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RESEARCH ARTICLE

Covariations and trade-offs of phosphorus (P) acquisition strategies in dioecious *Populus euphratica* as affected by soil water availability

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Abstract

1. Dioecious species may be particularly vulnerable to climate change because they often exhibit skewed sex ratios that are reinforced by the physiological and biological specialization of each sex to specific microhabitats. Yet, it is unclear how differences in functional traits between female and male plants lead to sex-specific responses to drought and whether these responses are associated with phosphorus (P) acquisition diverge or converge.
2. Here, we measured the morphological and physiological traits of roots, and the functional micro-organisms related to P acquisition in *Populus euphratica* females and males in the rhizosphere under different water availability.
3. The specific root length of females was greater than that of males, regardless of soil water availability. Therefore, the P concentration of females was significantly higher than that of males under well-watered conditions. In contrast, the physiological adjustment to drought showed distinct sexual patterns: males significantly increased the foliar manganese concentration and maintained higher acid phosphatase activities in the rhizosphere. Moreover, the arbuscular mycorrhizal hyphal biomass reduced less in males than in females under water deficiency. Soil water shortage also decreased the α diversity of phosphate solubilizing bacteria (PSB) and changed the co-occurrence network in the rhizosphere of females, but it had little effect on males. Consequently, the favourable physiological processes and effective maintenance of functional microbial homoeostasis in the rhizosphere were the reasons that enabled males to reduce P loss in leaves under water deficiency.
4. Our study indicated that, within *P. euphratica* populations, covariations and trade-offs simultaneously occurred among the three groups (root morphology, physiology and functional micro-organisms) of functional traits evaluated. More generally, the assessment of variations in sex-specific P acquisition strategies may help to understand the causes of sex ratio bias and how *P. euphratica* males and females mitigate resource shortage.

KEYWORDS
dioecy, drought, *phoD* gene communities, phosphorus acquisition, plant–soil–microbe interactions, root traits

1 | INTRODUCTION

The evolution of dioecious plants along with unique ecological characteristics has occurred more than 100 times from monoecious plants (Charlesworth, 2002). Skewed sex ratios have been observed in more than 50% of the reported dioecious plant species, the majority being biased toward males (Sinclair et al., 2012). Sex bias may be attributed to differences in nutritional requirements between females and males, caused by sexual functional traits and reproductive costs (Lei et al., 2017; Xia, He, Yu, Lv, et al., 2020). Females tend to bear greater reproductive costs than males due to the necessity to develop seeds and fruits (Juvany & Munne-Bosch, 2015). In addition to the absolute costs of reproduction that may differ between the two sexes, the seed and fruit production tend to rely heavily on water and phosphorus (P), whereas pollen production requires large amounts of nitrogen (N) (Bürli et al., 2022; Lei et al., 2017; Yu et al., 2022).

Because processes that devote more photosynthetic products to reproduction are more susceptible to resource depletion, sex-specific environmental pressures may lead to spatial segregation of the sexes or sex-specific mortality, resulting in sex ratio biases (Hultine et al., 2016). Female plants show greater sensitivity to drought (Hultine et al., 2016). The greater hydraulic transmission risk in females relative to males suggests that the impact of climate change may lead to higher mortality in females, resulting in male-biased sex ratios (Hultine et al., 2013). However, the effects of prolonged drought on mortality and nutrient acquisition strategies in dioecious plants are unknown.

Water availability strongly influences the expression and related processes of the P uptake of roots (Püschel et al., 2021; Zhang et al., 2020). In addition to limiting plants' water supply, drought causes insufficient nutrient uptake. Drought stress and associated reduction in water availability can reduce P diffusion and mass flow in the soil (Lambers, Chapin, et al., 2008; Pang, Zhao, et al., 2018), but also plants' P uptake through the reduction of mineralization processes (He & Dijkstra, 2014; Schimel et al., 2007).

