [37,38]; and genetic, morphological, and physiological responses to heavy metal (Pb, Zn, Cd, etc.) and salt stress [39,40].

To the best of our knowledge, no comparative study has been undertaken into the intra-annual growth dynamics of the two or more coexisting willows used microcores and their relation to climatic factors with respect to species-specific factors, which will help to clarify the climatic signals controlling the wood formation of different willow species to improve predictions of climate warming impacts on tree growth and species' distribution. Here, based on the xylogenesis monitoring by microcores method at biweekly/weekly intervals in 2018, we aimed (1) to characterize the dynamics of intra-annual growth (the timing of onset and end, as well as the growth rate of xylogenesis) of *Salix babylonica* and *Salix matsudana*, and (2) to relate the xylem growth with climatic variables, and further to compare the differences of the climate–growth relationship between *Salix babylonica* and *Salix matsudana*. We hypothesized that (1) both temperature and water availability may be climatic driving forces for wood formation in the transition zone from temperate zone to subtropical zone; (2) drought resistant *Salix matsudana* may be strongly responsive to water availability, as compared with *Salix babylonica*.

2. Materials and Methods

2.1. Study Site

The study was conducted on Kaiyuan Campus of Henan University of Science and Technology (34°36' N, 112°25' E, 142 m a.s.l., Figure 1), Central China. The site is located in warm, temperate climate, where the mean annual temperature is 14.2 °C and the annual

precipitation is 598 mm from 1960 to 2017. The study year of 2018 was relatively warm and wet, with 1.1 °C higher mean annual temperature and 223 mm surplus annual precipitation than the 1960–2017 average. In the study area, the herb is dominated by *Zoysia* spp. and shrubs are mainly *Cercis chinensis* and *Pittosporum tobira*. The main soil type is meadow cinnamon soil.

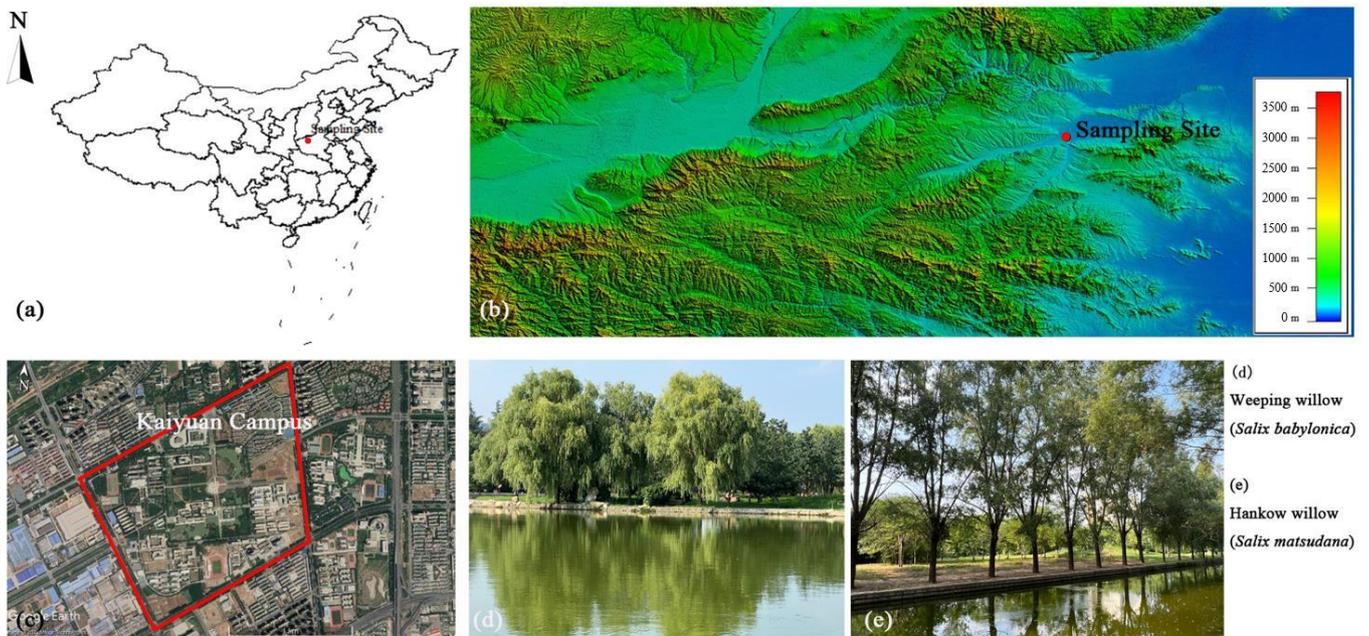


Figure 1. Geographical location of study site in central China (a,b), the study area landscape from Google Earth (c), and the photos of two tree species (d,e). Species photos were taken by Pengfei Luo.

