

Article



Xylem Formation in *Populus euphratica* and Its Response to Environmental Factors in the Lower Reaches of Tarim River, China

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Abstract: In order to gain a deeper understanding of the effects of environmental factors on the formation of Populus euphratica xylem, this study analysed the anatomical characteristics of Populus euphratica xylem and its response to environmental factors using wood anatomy as an example of Populus euphratica in the Yingsu section of the lower Tarim River. The results showed the following: (1) Throughout the growing season, the number of conduits of *Populus euphratica* in the two sample sites showed a slow increasing trend with the increase in groundwater burial depth, and the total conduit area showed an increasing and then decreasing trend with the increase in groundwater burial depth. The four indices of total, minimum, average, and maximum conduit areas in Populus euphratica xylem increased significantly with increasing temperatures during the growing season. (2) From the principal component analysis, the anatomical parameters of Populus euphratica xylem were found to be positively correlated with the depth of groundwater, average air temperature, maximum air temperature, minimum air temperature, surface temperature, relative humidity, and saturated water and air pressure deficit in the two sampling sites The most significant effects were found in the air temperature and depth of the groundwater. (3) The contribution of groundwater level and air temperature to different growth stages of *Populus euphratica* xylem was different. During the early part of the growing season of *Populus euphratica*, the air temperature was the main factor influencing the number of xylem conduits and total conduit area. As the growing season entered the middle stage, the air temperature and groundwater together affected the conduit parameters. In the later part of the growing season, groundwater became the most important factor affecting the number of conduits and the total conduit area. (4) The sensitivity analyses yielded a sensitive groundwater burial depth of 5.2 m for changes in the number of conduits in the xylem of the *Populus euphratica* and 5.9 m for changes in the total conduit area; the sensitive air temperature for the total conduit area in the xylem of the Populus euphratica was 22.0 °C, and the sensitive air temperature for the average conduit area was 18.5 °C. The results of this study can have important theoretical significance for understanding the Populus euphratica forests, as well as ecological water resource management in the lower Tarim River. They also provide scientific basis for the restoration and protection of Populus euphratica forests in the lower Tarim River.

Keywords: Populus euphratica; xylem anatomy; environmental factors; Tarim River

1. Introduction

The importance of forest ecosystems to terrestrial ecosystems as a central component of the global carbon cycle cannot be overstated [1,2]. In recent years, the continuous rise in temperature and the intensification of drought have led to changes in the hydrothermal supply and accelerated widespread forest mortality [3], so it is important to clarify the effects of hydrothermal changes on forest ecosystems and to protect them. In recent years, the development of microtree core technology can accurately reproduce the whole process



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). of tree formation layer cells, from dormancy to division and xylem production, and finely reflect the physiological process of tree radial growth and its response to the external environment during the year [4,5]. Therefore, the use of microtree core technology and wood anatomy to obtain xylem anatomical features, such as conduit size, density, and area on the annual rings sequence, and to analyse the effects of hydrothermal factors on the xylem anatomical features can better reflect the growth process of the tree and its response to key environmental factors [6,7].

The tree xylem anatomical features serve as a component of macroscopic growth in time and space, with xylem conduit features being important water-sparing tissues, and conduit features being closely related to water uptake, transport, and utilisation in trees [8]. Characteristics such as the structure and distribution of the conduit reflect the status and changes in environmental conditions during the year [9,10]. The larger the diameter of the conduit, the more efficient the conduit water transfer [11], and the response of the conduit to climatic factors depends mainly on the trade-off between hydraulic efficiency and water security, i.e., the number of conduits versus the area of the conduit, etc. [12,13]. The study of xylem conduit characteristics of trees was mainly carried out in non-porous and ring-porous wood, focusing on the cell size, cell wall thickness and conduit characteristics of Picea, Quercus, Larix, and Castanea [12,14,15]. Fewer studies were carried out on loose-porous species such as Betula, Fagus, etc., and very few studies on the wood conduit characteristics of Populus euphratica [16,17]. Currently, research on Populus tree whorl research focuses on the response or reconstruction of the whorl width to environmental factors. In the upper reaches of the Tarim River, it was found that [18] temperature is the main factor limiting the radial growth of *Populus euphratica* in the upper reaches of the Tarim River. In the lower reaches of the Tarim River, the relationship between the radial growth of Populus euphratica and the groundwater was analysed [19]. In addition, fewer studies have been carried out on the process of xylem formation in *Populus euphratica* and its response to the change in environmental factors from a more microscopic and precise scale.

