

RESEARCH ARTICLE

Sex-specific non-structural carbohydrate variation and hydraulics explain differences in drought resistance of *Populus euphratica* females and males along an aridity gradient

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Abstract

1. Non-structural carbohydrates (NSC) are essential for the osmotic adjustment and maintenance of the hydraulic functioning of trees, but knowledge about the relationship between NSC dynamics and hydraulics during drought stress is still limited, especially in dioecious plants.
2. We investigated photosynthetic carbon assimilation, xylem hydraulics and related functional traits and explored whether hydraulics are linked to NSC dynamics in the leaves and branches of *Populus euphratica* females and males along an aridity gradient in the Xinjiang Province, China.
3. Both sexes of *P. euphratica* had increased intrinsic water use efficiency (WUE), percent loss of conductivity (PLC) and xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}), but decreased net photosynthetic rate (P_n), sapwood-specific hydraulic conductivity (K_s) and hydraulic safety margin (leaf mid-day water potential- P_{50} , HSM_{50}) associated with the reduction in the soil water content. Furthermore, females and males have different hydraulic strategies related to NSC dynamics under low soil water conditions. Males had higher K_s , wood density (WD), HSM_{50} , P_n , WUE, leaf dry mass per area (LMA) and leaf soluble sugar levels and lower branch soluble sugar levels, PLC and P_{50} values than females under extreme drought conditions, indicating that males had a more resistant xylem and can maintain water flow and leaf turgor probably due to the greater availability of soluble sugars to be used for osmotic adjustments. In addition, females had a lower K_s , WD and LMA and higher branch soluble sugar levels and PLC, implying that females were more vulnerable to cavitation and required higher branch soluble sugar levels for embolism repair under extreme drought conditions.
4. *Synthesis.* Due to the spatial sexual segregation across resource gradients, dioecious plants are more vulnerable to rapid climate change. The different hydraulic strategies linked to NSC dynamics between females and males may result in a situation that one sex is more prone to an increasingly long and intense

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drought than the other one. This study improves our predictions for future climate change impacts on dioecious *P. euphratica* and provides theoretical knowledge for restoration and afforestation in *P. euphratica* forests.

KEYWORDS

dioecy, drought, hydraulics, non-structural carbohydrates, tree mortality

1 | INTRODUCTION

An increased frequency and intensity of drought induced by climate change (Allen et al., 2015; Dai, 2013; Zhang et al., 2020) has resulted in elevated tree mortality and forest dieback worldwide (Anderegg & Hillerislambers, 2016; Brodribb et al., 2020; Hammond et al., 2019, 2022; Hartmann et al., 2022; McDowell et al., 2022). Tree dieback and mortality have profound effects on the carbon sequestration and water flux of ecosystems, the maintenance of biodiversity and the composition of ecosystems (Hartmann et al., 2022; McDowell et al., 2022; Sterck et al., 2024). Choat et al. (2012) have reported that almost all forest trees in the world are close to the hydraulic safety margin. Xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}) and hydraulic safety margin (HSM_{50} , the difference between leaf mid-day water potential and P_{50}) are important indicators of tree embolism resistance and mortality (Camarero, 2021; De Kauwe et al., 2020; Mantova et al., 2022). A lower P_{50} value usually implies a safer hydraulic system and a lower risk of hydraulic failure (Li et al., 2024; Pratt & Jacobson, 2017). Most forests experience different levels of drought stress and may be very sensitive to drought events induced by climate change (Allen et al., 2010; Hammond et al., 2022; McDowell et al., 2022).

The capacity to maintain hydraulic safety is fundamental for trees to cope with drought stress, and it plays a key role in trees' survival, growth and distribution (Anderegg & Hillerislambers, 2016; Choat et al., 2012; Duan et al., 2022; Sack et al., 2016). The increased embolism resistance is normally associated with a declined hydraulic efficiency of the xylem under favourable conditions (Hao et al., 2008, 2013). However, Liu et al. (2021) found a weak trade-off between xylem hydraulic efficiency and safety in 499 woody species worldwide. On the other hand, Xiong and Flexas (2022) reported that there was no clear trade-off between hydraulic safety and efficiency, which depends on different leaf anatomical traits in each species. Overall, the present knowledge about hydraulic safety and efficiency is limited, especially in dioecious trees. In addition, the hydraulic function of trees not only affects drought resistance but it is also closely related to the photosynthetic rate and wood growth. The hydraulic efficiency of the xylem (the capacity of xylem to transport water) is fundamental for tree transpiration. Trees usually have a greater xylem hydraulic efficiency to support a higher rate of carbon fixation in resourceful environments (Sack & Holbrook, 2006; Wang et al., 2016; Yin et al., 2022, 2023). Thus, plants' hydraulic traits are closely linked

to carbohydrates, and both play key functional roles in plants' response to drought stress (Choat et al., 2018; Fang et al., 2021; Sterck et al., 2024).

Non-structural carbohydrates (NSC), the sum of starch and soluble sugars, are the main resources to support tree growth and metabolism, especially when trees are exposed to unfavourable conditions (Chapin et al., 1990; Richardson et al., 2013; Secchi & Zwieniecki, 2011). Under heat stress and/or drought stress, non-structural carbohydrates are important for supporting the respiration process and osmoregulation (Aranda et al., 2024; Asao et al., 2024). In addition, soluble sugars play a key role in plants' osmosis and turgor pressure and potentially allow water extraction from increasingly dry soil until the limit imposed by cavitation-dependent reduction in xylem conductance is reached (Kannenbergh & Phillips, 2020; Martinez-Vilalta et al., 2019). Under drought stress, trees usually convert starch to soluble sugars for the osmotic adjustment of water potential and turgor maintenance, resulting in declined starch and increased soluble sugar levels (Dickman et al., 2019; Li et al., 2018). In addition, stomatal closure to reduce the loss of water results in a decreased photosynthesis rate and photosynthetic carbon supply under drought stress (Wang & Wang, 2023). If the newly synthesized photosynthetic carbon supply cannot meet the basic carbon metabolism needs of trees, such as growth, respiration and defence, the carbon storage will be further depleted, resulting in a decreased NSC storage and overall reduction of the NSC level (Huang et al., 2021; McDowell et al., 2011; Peltier et al., 2023). A meta-analysis conducted by Li et al. (2018) showed that drought stress does not affect NSC storage in above-ground organs but decreased NSC storage in roots. Thus, in trees with long transport pathways, the storage and mobility of NSC in different organs play important roles in coping with drought stress (Adams et al., 2017; He et al., 2020; Oswald & Aubrey, 2024; Sala et al., 2010).

The decline in hydraulic conductivity induced by cavitation results in limited nutrient and water transport and decreased photosynthetic carbon assimilation due to stomatal closure in drought-stressed plants (Hartmann et al., 2018; Oswald & Aubrey, 2024). Thus, the hydraulic strategies of trees are closely related to carbon dynamics, for example, xylem water and nutrient transport and NSC availability (Duan et al., 2022; McDowell et al., 2022; Preisler et al., 2021; Sala et al., 2010). Trees should store more non-structural carbohydrates in environments with a higher embolism risk, since active embolism repair is energetically

expensive (Creek et al., 2018; Liu et al., 2019; Salleo et al., 2009). Thus, a decline in the availability of NSC may limit the capacity of plants to maintain turgor and water flow (Sapes et al., 2019; Sevanto et al., 2014). However, the present knowledge on how hydraulics links to the photosynthetic capacity and NSC dynamics in different plant organs (i.e. leaves and branches), especially in dioecious tree species, is limited.