2.2. Tree Selection and Lab Preparation

Three healthy and mature trees were randomly selected for both *Salix babylonica* and *Salix matsudana*. The diameter at breast height (1.3 m), tree height, and age of monitored *Salix babylonica* and *Salix matsudana* were 35.3 ± 1.8 cm and 25.5 ± 2 cm, 11.1 ± 0.2 m and 10.9 ± 0.4 m, and 16 ± 4 years and 13 ± 1 years, respectively.

From January to December 2018, microcores were sampled by 7–10 days intervals along the stem at breast height (1.3 m) using a Trepfor [41], which is an effective tool that has been widely accepted and used in dendroecology [20]. The microcores were 2 mm in diameter and 15 mm in length, containing the previous one to three xylem rings, cambium zone, and the adjacent phloem [42]. After sampling, the microcores were immediately put in 50% ethanol and glycerol mixed solution ($v:v = 1:1$) and stored at 4 °C to avoid tissue deterioration [43]. A total of 180 microcores were collected. In the laboratory, the microcores were dehydrated in successive ethanol solutions (50%, 70%, 90%, 95%, and 100%), xylene, and embedded in paraffin. Transverse sections of 8 μ m were cut using a Leica RM 2235 rotary microtome (Leica Microsystems, Wetzlar, Germany) and stained with 1% safranin and 0.5% fast green (in 95% ethanol) [44]. Next, the sections were observed under the Leica microscope (Leica DM 2500) to identify cambial activity and xylem differentiation.

2.3. Cambial Activity and Xylem Differentiation

In this research, cambial activity and xylem differentiation was divided into the cambial zone (CZ), radial enlargement phase (EN) and mature phase (M, Figure 2). Cambial cell was arranged in order, with thin cell wall and small cell diameter. The enlarging cell was defined as still showed thin cell walls but radial diameter was at least twice that of cambial cell. Both cambial cell and enlarging cell appeared blue-green after safranin and fast green stained [15]. Mature cell was cell wall finished the lignification, which appeared purplish red after being stained with safranin and fast green [45].