The Tarim River Basin has 89% of the *Populus* forest area in the whole territory [20], and the constructed ecosystem of desert riparian *Populus* forests is of indispensable importance for maintaining the ecological balance of the region and guaranteeing the sustainable development of oasis agriculture. However, over the past few decades, *Populus* forests have experienced large-scale decay and death, and their ecological functions have declined dramatically [21,22]. In the process of protecting and rescuing degraded *Populus* forests, the first task is to clarify the association between *Populus* growth and environmental factors. Therefore, based on the experimental data from the Yingsu section of the lower Tarim River, this study adopts the wood anatomy method and uses the microtree core technology to study the changes in the anatomical characteristics of the xylem under the environmental conditions of different lands. It analyses the response of these anatomical characteristics to the changes in the environmental factors, aiming to provide a scientific basis for the restoration of the *Populus* forests in the lower Tarim River.

2. Materials and Methods

2.1. Overview of the Study Area

The Tarim River is located in northwestern China, with a total length of 2137 km, making it the longest inland river in China. The sampling point selected for this study was located near the Daxihaizi Reservoir in the lower Tarim River in Xinjiang, specifically at the Yingsu section. The study area receives relatively little precipitation, with the mean annual precipitation ranging from 17.4 to 42.0 mm. Its mean annual temperature is 10.5 °C, and it experiences vigorous evaporation, with mean annual evaporation above 2500 mm. This makes it a typical arid area in China [23,24]. The vegetation of the region consists of temperate shrub desert, with woodlands dominated by trees, such as *Populus* and the *Tamarix ramosissima*, and herbaceous plants such as reeds *Phragmites australis* [25]. In order to gain a deeper understanding of the effects of environmental factors on the formation of *Populus euphratica* xylem, this study selected the sampling points TYA and TYB near the



river channel and 100 and 1500 m away from the river, in the Yingsu section, respectively, and the locations of the sampling points are shown in Figure 1.

Figure 1. Overview of the study area. TYA and TYB are sampling points. The same as below.

2.2. Experimental Design

Five well-established *Populus* trees of comparable age were selected around the monitoring wells TYA and TYB located at distances of 100 and 1500 m from the river in the Yingsu section of the lower Tarim River. Microtree core sampling was carried out weekly, from April to October 2020, using microgrowth cones to collect two to three microtree core samples at 1.3 m diameter at breast height (DBH) of the sample trees, with a total of 260 samples sampled 26 times. The distance between two adjacent samples was more than 3 cm to avoid mutual influence. The site and direction of the two samples before and after were consistent to avoid the error caused by the different growth rates of trees in different directions [26]. After sampling, the sample was quickly fixed in FAA solution to maintain the sample in its original state.

2.3. Sample Processing

After removing the samples from the FAA solution, a pencil was used to draw a line perpendicular to the direction of the vasculature, after which the samples were placed in an orderly manner in the embedding box and clearly labelled with their numbers. The samples were subjected to a stepwise dehydration process with ethanol, followed by transparency through limonene, and then steps such as immersion in paraffin and embedding. Using a rotary slicer, the samples were cut into 8 micron slices. Subsequently, the paraffin sections were fixed on slides through steps such as spreading and fishing followed by drying of the samples. After taking out the dried samples, limonene and anhydrous ethanol were used sequentially for dewaxing and transparency, after which the samples were stained with Senna (1 g Senna + 100 mL of distilled water) and Star Blue (0.5 g Star Blue + 2 mL of acetic acid + 100 mL of distilled water) for 15 min, and washed in 70% and 100% alcohol and xylene, respectively. After completing the staining, the sections were sealed with neutral gum and photographed under a $10 \times$ microscope to monitor the various growth stages of the xylem-forming layer in *Populus euphratica* throughout the growing season activity

(Figure 2). Because of the fixed-point continuous sampling, all anatomical parameters use cumulative parameter values, i.e., each measurement is cumulative from the previous annual cycle. Using Image-ProPlus 6.0, the characteristic parameters of conduits in *Populus euphratica* xylem were measured, including the number of conduits, the density of conduits, the total conduit area, the average conduit area, the minimum conduit area, and the maximum conduit area.



