DIFFERENCES IN THE STRUCTURAL AND FUNCTIONAL TRAITS OF *POPULUS EUPHRATICA* AND *POPULUS PRUINOSA* WITH TREE HEIGHT

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Abstract. *Populus euphratica* Oliv. and *Populus pruinosa* Schrenk are distributed on the banks of desert rivers in arid and semi-arid regions. By studying the variation of the structural and functional traits of *P. euphratica* and *P. pruinosa* with tree height, the differences in the structural and functional traits of the heteromorphic leaves were compared. The study determined the changes of the morphological structure, photosynthetic water physiology, osmotic adjustment substances and endogenous hormone content of the two species with the height of the tree. The results showed that with the increase of tree height, the leaf area (LA), leaf thickness (LT), palisade tissue thickness (PT), main vein xylem area (MXA), vessel area (VA), vessel number (VN) and net photosynthetic rate (Pn) of *P. euphratica* and *P. pruinose*, $\delta^{13}C$, proline content, malondialdehyde (MDA) and endogenous hormone GA_3, IAA, ZR content showed an increasing trend, and there was a significant positive correlation with tree height. The Pn at 10 m, the Tr at 6 m, 8 m, and 10 m, the $\delta^{13}C$ and the content of MDA, soluble protein, ABA, and IAA at each height for *P. euphratica* is significantly larger than *P. pruinosa*. These results suggested that *P. euphratica* have the more stronger ability to resistance to drought than *P. pruinosa* for its more invests in leaves, more xerophytic leaf morphology and anatomical structure, higher photosynthetic water use efficiency, stronger ability of osmotic adjustment.
Keywords: *desert poplars, heteromorphic leaves, morphological structure, osmotic adjustment, endogenous hormones, photosynthetic water physiology*

Abbreviations: LI = leaf index; LA = leaf area; LT = leaf thickness; SLA = Specific Leaf Area; PT = Palisade tissue thickness; PSR = Ratio of palisade tissue to spongy tissue; MVBA = Main vein vascular bundle area; MXA = Main vein xylem area; XVBR = Main vein xylem/main vascular bundle area; VA = Vessel area; Pn = Photosynthetic rate; Tr = Transpiration rate; Gs = Stomatal conductance; Ci = Intercellular CO_2 concentration; WUEi = Instantaneous water use efficiency; $\delta^{13}C$ = Stable carbon isotope value; Pro = Proline; MDA = Malondialdehyde; SS = Soluble sugar; SP = Soluble protein; BA = Abscisic acid; GA_3 = Gibberellin; IAA = Indoleacetic acid; ZR = Zeatin Riboside

Introduction

Populus euphratica Oliv. and *Populus pruinosa* Schrenk. have different distribution areas. The total area of *P. euphratica* forests in the world is about 6.48×10^5 hm^2, and its distribution spans across the three continents of Europe, Asia and Africa. Among them, 60% of *P. euphratica* in the world is distributed in China, and 91.1% of *P. euphratica* in China is concentrated in the Tarim River Basin in Xinjiang (Wang, 1996), while *P. pruinosa* is only distributed in the Tarim Basin in China, and both are the dominant riparian tree species of the Tarim River (Li et al., 2021). The phenomenon of plant leaf morphology changes along the longitudinal axis is called heterophylly, which is the

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result of leaf phenotypic plasticity and helps plants adapt to environmental changes (Nakayama et al., 2017; Zeng et al., 2019), while *Populus euphratica* and *P. pruinosa* are heteromorphic leaf plants, but their leaves have morphological differences. For example, from the base to the top of the crown, the leaves of mature *Populus euphratica* will appear in four leaf shapes: strip, lanceolate, ovate and broad-ovate. In contrast, *P. pruinosa* is found on seedlings, saplings and adult trees, and oval, round and broad-ovate-shaped leaves appear in sequence (Liu et al., 2016; Yu et al., 2020).

Leaves are the most sensitive organs to environmental factors and show different adaptation strategies in different environments (Bao et al., 2009; Zirbel et al., 2017). The different canopies of trees often produce vertical gradients due to the projection of sunlight, which causes differences in the anatomical structure and physiological metabolism of the leaves on the upper and lower layers of the canopy (Aranda et al., 2004; Niinemets et al., 2015). At the same time, as the water potential of the xylem of the tree decreases as the height of the tree increases, the difference in water pressure in the height gradient will affect the morphological structure of the leaves of the corresponding tree height. The upper leaves of the tree can only hinder the water loss through a more obvious xeromorphic structure in order to cope with water stress caused by tree height (He et al., 2008; Ryan et al., 1997). Previous studies have shown that the heteromorphic leaves of *P. euphratica* are isofaceted, with thick stratum corneum, subcutaneous layer and subporous chambers, containing more mucous cells, and showing obvious xerophytic structural characteristics. However, from stomata density, stomata size, compared with the degree of stomata subsidence and the degree of mesophyll development, the broad-ovate xerophyte structure is more developed than other leaf shapes and has a stronger ability to resist adversity (Bai et al., 2011; Wang, 1996; Yang et al., 2004; Zhao et al., 2016; Zheng et al., 2007). Leaf area, leaf thickness and petiole length of *P. euphratica* and *P. pruinosa*, showed the positive correlation with the diameter at breast height and tree height (Liu et al., 2016; Zhao et al., 2016). At the same time, the ABA and ZR content of *P. euphratica* showed an increasing trend with the increase of tree age and tree height (Huang et al., 2010a, b). In coniferous trees, the net photosynthetic rate usually decreases with the increase in tree height (Ishii et al., 2008), while in broad-leaved trees, the net photosynthetic rate varies with the height of the tree (Miyata et al., 2016; Sendall et al., 2013; Zhang et al., 2009). At different canopy heights of the same tree, the broad-ovate leaves at the top of the *P. euphratica* canopy have stronger photosynthetic capacity, osmotic adjustment capacity and water use efficiency than the rest of the leaf shape (Bai et al., 2011; Zhai et al., 2020; Zheng et al., 2007), with more effective energy distribution and utilization strategies. In addition, the salt and drought stress studies on *P. euphratica* and *P. pruinosa* seedlings have shown that *P. euphratica* and *P. pruinosa* have species-specific variations. Under the influence of drought stress, salt stress and interactions, *P. euphratica* suffers a greater negative impact than *P. pruinosa* (Yu et al., 2020).

For woody plants, growth is not only affected by environmental soil drought, but also by changes in water potential caused by changes in their height (Ryan and Yoder, 1997). Previous studies on the heteromorphic leaves of *P. euphratica* under suitable water conditions found that the morphology, anatomical structure and physiological characteristics of the leaves are related to the coronal position, and they change synergistically along the tree height gradient (Li et al., 2021; Zhai et al., 2020). However, there is currently no research under soil drought conditions. In addition, the changes in the morphological structure and photosynthetic water physiology of *P. pruinosa* with tree

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height are still unclear. We hypothesized that under soil drought stress, *P. euphratica* and *P. pruinosa* have different adaptation strategies for leaf traits as the height of the tree increases, and *P. euphratica* shows stronger adaptability than *P. pruinosa*.

Materials and methods

Study area

The study area, located in the north-western margin of the Tarim Basin in Xinjiang Province of China, has a typical temperate desert climate. The annual average annual rainfall is approximately 50 mm, the potential evaporation reaches up to 1,900 mm, the yearlyannual average temperature is 10.8 °C, and the average annual average sunshine hours duration is 2,900 h (Zhai et al., 2020). As sampling points for comparison located in Shaya County (82°00’22.69″ E, 40°41’10. 91″ N, 977 m a.s.l.), with a groundwater level of 5 m (*Fig. A1*).

Plant samples and sampling method

In the sampling area, 5 *Populus euphratica* and 5 *Populus pruinosa* with diameter at breast height of 15 cm, tree age of 12 years and height of 10 m were selected, respectively. Samples were obtained at heights of 2, 4, 6, 8, and 10 m starting from the base of the trunk of each tree. We collected 30 branches from each sampling layer, selected the fourth node leaf from each branch, and took 30 leaves in total. A portion of the leaves was quickly frozen with liquid nitrogen and stored at -80 °C to determine the content of proline, malondialdehyde, soluble sugar, and hormones; another sample of the leaves was fixed with formalin-alcohol-glacial acetic acid mixed fixative (FAA). The fixed samples were used to prepare tissue sections; a part of the leaves was used to determine the morphological indicators of abnormal leaves. Sampling was done during the vigorous growth period of *P. euphratica* in mid-July. The leaf photosynthetic index was measured from 11:00 to 13:00 on clear and cloudless days.