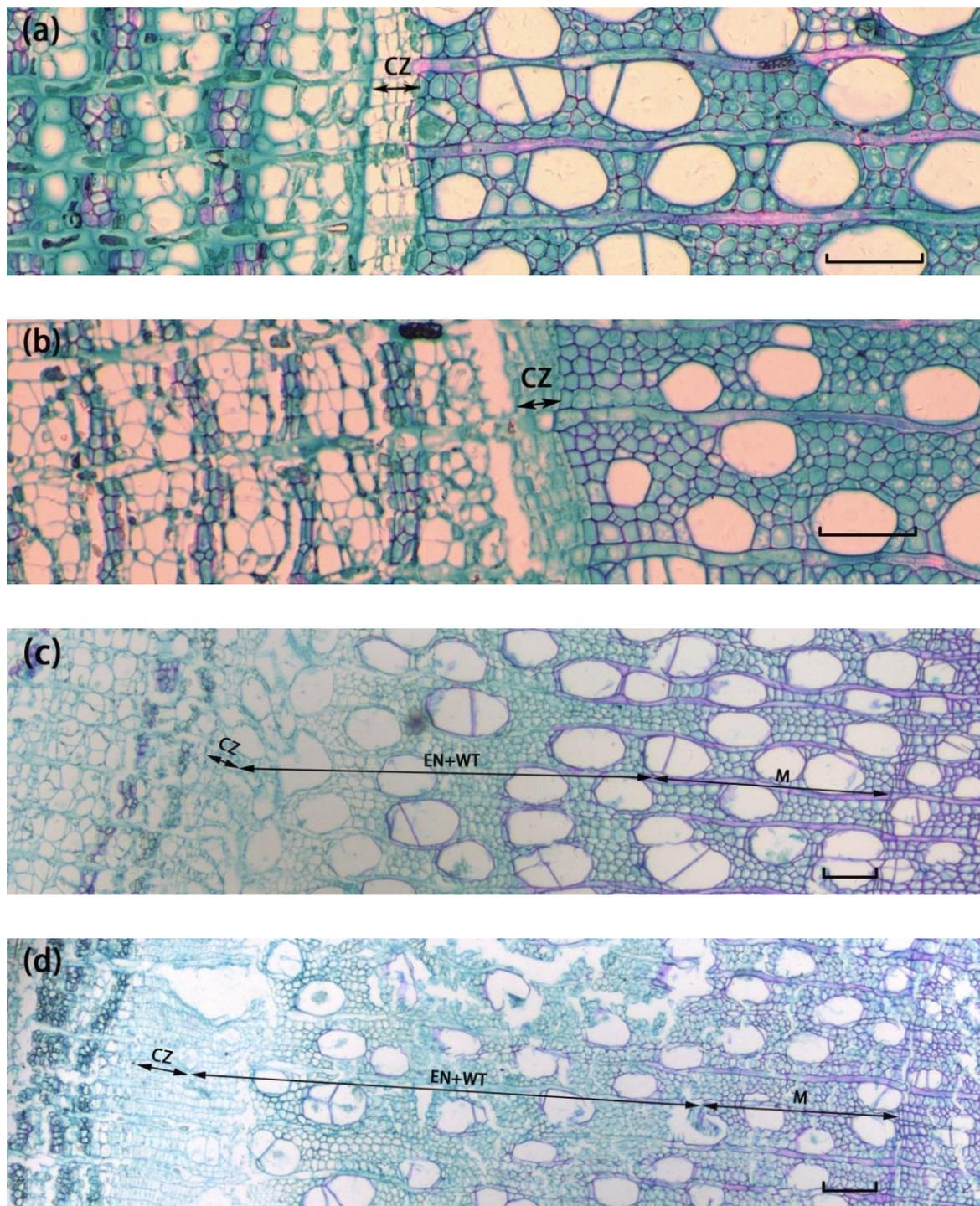


Figure 2. Phases of wood formation of *Salix babylonica* (a,c) and *Salix matsudana* (b,d) in 2018. (a,b): on 10 March, no new xylem cell production was observed and the cambial zone (CZ) consisted of five to six cells and four to five cells for *Salix babylonica* (a,c) and *Salix matsudana*, respectively. (c,d): In the middle of the growing season (4 May) enlarging (EN), wall-thickening (WT), and mature (M) cells in xylem. Scale bar = 100 μ m.

When at least one row of enlarging cell was observed, cambial activity and xylem differentiation were considered to be onset in the xylem. When no enlarging cell was observed and cell division was stopped, cambial activity was considered to have ceased. When the last cell in wall-thickening phase matured at the end of the growing period, xylem differentiation was completed [46].

For each section, the number of cells in the cambial zone was counted, and the radial growth increment of xylem was measured along three radial files using Image J [47]. For each tree, four stages were used to assess the process of xylem differentiation, including first enlarging cell, first mature cell, end of cambial activity, and completion lignifications. For each stage, differences between two species were compared by non-parametric test.

2.4. Intra-Annual Xylem Growth Fitting

To assess the dynamics of xylem growth, the xylem increment was modeled for each tree with a Gompertz function, using nonlinear regression procedure by Origin software (OriginLab Corporation, Northampton, MA, USA) [48]. The Gompertz equation was defined as:

$$Y = Ae^{-e^{-k(x-x_c)}}$$

where Y is the accumulation xylem growth, x is the time expressed as DOY (day of the year), A is upper asymptote (maximum growth expressed), k is the rate of change of the shape, and x_c is the date of the inflection point.

In addition, the xylem growth rate can be estimated by first-order derivation of the fitted function [49]. The maximum production rate (r_{max}) and the average rate of wood production (r_{mean}) were computed as [50]:

$$r_{max} = kA/e$$

$$r_{mean} = (9/40)er_{max}$$

2.5. Climate and Growth Relationship Analysis

Daily climate data were obtained from the nearest state meteorological station in Mengjin, which was located approximately 20 km from the site (34°49' N, 112°26' E, 333 m a.s.l.). These data were corrected and assessed with high quality of less than 1% missing rate and nearly 100% accuracy, which could be acquired from China Meteorological Science Data Sharing Network (<http://data.cma.cn>) (accessed on 1 September 2020).

The effects of climate factors and tree species on the xylem growth increment and xylem growth rate were analyzed separately using linear mixed models, where the tree species and climate variables—including air mean temperature, ground surface temperature, precipitation, relative humidity, vapor pressure deficit, and sunshine duration—were designated as fixed effects, whereas individual trees were designated as random effects. All statistical analyses were conducted using R version 3.4.0 (Vienna, Austria) [51]. Daily vapor pressure deficit (VPD) was calculated from daily mean values of air temperature and relative humidity [52]. Cumulative precipitation and daily mean values of other climatic factors were calculated between two sampling intervals. Xylem growth increment and growth rate (fitting value) of each of the two sampling intervals were also calculated.