Figure 2. Cell morphology at various stages of xylem differentiation in *Populus euphratica.* CZ: Cambium; EM: enlarged cell; WT: thickened cell wall; MC: mature cell.

2.4. Data Processing

Data on air temperature in the study area were obtained from the lower Tarim River Teganlik meteorological station. Groundwater bathymetry change data were obtained from the Tarim River Basin Authority. The temperature and depth of groundwater were measured at the same time for each sampling event, and the depth of groundwater ranged from 3.2 to approximately 4.8 m in TYA and from 4.4 to approximately 6.7 m in TYB during the growing season (Figure 3). The data were statistically analysed using Excel 2010 software, and Pearson correlation analysis using SPSS 21.0 software was used to analyse the correlation between the xylem anatomical parameters of the *Populus euphratica* and the water table and air temperature, and to identify the xylem anatomical parameters of the poplar that have significant correlation with the water table and air temperature. Partial correlation analysis was used to analyse the contribution of groundwater and air temperature to the effect of each parameter on the xylem conduits of *Populus euphratica*. Polynomial regressions of significantly correlated *Populus euphratica* xylem conduit parameters were fitted to groundwater levels and air temperatures using Origin 2018 software. The rate of change of the function was obtained by first-order derivation of the fitted function using sensitivity analysis, and the point where the second-order derivation is zero and the third-order derivation is not zero is taken as the inflection point of the function, which is taken as the sensitivity point of the main parameters of the xylem as a function of the changes in hydrothermal factors [27].



Figure 3. Changes in groundwater depth and average temperature at sampling sites in 2020. D: groundwater depth, T: temperature (the same as below).

3. Results

3.1. Intra-Annual Variation in Xylem Formation in Populus euphratica

According to Figure 4, the number of conduits and the total conduit area in the xylem of *Populus euphratica* showed a linear growth trend in both sampling plots throughout the growing season. There was little difference between the number of conduits in TYA and TYB at the beginning of the growing season, and the number of conduits in TYA was greater than that in TYB at the end stage of the growth cycle, after DOY221 (day of year). In terms of conduit density, the TYA conduit density was greater than that in TYB in the beginning of the growing season, and the TYB conduit density was greater than that of TYA from late to mid growing season, starting with DOY144. In terms of total conduit area, there was little difference in the total conduit area between the two samples during the first and middle parts of the growing season. However, later in the growing season, the total conduit area was generally larger in TYA than in TYB. Throughout the growing season, the trends in the number of xylem conduits and the total conduit area of *Populus euphratica* were basically the same in the two sample sites. There was a rapid rise in the xylem minimum conduit area at the beginning of the growing season in both samples, and the TYA minimum conduit area was generally larger than that in TYB throughout the growing season. At the beginning of the growing season, the mean conduit area of both TYA and TYB began to increase rapidly. The mean conduit area of TYA began to fluctuate and decrease around DOY172, and the mean conduit area of TYB reached a maximum value around DOY137, and then fluctuated and decreased. The maximum conduit area increased at a faster rate at the beginning of the growing season and fluctuated in both samples from the middle of the growing season. Throughout the growing season, the number of conduits, total conduit area, minimum conduit area, average conduit area, and maximum conduit area in the xylem of TYA, with shallower groundwater burial, were generally higher than those of TYB, with deeper groundwater burial (Table 1).

Table 1. Characteristics of xylem conduits of *Populus euphratica* across different locations.

Site	Tree Age (Year)	DBH (m)	Vessel Number	Vessel Density (×10 ⁻⁶ ind ·µm ⁻²)	Total Vessel Area (×10 ³ μm ²)	Minimum Vessel Area (×10 ³ μm ²)	Average Vessel Area (×10 ³ μm ²)	Maximum Vessel Area (×10 ³ μm ²)
TYA TYB	32.87 28.45	52.84 45	$\begin{array}{c} 316.4 \pm 208.7 \\ 264.34 \pm 153.3 \end{array}$	$\begin{array}{c} 39.46 \pm 7.74 \\ 44.48 \pm 9.83 \end{array}$	$\begin{array}{c} 964.03 \pm 556.13 \\ 833.78 \pm 432.52 \end{array}$	$\begin{array}{c} 0.46 \pm 0.12 \\ 0.33 \pm 0.10 \end{array}$	$\begin{array}{c} 2.94 \pm 1.22 \\ 2.75 \pm 1.10 \end{array}$	$\begin{array}{c} 11.96 \pm 3.85 \\ 11.50 \pm 6.19 \end{array}$

Note: DHB: Diameter at breast height.