Dioecious plants account for only 5%–6% of all plant species (Renner, 2014), but they play key roles in maintaining the function and stability of ecosystems (Field et al., 2013; Hultine et al., 2016, 2018; Juvany & Munné-Bosch, 2015; Keram et al., 2021). Females with high reproduction investments to produce flowers and seeds usually are more sensitive to unfavourable environments (Hultine et al., 2016; Lei et al., 2017; Xia et al., 2020; Yu, Tang, et al., 2023). For example, Olano et al. (2017) reported that *Juniperus thurifera* females had a greater hydraulic efficiency over safety, whereas males showed a more conservative strategy, especially at drier sites. Liu et al. (2023) found that long-shoot leaves in *Ginkgo biloba* males had a higher leaf hydraulic conductance and leaf water potential of 50% loss in K_{leaf} compared to females. In addition, *Acer pensylvanicum* females had high concentrations of NSCs throughout the dying process (Blake-Mahmud & Struwe, 2020), and *Juniperus thurifera* females had higher levels of carbohydrates and greater growth rates under favourable conditions (DeSoto et al., 2016). *Populus euphratica* Oliver is a dioecious tree species, and about 90% of its distribution area is within the Tarim River watershed in China (Wang et al., 1995). Previous studies have reported that *P. euphratica* males have a higher resistance than females under drought and salinity stress (Yu, Huang, et al., 2023), and males have a higher leaf nitrogen resorption efficiency, while females have a higher leaf phosphorus (P) resorption efficiency for the reproductive investment under extreme drought conditions (Yu et al., 2022). In addition, Lan et al. (2024) found that *P. euphratica* females obtain more phosphorus (P) by releasing organic acids to mobilize P from precipitated P during the mid-growing season. Yet, there is still a knowledge gap in the understanding of (i) whether *P. euphratica* females and males have different hydraulic responses to a water-limited environment, (ii) whether hydraulics relate to NSC dynamics and (iii) whether there are sexual differences in the scaling of hydraulic traits with NSC under drought.

Climate change and human activities have increased water scarcity along the Tarim River, resulting in a serious decline of *P. euphratica* forests (Chen, Li, Xu, et al., 2015; Halik et al., 2019; Ling et al., 2015). For example, Keram et al. (2021) have reported that the mortality of young and middle-aged gap makers in *P. euphratica* forests has significantly increased over recent decades, primarily due to the regional water shortage. In this study, we compared photosynthetic carbon assimilation, xylem hydraulics and related functional traits and NSC dynamics in different organs between *P. euphratica* females and males along a water availability gradient on the Tarim River basin in the Xinjiang Province, China. Specifically, we aimed to answer the following questions: (1) Do hydraulic and related functional traits show sex-specific responses in *P. euphratica*? (2) How does NSC dynamics

in different organs link to hydraulics in *P. euphratica* females and males under drought conditions?

2 | MATERIALS AND METHODS

2.1 | Study area and plant materials

The study was conducted at four natural *P. euphratica* forest sites, Sanhe, Shaya, Luntai and Yuli, located from west to east along the Tarim River, Xinjiang Province, China (Figure 1). The soil water content decreased along the Tarim River from Sanhe to the east (Figure 1). This area is classified as a typical temperate desert climate with an average annual temperature of about 10°C, mean annual precipitation of less than 50 mm and annual potential evaporation of about 2800 mm (Guo et al., 2021; Yu et al., 2022). The height and diameter of trees, soil physicochemical traits, annual temperature and other environmental factors are described in Table S1.

At the beginning of April 2018, we selected naturally established, non-disturbed *P. euphratica* forests with a similar canopy height and species composition (Yu et al., 2022). In each forest, we marked female and male individuals according to their flower traits during the flowering period, 5–10 individuals per sex (Guo et al., 2021). The marked trees were 10–100 m apart from each other in order to minimize the possibility of including identical clones. Early August 2021, leaves with a similar size from sun-exposed branches on the south-facing side of five male and female trees, three different leaves per plant, were sampled for measurements. Five soil samples per sex at each site were collected for the soil water content (SWC) measurements. About 5 g soil was collected from 100 to 130 cm depth per sex at each forest site, weighed immediately and dried at 80°C for 72 h to a constant mass for the SWC measurements (Guo et al., 2021).

2.2 | Leaf photosynthesis and morphological measurements

In early August 2021, the light-saturated net photosynthetic rate (P_n) and stomatal conductance of fully mature healthy leaves from five male and female plants, three different leaves per plant were measured with a LI-COR 6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) between 08:00–11:30 AM. Before each photosynthesis measurement, the selected leaf was illuminated with saturated PPFD of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ for about 5–20 min for full photosynthetic induction as assessed by changes in stomatal conductance and photosynthesis rate. Once the full induction was achieved, the P_n value was recorded. The measurements were conducted in the following conditions: leaf temperature, 25°C; air vapour pressure deficit, $1.5 \pm 0.5 \text{ kPa}$; relative humidity, 50%; light intensity (PPFD), $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$; and CO_2 concentration, $400 \pm 5 \mu\text{mol mol}^{-1}$. The intrinsic water use efficiency (WUE) was calculated as the ratio of net photosynthetic rate to stomatal conductance. The leaf area was calculated with a resolution scanner (Cannon Scanner 5600F, Chengdu,