Determination of the morphological and anatomical structural indexes of heteromorphic leaves

We used a scanner (MRS-9600TFU2, China) and the LA-S plant image analysis software to measure the leaf length, leaf width, and leaf area of *P. euphratica and P. pruinosa*. The leaf shape index (LI) was calculated on the basis of the leaf length/width ratio. The collected leaves were processed for deactivation (10 min) at 105 °C and heated at 65 °C to a constant weight. After the sample reached a constant weight, the material was cooled to room temperature (25 °C) in a desiccator and weighed with an electronic balance with an accuracy of 0.001 g; the specific leaf area (SLA) was then calculated.

The leaf blade was cut transversely at its widest section. The material that retained the primary vein and leaf margin was selected and fixed in a formalin–acetic acid–alcohol (FAA) solution. Paraffin-embedded tissue sections (8 µm thick) were prepared, double-stained with safranin–fast green, and mounted in a neutral resin. Observation and determination of the palisade tissue (PT), main vein vascular bundle area (MVBA), main vein xylem area (MXA), main vein xylem area (VA) were performed using a Leica microscope (Leica DM4 B, Wetzlar, Germany). The gate-to-sea ratio (PSR), main vein xylem, vascular bundle area ratio (XVBR), five fields of view per leaf, 20 values

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per field of view, and average value of leaf anatomical structure parameters of five fields of view were taken as the parameter values of anatomical structural index of each leaf.

Determination of gas exchange indices of heteromorphic leaves

Branch shears were used to cut branches of the current year. The branches were wrapped immediately with fresh-keeping film to cover the cut ends. The fourth node leaves from the base of the branches were used to measure the gas exchange parameters with a LI-COR 6400 portable photosynthesis measuring system (LI-COR, Lincoln, NE). The net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), and intercellular CO_2 concentration (C_i) values were obtained.

The photosynthetic physiological indices of the leaves were measured with the Li-6400 photosynthesis instrument, and the instantaneous water use efficiency (WUE_i = Pn/Tr) of the irregular leaves was calculated. The leaf samples were washed and air-dried, then dried at 65 °C for 36 h, pulverised with a grinder, and passed through a 90-mesh sieve to prepare test samples. The carbon isotope analysis of the plant samples was prepared using a glass vacuum system. The furnace temperature of the burner was controlled at 1,000 °C. The system was evacuated and O_2 was passed through. The porcelain spoon containing the sample of *P. euphratica* leaves was placed in the combustion tube in the high-temperature zone. After burning for 2 min, the CO_2 gas was collected and purified by freezing. A stable gas isotope mass spectrometer (Thermo Fisher Scientific, Inc., Waltham, MA) was used to analyse the carbon isotope composition ($\delta^{13}C$ value) of the purified CO_2 gas.

Determination of physiological and biochemical indices of heteromorphic leaves

The acid ninhydrin method was used to determine the leaf proline content. The MDA content was determined with the thiobarbituric acid colour method, and the SS content was determined with the anthrone colourimetry method. The Coomassie brilliant blue G-250 dyeing method was used to determine the SP content of leaves (Zhai et al., 2020).

Determination of endogenous hormone content in heteromorphic leaves

We took the leaves (without petioles) at the fourth node of the branches, quickly froze them with liquid nitrogen, and stored them at -80 °C. The enzyme-linked immunoassay method was used to determine the content of abscisic acid (ABA), gibberellin (GA_3), indoleacetic acid (IAA), and zeatin riboside (ZR).

Statistical analysis

Statistical analyses were performed using the Statistical Package for the Social Sciences (SPSS, Chicago, IL, USA) version 18.0. Tukey's HSD test was conducted to detect significant differences between different heights and different tree species. All statistical effects were considered significant at $P < 0.05$. All data were normally distributed and single-peaked. In addition, pearson correlation analysis was used to analyze the correlation between the indicators, comprehensive evaluation of drought resistance of P. pruinosa and *P. euphratica* by membership function method. We used linear regression analysis to evaluate the impact of endogenous hormone on structural traits.

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Results

Changes in the morphological characters of heteromorphic leaves with the increase of tree height

P. euphratica and *P. pruinosa* heteromorphic leaf morphology changes significantly with the increase of tree height (*Fig. 1a-c*). For example, the leaf shape index (LI) at a height of 2 m is significantly larger than the other heights. LA and LT show an increasing trend with the increase of tree height, and have a significant positive correlation with tree height (*Tables A1* and *A2*). From the height of the tree from 2 m to 10 m, the LA of *P. euphratica* increased by 73.79%, which was greater than the 22.54% increase of *P. pruinosa,* and the SLA of *P. euphratica* decreased by 18.32%, which was less than the decrease of 38.47% of *P. pruinosa*, and the height of the top (10 m) of the LA and SLA of *P. euphratica* were significantly larger than *P. pruinosa*, and the LT at 8 m and 10 m of *P. euphratica* was significantly larger than that of *P. pruinosa*.

Correlation analysis showed that the LA of *P. euphratica* and *P. pruinosa* showed a significant positive correlation with LT and a significant negative correlation with the LI. The SLA of *P. pruinosa* showed a significant negative correlation with LT, while *P. euphratica* had no significant correlation (*Tables A1* and *A2*), indicating that the relationship between *P. euphratica* and *P. pruinosa* with the increase of the height of the leaf morphology is different.

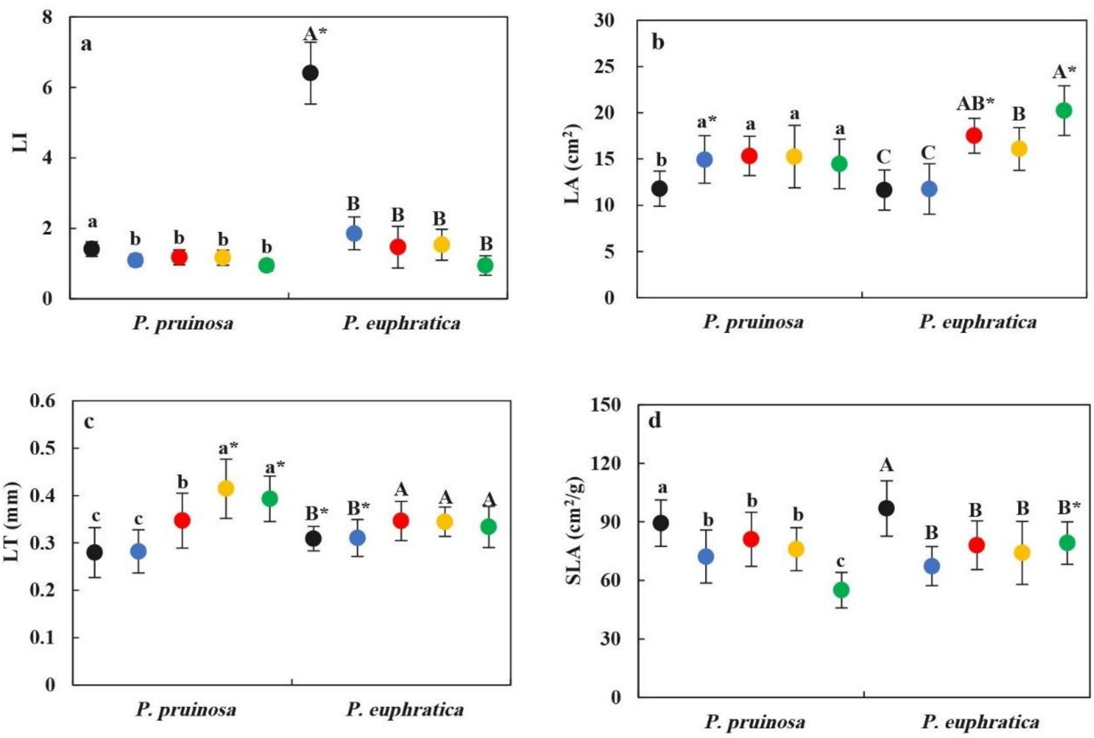

Figure 1. *Changes in morphological characteristics of heteromorphic leaves with tree height of P. pruinosa and P. euphratica. Each value is the mean ± SE. Note: The black dot indicates the height of the 2 m tree, the blue dot indicates the height of the 4 m tree, the red dot indicates the height of the 6 m tree, the yellow dot indicates the height of the tree 8 m, and the green dot indicates the height of the 10 m tree. According to Tukey's HSD test, lowercase and uppercase letters represent the significance of the difference between different sampling heights of P. pruinosa and P. euphratica. * The representing the comparison of the same height among species was significantly higher value (P < 0.05)*

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Changes of anatomical structure characters of heteromorphic leaves with increase tree height

P. euphratica and *P. pruinosa* heteromorphic leaf PT, MXA, VA, and VN showed an increasing trend with the increase of tree height (*Fig. 2a-f*), and there was a significant positive correlation with tree height (*Tables A1* and *A2*). *P. euphratica* PSR, XVBR increased with the increase of tree height, and showed a significant positive correlation with tree height, while *P. pruinosa* had no significant correlation, indicating that the characteristics of the xerophytic structure of *P. euphratica* the increase in tree height is reflected in more aspects than *P. pruinosa*. At the same time, it was also found that the PT, MXA, XVBR, and VA at 8 m and 10 m were significantly larger than that of *P. pruinosa*. From the height of the tree from 2 m with 10 m, *P. euphratica* of PSR increased by 26.03%, which is obviously greater than the 0.37% increase of *P. pruinosa*, indicating that the xerophytic structural characteristics of the top leaves of the tree height are more obvious than that of *P. pruinosa*.