3. Results

3.1. Cambial Activity

Dynamics of the number of cambial cells in *Salix babylonica* and *Salix matsudana* showed a “single peak” during 2018 growing season (Figure 3). *Salix babylonica* started cambial activity at the end of March (DOY85 ± 9) and reached its maximum (12 ± 1 cells) at the end of May (DOY153 ± 9). After that, the number of cambial cells began to decline continuously until the middle of October (DOY290 ± 14). When cambial activity nearly stopped, the number of cambial cells remained at five to six. Compared with *Salix babylonica*, the onset and end timing of cambial activity of *Salix matsudana* were seven days earlier (DOY78 ± 4) and five days earlier (DOY285 ± 0), respectively. However, the timing reached the maximum value of cambial cells was two days earlier (DOY151 ± 3) than *Salix babylonica*, which was stable at nine to ten cells. During the dormancy in autumn, the number of cambial cells of *Salix matsudana* was stable at four to five, less than that of *Salix babylonica*.

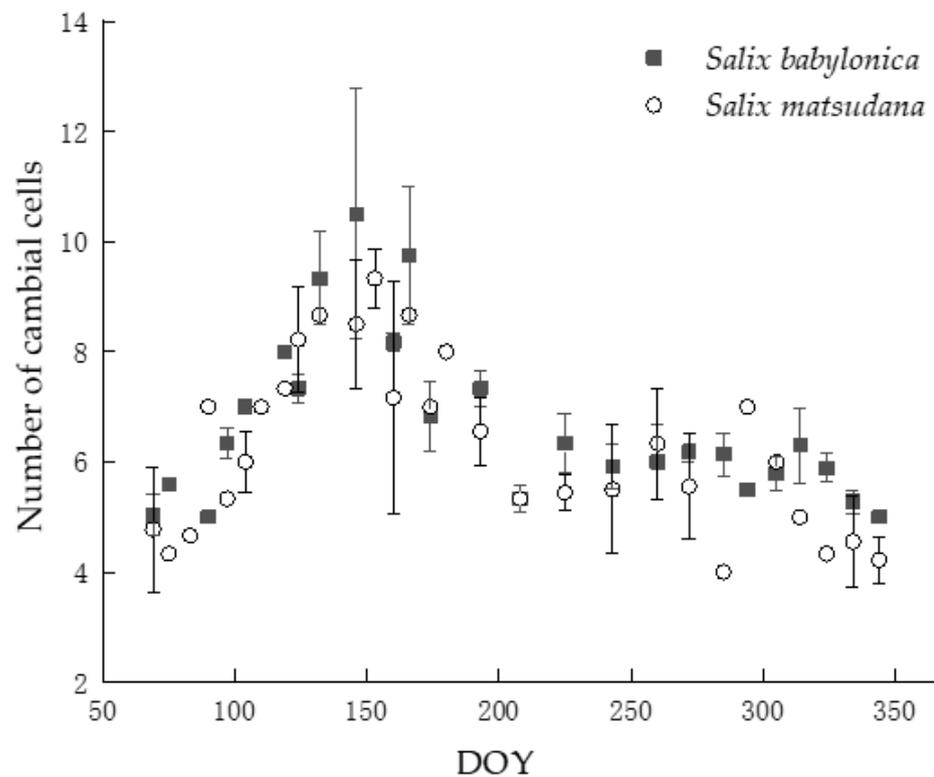


Figure 3. Number of cells observed in the cambial zone of *Salix babylonica* and *Salix matsudana* during 2018. Dots and bars represent average number of cells and standard deviations among three trees, respectively.

3.2. Xylem Differentiation

Both species exhibited almost similar stem xylem differentiation process (Table 1, $p > 0.05$). The timing of the first mature cell in the xylem of *Salix babylonica* was occurred around late April (DOY111 \pm 6). In the middle of November (DOY321 \pm 5), the last formed xylem cell of *Salix babylonica* was completed. For *Salix matsudana*, the first mature cell appeared two days later (DOY113 \pm 4) than that of *Salix babylonica*. After that, the last formed latewood cell finished lignification in the beginning of November (DOY311 \pm 4). Correspondingly, the duration of xylogenesis was 236 days and 233 days for *Salix babylonica* and *Salix matsudana*, respectively.

Table 1. Xylem differentiation of *Salix babylonica* and *Salix matsudana*.