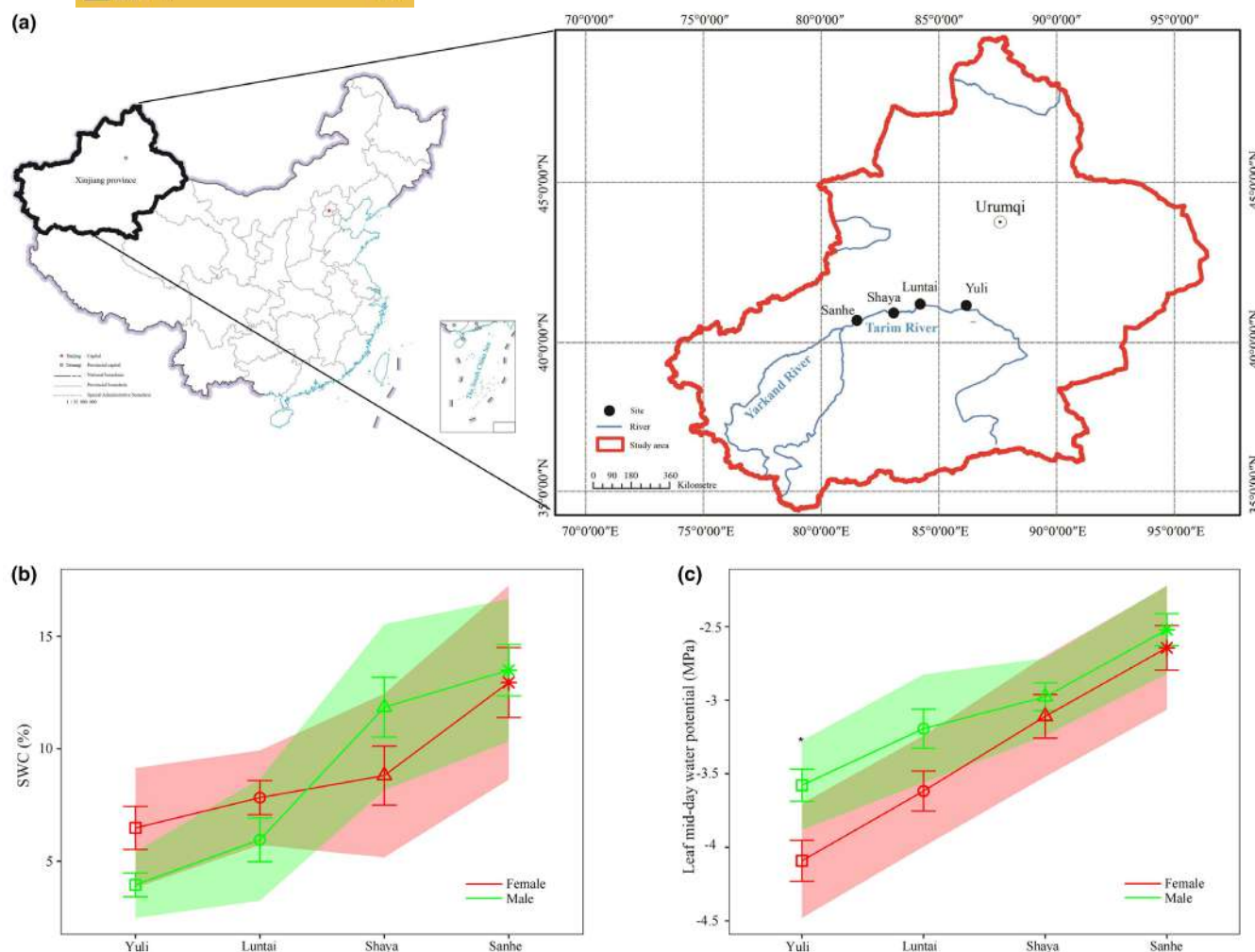


FIGURE 1 The (a) research sites, (b) soil water content (SWC) and (c) leaf mid-day water potential with 95% confidence interval in *P. euphratica* females and males at different natural forest sites. Each value is the mean $\pm$ SE ($n=5$). Red and green colours indicate *P. euphratica* females and males, respectively. The asterisks denote significant differences between the sexes based on independent samples *t*-tests. Statistical significance: * $p < 0.05$.

China) and ImageJ imaging software (National Institutes of Health, MD, USA). Leaves of five female and male trees at each site were oven-dried at 70°C to a constant mass to calculate the leaf dry mass. Then, the leaf mass per area (LMA) was calculated as the ratio of leaf dry mass to leaf area.

2.3 | Estimation of non-structural carbohydrate (NSC) contents

Starch and soluble sugar contents in the sampled leaves and branches used for hydraulic measurements were determined according to the anthrone method (Yemm & Willis, 1954). Briefly, about 50 mg of powdered sample was put into 10-ml centrifuge tubes, followed by incubation in 80% (v/v) ethanol at 80°C for 30 min and centrifugation at 5000g for 10 min. The extraction solution was used for soluble sugar measurements and the residue for starch measurements. Full details of the measurement protocols are available in Song et al. (2017). The total non-structural

carbohydrate content (NSC) was calculated as the sum of soluble sugars and starch.

2.4 | Hydraulic trait and wood density measurements

About 1-m long branches (10 replicates per sex at each site) were collected before dawn for hydraulic measurements. After harvesting, the cut end of each branch was immediately recut under water to remove potentially embolic xylem vessels. The cut ends were kept under water, and the samples were wrapped in black plastic bags and immediately transported to the laboratory, where a stem section of about 20 cm was cut off from the sampled 1-m long branches using a tubing device to measure hydraulic conductivity (Sperry & Tyree, 1988). After peeling off the bark and re-cutting both ends of the stem sections, the segments were attached to the tubing device with a 20-mM KCl solution (Scoffoni et al., 2017) under a 50-cm high water column pressure (Sperry & Tyree, 1988). The flow rate was

measured by recording the volume of liquid flowing through the segment with a graduated pipette during a certain period of time. Branch hydraulic conductivity (K_h , $\text{kg m s}^{-1} \text{MPa}^{-1}$) is the volume of liquid flowing through the stem segment per unit time:

$$K_h = J_v(L/P),$$

where J_v is the mass of liquid flowing through the segment during a certain period of time, P (0.005 MPa) is the hydrostatic pressure used and L is the length of the stem segment (m). After K_h measurements, the stem segments were flushed over 20 min with degassed 20 mM KCl solution under 0.1 MPa pressure for refilling embolized vessels and reversing embolism (Li et al., 2021). Then, the maximum hydraulic conductivity ($K_{\max}$) was obtained by the same method used for measuring K_h , and the percent loss of conductivity (PLC) of the stem was calculated (Tyree & Sperry, 1989):

$$\text{PLC} (\%) = 100(1 - K_h/K_{\max})$$

The segments used for hydraulic conductivity were selected for the sapwood area (SA) determination according to Fang et al. (2021). For the SA measurement, the middle part of each segment used for conductivity measurement was connected to a tubing device allowing 0.1% magenta solution to flow through the xylem under a hydrostatic pressure of 0.005 MPa (Sperry et al., 1988). Then, the segment cross sections were scanned, and the images were calculated using ImageJ imaging software (National Institutes of Health, MD, USA). Sapwood-specific hydraulic conductivities (K_s , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) were calculated as K_h divided by SA.

After K_h measurements, the stem branch sections were fixed into a rotor and centrifuged with increasing speeds to generate negative pressures in the xylem ranging from -0.5 to -5.5 MPa for the induction of embolism (Alder et al., 1997). The stem segments were kept spinning for 3 min at each speed level, and K_h measurements were conducted after each spinning treatment. The stem vulnerability curve was constructed by plotting PLC values against the corresponding negative pressure generated by centrifugation. Each vulnerability curve was fitted with an exponential sigmoid model to calculate the xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}). In addition, about 2-cm long segment samples from each branch were selected for volume measurements by a water displacement method. Stem samples were oven-dried at 70°C to a constant mass, and wood density (WD) was calculated. A pressure chamber (PMS1505D, Albany, OR, USA) was used to measure the leaf mid-day water potential at mid-day (12:00–14:00) for five male and female plants; three different leaves per plant were used. The hydraulic safety margin was quantified as the difference between leaf mid-day water potential and P_{50} .

2.5 | Statistical analyses

Differences between sexes in soluble sugar, starch and NSC contents of leaves and branches, K_s , PLC, WD, P_n , WUE, LMA, P_{50} and HSM_{50} were analysed by independent samples t -tests. Linear correlation (Pearson)

and regression analyses were used to examine the relationships between the soil water content and soluble sugar, starch and NSC contents of leaves and branches, K_s , PLC, P_n , WUE, LMA, P_{50} and HSM_{50} ; between soluble sugars and PLC, WD, P_n and LMA; and between K_s and P_n , PLC and leaf mid-day water potential in *P. euphratica* females and males across different natural forest sites using the R software and RStudio (R version 4.3.3 for Windows) with R package 'tidyverse' and 'ggpmisc' (Aphalo, 2024; Wickham et al., 2019). The effects of sex and site and their interactions were determined using a two-way analysis of variance (ANOVA). A principal component analysis (PCA) was used to test associations among studied traits using the R software and RStudio (R version 4.3.3 for Windows) with R package 'FactoMineR'. All other data analyses were conducted with the SPSS ver. 18.0.