Changes in gas exchange capability of heteromorphic leaves with increase of tree height

The photosynthetic capacity of *P. euphratica* and *P. pruinosa* showed an increasing trend with the increase of tree height (*Fig. 3a-d*). The Pn, Tr with tree height are significantly positively correlated (*Tables A1* and *A2*). From the height of 2 m to 10 m, the Pn of *P. euphratica* and *P. pruinosa* were increased by 49.36% and 33.95%, and the Tr increased by 86.76% and 20.28% respectively. At the same time, the Ci of *P. euphratica* at a height of 10 m was significantly lower than that of other heights, while the Ci of *P. euphratica* had no significant difference at different tree heights. In addition, the Pn, Tr and Gs of *P. euphratica* heteromorphic leaves are significantly positively correlated with LA, while only the Pn of *P. pruinosa* is significantly positively correlated with LA, indicating that with the increase of tree height under drought stress conditions, The photosynthetic capacity of *P. euphratica* and *P. pruinosa* have different changes.

The $\delta^{13}C$ of the heteromorphic leaves of *P. euphratica* and *P. pruinosa* showed an increasing trend with the increase of tree height (*Fig. 4b*). Although there is no significant change in WUE_i, the $\delta^{13}C$ value is positively correlated with tree height (*Tables A1* and *A2*). The $\delta^{13}C$ value of *P. euphratica* is significantly positively correlated with the Pn and LA, indicating that the water use efficiency increases with the height of the tree and is closely related to the height and LA of the tree where the heteromorphic leaves are located. Compared with different species, *P. euphratica* had significantly higher $\delta^{13}C$ values than those of *P. pruinosa* in different heights, and the long-term water use efficiency of *P. euphratica* was higher than that of *P. pruinosa*.

Changes in physiological characteristics of heteromorphic leaves with increase of tree height

The Pro content of the heteromorphic leaves of *P. euphratica* at a height of 2 m was significantly smaller than the other heights, and the proline content of *P. pruinosa* at 2 m was significantly less than that of 8 m. From 2 m to 10 m, the increase in Pro content of *P. euphratica* is twice that of *P. pruinosa* (*Fig. 5a-d*). The Pro content of 8 m and 10 m and the content of MDA and SP in each height of *P. euphratica* were

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significantly higher than those of *P. pruinosa*, indicating that the osmotic adjustment ability of the heteromorphic leaves at the top of the crown of *P. euphratica* was stronger than that of *P. pruinosa*.

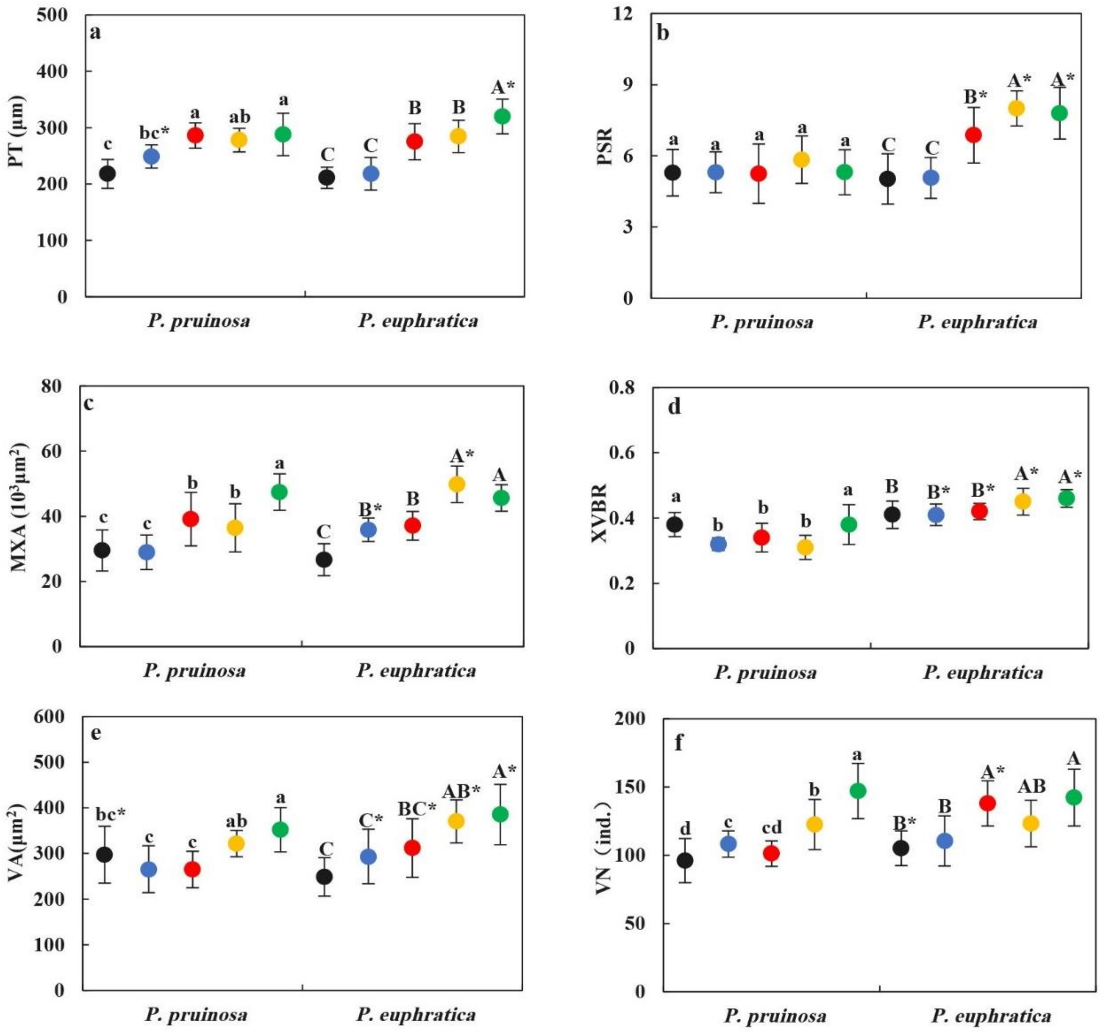

***Figure 2.** Changes in anatomical structure characters of heteromorphic leaves with tree height of P. pruinosa and P. euphratica. Each value is the mean ± SE. Note: The black dot indicates the height of the 2 m tree, the blue dot indicates the height of the 4 m tree, the red dot indicates the height of the 6 m tree, the yellow dot indicates the height of the tree 8 m, and the green dot indicates the height of the 10 m tree. According to Tukey's HSD test, lowercase and uppercase letters represent the significance of the difference between different sampling heights of P. pruinosa and P. euphratica. * The representing the comparison of the same height among species was significantly higher value (P < 0.05)*

Correlation analysis showed that the Pro content of *P. euphratica* was significantly positively correlated with tree height, LA, RT, PSR, VA, and Pn, while the Pro content of *P. pruinosa* was only relate LA and Pn significantly positive correlation (*Tables A1* and *A2*), It shows that the increase of Pro content with the height of the tree is closely related to the increase of the height and LA of the tree where the heteromorphic leaves are located.