Drought also strongly influences the expression and related processes of the P uptake of roots (Püschel et al., 2021; Zhang et al., 2020). P acquisition strategies of plants are usually related to the expression of P acquisition traits (Wen et al., 2021). Multiple factors affect P acquisition, such as the morphology and physiological characteristics of roots (Wendling et al., 2016), and root-related micro-organisms (Richardson et al., 2011; Schimel, 2018). Plant adaptation to P deficiency requires higher carbon costs. Morphological adjustments of roots, formation of arbuscular mycorrhizas and exudation of carboxylates are considered to be carbon-demanding processes (Ryan et al., 2012). Thus, there may be trade-offs or covariations among P acquisition traits (Han et al., 2022; Wen et al., 2021). Multiple correlations have been found between root morphology and exudates, and rhizosphere microbes (Funayama-Noguchi et al., 2021; Honvault, Houben, Firmin, et al., 2021). For instance, thick roots benefit from stronger symbiotic AMF associations (Chen et al., 2016). In addition, morphological traits of roots are negatively correlated with various physiological traits (Lyu et al., 2016; Wen et al., 2019). Moreover, an increased microbial abundance and activity caused by root exudates contribute to P mobilization (Wang & Lambers, 2020).

Functional traits may differ significantly between males and females across resource gradients (Juvany & Munne-Bosch, 2015; Liu et al., 2021; Melnikova et al., 2017). There may be trade-off in root functional traits between genders, reflecting different below-ground strategies to improve P acquisition (Xia, He, Yu, Lv, et al., 2020). However, sexual variations in the root traits of mature dioecious plants, their associations with functional micro-organisms related to P acquisition, and their joint responses to water availability are largely unknown, yet critical for evaluating the effects of dioecious plants on P acquisition and cycling, and ecosystem functions.

Populus euphratica trees are an important component of desert ecosystems. They are very sensitive and vulnerable to global change, and their primary productivity will change in the future when drought becomes more extreme and frequent (Luo et al., 2021; Tao et al., 2016; Xia et al., 2021). The Chinese government has taken targeted measures to restore *P. euphratica* populations. Irrigation by groundwater near the Tarim River has significantly promoted the recovery of *P. euphratica* (Li, Yu, et al., 2013). However, it was unclear whether the effects of improved water availability are associated with human-induced changes that affect the nutrient acquisition strategies of female and male individuals in diverging or converging ways. Here, multiple below-ground functional traits of *P. euphratica* females and males were measured together with AM hyphal biomass and composition of *phoD* communities in the rhizosphere under different water availability conditions. We hypothesized that (1) water shortage reduces P acquisition but the negative effect is greater in females; (2) the P acquisition strategies of the two sexes show distinct functional traits and plasticity in roots and associated functional micro-organisms under different water availability conditions; (3) there are trade-offs or covariations among root morphology, physiology and functional microbes for P acquisition.

2 | MATERIALS AND METHODS

2.1 | Field experiment

The experiment was conducted on the northwestern border of the Tarim Basin in China's Xinjiang Autonomous Region. The annual mean air temperature is 10.8°C, with 50 mm of precipitation. The soil type was determined to be calcic xerosol.

A factorial experiment was set up comprising two genders and two soil water levels. There was a total of four treatment combinations, each with six replicates. A total of 24 15 m × 10 m plots were situated at upper reaches of the Tarim River (81°17′E, 40°32′N–40°81′N). *P. euphratica* individuals were planted as vegetation restoration trees in 2003. During the first 5 years, all plots were irrigated. However, only half of the plots were randomly assigned to irrigation from 2009 to 2021 in March and April for half of a month (well-watered treatments), while the other half would receive only

ambient precipitation (water deficiency treatments). The irrigation was set at 8 h per day at about 50 m^3 h^{-1} and the soil relative water content, throughout the top 60 cm depth, was maintained at 90% during the irrigation period. The soil properties under different water management conditions were listed (see Table S1). We identified the sex of each tree throughout the blooming season based on the flower morphology. After rigorous investigations, we found that the sex ratio (females to males) was 0.86 in the well-watered conditions, whereas 0.64 under water deficiency, showing apparent male bias. In each well-watered and water deficiency treatment, three *P. euphratica* females or males were selected as one replicate within a plot.