3 | RESULTS

3.1 | Changes in soil water content, leaf mid-day water potential and photosynthesis along the soil water availability gradient

The soil water content (SWC) and leaf mid-day water potential (WP) of both sexes increased along the Tarim River from Yuli to Sanhe site (Figure 1). The SWC showed no significant differences between females and males at any forest site, while WP of males was higher than that of females under low SWC conditions (e.g. Yuli site). In addition, the net photosynthetic rate (P_n) of both sexes increased along with SWC, but the intrinsic water use efficiency (WUE) of both sexes and leaf dry mass per area (LMA) of males decreased with an increasing soil water content (Figure S1). Compared with *P. euphratica* females, males had significantly higher P_n , WUE and LMA in low SWC conditions, for example, Luntai and Yuli sites (Figure 2). Furthermore, sex $\times$ site interactions were significant for P_n and WUE (Table S2).

3.2 | Changes in leaf and branch non-structural carbohydrate contents along the soil water availability gradient

Leaf starch and NSC contents increased with the soil water content in females, while the male leaf soluble sugar content decreased and starch content increased with an increasing soil water content ($p < 0.05$, Figure S2). In addition, leaf soluble sugar and NSC contents of males were higher than those in females in low SWC conditions, for example, Luntai and Yuli forest sites ($p < 0.05$, Figure 3). The branch starch content increased with an increasing soil water content in females, but an opposite trend was observed in males ($p < 0.05$, Figure S2). Furthermore, *P. euphratica* males had higher branch starch levels, but lower branch soluble sugar contents than females in low SWC conditions (Figure 3). Additionally, sex $\times$ site interactions were significant for leaf soluble sugar and NSC contents, and for branch soluble sugar, starch and NSC contents (Table S2).

3.3 | Changes in branch hydraulic characteristics along the soil water availability gradient

The sapwood-specific hydraulic conductivity (K_s) and hydraulic safety margin (leaf mid-day water potential- P_{50} , HSM_{50}) of both sexes increased with the soil water content, but the percent loss of hydraulic conductivity (PLC) and the xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}) decreased in both sexes with an increasing soil water content (Figure 5, Figures S3 and S4). Compared with *P. euphratica* females, males had higher K_s , HSM_{50} and wood density (WD), but lower PLC and P_{50} in low SWC conditions, for example, Yuli site (Figure 4, Figure S5). In addition, sex $\times$ site interactions were significant for PLC, K_s and P_{50} (Table S2).

3.4 | Correlations among hydraulic traits, net photosynthesis rate and non-structural carbohydrate contents, and differences in trait combinations in males and females

In males, the leaf soluble sugar content increased linearly with increasing LMA ($p < 0.05$, Figure S6), and the branch soluble sugar content increased linearly with P_n , but decreased with PLC and WD ($p < 0.05$, Figure 6). However, in females, the branch soluble sugar content increased linearly with PLC, but decreased with P_n along the soil water availability gradient (Figure 6). The sapwood-specific hydraulic conductivity (K_s) increased linearly with P_n and leaf mid-day water potential in both sexes along the soil water availability gradient (Figure S7). Furthermore, in males, the leaf soluble sugar content

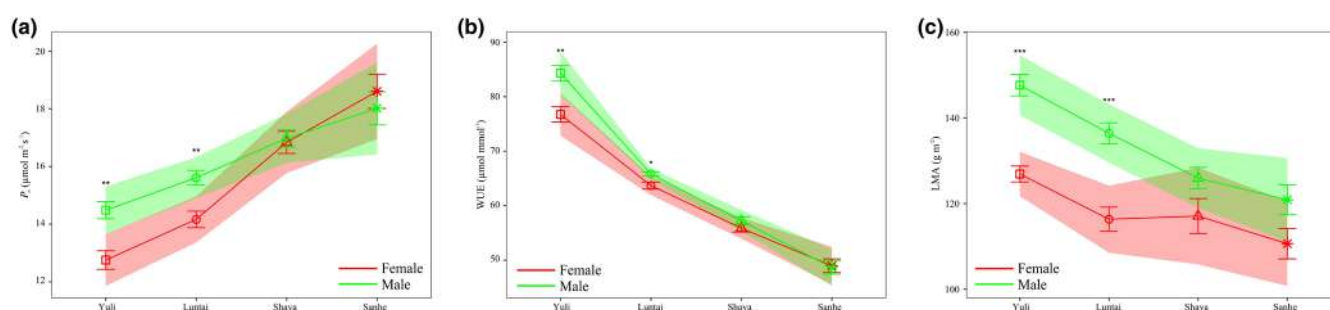


FIGURE 2 The (a) net photosynthetic rate (P_n), (b) intrinsic water use efficiency (WUE) and (c) leaf dry mass per area (LMA) with a 95% confidence interval in *P. euphratica* females and males at different natural forest sites. Each value is the mean $\pm$ SE ($n=5$). Red and green colours indicate *P. euphratica* females and males, respectively. The asterisks denote significant differences between the sexes based on independent samples *t*-tests. Statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p \leq 0.001$.

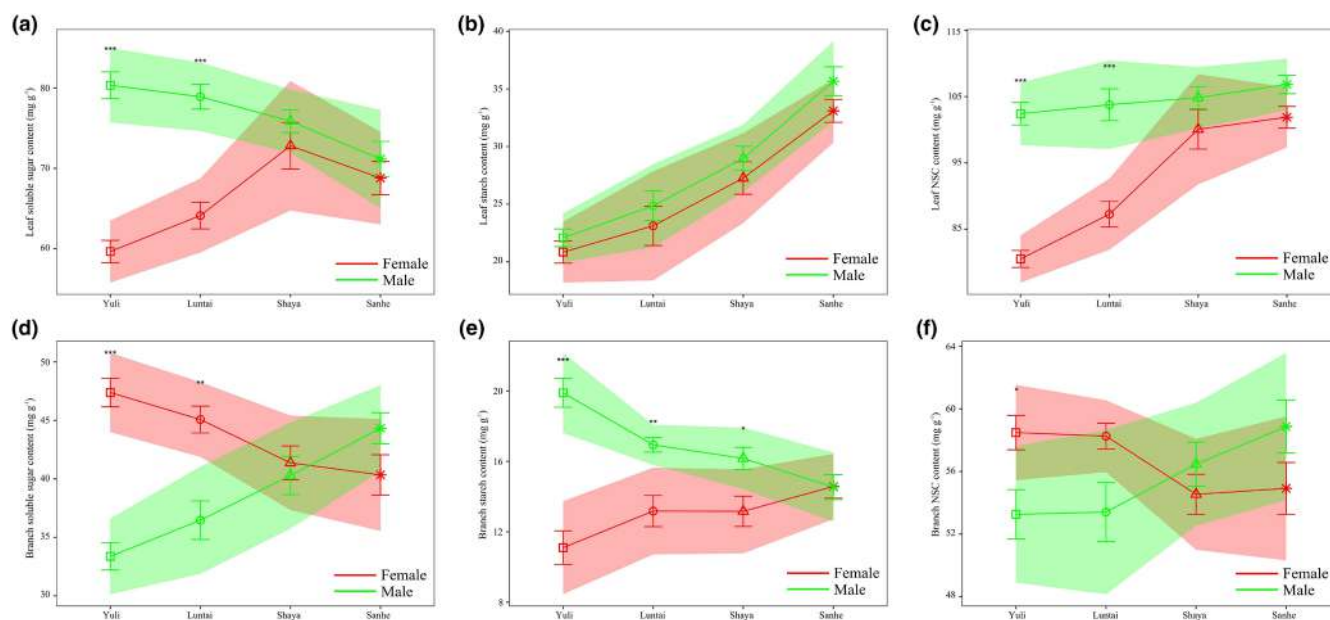


FIGURE 3 The (a) leaf soluble sugar, (b) leaf starch, (c) leaf total NSC, (d) branch soluble sugar, (e) branch starch and (f) branch total NSC contents per dry mass with a 95% confidence interval in *P. euphratica* females and males at different natural forest sites. Each value is the mean $\pm$ SE ($n=5$). Red and green colours indicate *P. euphratica* females and males, respectively. The asterisks denote significant differences between the sexes based on independent samples *t*-tests. Statistical significance: * $p < 0.05$; ** $p < 0.01$; *** $p \leq 0.001$.