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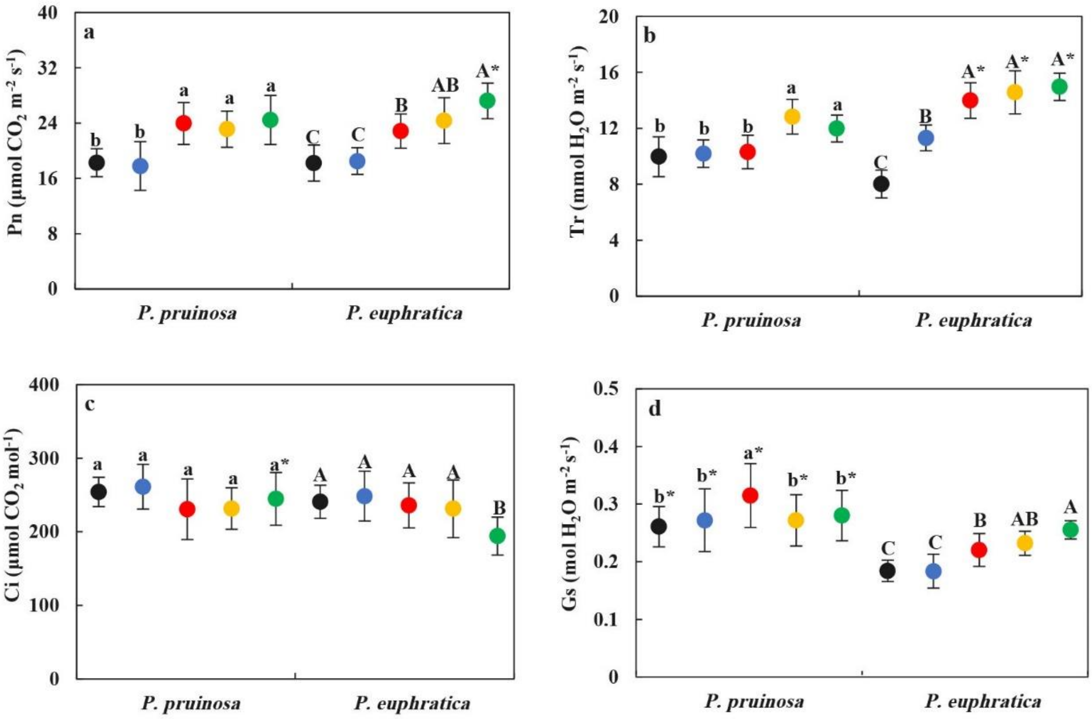

Figure 3. *Changes in photosynthetic physiological parameters of heteromorphic leaves with tree height of P. pruinosa and P. euphratica. Each value is the mean ± SE. Note: The black dot indicates the height of the 2 m tree, the blue dot indicates the height of the 4 m tree, the red dot indicates the height of the 6 m tree, the yellow dot indicates the height of the tree 8 m, and the green dot indicates the height of the 10 m tree. According to Tukey's HSD test, lowercase and uppercase letters represent the significance of the difference between different sampling heights of P. pruinosa and P. euphratica. * The representing the comparison of the same height among species was significantly higher value (P < 0.05)*

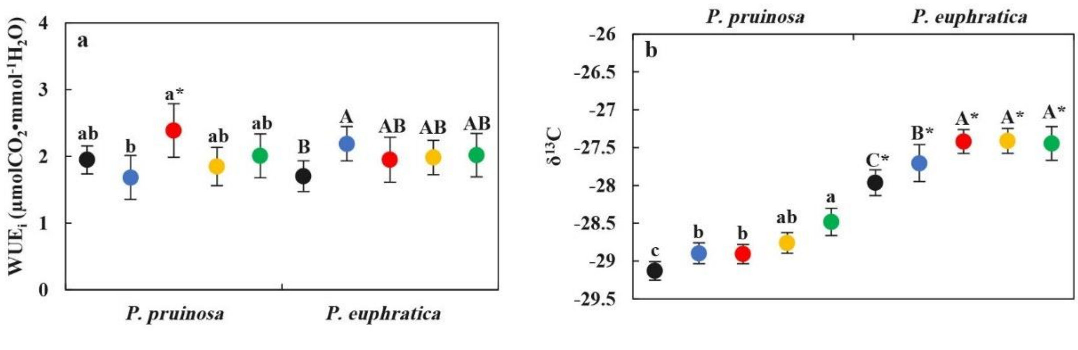

Figure 4. *Changes in water use efficiency of heteromorphic leaves with tree height of P. pruinosa and P. euphratica. Each value is the mean ± SE. Note: The black dot indicates the height of the 2 m tree, the blue dot indicates the height of the 4 m tree, the red dot indicates the height of the 6 m tree, the yellow dot indicates the height of the tree 8 m, and the green dot indicates the height of the 10 m tree. According to Tukey's HSD test, lowercase and uppercase letters represent the significance of the difference between different sampling heights of P. pruinosa and P. euphratica. * The representing the comparison of the same height among species was significantly higher value (P < 0.05)*

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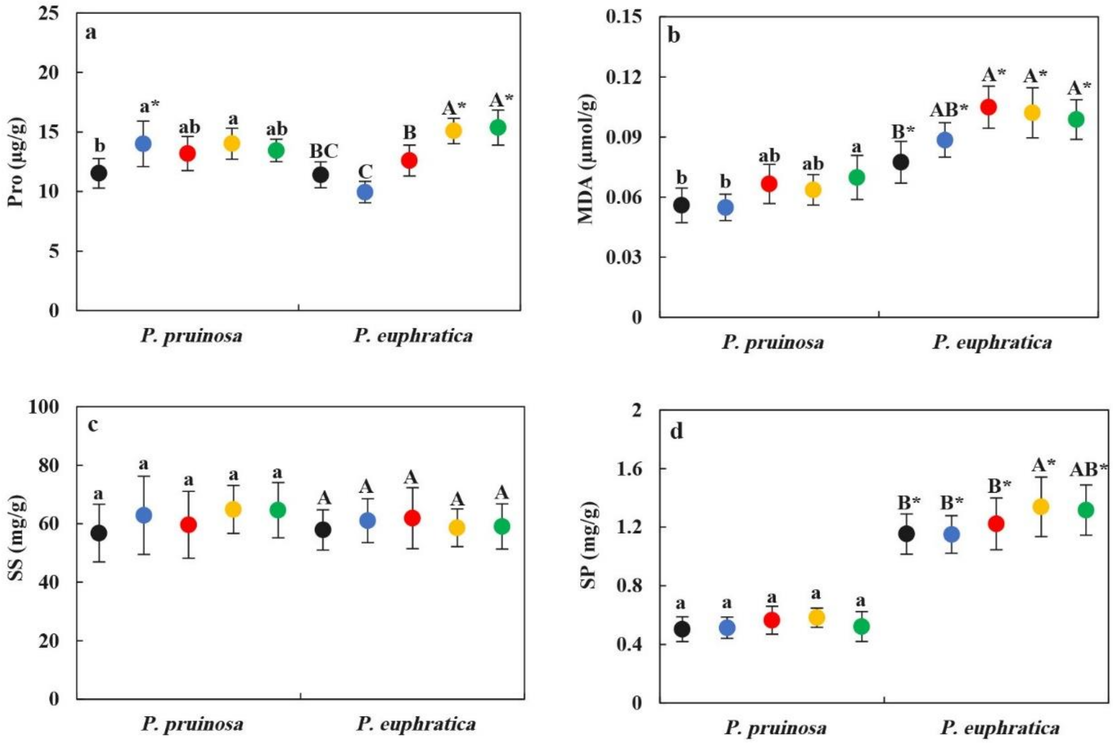

Figure 5. *Changes in physiological characteristics of heteromorphic leaves with tree height of P. pruinosa and P. euphratica. Each value is the mean ± SE. Note: The black dot indicates the height of the 2 m tree, the blue dot indicates the height of the 4 m tree, the red dot indicates the height of the 6 m tree, the yellow dot indicates the height of the tree 8 m, and the green dot indicates the height of the 10 m tree. According to Tukey's HSD test, lowercase and uppercase letters represent the significance of the difference between different sampling heights of P. pruinosa and P. euphratica. * The representing the comparison of the same height among species was significantly higher value (P < 0.05)*

Changes in endogenous hormones of heteromorphic leaves with increase of tree height

The content of GA_3, IAA, and ZR in the heteromorphic leaves of *P. euphratica* and *P. pruinosa* all showed an increasing trend with the increase of tree height (*Fig. 6a-d*), and the contents of GA_3, IAA and ZR in the heteromorphic leaves were significantly positively correlated with the height of the tree (*Tables A1* and *A2*). The ABA content of *P. euphratica* showed a decreasing trend with the increase of tree height, while *P. pruinosa* showed an increasing trend. From the height of 2 m to 10 m, the increase of GA_3, IAA and ZR content of *P. euphratica* is about 2 times, 4 times and 2 times of that of *P. pruinose* respectively.