	First Enlarging Cell	First Mature Cell	End of Cambial Activity	Completion Lignification
<i>Salix babylonica</i>	85 \pm 9	111 \pm 6	290 \pm 14	321 \pm 5
<i>Salix matsudana</i>	78 \pm 4	113 \pm 4	285 \pm 0	311 \pm 4
<i>z</i>	−0.943	−0.471	−0.696	−1.65
<i>p</i>	0.346	0.653	0.487	0.099

Date was expressed as day of the year (DOY).

3.3. Xylem Growth Comparison

The Gompertz function adequately fitted the xylem growth of *Salix babylonica* and *Salix matsudana*, which the adjusted R^2 values were 0.95 and 0.88 ($p < 0.001$), respectively. The average width of xylem (A) was 8525 \pm 1201 μm and 7603 \pm 826 μm for *Salix babylonica* and *Salix matsudana*, respectively (Table 2). The average xylem width growth rate (r_{mean}) was 48.77 $\mu\text{m d}^{-1}$ and 40.52 $\mu\text{m d}^{-1}$ for *Salix babylonica* and *Salix matsudana*, respectively. As expected, the maximum xylem growth rate was 13.75 $\mu\text{m d}^{-1}$, higher than that of *Salix matsudana*, and the date of maximum xylem growth rate (x_c) occurred in early

June (DOY155 ± 5) and late May (DOY146 ± 5) for *Salix babylonica* and *Salix matsudana*, respectively.

Table 2. Measured and fitted values of radial growth increment in 2018.

		Measured Value (μm)	A (μm)	r_{mean} (μm/d)	r_{max} (μm/d)	x_c (DOY)
<i>Salix babylonica</i>	1	7870	7154	45.59	74.54	150
	2	9106		47.48	77.64	161
	3	7634	8342	53.25	87.07	153
<i>Salix matsudana</i>	1	7742	8636	34.53	56.45	153
	2	6778	7560	37.98	62.10	145
	3	5329	6614	49.05	80.20	140

A = upper asymptote (maximum growth), r_{mean} = the mean radial growth rate, r_{max} = the maximum radial growth rate, x_c = the date of the maximum growth rate occurrence (the inflection point), DOY = day of the year. The fitted values (A, r_{mean} , r_{max} and x_c) were modeled by Gompertz function.

3.4. Climate–Xylem Growth Relationship

Both temperature (air temperature and ground surface temperature) and water availability (precipitation, relative humidity, and vapor pressure deficit) had a significant effect on the xylem growth increment for both *Salix babylonica* and *Salix matsudana* (Table 3). The xylem increments in response to water availability were similar between species. However, the effect of temperature on the width of xylem growth of *Salix matsudana* was stronger, compared with *Salix babylonica*, as indicated by the significant interaction term in the model (Table 3). The xylem growth increment of both species was not affected by sunshine duration ($p > 0.05$).

Table 3. Effects of daily climate factors on the xylem growth increment and xylem growth rate of *Salix babylonica* and *Salix matsudana*. In the models, *Salix babylonica* represents the reference group.

Model Parameters	Xylem Growth Increment			Xylem Growth Rate		
	Estimate	SE	t-Value	Estimate	SE	t-Value
Air temperature						
Intercept	−153.31	40.04	−3.83 ***	−12.15	5.70	−2.13 *
Ta	21.65	2.02	10.74 ***	2.22	0.29	7.75 ***
<i>S. matsudana</i>	−119.31	56.62	−2.11 *	−12.46	8.06	−1.55
Ta × <i>S. matsudana</i>	8.13	2.85	2.85 **	0.82	0.41	2.03 *
Ground surface temperature						
Intercept	−124.81	41.12	−3.04 **	−10.68	5.52	−1.94
GST	17.87	1.83	9.77 ***	1.91	0.25	7.77 ***
<i>S. matsudana</i>	−105.14	58.16	−1.81	−11.32	7.80	−1.45
GST × <i>S. matsudana</i>	6.55	2.59	2.53 *	0.68	0.35	1.95
Precipitation						
Intercept	158.99	28.14	5.65 ***	23.42	3.70	6.32 ***
PRE	3.41	0.73	4.66 ***	0.22	0.10	2.26 *
<i>S. matsudana</i>	−6.04	39.80	−0.15	−0.33	5.24	−0.06
PRE × <i>S. matsudana</i>	1.44	1.04	1.39	0.12	0.14	0.87
Relative humidity						
Intercept	4.33	102.01	0.04	23.40	12.60	1.86
RH	398.63	161.96	2.46 *	9.40	20.00	0.47
<i>S. matsudana</i>	−77.97	144.29	−0.54	−4.44	17.82	−0.25
RH × <i>S. matsudana</i>	178.89	229.05	0.78	11.81	28.29	0.42
Vapor pressure deficit						
Intercept	110.24	50.28	2.19 *	5.84	5.48	1.06
VPD	151.74	62.57	3.08 **	25.51	5.38	4.74 ***
<i>S. matsudana</i>	−17.66	71.11	−0.25	−4.67	7.76	−0.60
VPD × <i>S. matsudana</i>	54.12	69.67	0.78	8.18	7.60	1.08

Table 3. Cont.