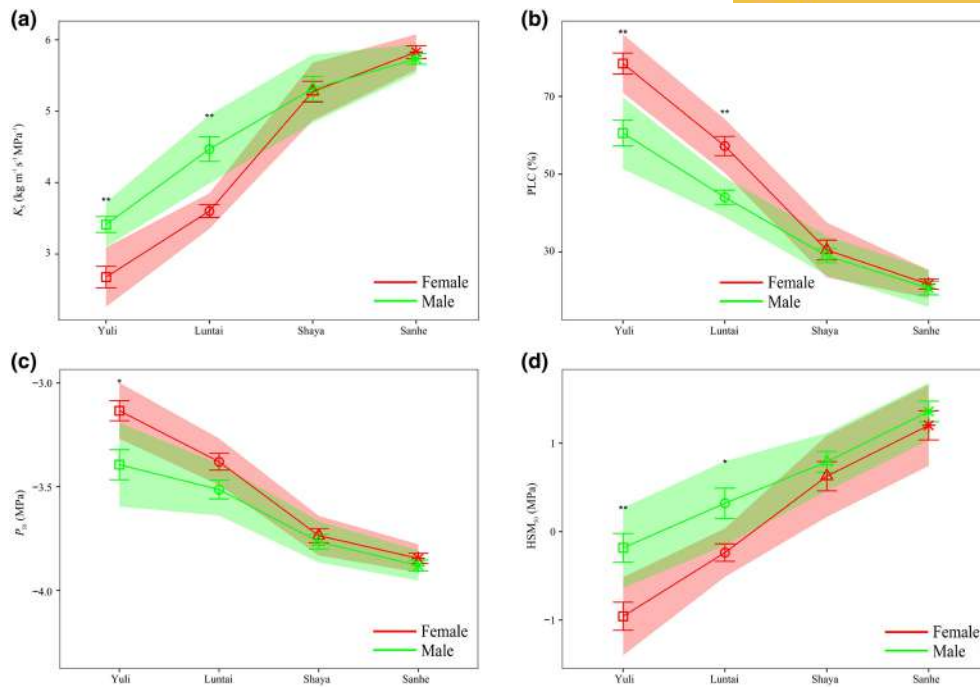


FIGURE 4 The (a) sapwood-specific hydraulic conductivity (K_s), (b) percentage loss of conductivity (PLC), (c) xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}) and (d) hydraulic safety margins (leaf mid-day water potential- P_{50} , HSM_{50}) with a 95% confidence interval in *P. euphratica* females and males at different natural forest sites. Each value is the mean $\pm$ SE ($n=5$). Red and green colours indicate *P. euphratica* females and males, respectively. The asterisks denote significant differences between the sexes based on independent samples *t*-tests. Statistical significance: * $p < 0.05$; ** $p < 0.01$.

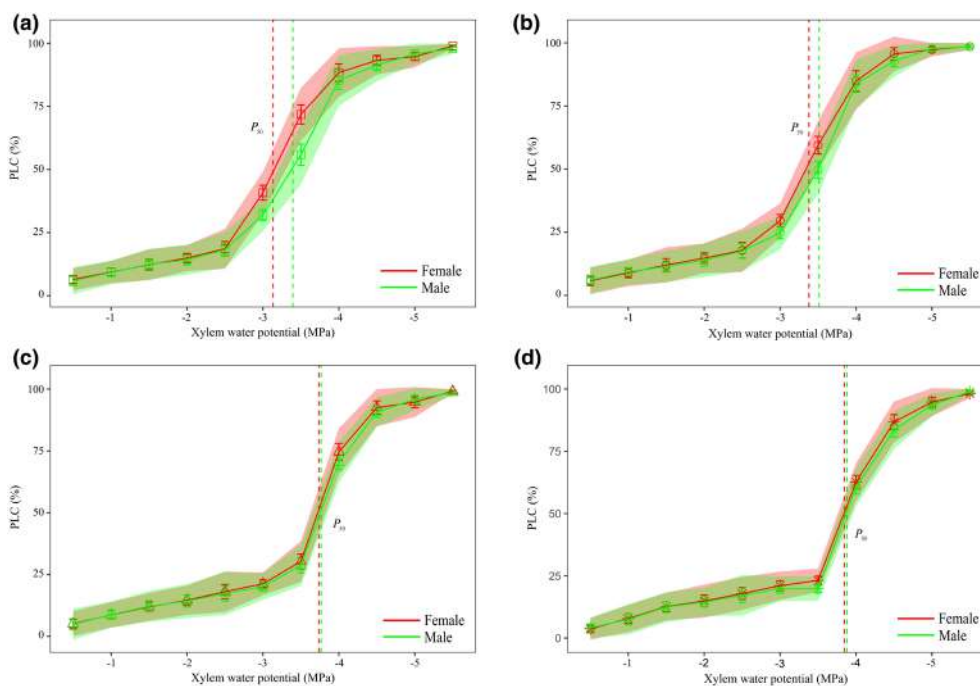


FIGURE 5 Branch hydraulic vulnerability curves showing the response of the percentage loss of hydraulic conductivity (PLC) to a decreasing xylem water potential with a 95% confidence interval in *P. euphratica* females and males at (a) Yuli site, (b) Luntai site, (c) Shaya site and (d) Sanhe site. Red and green colours indicate *P. euphratica* females and males, respectively. The dashed vertical lines denote xylem water potentials corresponding to PLC of 50% (P_{50}).