Figure 4. Variation of conduit parameters of Populus euphratica across different sub-locations.

3.2. *Response of Populus euphratica Xylem Anatomical Parameters to Environmental Factors* 3.2.1. Principal Component Analysis of Anatomical Parameters of *Populus euphratica* Xylem

After principal component analysis, it was found that there were differences in the xylem anatomical parameters of Populus euphratica under different groundwater burial depth conditions. Particularly, in the sample TYA, the groundwater level is higher (as shown in Tables 2 and 3), with the first principal component explaining 44.65% of the variance, the second principal component explaining 33.20%, and the two principal components in total explaining 77.85% of the variance. This suggests that the response of Populus euphratica xylem conduit parameters to the environment is relatively focussed in environments with relatively good moisture conditions. The first principal component contains information on the number of conduits (0.89) and the density of conduits (0.81), and the second principal component contains information on the minimum conduit area (0.79) and the average conduit area (0.71). The first principal component explained 54.83% of the variance, the second explained 31.63% of the variance, and the two principal components together explained 86.46% of the variance for the sample site TYB, which has a lower water table and poorer moisture conditions. This suggests that the response of Populus euphratica xylem conduit parameters to the environment is also relatively focussed in low-water environments. The first principal component contains information on the number of conduits (0.91) and the density of conduits (0.87), while the second principal component contains information on the average conduit area (0.80) and the maximum conduit area (0.72).

Site	Main Component	Trait Root (Math.)	Variance Contribution/%	Cumulative Variance Contribution/%
	1	2.68	44.65	44.65
ТYA	2	1.20	33.20	77.85
T)/D	1	3.29	54.83	54.83
ТYВ	2	1.90	31.63	86.46

Table 2. Principal component information of xylem anatomical parameters in *Populus euphratica*.

Site	Anatomical Parameters	Principal Component 1	Principal Component 2
	Vessel number	0.89	0.196
	Vessel density	0.811	-0.531
	Total vessel area	-0.41	0.241
ТYA	Minimum vessel	0.408	0.799
	Average vessel area	0.671	0.717
	Maximum vessel area	0.666	-0.678
	Vessel number	0.907	0.02
	Vessel density	0.872	0.188
TT) / D	Total vessel area	0.794	-0.574
ТҮВ	Minimum vessel	0.756	-0.616
	Average vessel area	0.397	0.796
	Maximum vessel area	0.589	0.72

Table 3. Contributions of factors to the first and second principal components of the xylem anatomical parameters of *Populus euphratica*.

3.2.2. Principal Components of Xylem Parameters of *Populus euphratica* in Relation to Environmental Factors

Based on the principal component analysis, the principal component function values of the xylem anatomical parameters of *Populus euphratica* in the two sample plots were correlated with the environmental factors, and the results are shown in Figure 5. The principal component function values of the xylem anatomical parameters of Populus euphratica in the two sample plots were positively correlated with the depth of the groundwater, the average air temperature, the maximum air temperature, the minimum air temperature, the surface temperature, relative humidity, and saturated water and air pressure deficits, among which the depth of the groundwater, the average air temperature, the maximum air temperature, the minimum air temperature, and the relative humidity showed significant positive correlations, with the minimum air temperature, surface temperature, and relative humidity being notable. The principal component function values of the anatomical parameters of Populus euphratica xylem were negatively correlated with wind speed and air pressure in both sample sites. The principal component function values of the xylem anatomical parameters of TYA and TYB Populus euphratica were all significantly negatively correlated with air pressure, with the principal component function values of the xylem anatomical parameters of TYA also being significantly negatively correlated with the wind speed.