Model Parameters	Xylem Growth Increment			Xylem Growth Rate		
	Estimate	SE	t-Value	Estimate	SE	t-Value
Sunshine duration						
Intercept	132.77	65.75	2.02 *	7.34	7.51	0.98
SSD	17.90	9.46	1.89	3.36	1.08	3.11 **
<i>S. matsudana</i>	14.12	92.98	0.15	0.91	10.61	0.09
SSD × <i>S. matsudana</i>	2.73	13.38	0.20	0.29	1.53	0.19

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

The xylem growth rate was also significantly affected by temperature (air temperature and ground surface temperature), water availability (precipitation and vapor pressure deficit), and sunshine duration. However, the effect of relative humidity on the growth rate was not significant. In addition, the growth rate of *Salix matsudana* increased more rapidly with the increase in air temperature, compared with *Salix babylonica*.

4. Discussion

4.1. Cambial Activity of Two Willows in Warm Temperate Zone

In this study, the onset and cessation timing of cambial activity of *Salix babylonica* and *Salix matsudana* are basically the same (Table 1), which were in the middle/late March (DOY 85 ± 9 and DOY 78 ± 4) and the middle October (DOY 290 ± 14 and DOY 285 ± 0), respectively. Correspondingly, the duration of cambial activity was 205 days and 207 days for *Salix babylonica* and *Salix matsudana*, respectively.

In Qilian Mountains, a cold and arid environment on the northeastern Tibetan Plateau, the duration of cambial activity of *Juniperus przewalskii* was shorter, lasting around 90 days, which started in mid-May to mid-August [27]. In the warm temperate zone, Zhang et al. reported that the duration of cambial activity of *Pinus massoniana* Willd lasted for about 240 days [53]. Unlike the complete dormancy of cambial cells in temperate and boreal trees, there might be a semi-dormancy in subtropical pine in January. As a result, the duration of cambial activity of *Pinus massoniana* in subtropical China was four or six months longer than temperate and boreal trees, which was more than 300 days [29].

It is generally considered that air temperature is the main environmental factor that controls the initiation of cambial activity. Once the daily mean air temperature reaches 6–8 °C, the tree cambium begins to be active [25]. As the seasonal average air temperature increases with decreasing latitude, an earlier onset of tree's cambial activity along the latitude gradient is reasonable. Therefore, it could explain why in the Qilian Mountains, compared to the warm temperate zone and the subtropical zone, the onset timing of cambial activity was in mid-May, rather than mid-March or mid-February. In addition, the duration of cambial activity became longer, from approximately 90 days to 240 days, to almost all year.

4.2. Xylem Growth with High Growth Rate

Based on the measured values, the width of intra-annual xylem growth of *Salix babylonica* and *Salix matsudana* was $8203 \pm 646 \mu\text{m}$ and $6616 \pm 992 \mu\text{m}$, respectively (Table 2). Similarly, the annual xylem increment of *Salix matsudana* at the cambial age of 12a–14a was about 7000 μm , which was analyzed by analytical wood in a semi-arid and semi-humid area [54]. By using the dendrometer method, Ma et al. found that the average annual xylem increment of *Salix matsudana* was 6637 μm during 2016–2019 in Beijing [55], which is in line with our findings. Although the relevant research on *Salix babylonica* is lacking, these studies supported that using the microcore method to monitor the intra-annual xylem growth process of willow is feasible. Additionally, the result of our work showed that *Salix matsudana* was in a favorable growing condition.

The growing season for both species was from March to November (Figure 4), and the daily average growth rate was 48.77 μm and 40.52 μm for *Salix babylonica* and *Salix matsu-*

dana (Table 2), respectively, which were fitted by Gompertz model. The average growth rates of these two *Salix* were much higher than some trees in tropical and subtropical zones, which was $3.0 \mu\text{m d}^{-1}$ and $14.8 \mu\text{m d}^{-1}$ of *Hopea pierrei* in tropic and *Cunninghamia lanceolata* in subtropic, respectively [56,57]. This behavior could be largely explained by willow's genetic differences, related to the species-specific capacity to fast-growing under-favorable water conditions [58]. In addition to that, tree species in warm temperate tend to complete growth during a shorter growing season but with a higher growth rate, in comparison with trees in tropical and subtropical zones.