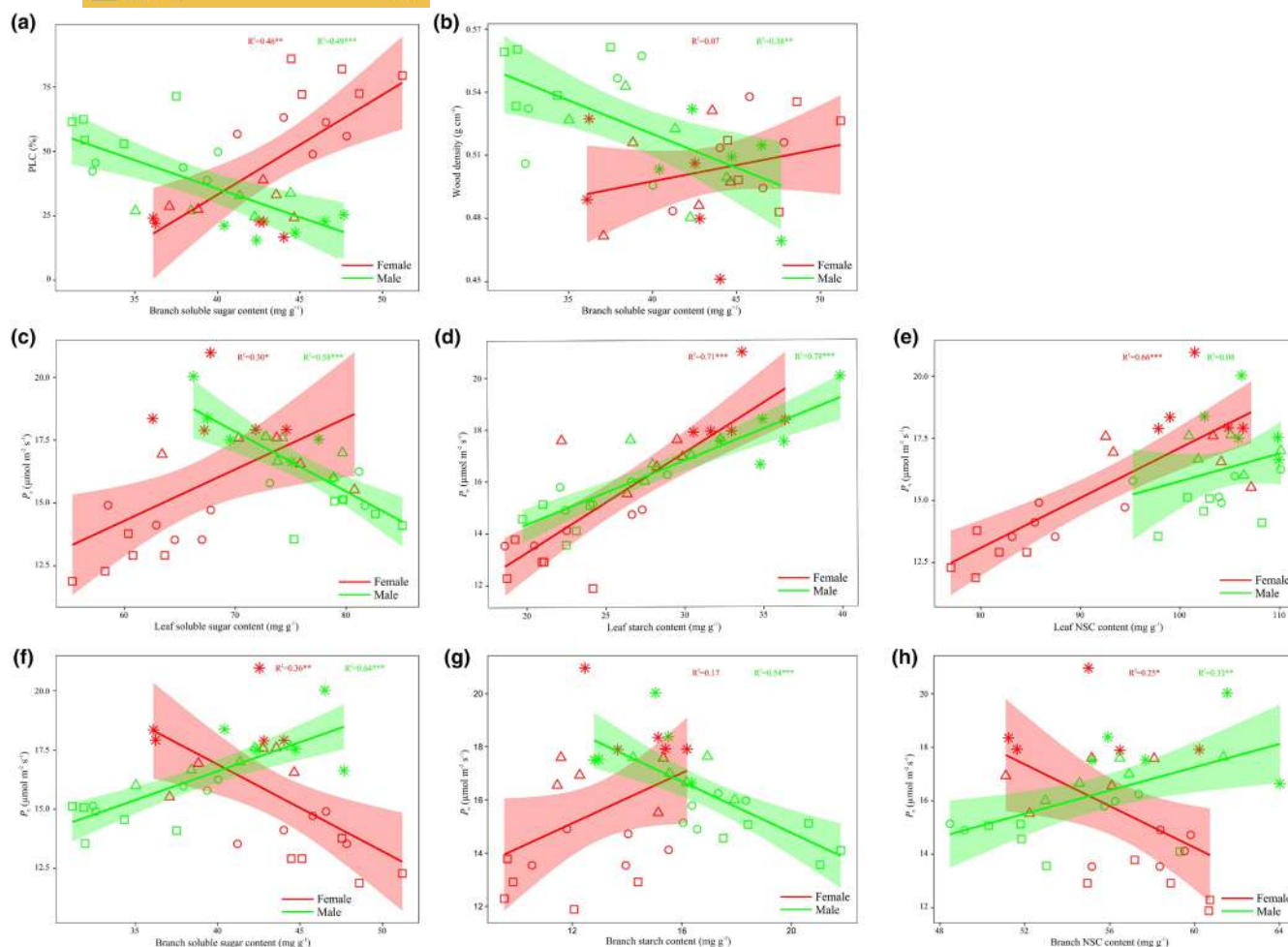


FIGURE 6 Correlations between branch soluble sugar content and (a) percent loss of hydraulic conductivity (PLC) and (b) wood density (WD), and correlations between net photosynthetic rate (P_n) and (c) leaf soluble sugar, (d) leaf starch, (e) leaf NSC, (f) branch soluble sugar, (g) branch starch and (h) branch NSC contents with a 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1), respectively. The sites are ranked according to the soil water content in the rooting zone as Sanhe > Shaya > Luntai > Yuli (Figure 1). R^2 is the explained variance. Statistical significance (P) is shown: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

was positively correlated with LMA, while the branch soluble sugar content was negatively correlated with PLC and WD (Table S3). In females, the branch soluble sugar content was positively correlated with PLC, but negatively with P_n (Table S3).

3.5 | Principal component analysis

The simultaneous consideration of all traits in the principal component analysis (PCA) indicated that females and males were separated by PC2 and grouped with positive and negative loadings of PCA in low SWC conditions (Figure S8). In addition, according to PCA, PC1 explained 50.7% of the total variance of the studied traits. The negative loadings are traits with high WUE, PLC and P_{50} in females in low SWC conditions, and with positive loading are traits with high leaf NSC and starch contents, leaf mid-day water potential, sapwood-specific hydraulic conductivity, HSM₅₀ and net photosynthetic rate

in both sexes in medium and high SWC conditions. PC2 explained 26.3% of the total variance of the studied traits. The positive loadings are traits with high wood density, LMA, branch starch and leaf soluble sugar contents in males in low SWC conditions, and with negative loading are traits with high branch soluble sugar contents in females in low SWC conditions (Figure S8).

4 | DISCUSSION

4.1 | Hydraulics and NSC dynamics along the soil water availability gradient

In the present study, we found that *P. euphratica* females and males had differences in the magnitude and combinations of hydraulic traits, and that the sex differences in hydraulics were associated with sex-specific variation in NSC along the soil water availability gradient. The

decreasing trends in the soil water content (SWC) and corresponding reduction in leaf water potential along the Tarim River (Figure 1) imply that *P. euphratica* experienced a challenging water status and was likely to suffer from embolism. Compared to high SWC conditions (e.g. Sanhe site), both sexes had increased (less negative) P_{50} and decreased HSM_{50} under low SWC conditions (Figure 4), which indicated an elevated embolism and hydraulic failure risk (Choat et al., 2018; Dai et al., 2025). Furthermore, males showed significantly lower P_{50} and higher HSM_{50} than females under low SWC conditions (e.g. Yuli site), implying males had a stronger embolism resistance and safer hydraulic system. Previous studies have reported that embolism is responsible for a reduction in K_s in trees exposed to drought stress conditions (Balducci et al., 2014; Fang et al., 2021; Sperry & Hacke, 2002). In low SWC conditions (e.g. Luntai and Yuli sites), the risk of xylem embolism significantly increased in *P. euphratica*, resulting in an extensive loss of hydraulic conductivity (Figure 4, Figure S3). This is consistent with Hukin et al. (2005), who concluded that *P. euphratica* is a relatively cavitation-sensitive species. In addition, females had significantly higher PLC and lower hydraulic conductivity in low SWC conditions (e.g. Luntai and Yuli sites), indicating that males had a more cavitation-resistant xylem. Higher resistance of males is further supported by overall higher K_s , WD, LMA, HSM_{50} and lower P_{50} values in males (Figures 2 and 4, Figure S5). Under drought stress, increased LMA may result from an enhanced leaf density, which plays an important role in water extraction from dry soil and makes trees better adapted to drought (Limousin et al., 2010; Niinemets, 2001; Poorter et al., 2009; Wu et al., 2022; Yu et al., 2022). These results collectively demonstrated that *Populus* males have stronger resistance under limited water conditions (Chen et al., 2014; Juvany & Munné-Bosch, 2015; Yu, Huang, et al., 2023). In addition, *P. euphratica* males have a higher leaf thickness (Yu et al., 2022) and LMA under extreme drought conditions, suggesting that male leaves have a greater investment in support tissues and thicker cell walls, which are modifications that increase foliage resistance to drought (Niinemets, 1999).