In order to explore in depth the main factors leading to changes in the conduit of *Populus euphratica*, this study analysed the relationship between these environmental factors (Figure 6), showing that the mean air temperature is significantly and positively correlated with maximum, minimum, and surface temperatures, and significantly and negatively correlated with mean barometric pressure. Thus, the mean and maximum air temperatures, minimum air temperatures, surface air temperatures, and mean barometric pressure can be used as key factors in analysing changes in xylem conduits in *Populus euphratica*. The depth to groundwater was significantly positively correlated with relative humidity in both sites, so the key environmental factors affecting the growth of *Populus euphratica* were air temperature and depth to groundwater.



Figure 5. Correlation coefficients of principal components of xylem parameters of *Populus euphratica* with environmental factors. GD: groundwater depth, Tamean: average temperatures, Tamax: maximum temperature, Tamin: minimum temperature, LST: surface temperature, RH: relative humidity, WSmean: average wind speed, Pmean: average pressure, VPD: water–gas pressure difference (the same as below).



Figure 6. Relationships between environmental factors associated with xylem principal components.

3.3. Populus euphratica Xylem Conduit Parameters in Relation to Temperature and Depth of Groundwater Burial

From the correlation between the xylem conduit parameters and groundwater burial depth of *Populus euphratica* (Figure 7), the groundwater burial depths of the monitoring wells TYA and TYB were both significantlyand positively correlated with the number of xylem conduits and the total conduit area of *Populus euphratica*, whereas the groundwater burial depth of TYB was also significantly and positively correlated with the maximum conduit area. In terms of the correlation between the xylem conduit parameters and the mean air temperature, the air temperatures at the monitoring wells TYA and TYB were significantly and positively correlated with the total, minimum, mean, and maximum

xylem conduit areas of the *Populus euphratica*. Therefore, the number of xylem conduits and the total conduit area of *Populus euphratica* can be used as key indicators to analyse the relationship between xylem formation and groundwater in *Populus euphratica*. The total conduit area, minimum conduit area, average conduit area, and maximum conduit area of *Populus euphratica* xylem can be used as key indicators to analyse the relationship between xylem formation and air temperature in *Populus euphratica*. Regressions of groundwater burial depth, air temperature, and key indicators of xylem conduit parameters of *Populus euphratica* were fitted, and the fitted equations all passed the 99% significance test (Figure 8). Sensitivity analyses of the fitted polynomial function revealed a sensitivity of groundwater burial depth of 5.2 m to changes in the number of conduits in the xylem of *Populus euphratica*, a sensitivity of groundwater level of 5.9 m to changes in the total conduit area, sensitivity of air temperature of 22.0 °C to the total conduit area and 18.5 °C to the average conduit area, and insensitivity of the minimum conduit area and maximum conduit area to the effects of changes in air temperature.

3.4. Contribution of Hydrothermal Factors to the Effect of Various Parameters of the Xylem Conduit of Populus euphratica

Exploring the contribution of hydrothermal factors to the effects of key indicators of xylem conduit parameters in Populus euphratica in different sub-locations involves using partial correlation analysis techniques (Figure 9). Based on the observation of conduit number and total area, the contribution of groundwater and air temperature to the effect of TYA and TYB on the conduit number and total area of *Populus euphratica* xylem over time showed approximately the same trend, which was mainly as follows: early in the growing season, the contribution of air temperature was greater than that of the depth of groundwater to the growth of *Populus euphratica* xylem, and with the passage of time, the contribution of groundwater began to be higher than that of air temperature. However, the inflection points of changes in the contribution of hydrothermal factors differed in time for different sites. The number of xylem conduits of Populus euphratica in the TYB sample, with deeper groundwater burial, was affected by the depth of groundwater burial about 12 day earlier than in the TYA sample, which has shallower groundwater burial. The total conduit area indicator was affected by the depth of groundwater burial about 2 day earlier than in the TYA sample, which has deeper groundwater burial. The total conduit area indicator was also affected by the depth of groundwater burial. In terms of conduit density, no significant difference was observed in the contribution of hydrothermal factors to the effect of each indicator of conduit density in *Populus euphratica* xylem in the TYA sample site, but the TYB conduit density had a large contribution to the average temperature midway through the growing season, and a large contribution to the depth of groundwater burial early and late in the growing season. In terms of minimum conduit area, average conduit area, and maximum conduit area, during the whole growing season, the trends in the contributions of groundwater burial depth and air temperature were the same in the two sample sites, showing that the air temperature and groundwater factors jointly affected the changes in the xylem conduit parameters of the Populus euphratica. However, TYB, where the depth of the groundwater was deeper, appeared to experience the joint influence of air temperature and groundwater burial depth on the xylem conduit parameters of the *Populus euphratica* earlier than TYA.