We sampled fine roots and leaves from well-watered and water deficiency plots in July 2021. Three fine root (average diameter 2 mm) samples were taken from the rhizosphere of each tree. Soil from the rhizosphere was carefully separated from fine roots. Within each plot, three samples (root or rhizosphere soil) from each sex resulted in a mixed sample that was regarded as a replication. Rhizosphere soil samples were stored at −80°C until pH, soil acid phosphatases and microbial parameters were determined.

2.2 | Plant measurements

2.2.1 | Plant P and foliar manganese (Mn) concentrations

The leaf samples were oven-dried at 70°C for 48 h, after which they were weighed and homogenized for P and Mn concentration measurements. The concentration of P and Mn in leaves was determined by an inductively coupled plasma optical emission spectrometer (ICP-OES) Model 5300DV (Perkin Elmer) (Pang, Bansal, et al., 2018).

2.2.2 | Root traits

After harvest, the fine root samples were selected. They were washed carefully using deionized water, and the fresh weight of root segments was measured. Then, the root samples were scanned by the scanner (Epson V700), and the Win-RHIZO system (Régent instrument Inc.) was used to analyse the total root length and root volume. All samples were dried at 70°C for 48 h to determine the specific root length (SRL). The root tissue density (RTD) was the ratio of the fresh weight of root segments to the root volume.

2.3 | Soil analyses

2.3.1 | Soil pH and acid phosphatase measurements

The determination of soil pH and acid phosphatase activities followed Xia, He, Yu, Lv, et al. (2020). The pH of the rhizosphere solutions was measured using a pH metre. The analyses of acid phosphatase activities in the rhizosphere soil were conducted as follows: 0.5 ml aliquots of soil suspensions were transferred into 2-ml Eppendorf vials. Then, 0.4 ml acetate buffer (pH 5.2) and 0.1 ml substrate (pNPP [p-nitrophenylphosphate]; Sigma-Aldrich) were added and the solutions were incubated at 30°C for 30 min. The reactions were terminated by adding 0.5 ml 0.5 M NaOH. In the case of controls, NaOH was added before incubation. A spectrophotometer was used to measure the absorbance of the solutions at 405 nm.

2.3.2 | Phospholipid fatty acid and neutral lipid fatty acid determination

Frozen rhizosphere soil was freeze dried for 48 h. The extraction procedures of phospholipid fatty acids (PLFAs) and neutral lipid fatty acids (NLFAs) were based on Honvault, Houben, Firmin, et al. (2021). For measuring AM hyphal biomass, the amount of 16:1ω5c PLFA and 16:1ω5c NLFA in the rhizosphere were determined and used as living and recently died AM biomarkers respectively (Honvault, Houben, Firmin, et al., 2021).

2.3.3 | DNA extraction and *phoD* gene amplification

Total DNA was extracted from rhizosphere soils using the Dneasy® PowerSoil® Pro Kit (QIAGEN) following manufacturer's instructions. The purity and concentration of DNA were then determined using 1% agarose gel electrophoresis. The *phoD* gene amplification was conducted with F733 (5′-TGGGAYGATCAYGARGT-3′) and R1083 (5′-CTGSGCSAKSACRTTCCA-3′) primers (Ragot et al., 2015). PCR conditions were as follows: 94°C for 5 min; 30 cycles at 94°C for 30 s, 52°C for 30 s and 72°C for 30 s; and 72°C for 10 min. PCR products were sequenced on the Illumina HiSeq PE250 sequencing platform (Illumina).

Raw reads were merged by USEARCH v10.0 (http://www.drive5.com/usearch/) and quality filtered, after which singletons were removed by fastp (version 0.14.1, https://github.com/OpenGene/fastp). By default, the sequences were clustered into OTUs (operational taxonomic units) with 80% consistency for *phoD* harbouring bacteria (Tan et al., 2013). The BLAST method in the Qiime software (version 1.9.1) and Unite database were used for *phoD* harbouring bacterial OTU taxonomic classification. Bacterial sequencing data were rarefied to a minimum sequencing depth of 43,000 reads.