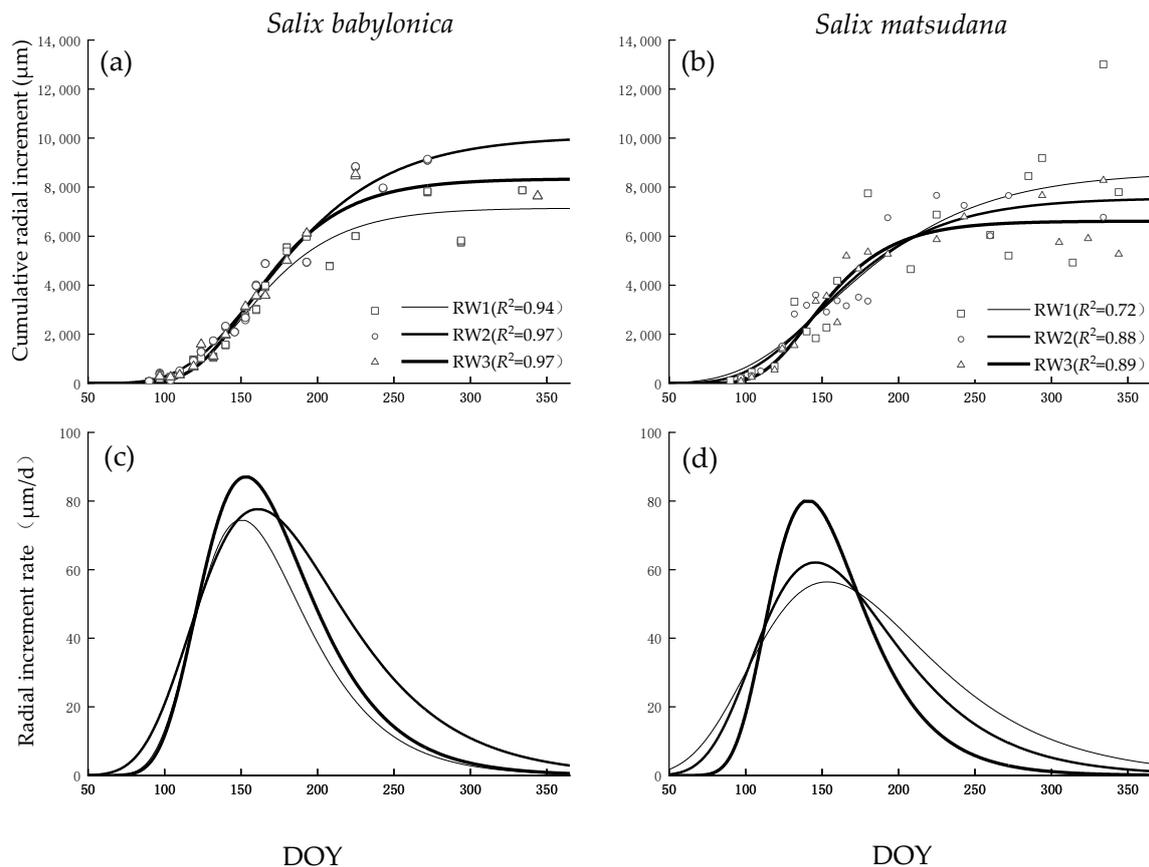


Figure 4. (a,b) Intra-annual xylem growth dynamics and (c,d) the daily growth rate of *Salix babylonica* and *Salix matsudana*. Dots and lines represent the measured value and fitted value by the Gompertz function, respectively.

The maximum xylem growth rate were observed around early June ($\text{DOY}155 \pm 5$) and late May ($\text{DOY}146 \pm 5$) for *Salix babylonica* and *Salix matsudana*, respectively, which were significantly earlier than the time of the summer solstice. It is documented for several tree species that the time at which the rate of xylem growth is peaking is synchronized with the summer solstice, especially in cold boreal forest [59,60]. This discrepancy of the timing of maximum growth rate in our result may be explained by between-sites variation in photosynthetically active radiation (PAR). In boreal forest, due to the low annual air temperature ($1\text{--}3 \text{ }^\circ\text{C}$), the maximum PAR has often been associated with the summer solstice when day length peaked [47]. In contrast, our study site was located in warm temperate zones, and the mean annual air temperature was considerably high with $14.2 \text{ }^\circ\text{C}$ (1960–2017). Thus, favorable PAR condition for tree growth can be reached before summer solstice. Additionally, the short-term drought in June 2018 (63 mm) might be another reasonable trigger for the earlier occurrence of maximum growth rate before summer solstice.