Correlation analysis showed that the content of IAA and ZR in the heteromorphic leaves of *P. euphratica* and *P. pruinose* were significantly positively correlated with the Pn. The content of GA_3 and IAA was significantly positively correlated with tree height and LA, PT, MXA, and VN. At the same time, GA_3 content was significantly positively correlated with Pro content, indicating that under drought stress, the endogenous hormone changes of *P. euphratica* and *P. pruinose* with the increase of tree height are closely related to leaf morphology and physiological functions.

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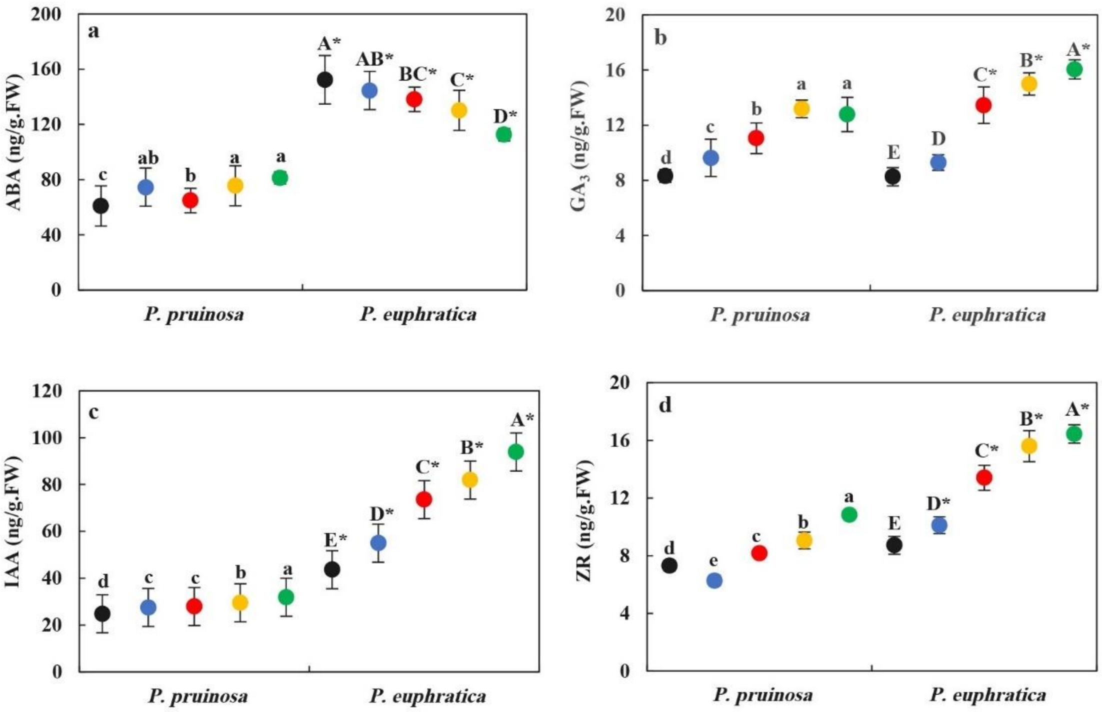

Figure 6. *Changes in endogenous hormones of heteromorphic leaves with tree height of P. pruinosa and P. euphratica. Each value is the mean ± SE. Note: The black dot indicates the height of the 2 m tree, the blue dot indicates the height of the 4 m tree, the red dot indicates the height of the 6 m tree, the yellow dot indicates the height of the tree 8 m, and the green dot indicates the height of the 10 m tree. According to Tukey's HSD test, lowercase and uppercase letters represent the significance of the difference between different sampling heights of P. pruinosa and P. euphratica. * The representing the comparison of the same height among species was significantly higher value (P < 0.05)*

Effects of endogenous hormones on the structural traits of heteromorphic leaves

The endogenous hormone content was used as the independent variable, and the leaf morphology and anatomical structure traits were respectively used as the dependent variable for stepwise regression analysis. The results showed that there is a very significant linear relationship between the dependent variable Y and the independent variable X (*Tables 1* and *2*). It is found that the content of IAA affects the change of *P. euphratica* LI, and also affects the change of LT and the anatomical structure characteristics of the main vein of the leaf, such as the MXA and the VN; In addition, GA_3 content also affects the changes in PT, XVBR, and VA. With the increase of tree height, *P. euphratica* heteromorphic leaf LA, PT, and MXA are mainly affected by the content of GA_3, ZR, and IAA respectively, and the PSR is mainly affected by the content of ABA.

Similarly, the content of endogenous hormone IAA in *P. pruinose* heteromorphic leaves affects the change of LI. Unlike *P. euphratica*, the IAA content of heteromorphic leaves of *P. pruinose* also mainly affects LA, SLA and PT, while GA_3 content is mainly affects the change of LT. With the increase of tree height, the LA and PT of *P. pruinose* are mainly affected by the content of IAA, and the MXA of the main vein is mainly affected by the content of ZR.

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Table 1. *Stepwise regression model of P. euphratica heteromorphic leaf structure traits and endogenous hormones*

Model	Dependent variable (Y)	Regression equation	R	R^2	F	Sig.
LI	Y_1	$Y_1 = 7.373-0.07X_3$	0.73	0.53	25.99	0.00
LA	Y_2	$Y_2 = 1.65 + 0.62X_2 + 0.48X_4$	0.84	0.71	26.47	0.00
LT	Y_3	$Y_3 = 0.27 + 0.001X_3$	0.56	0.31	10.29	0.00
PT	Y_4	$Y_4 = 115.01 + 3.85X_2 + 7.71X_4$	0.85	0.73	29.41	0.00
PSR	Y_5	$Y_5 = 12.22-0.04X_1$	0.43	0.19	5.24	0.03
MXA	Y_6	$Y_6 = 15477.67 + 344.85X_3$	0.73	0.53	25.81	0.00
XVBR	Y_7	$Y_7 = 0.31 + 0.01X_2$	0.65	0.42	16.45	0.00
VA	Y_8	$Y_8 = 134.92 + 5.85X_2 + 9.10X_4$	0.85	0.72	28.72	0.00
VN	Y_9	$Y_9 = 93.08 + 0.49X_3$	0.57	0.33	11.26	0.00

Y_1: LI; Y_2: LA; Y_3: LT; Y_4: PT; Y_5: PSR; Y_6: MXA; Y_7: XVBR; Y_8: VA; Y_9: VN; X_1: ABA; X_2: GA_3; X_3: IAA; X_4: ZR

Table 2. *Stepwise regression model of P. pruinosa heteromorphic leaf structure traits and endogenous hormones*

Model	Dependent variable (Y)	Regression equation	R	R^2	F	Sig.
LI	Y_1	$Y_1 = 1.90-0.03X_3$	0.52	0.27	8.59	0.00
LA	Y_2	$Y_2 = 6.48 + 0.28X_3$	0.41	0.17	4.75	0.04
LT	Y_3	$Y_3 = 83.83 + 23.78X_2$	0.80	0.64	40.99	0.00
SLA	Y_4	$Y_4 = 182.10-3.78X_3$	0.76	0.57	30.95	0.00
PT	Y_5	$Y_5 = 3.23 + 9.24X_3$	0.71	0.51	23.74	0.00
MXA	Y_6	$Y_6 = 3594.08 + 3923.81X_4$	0.81	0.66	44.57	0.00
VA	Y_7	$Y_7 = 146.61 + 18.20X_4$	0.64	0.42	16.44	0.00
VN	Y_8	$Y_8 = 24.82 + 11.19X_4$	0.68	0.46	19.92	0.00

Y_1: LI; Y_2: LA; Y_3: LT; Y_4: SLA; Y_5: PT; Y_6: MXA; Y_7: VA; Y_8: VN; X_1: ABA; X_2: GA_3; X_3: IAA; X_4: ZR

Comparison of drought resistance of P. euphratica and P. pruinose

The membership function method was used to comprehensively analyze the drought resistance of *P. euphratica* and *P. pruinose* with different heights and heteromorphic leaves. The results show (*Table A3*) that the average membership function value of *P. euphratica* at 6 m, 8 m, and 10 m is 0.52, which is greater than the average function value at 2 m and 4 m. The average membership function value of *P. pruinose* at 8 m and 10 m is greater than 2 m and 4 m. It shows that the broad oval leaves of *P. euphratica* and *P. pruinose* with large crowns are larger than the heteromorphic leaves at the bottom under drought resistance. Comparing the two species, the average membership function value of each height is that *P. euphratica* is greater than that of *P. pruinose*.