When trees are exposed to drought stress, stomatal conductance decreases, leading to a reduction in the photosynthetic carbon assimilation (Wang et al., 2021; Yu, Huang, et al., 2023). The immediate result will be a decrease in the synthesis of non-structural carbohydrates and possibly a start in the use of plants' NSC carbon reserves to support metabolism. In fact, soluble sugars support the respiration process and osmoregulation, and their concentration might increase upon drought and/or heat stress due to starch breakdown to maintain leaf turgor under lowering leaf water potential (Aranda et al., 2024; Asao et al., 2024; Dietze et al., 2014; Hartmann & Trumbore, 2016; Kannenberg & Phillips, 2020; O'Brien et al., 2014). The mobility, transport and conversion of NSC play key roles in plant drought recovery. For example, Dickman et al. (2019) studied 23 tree species during the 2015–2016 El Niño drought and found that total leaf and branch NSC was homeostatic, but the NSC proportions of soluble sugars and starch were shifted by drought. In addition, a recent review has reported that the starch-to-sugar conversion may promote soluble sugar accumulation and delay a 'sugar deficit' under stressful conditions (Dong & Beckles, 2019). The soluble sugar content of

leaves was found to increase and their starch content to decrease in drought-stressed males, implying that starch was converted to soluble sugars (Huang et al., 2021; Li et al., 2018). Our results further indicate that branch starch was converted to soluble sugars, suggesting an almost invariable NSC in females across the water availability gradient (Figure 3, Figure S2). In contrast, branch NSC of males showed a slight decline and a shift in the NSC composition towards starch, thus increasing the severity of water limitation (Figure 3, Figure S2).

4.2 | Relationships among hydraulics, net photosynthetic rate and NSC through the water availability gradient

We observed that branch soluble sugars of females decreased linearly with P_n along the soil water availability gradient, while the males exhibited a positive relationship (Figure 6). The reason for a negative relationship in females might indicate that higher levels of branch soluble sugars induced a decline in the sink strength and phloem transport, thus ultimately resulting in a feedback inhibition of the photosynthetic rate (McCormick et al., 2009; Paul & Foyer, 2001). However, such a feedback inhibition is not evident in leaf sugar contents (Figure 3, Figure S2). Nevertheless, compared with females, the males maintained an overall higher sugar content in leaves and had a greater starch content in branches under a lower water availability (Figure 3, Figure S2). This highlights sex-specific sink–source relationships meaning that males with higher levels of soluble sugars may support a greater share of sugar-dependent osmotic potential and improve the foliage resistance to a low water availability. Previous studies have demonstrated that the leaf vein density is closely correlated with the phloem transport capacity (Sack et al., 2012; Sack & Scoffoni, 2013). This is relevant given the evidence that *P. euphratica* females have a lower leaf vein density than males (Yu et al., 2022), and accordingly a lower phloem transport capacity.

In this study, branch soluble sugars of males decreased with an increasing wood density (Figure 6, Table S3). There are several explanations for this observation. A higher density is usually associated with a greater share of support tissues, such as thicker cell walls, a denser packing of cells and a smaller fraction of storage parenchyma (Dickman et al., 2019). In fact, when all data were pooled, females showed the same negative relationship, although their wood density was on average lower, suggesting a greater fraction of storage compartments (Figure S5). On the other hand, females had a lower sapwood-specific hydraulic conductivity associated with higher levels of branch soluble sugars, and their branch sugar content was positively correlated with PLC (Figure 6). These relationships partly reflect correlated changes in sink–source relationships and PLC as driven by water availability (Figure 4, Figure S3). Nevertheless, it has been demonstrated that soluble sugars can repair embolism and maintain hydraulic functions to alleviate drought stress (Klein et al., 2018; Secchi et al., 2011; Trifilò et al., 2019), indicating that females are more vulnerable to cavitation and require higher levels of branch soluble sugars for embolism repair under drought conditions (Figure 7).

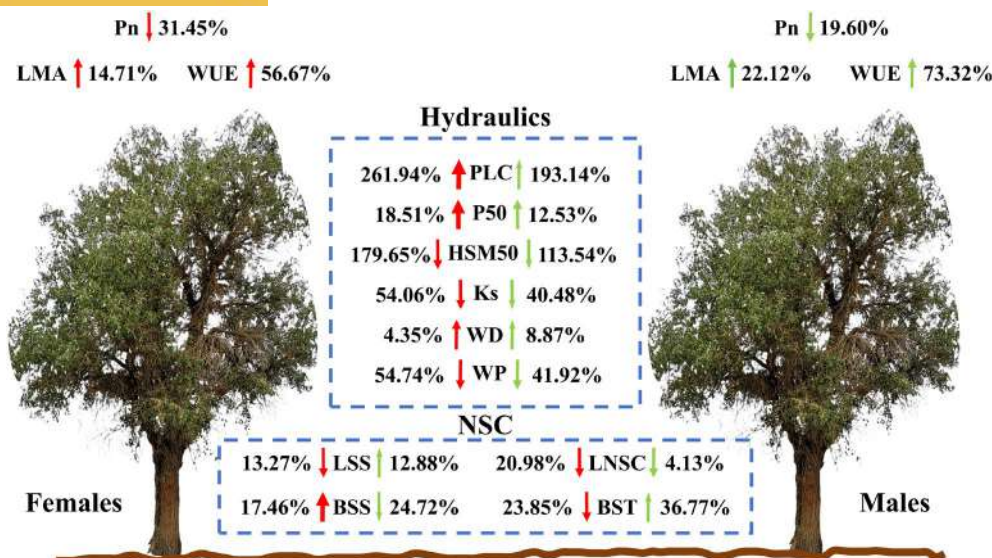


FIGURE 7 A simplified conceptual framework for hydraulics and NSC dynamics of *P. euphratica* females and males in low soil water content conditions. The upward arrows represent an increase, and downward arrows represent a decrease in key traits at the low soil water content site (Yuli) compared to the high soil water content site (Sanhe). The red and green arrows indicate females and males, respectively. The larger red arrows (e.g. PLC, P_{50} , BSS) indicate that these traits were significantly higher in females than in males, while the other traits were higher in males at the low soil water content site (Yuli). P_n , net photosynthetic rate; WUE, intrinsic water use efficiency; LMA, leaf dry mass per area; LSS, leaf soluble sugar content; LNSC, leaf total NSC content; BSS, branch soluble sugar content; BST, branch starch content; PLC, percent loss of hydraulic conductivity; K_s , sapwood-specific hydraulic conductivity; P_{50} , the xylem pressure inducing 50% loss of hydraulic conductivity; HSM₅₀, hydraulic safety margin (leaf mid-day water potential- P_{50}); WD, wood density; WP, leaf mid-day water potential.

4.3 | Mechanisms of drought-induced mortality in *P. euphratica* females and males

From 1960 to 2010, the air temperature of the Tarim River Basin has increased by 0.33–0.39°C every 10 years, and this area may be one of the most sensitive areas to climate change effects (Chen et al., 2012; Zhou et al., 2020). High potential evapotranspiration in arid environments amplifies the impacts of global change (Su et al., 2018), implying that this area may experience more frequent and severe droughts under future climate change (Chen, Li, & Fan, 2015; Zhou et al., 2020). Hydraulic failure and carbon starvation are the primary physiological mechanisms of drought-induced mortality in tree species (McDowell et al., 2008; Niinemets, 2010). A lower water potential as well as a higher vulnerability to embolism results in higher risks of mortality due to hydraulic failure under extreme drought conditions (McDowell et al., 2008; Rowland et al., 2015; Sperry & Tyree, 1988). Differently from hydraulics-dependent mortality, carbon starvation usually occurs after stomatal closure under drought stress, when the plants' sustained need to maintain respiration exceeds the amount of carbon stored in NSC, and either the carbon reserves are depleted or the stored NSC cannot be used where they are needed, resulting in plant death (McDowell et al., 2011; Sala et al., 2010; Sevanto et al., 2014).