Figure 7. Correlation coefficients between xylem vessel parameters of *Populus euphratica* and ground-water depth and temperature in different sites (D: groundwater depth, T: temperature).



Figure 8. Relationship between each parameter of *Populus euphratica* xylem conduit and hydrothermal factors. **: *p* < 0.01.



Figure 9. Contribution of water-heat factors to xylem vessel parameters of Populus euphratica.

4. Discussion

4.1. Relationship between Anatomical Characteristics of Populus euphratica Xylem and Depth of Groundwater Burial

Trees are able to adapt and respond to environmental changes [28,29], and this is especially true of xylem conduits, as water transporters for tree growth. In this study, the number of conduits, total conduit area, average conduit area, minimum conduit area, and maximum conduit area of the xylem in TYA, with shallower groundwater burial depth, were overall higher than those in TYB, with deeper groundwater burial depth. This might be due to the fact that TYA had better water conditions, which either directly or indirectly affected the water supply of the trees and thus the xylem growth; thus, the xylem growth of *Populus euphratica* in TYA was better than that in TYB. This is consistent with the results of other studies [30]. The number and total area of xylem conduits in *Populus euphratica* xylem in TYA, with shallower groundwater depth, were higher than those in TYB, and the density of the conduits was lower than in TYB. This difference may be due to the

better water conditions in TYA, where the better water supply conditions promoted the acceleration of the cell division rate [31], which increased the number and area of the cells. Therefore, both the number and total area of xylem conduits in Populus euphratica in TYA were higher than those in TYB, and the density of the conduits was lower in TYA. TYA had a low density of conduits, probably because although the number of conduits was high, the density of conduits was sparse due to the large area of individual conduits. In this study, the number of xylem conduits and total conduit area of Populus euphratica were significantly and positively correlated with the depth of groundwater burial, which may be influenced by the seasonal rhythms of xylem growth, which itself happens to be coupled with intra-annual variations in groundwater. The number of xylem conduits and the total conduit area of *Populus euphratica* showed a significant correlation with the depth of groundwater burial, indicating that the total conduit area and the number of conduits are closely related to groundwater. This relationship may be due to the fact that the status of radial growth of Populus euphratica during the year is mainly dependent on the increase in the number and area of xylem cells. An adequate supply of water in the xylem will promote an increase in the cell area and in the number of cells [32]. Xylem conduit as an effective tool for water transmission in trees can directly affect the water-conducting capacity of the xylem, and the water status of trees in the growth process is mainly reflected by the characteristics of the conduit. According to Hagen–Poiseuill's law [33], an increase in the radius of the conduit leads to a fourfold increase in the corresponding water transport efficiency. Therefore, fluctuations in hydraulic efficiency are due to changes in the conduit area caused by changes in the radius of the conduit. The maximum xylem conduit area of TYB and the depth of groundwater were significantly correlated with the tree's conduit area and the xylem's hydraulic transport efficiency. This correlation may be attributed to the influence of the tree's conduit area and hydraulic transport efficiency, where higher levels of xylem conduits affect the growth of trees, reflecting the water condition mainly by the characteristics of the xylem. This may be due to the fact that the xylem hydraulic transport efficiency is related to the conduit area of trees, and a high or low efficiency of xylem hydraulic transport affects the water supply conditions, which in turn affect cell development. Good water supply conditions are conducive to the development of the cell, resulting in a larger maximum conduit area. However, the low efficiency of hydraulic transport leads to poor water supply conditions, resulting in imperfect development of the cells and a smaller maximum conduit area.