Discussion

Adaptation strategies of heteromorphic leaf structure traits with increasing tree height

As the water potential of the xylem of the tree decreases as the height of the tree increases, the difference in water pressure in the height gradient will affect the morphology and structure of the leaves at the corresponding tree height. The upper leaves

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of the tree can only hinder water loss through a more obvious xeromorphic structure to cope with water stress (He et al., 2008; Ryan and Yoder, 1997). For example, the leaf size of *Eucalyptu srobusta* decreases with the increase of tree age and tree height, reducing the area of transpiration and photosynthesis (England et al., 2005). The LA of *Parashorea chinensis* also decreases along the height of the tree, while the anatomical structure of the leaf shows a stronger xerophytic structure as the height of the tree increases, such as PT, PSR increases with the increase of tree height (He et al., 2008). *P. euphratica* exhibits LA, PT and PSR at different developmental stages, which increase with the increase in diameter at breast height and the height of the heteromorphic leaves, the heteromorphic leaves show a stronger xerophytic structure as the height of the tree increases features (Zhai et al., 2020). In the results of this study, *P. euphratica* under soil drought stress conditions increased the LA, LT, PT, MXA with the increase of tree height, the xeromorphic structural characteristics increased with the increase of tree height. The change rule is consistent with the above results Similarly, under soil drought conditions, with the increase of tree height, *P. pruinose* also has obvious xerophytic characteristics as the leaf area increases, and the change pattern is similar to that of *P. euphratica*.

The size of the leaf strongly affects its anatomical characteristics, and the anatomical characteristics are reflected in the mechanical support and physiological capabilities of the leaf. The increase in leaf area will inevitably require an increase in supporting tissue and transpiration rate. *P. euphratica* and *P. pruinose* have the largest LA at the top of the crown, the LA has a significant positive correlation with the PT, MXA and Tr. The LT of the heteromorphic leaves at the top of the canopy is also the largest, which is good for water storage and reduces transpiration. The PT and MXA increase with the increase of tree height, reflecting the enhancement of leaf water transport efficiency, mechanical support and physiological ability, at the same time, the investment of leaves in the mesophyll fence organization and vascular organization is also the main reason why the specific leaf area decreases with the height of the tree. Leaf anatomical characteristics are related to CO_2 diffusion resistance (Crous et al., 2021; Terashima et al., 2011), The thicker leaves at the top of *P. euphratica* and *P. pruinose* have more palisade layers and dense mesophyll, leaving less intercellular air space in the upper leaves of the canopy, reducing the internal limitation of CO_2 transfer during photosynthesis, which is conducive to the enhancement of photosynthetic capacity. Comparing the two at the same height, it is found that the anatomical structures such as the LA at the top (10 m) of the tree height, PT, and MXA were *P. euphratica* was significantly larger than *P. pruinose*. In addition, *P. euphratica* PSR, VBXR with tree height were significantly positively correlated. In response to soil drought stress, *P. euphratica* and *P. pruinose* showed different adaptation strategies in leaf morphology. *P. pruinose* mainly enhances the xerophytic structure characteristics through the increase of LT, PT, MXA, VA increase and SLA decrease. *P. euphratica* mainly enhances the characteristics of xerophytic structure through coordinated changes in the PSR and XVBR in addition to the LA, PT, MXA, and VA. In addition, with the increase of tree height, *P. euphratica* reduced the percentage of SLA less than that of *P. pruinose*, which shows that *P. euphratica* has the ability to utilize resources while increasing drought resistance.

Adaptation strategies of heteromorphic leaf functional traits with increasing tree height

The leaves at the top of the canopy must maintain photosynthetic and hydraulic functions under high light and high evaporation requirements (Shiraki et al., 2017). The

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photosynthetic efficiency of an adult *P. euphratica* leaf broad-ovate leaf is significantly greater than that of striped leaf (Bai et al., 2011; Su et al., 2003; Zhai et al., 2020), broad oval leaves have a relatively large photosynthetic area, better light resources, a relatively large net photosynthetic rate, and higher photosynthetic efficiency can accumulate more photosynthetic products (Wang et al., 2014). In addition, the osmotic adjustment of many species allows them to maintain normal functions during droughts (Martorell et al., 2015; Merchant et al., 2007). Plants can cope with stress by absorbing water to the maximum, minimizing water loss or accumulating some osmotic regulators, thereby avoiding drought (Ma et al., 2014). The osmotic adjustment ability of *P. euphratica* broad-ovate leaves is stronger than that of other leaves (Wang et al., 2011; Yang, 2004). Under suitable water conditions, the net photosynthetic rate, transpiration rate, stomatal conductance, instantaneous water use efficiency, $\delta^{13}C$, proline, and malondialdehyde content of *P. euphratica* heteromorphic leaves all increase with the increase of diameter step and sampling height, the photosynthetic capacity and osmotic adjustment capacity of broad oval leaves are stronger than other leaves (Wang et al., 2011, 2014; Zhai et al., 2020). This study shows that under soil drought stress, the photosynthetic capacity, water use efficiency and osmotic adjustment ability of *P. euphratica* and *P. pruinose* with the increase of tree height increase with the increase of tree height, which is similar to the change law of *P. euphratica* under suitable water conditions.

Leaf anatomy has a great influence on photosynthetic capacity, for example, thicker fence tissue can maximize light absorption (Coble et al., 2016), The MXA provides support for the high photosynthetic rate (Johnson et al., 2012), and the transportation of water in the leaves is the key to maintaining the high photosynthetic rate. Investment in water transportation systems is also an important part of reducing the limitation of photosynthesis. The Pn of *P. euphratica* and *P. pruinose* canopy top leaves was higher than the other heights, and was significantly correlated with the PT, VN, and the $\delta^{13}C$ value. At the same time, the Pn of *P. euphratica* was also significantly positively correlated with the MXA. Because the heteromorphic leaves of *P. euphratica* and *P. pruinose* have thicker PT, larger MXA and $\delta^{13}C$ value in the high canopy layer, it shows that the efficiency of water transportation is improved while the efficiency of long-term water use is also enhanced, this is conducive to the enhancement of photosynthetic capacity. Compared with the two species, the photosynthetic capacity, long-term water use efficiency and osmotic adjustment ability of the top leaves of the tree height showed that *P. euphratica* was stronger than *P. pruinose*. As we mentioned earlier, the LA at the top of the canopy, PT, and MXA of *P. euphratica* are significantly larger than that of *P. pruinose*, which provides the basis for strong stomata exchange capacity, the Pn of *P. euphratica* is significantly positively correlated with Gs, while *P. pruinose* has no significant correlation with Gs, but it is significantly negatively correlated with the C_i, this may be related to the dense accumulation of palisade tissue to reduce the internal limitation of CO_2 transfer in photosynthesis. In addition, the content of proline and soluble protein in the broad ovoid leaves of *P. euphratica* canopy is significantly greater than that of *P. pruinose*, and the net photosynthetic rate is significantly positively correlated with proline, the increase in the content of these osmotic adjustment substances can maintain a certain osmotic potential, provide a certain water absorption capacity, and ensure a normal physiological response.

Hormones not only coordinate internal developmental procedures, but also drive adaptability with external assistance (Ali et al., 2020). They can induce the accumulation of soluble osmotic substances through regulation of intracellular

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metabolism and enhance the chances of survival of plants in adversity (Yao et al., 2011). Li (2017) research shows that the hormone content of *P. euphratica* leaves changes with the change of the morphology of the abnormal leaves, which reflects the physiological adjustment of *P. euphratica* to adapt to arid desert environment (Li et al., 2017). This study showed that the content of endogenous hormones GA_3, IAA, and ZR in *P. euphratica* and *P. pruinose* leaves increased with the increase of tree height, similar to the change trend of proline and soluble protein content, and GA_3 and proline showed a significant positive correlation. Under soil drought conditions, *P. euphratica* responds to drought endogenous hormone ABA content stronger than *P. pruinose*, and its ABA content at each height is significantly greater than *P. pruinose*, at the same time, the endogenous hormone ABA content of *P. euphratica* heteromorphic leaves showed a decreasing trend with the increase of tree height, while that of *P. pruinose* was the opposite. When plants are subjected to drought stress, ABA accumulates rapidly in the body, which promotes the closure of stomata and reduces transpiration. The ABA content at the top of the *P. pruinose* canopy is the highest compared to the rest of the canopy, however broad ovoid leaves of *P. euphratica* have the lowest ABA content, and the net photosynthetic rate and stomatal conductance are significantly negatively correlated with ABA content. lower ABA content can reduce the negative impact on the photosynthetic capacity of heteromorphic leaves and provide support for the enhancement of photosynthetic capacity. To cope with the water stress caused by soil drought and tree height increase, as far as the endogenous hormone ABA in the heteromorphic leaves is concerned, compared with *P. euphratica*, *P. pruinose* chose a more conservative adaptation strategy.