2.4 | Statistical analyses

Differences in the foliar and root P concentrations, root traits, AM hyphal biomass and α diversity of *phoD* communities between water

management conditions and sexes were identified by independent samples *t* tests.

Bray–Curtis dissimilarities were calculated and implemented in NMDS, and principal coordinate analyses (PCoAs) were used to visualize *phoD* community differences between sexes and water management effects. A PerMANOVA model was also implemented to discern the amount of variation attributed to drought, sex and interactions. We used a two-way ANOVA to determine whether the water management or sex influenced the composition of *phoD* communities on phylum levels and visualized them by the GGPLOT2 package in R.

We analysed *phoD* harbouring bacterial community networks for each treatment separately. We focused on the relative abundance of top 100 OTUs of each group. Robust correlations with Spearman's correlation coefficients ($|r|>0.60$) with false discovery rate (FDR) corrections ($p<0.05$) were used to construct networks. The co-occurrence networks were conducted using the 'IGRAPH' package in R (Csardi & Nepusz, 2006) and visualized using the interactive Gephi platform (https://gephi.org). The parameters in networks of nodes (degree, betweenness, closeness and eigenvector) were obtained and one-way ANOVAs were used to determine differences among the four groups.

Morphological and physiological traits of roots, and AM hyphal biomass were analysed using the canonical correspondence analysis (CCA) by VEGAN and GGPLOT2 packages in R (Oksanen et al., 2015; Wickham, 2016). The permutation test was used to test the significance of seven indicators for the correlation of *phoD* community changes. Thereafter, a variance partitioning analysis (VPA) was used to determine the proportions root morphology, physiology and AM hyphal biomass explained of the changes in *phoD* harbouring bacterial communities. The regression analyses of rhizosphere pH, acid phosphatase activities and AMF hyphal biomass in relation to SRL, and rhizosphere pH, AMF hyphal biomass and Shannon diversity of *phoD* bacterial communities in relation to acid phosphatase activities were also performed using GGPLOT2 in R.

Furthermore, to visualize the complex relationships among variables, we performed structural equation modelling (SEM) to estimate the direct and indirect factors determining P acquisition strategies of dioecious *P. euphratica* in different soil types (see, Grace et al., 2010). According to the method of Jiang et al. (2019), we classified all variables into four groups, including root morphology traits (SRL and RTD), root physiology traits (foliar Mn^{2+}, rhizosphere pH and acid phosphatase activity), *phoD* community diversity and composition (values of PCoA1 axis based on Bray–Curtis analysis) and AM hyphal biomass (16:1ω5c PLFA and 16:1ω5c NLFA). All included factors were subjected to logarithmic transformation to meet the assumptions of normality. The SEM analysis was conducted in R with 'LAVAAN' and 'PIECEWISESEM' packages (Lefcheck, 2016; Rosseel, 2012). The criteria for the evaluation of structural equation modelling fit, such as the *p*-values, χ^2 values and goodness-of-fit index (GFI), were adopted according to Grace et al. (2010).

3 | RESULTS

3.1 | Foliar and root P concentrations of dioecious *P. euphratica* under different water availability conditions

Water management significantly affected foliar and root P concentrations of *P. euphratica* females and males: they were significantly lower under water deficiency than under well-watered conditions. Under water deficiency, the foliar P concentration decreased by 29.30% in females and 18.72% in males, and the root P concentration decreased in females and males by 63.84% and 63.08% respectively (Figure 1). Under well-watered conditions, we found sexual differences in foliar and root P concentrations,