In our study, *P. euphratica* males showed a higher resistance to drought stress (higher WUE, hydraulic conductance, WD, LMA and HSM₅₀, lower PLC and P_{50} values) and higher leaf soluble sugar levels that contributed to the maintenance of leaf turgor in low SWC conditions (e.g. Yuli site). In contrast, females showed more vulnerable hydraulics (lower hydraulic conductance, WD and LMA) and higher PLC,

indicating that females are more likely to experience hydraulic dysfunction in low SWC conditions. Furthermore, females experienced a negative hydraulic safety margin (HSM₅₀) at both Luntai and Yuli sites, while male plants only at the very dry Yuli site. Such a lower drought resistance in females is in agreement with findings of the overall lower abiotic stress resistance in females (Hultine et al., 2016; Juvany & Munné-Bosch, 2015; Yu et al., 2022), reflecting their inherently greater investments in the reproductive function. Under increasingly long and intense drought, *P. euphratica* females may experience higher risks of hydraulic failure, while males with a more resistant xylem and a greater need of soluble sugars to maintain the leaf water status might suffer from carbon depletion. Overall, our data showed the presence of sex-dependent drought adaptation strategies along a soil water gradient in the dioecious *P. euphratica*. However, in the future, we are encouraged to conduct experiments specifically on mortality mechanisms in dioecious plants.

5 | CONCLUSIONS

As far as we know, this study pioneers in investigations on the hydraulics associated with NSC dynamics in different organs in dioecious plants. Our results showed that both sexes of *P. euphratica* had decreased net photosynthetic rate (P_n), sapwood-specific hydraulic conductivity (K_s) and HSM₅₀, but increased intrinsic water use efficiency (WUE), the percent loss of hydraulic conductivity (PLC) and P_{50} to cope with the reduction in the soil water content along the Tarim River. In addition, we found that *P. euphratica* females and males have

different hydraulic strategies related to NSC dynamics under low soil water conditions. Males had higher leaf soluble sugar levels, K_s , wood density and HSM_{50} , as well as lower levels of branch soluble sugars, PLC and P_{50} values compared to females, indicating that males with a resistant xylem and leaf starch converted into soluble sugars are able to maintain their leaf water status under extreme drought (e.g. at the most water-limited Yuli site). On the other hand, females had lower K_s associated with higher levels of branch soluble sugars, which positively correlated with PLC, implying that females are more vulnerable to cavitation and might require higher levels of branch soluble sugars for embolism repair under extreme drought conditions. Previous studies have demonstrated that dioecious plants are more vulnerable to future climate change due to the spatial sexual segregation across resource gradients (Hultine et al., 2016). The different hydraulic strategies linked to NSC dynamics between females and males may result in a situation in which one sex is more prone to future climate change than another. Thus, our results are helpful for the afforestation and protection measures in *P. euphratica* forests under climate change with increasingly long and intense drought.

AUTHOR CONTRIBUTIONS

Lei Yu: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing—original draft. Haixiang Dai and Lidong Fang: Data curation and investigation. Helena Korpelainen and Ülo Niinemets: Validation and writing—review and editing. Chunyang Li: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; validation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Date is available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.zcrjdfnrq> (Yu et al., 2025).

FIELDWORK PERMITS

We did not need permission for fieldwork.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Correlations between soil water content and (a) net photosynthetic rate (P_n), (b) intrinsic water use efficiency (WUE) and (c) leaf dry mass per area (LMA) with 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1), respectively. The sites are ranked according to soil water content in the rooting zone as Sanhe > Shaya > Luntai > Yuli (Figure 1). R^2 is the explained variance; statistical significance (p): * $p < 0.05$; *** $p \leq 0.001$.

Figure S2. Correlations between soil water content and (a) leaf soluble sugar, (b) leaf starch, (c) leaf total NSC, (d) branch soluble sugar, (e) branch starch and (f) branch total NSC contents per dry mass with 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Total NSC is the sum of soluble sugars and starch. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1), respectively. The sites are ranked according to soil water content in the rooting zone as Sanhe > Shaya > Luntai > Yuli (Figure 1). R^2 is the explained variance; statistical significance (p): * $p < 0.05$; *** $p \leq 0.001$.

Figure S3. Correlations between soil water content and (a) sapwood-specific hydraulic conductivity (K_s) and (b) percent loss of hydraulic conductivity (PLC) with 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1),

respectively. The sites are ranked according to soil water content in the rooting zone as Sanhe>Shaya>Luntai>Yuli (Figure 1). R^2 is the explained variance; statistical significance (p): ** $p < 0.01$; *** $p \leq 0.001$.

Figure S4. Correlations between soil water content and (a) the xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}) and (b) hydraulic safety margin (leaf mid-day water potential- P_{50} , HSM_{50}) with 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1), respectively. The sites are ranked according to soil water content in the rooting zone as Sanhe>Shaya>Luntai>Yuli (Figure 1). R^2 is the explained variance; statistical significance (p): ** $p < 0.01$; *** $p \leq 0.001$.

Figure S5. Wood density (WD) with 95% confidence interval in *P. euphratica* females and males at different natural forest sites. Each value is the mean $\pm$ SE ($n=5$). Red and green symbols indicate *P. euphratica* females and males, respectively. The asterisks denote significant differences between the sexes based on independent samples t -tests. Statistical significance: * $p < 0.05$.

Figure S6. Correlations between leaf soluble sugar content and leaf dry mass per area with 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1), respectively. The sites are ranked according to soil water content in the rooting zone as Sanhe>Shaya>Luntai>Yuli (Figure 1). R^2 is the explained variance; statistical significance (p): ** $p < 0.01$.

Figure S7. Correlations between sapwood-specific hydraulic conductivity (K_s) and net photosynthetic rate (P_n , a) and leaf mid-day water potential (b) with 95% confidence interval in *P. euphratica* females and males across four natural forest sites with varying water availability. Red symbols indicate females and green symbols indicate males. The stars, triangles, circles and squares indicate *P. euphratica* individuals sampled at Sanhe, Shaya, Luntai and Yuli sites (Figure 1),

respectively. The sites are ranked according to soil water content in the rooting zone as Sanhe>Shaya>Luntai>Yuli (Figure 1). R^2 is the explained variance; statistical significance (p): *** $p \leq 0.001$.

Figure S8. The (a) principal component analysis (PCA), (b) eigenvalues and (c) explained variance based on studied traits in *P. euphratica* females and males across four natural forest sites with varying water availability. Red and green symbols indicate *P. euphratica* females and males, respectively. The asterisks, triangles, circles and squares indicate *P. euphratica* individuals at Sanhe, Shaya, Luntai and Yuli sites, respectively. LSS, leaf soluble sugar content; LST, leaf starch content; LNSC, leaf total NSC content; BSS, branch soluble sugar content; BST, branch starch content; BNSC, branch NSC content; WD, wood density; PLC, percent loss of hydraulic conductivity; K_s , sapwood-specific hydraulic conductivity; P_{50} , the xylem pressure inducing 50% loss of hydraulic conductivity; HSM_{50} , hydraulic safety margin (leaf mid-day water potential- P_{50}); WP, leaf mid-day water potential; P_n , light-saturated net photosynthetic rate; LMA, leaf dry mass per area; WUE, intrinsic water use efficiency.

Table S1. The research sites and their characteristics.

Table S2. p values of two-way ANOVAs conducted for photosynthesis, non-structural carbohydrates, and hydraulic traits in *P. euphratica* females and males across different natural forest sites of varying water availability.

Table S3. Pearson correlation coefficients among the studied parameters in *P. euphratica* females (upper triangular part of the matrix) and males (lower part) across different natural forest sites of varying water availability (Figure 1).

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