Phytohormones especially GA_3, IAA, ABA, ZR affect the formation and development of many plante heteromorphic leaves (Li et al., 2019; Nakayama et al., 2017). Auxin affects the structure of leaf cells, increases the morphology and development of cell volume (Barkoulas et al., 2008), affects the formation of leaf vascular tissue and the morphology and development of leaves (Avsian-Kretchmer et al., 2002; Donner et al., 2009). Although the endogenous hormone IAA of *P. euphratica* and *P. pruinose* affects the change of LI, the main influence points on the anatomical structure are different, the leaf hormone IAA of *P. euphratica* and *P. pruinose* mainly affects MXA and PT, respectively. In addition, the leaf IAA of *P. euphratica* and *P. pruinose* showed a significant positive correlation with MXA, PT, and Pn, *P. euphratica* IAA affects the water transport efficiency of the main vein to ensure normal photosynthetic physiology, while *P. pruinose* IAA affects the thickness of the fence tissue to ensure photosynthetic capacity. In addition, the ABA content of *P. euphratica* hormone is significantly negatively correlated with PT, PSR, Pn, Tr, and Gs, which can support the enhancement of gas exchange capacity by influencing the change of PSR.

Conclusions

Adaptation strategies of heteromorphic leaf structure traits with increasing tree height *P. euphratica* and *P. pruinose* have different response strategies to water stress caused by tree height. With the increase of tree height, the abnormal leaves of the two species strengthen the xerophytic structure through the increase of leaf area, palisade tissue, main vein xylem area, duct area and reduction of specific leaf area. In addition, *P. euphratica* also enhances the xerophytic structure characteristics through the changes in the PSR and the XVBR. The functional traits of *P. euphratica*, such as photosynthetic

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capacity and osmotic adjustment ability, are stronger than those of *P. pruinose*. It is because the LA at the top of the canopy, the PT, PSR, MXA, the $\delta^{13}C$ value, the proline, and the soluble protein content show that *P. euphratica* is significantly larger than that of *P. pruinose*. At the same time, endogenous hormones also participate in the enhancement of osmotic regulation. The different influencing factors of the endogenous hormone IAA is also one of the reasons for the different adaptation strategies of the two. IAA mainly affects the water transport efficiency of the main veins of *P. euphratica*, and mainly affects the leaf morphology of *P. pruinose*. In addition, the comprehensive comparison of membership function method shows that the drought resistance of *P. euphratica* heteromorphic leaves is greater than that of *P. pruinose.*

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APPENDIX

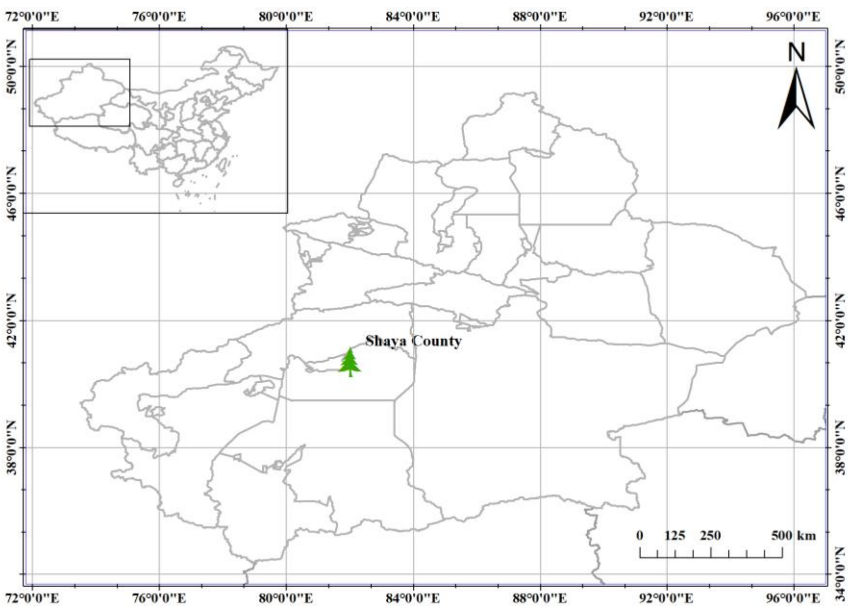

Figure A1. *Overview of the study area*

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Table A1. *Correlation analysis of structural and functional traits of P. euphratica*

R	H	LI	LA	LT	SLA	PT	PSR	MXA	XA/VBA	VA	VN	Pn	Tr	Ci	Gs	WUEi	$\delta^{13}C$	Pro	MDA	SS	SP	ABA	GA3	IAA	ZR
LI	-0.73**	1																							
LA	0.67**	-0.65**	1																						
LT	0.65*	-0.57**	0.49*	1																					
SLA	0.34	0.55**	-0.09	-0.31	1																				
PT	0.87**	-0.66**	0.63**	0.27	0.24	1																			
PSR	0.82**	-0.57**	0.54**	0.07	0.24	0.71**	1																		
MXA	0.90**	-0.74**	0.50**	0.20	0.03	0.73**	0.81**	1																	
XVBR	0.71*	-0.23	0.55*	0.31	0.23	0.24	0.12	0.52**	1																
VA	0.95**	-0.69**	0.60**	0.19	0.28	0.73**	0.77**	0.66**	0.46*	1															
VN	0.67**	-0.62**	0.65**	0.26	-0.18	0.60**	0.32	0.55**	0.23	0.53**	1														
Pn	0.73**	-0.38	0.58**	0.25	0.29	0.46*	0.63**	0.41*	0.22	0.62**	0.54**	1													
Tr	0.65**	-0.42*	0.56**	0.28	0.04	0.47*	0.41*	0.51**	0.05	0.67**	0.49*	0.50*	1												
Ci	-0.70**	0.45*	-0.34	0.21	-0.59**	-0.60**	-0.59**	-0.17	-0.41*	-0.20	-0.33	-0.27	-0.065	1											
Gs	0.45*	-0.15	0.63**	0.27	0.35	0.32	0.16	0.17	0.27	0.48*	0.46*	0.54**	0.44*	-0.23	1										
WUEi	0.07	-0.08	-0.01	-0.11	0.17	-0.09	-0.05	0.02	-0.02	0.08	0.31	-0.14	-0.13	-0.08	0.07	1									
$\delta^{13}C$	-0.73*	0.63**	0.71*	0.18	0.23	-0.31	-0.18	0.34	0.33	0.28	0.23	0.63*	0.30	-0.15	0.30	-0.13	1								
Pro	0.71**	-0.32	0.60**	0.11	0.45*	0.51**	0.64**	0.39	0.29	0.47*	0.29	0.55**	0.22	-0.35	0.29	0.02	-0.01	1							
MDA	0.43*	-0.23	0.41*	-0.22	-0.20	0.14	-0.14	0.49*	0.46*	0.29	0.39	0.07	-0.03	-0.05	-0.01	0.39*	-0.07	0.31	1						
SS	0.01	-0.14	0.23	0.15	-0.13	0.07	-0.25	0.17	-0.09	0.04	0.08	0.15	0.29	-0.18	-0.25	-0.33	0.14	0.11	-0.16	1					
SP	0.41*	-0.25	0.17	-0.06	0.25	0.17	0.18	0.21	0.19	0.10	0.07	0.36	0.04	-0.01	0.25	0.03	0.13	0.24	0.05	-0.24	1				
ABA	-0.86**	0.61**	-0.47*	0.04	-0.36	-0.69**	-0.73**	-0.72**	-0.06	-0.76**	-0.45*	-0.51**	-0.53**	0.80**	-0.13	-0.02	0.23	-0.49*	-0.17	0.23	-0.33	1			
GA$_3$	0.81**	-0.55**	0.82**	0.45*	0.27	0.76**	0.65**	0.75**	0.53**	0.79**	0.40*	0.63**	0.53**	-0.39	0.68**	0.03	-0.21	0.74**	-0.07	0.28	0.28	-0.45*	1		
IAA	0.95**	-0.67**	0.72**	0.25	0.38	0.77**	0.72**	0.85**	0.41*	0.93**	0.57**	0.70**	0.70**	-0.61**	0.59**	0.14	-0.19	0.78**	0.09	0.17	0.54**	-0.78**	0.84**	1	
ZR	0.80**	-0.55**	0.76**	0.43*	0.23	0.74**	0.62**	0.77**	0.53**	0.80**	0.52**	0.62**	0.53**	-0.35	0.66**	0.04	-0.18	0.72**	-0.05	0.29	0.28	-0.44*	0.98**	0.84**	1