4.3. Higher Climate Growth Sensitivity in *Salix matsudana* Than *Salix babylonica*

Our results supported the first hypothesis that both temperature and water availability affected the xylem growth of two willows (Table 3). In cold climates, tree phenology is primarily controlled by temperature [30]. It is generally accepted that at high latitudes, the effect of temperature not only determines the onset of the growing season but also plays a key role for the end of the growing season [45]. However, in arid and semi-arid regions, water availability becomes a limiting factor for xylem formation [61]. Precipitation rather than temperature primarily controls xylem growth in drought-exposed trees. In warm temperate regions, both temperature and water availability might be effective climatic factors for tree growth. These variability responses of xylem growth to climatic drivers are essential to link species-specific capacity and plant-level growth phases with the environmental factors [62]. In this study, the daily mean air temperature for cambium onset and xylem growth ending of both willows was around 13.6 °C and 15.4 °C, respectively. From May to July, total precipitation was 460 mm, which accounted for 56% of the annual precipitation (Figure 5). During the same period, the width of xylem growth accounted for 67.6% of the total annual xylem increment.

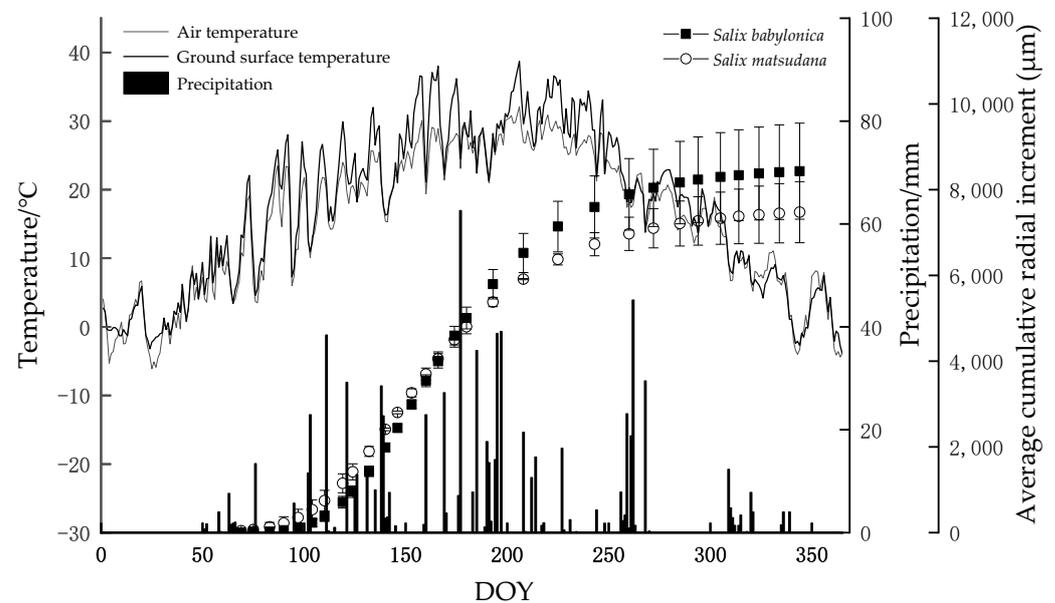


Figure 5. Intra-annual xylem growth of *Salix babylonica* and *Salix matsudana* fitted by Gompertz function and the corresponding main climatic factors during 2018 growing season.

Compared with *Salix matsudana*, *Salix babylonica* seemed to grow better at study site with higher xylem increment and faster growth rate. The higher sensitivity of xylogenesis in *Salix matsudana* to temperature may relate to inter-specific competition for *Salix matsudana* to adjust its growth rate than that of *Salix babylonica* (Table 3). On the other hand, the ecophysiological discrepancies between the two species may also explain the different xylem growth performances, of which the vessel diameter was smaller and vessel length was shorter in *Salix matsudana* than that of *Salix babylonica* [37,38]. This may result in *Salix matsudana* having limited plastic response in water transportation for xylem growth [34]. These findings suggest the xylem growth of *Salix babylonica* is clearly more conservative with respect to environmental conditions than *Salix matsudana*. However, conservative responses of *Salix babylonica* (lower sensitivity to warming temperature) may be able to minimize the growth risk better, which is caused by increasing climate warming. Therefore, when the degree of water stress imposed on the trees is released, *Salix babylonica* is probably competitively superior to *Salix matsudana* in the xylem growth at mesic site.

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