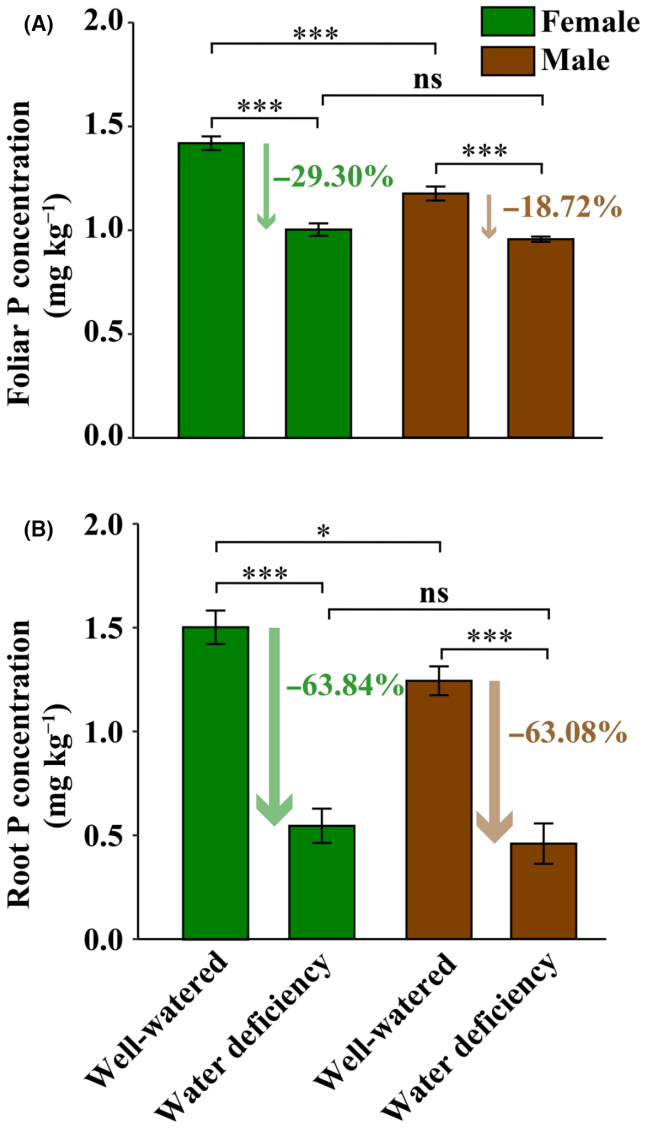

FIGURE 1 Effects of sex and water management on foliar P (A) and root P concentrations (B) of *Populus euphratica*. Data are means ± SE ($n = 6$). * denotes significant differences between two treatments: $^*p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$, according to *t* test of two independent samples.

females having significantly higher concentrations compared to males, whereas there was no sexual difference under water deficiency (Figure 1).

3.2 | Morphological and physiological traits of roots, AM hyphal biomass and the composition of the *phoD* community under different water availability conditions

Sex-specific differences were detected in the morphological traits of roots under both water deficiency and well-watered conditions (Figure S1). Sex-specific differences in SRL were found to be independent of soil water availability, females having significantly higher values than males (Figure 2A). However, SRL was significantly greater in both females and males under water deficiency than under well-watered conditions. RTD was significantly higher in males than in females under water deficiency (Figure 2B).

The rhizosphere pH of females and males showed a significant increase caused by water shortage. There were sex-specific differences in foliar Mn^{2+} concentrations and acid phosphatase activities under water deficiency, males having significantly greater levels than females. Compared with well-watered conditions, foliar Mn^{2+} concentrations of males significantly increased under water deficiency; however, the acid phosphatase activity of females significantly decreased (Figure 2C–E).

Water management significantly affected the AM hyphal biomass of females and males, being lower under water deficiency than under well-watered conditions. However, sex-specific differences were found independent of water availability, males being substantially taller than females (Figure 2F,G). In addition, α diversity of the *phoD* community, including chao1, richness and Shannon, was analysed. Compared with well-watered conditions, these diversity indexes significantly reduced under water deficiency in females but not in males (Figure 2H–J). β-diversity patterns of the *phoD* harbouring bacterial community were visualized with NMDS plots with the stress value 0.046 (Figure S2a). Principal coordinate analyses (PCoA) showed that the community composition differed strongly between well-watered and water deficiency conditions, as demonstrated by PerMANOVA ($p < 0.001$; Figure S2b). The variation partitioning analysis (VPA) showed that 24.78% of variation in the *phoD* community