4.2. Relationship between Anatomical Characteristics of Populus euphratica Xylem and Air Temperature

Air temperature has an important effect on the anatomical characteristics of *Populus* euphratica xylem. In this study, we found that the parameters of Populus euphratica xylem anatomy in the Yingsu section of the lower Tarim River were positively correlated with the average air temperature to different degrees, indicating that the increase in air temperature can promote the growth of *Populus euphratica* xylem, which is consistent with the conclusion of a study which found that the total conduit area of the water hyacinth in the northeast region was significantly positively correlated with the air temperature [30]. This may be due to the fact that although there are differences in climatic conditions, soil fertility, altitude, as well as the tree species in the different study areas, the temperature can promote cell development to a certain extent and favour tree growth. Most studies have shown that tree growth in arid regions is mainly affected by water conditions [34,35]. It has been found that tree conduit area in arid areas is significantly correlated with precipitation and not with temperature [36]. Although the present study area is in an arid zone, the total conduit area, mean conduit area, maximum conduit area, and minimum conduit area of Populus *euphratica* xylem were significantly and positively correlated with the mean air temperature. The inconsistency of the above findings may be due to the fact that although the lower Tarim River is in an arid zone, the differences in climatic conditions and topography between the study areas caused the differences in the findings. Alternatively, they may be due to the fact

that the temperatures in the lower Tarim River are favourable during the growing season, and the trees photosynthesize efficiently, thus positively affecting the various parameters of the xylem anatomy.

4.3. Contribution of Air Temperature and Groundwater to Various Parameters of Xylem Anatomy

The contribution of groundwater and air temperature to the number of conduits and total conduit area of Populus euphratica in the two sampling sites showed basically the same trend, with the contribution of air temperature being higher than that of groundwater at the beginning of the growing season, and the contribution of groundwater being gradually higher than that of air temperature midway through the growing season. This may be due to the fact that temperature is the main limiting factor for tree growth during the pre-growing season, and cellular activity starts when the outdoor temperature is above the minimum threshold value for xylem cell activity [37], with higher temperatures accelerating the rate of cell division and improving photosynthetic efficiency. Midway through the growing season, with the warming of the temperature, the effect of temperature gradually declined, while the end of May began to be an important period of the formation of the annual rings of the *Populus euphratica*. The radial growth of the *Populus euphratica* is mainly dominated by the transfer of water within the tree and the differentiation of the cells. The trees have a higher water demand, which leads to the gradual dominance of the contribution of groundwater [38]. In this study, it was found that TYB, with a deeper water table, was dominated by groundwater instead of air temperature earlier compared to TYA, with a shallower water table and better water conditions. This may be due to the fact that the air temperature at the beginning of the growing season directly affects the cell division rate and the activity cycle of the cells [39], while the gradual increase in air temperature in the middle of the season leads to an increased evapotranspiration and enhanced water consumption by Populus euphratica. Compared with TYA, where the water table is shallow and the water supply is relatively sufficient, TYB Populus euphratica relies on groundwater earlier to satisfy its water demand. The present study showed that the formation of *Populus euphratica* xylem in the lower Tarim River was significantly affected by hydrothermal factors, and similarly, poplar xylem cells were subject to growth rhythms. Due to the limitation of the sampling site, the present study did not take into account the growth rhythms of Populus euphratica xylem cells when exploring the effects of air temperature and groundwater on the parameters of poplar xylem, which is a direction for future research.

5. Conclusions

(1) Throughout the growing season, the number of conduits in *Populus euphratica* showed a slow increasing trend with the increase in groundwater burial depth, and the total conduit area showed an increasing and then decreasing trend with the increase in groundwater burial depth. The total conduit area, the minimum conduit area, the average conduit area, and the maximum conduit area of Populus euphraticar xylem increased significantly with the increase in temperature during the growing season. (2) The key environmental factors affecting *Populus euphratica* growth are temperature and the depth of groundwater burial. (3) The contribution of groundwater level and air temperature to different growth stages of *Populus euphratica* xylem was different. In the early stage of the growing season, the air temperature made the greatest contribution to the number of conduits and the total conduit area of Populus euphratica xylem; in the middle stage of the growing season, the air temperature and groundwater jointly affected the parameters of each conduit; and in the late stage of the growing season, groundwater made the greatest contribution to the number of conduits and the total conduit area. (4) The sensitive groundwater level interval affecting the growth of Populus euphratica xylem is 5.2–5.9 m, and the sensitive air temperature range is 18.5-22 °C.

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