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Table A2. *Correlation analysis of structural and functional traits of P. pruinosa*

R	H	LI	LA	LT	SLA	PT	PSR	MXA	XA/VBA	VA	VN	Pn	Tr	Ci	Gs	WUEi	$\delta^{13}C$	Pro	MDA	SS	SP	ABA	GA3	IAA	ZR
LI	-0.53**	1.00																							
LA	0.43*	-0.77**	1.00																						
LT	0.82**	-0.33	0.43*	1.00																					
SLA	-0.68**	0.49*	-0.27	-0.43*	1.00																				
PT	0.71**	-0.50*	0.51**	0.50**	-0.46*	1.00																			
PSR	0.08	0.02	0.11	0.05	-0.02	0.36	1.00																		
MXA	0.78**	-0.37	0.29	0.53**	-0.54**	0.51**	-0.13	1.00																	
XVBR	0.02	0.30	-0.32	0.12	-0.13	-0.11	0.27	0.18	1.00																
VA	0.49*	-0.09	-0.02	0.50**	-0.17	0.21	0.02	0.28	0.15	1.00															
VN	0.76**	-0.47*	0.30	0.64**	-0.63**	0.48*	0.32	0.54**	0.35	0.50*	1.00														
Pn	0.53**	-0.30	0.52**	0.67**	-0.18	0.44*	0.45*	0.37	0.13	0.32	0.51**	1.00													
Tr	0.30	-0.10	0.03	0.39	-0.29	-0.03	0.11	0.21	0.33	0.02	0.29	0.40*	1.00												
Ci	-0.22	-0.12	-0.10	-0.32	0.04	-0.21	-0.52**	-0.09	-0.23	0.12	-0.22	-0.56**	-0.46*	1.00											
Gs	0.04	-0.12	0.07	0.04	0.00	0.00	0.27	0.14	0.19	-0.32	0.25	0.34	0.34	-0.45*	1.00										
WUEi	0.07	-0.14	0.39	0.16	0.05	0.28	0.34	0.15	0.13	0.16	0.19	0.52**	-0.26	-0.32	0.14	1.00									
$\delta^{13}C$	0.52**	-0.38	0.30	0.55**	-0.44*	0.41*	0.21	0.36	0.34	0.41*	0.55**	0.46*	0.30	-0.06	0.03	0.24	1.00								
Pro	0.35	-0.62**	0.51**	0.27	-0.46*	0.37	0.20	0.18	-0.25	-0.23	0.30	0.41*	0.22	-0.19	0.23	-0.09	0.27	1.00							
MDA	0.62**	-0.35	0.38	0.61**	-0.44*	0.41*	-0.07	0.67**	0.05	0.29	0.46*	0.51**	0.31	-0.15	0.24	0.33	0.57**	0.33	1.00						
SS	0.40*	-0.47*	0.19	0.32	-0.44*	0.22	-0.05	0.16	-0.05	0.22	0.46*	0.11	0.08	0.26	-0.05	-0.17	0.30	0.40*	0.16	1.00					
SP	0.20	0.19	0.03	0.15	0.05	0.26	0.23	0.22	0.05	-0.13	0.00	0.22	0.25	-0.26	0.05	-0.10	0.01	-0.07	0.15	-0.11	1.00				
ABA	0.49*	-0.48*	0.24	0.24	-0.41*	0.49*	-0.16	0.37	-0.38	0.46*	0.31	0.02	-0.02	0.32	-0.31	-0.17	0.21	0.30	0.22	0.39	0.00	1.00			
GA_3	0.85**	-0.39*	0.36	0.80**	-0.49*	0.51**	0.19	0.60**	0.10	0.31	0.66**	0.58**	0.47*	-0.50*	0.19	0.09	0.50*	0.40*	0.51**	0.33	0.30	0.19	1.00		
IAA	0.86**	-0.52**	0.41*	0.58**	-0.75**	0.71**	0.02	0.65**	-0.16	0.42*	0.64**	0.41*	0.15	-0.14	-0.13	0.11	0.34	0.26	0.47*	0.36	0.09	0.60**	0.63**	1.00	
ZR	0.88**	-0.22	0.18	0.77**	-0.58**	0.56**	-0.03	0.81**	0.21	0.66**	0.68**	0.45*	0.24	-0.17	-0.06	0.09	0.42*	0.08	0.60**	0.29	0.12	0.44*	0.68**	0.78**	1.00

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Table A3. *Evaluation and analysis on drought resistance of P. pruinosa and P. euphratica by membership function method*

Index	*P. pruinosa*					*P. euphratica*				
H	2m	4m	6m	8m	10m	2m	4m	6m	8m	10m
LI	0.51	0.47	0.46	0.36	0.77	0.48	0.36	0.53	0.63	0.55
LA	0.40	0.49	0.59	0.44	0.50	0.59	0.42	0.51	0.39	0.26
LT	0.40	0.51	0.49	0.51	0.41	0.67	0.67	0.56	0.40	0.53
SLA	0.46	0.62	0.50	0.52	0.61	0.52	0.62	0.63	0.51	0.64
PT	0.39	0.60	0.39	0.57	0.36	0.56	0.44	0.53	0.49	0.39
PSR	0.36	0.32	0.45	0.44	0.58	0.40	0.66	0.43	0.51	0.57
MXA	0.33	0.64	0.49	0.47	0.44	0.51	0.57	0.63	0.46	0.57
XVBR	0.36	0.45	0.63	0.38	0.50	0.54	0.43	0.45	0.64	0.50
VA	0.46	0.53	0.66	0.47	0.57	0.46	0.66	0.51	0.61	0.35
VN	0.63	0.63	0.36	0.54	0.40	0.53	0.39	0.43	0.47	0.58
Pn	0.41	0.40	0.43	0.43	0.54	0.57	0.38	0.70	0.58	0.33
Tr	0.52	0.27	0.57	0.56	0.54	0.45	0.58	0.62	0.54	0.53
Ci	0.27	0.38	0.44	0.42	0.41	0.44	0.47	0.47	0.67	0.59
Gs	0.44	0.54	0.58	0.66	0.40	0.33	0.54	0.57	0.40	0.67
WUE_i	0.43	0.46	0.29	0.65	0.60	0.52	0.27	0.35	0.52	0.57
$\delta^{13}C$	0.39	0.57	0.34	0.46	0.46	0.49	0.36	0.62	0.48	0.39
Pro	0.52	0.43	0.53	0.49	0.52	0.31	0.38	0.44	0.58	0.53
MDA	0.51	0.41	0.47	0.49	0.44	0.49	0.57	0.56	0.42	0.53
SS	0.58	0.54	0.53	0.57	0.37	0.49	0.50	0.47	0.66	0.55
SP	0.56	0.42	0.39	0.39	0.45	0.34	0.57	0.28	0.40	0.29
ABA	0.59	0.54	0.61	0.47	0.52	0.43	0.57	0.65	0.59	0.66
GA_3	0.38	0.47	0.60	0.38	0.50	0.48	0.56	0.63	0.45	0.51
IAA	0.52	0.42	0.55	0.44	0.42	0.40	0.41	0.36	0.34	0.53
ZR	0.54	0.40	0.48	0.60	0.39	0.52	0.40	0.38	0.58	0.75
Average	0.45	0.48	0.49	0.49	0.49	0.48	0.49	0.51	0.51	0.52

N = 450. LI: leaf index; LA: leaf area; LT: leaf thickness; SLA: Specific Leaf Area; PT: Palisade tissue thickness; PSR: Ratio of palisade tissue to spongy tissue; MXA: The main vein xylem area; XVBR: Main vein xylem/main vascular bundle area; VA: Vessel area; VN: Vessel number; Pn: Photosynthetic rate; Tr: Transpiration rate; Gs: Stomatal conductance; C_i: Intercellular CO_2 concentration; WUE_i: Instantaneous water use efficiency; $\delta^{13}C$: Stable carbon isotope values; Pro: Proline; MDA: Malondialdehyde; SS: Soluble sugar; SP: Soluble protein; ABA: Abscisic acid; GA_3: Gibberellin; IAA: Indoleacetic acid; ZR: Zeatin Riboside

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