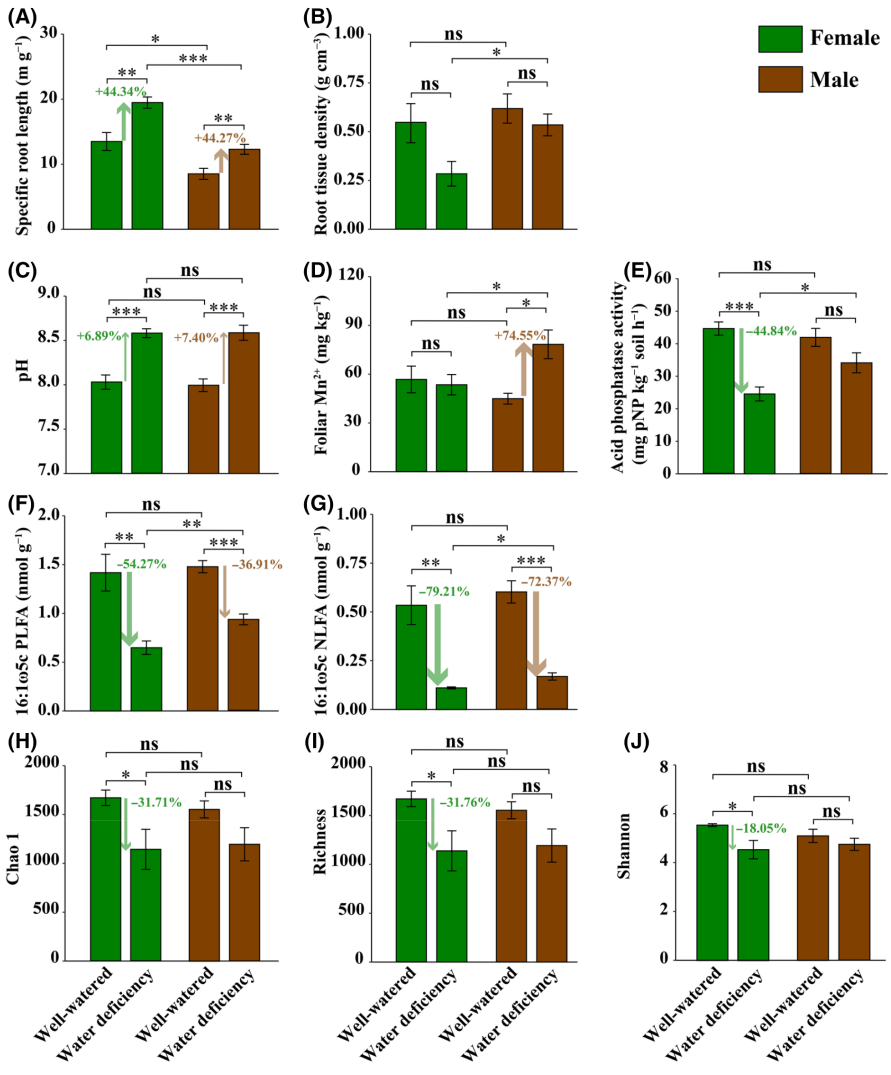

FIGURE 2 Effects of sex and water management on specific root length (A), root tissue density (B), rhizosphere pH (C), foliar Mn^{2+} (D), acid phosphatase activity (E), phospholipid fatty acid (PLFA) biomarkers 16:1ω5c (F), neutral lipid fatty acid (NLFA) biomarkers 16:1ω5c (G), and α diversity: Chao 1 (H), richness (I) and Shannon (J) of *phoD* harboured bacterial communities of *Populus euphratica*. Data are means ± SE ($n = 6$). * denotes significant differences between sites and sexes: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, according to *t* test of two independent samples.

composition was explained by water management, while sex and management × sex had no significant effects (Figure S2a). The taxonomic composition of the *phoD* gene at the phylum level (relative abundances >0.01%) is shown in Figure S2c. The relative abundance of Actinobacteria and Planctomycetes was significantly greater under water deficiency, while the relative abundance of Cyanobacteria was significantly lower under water deficiency (Figure S2c). However, sex did not have a significant effect on the relative abundance at the phylum level (Figure S2c).

3.3 | Relationships among morphological and physiological traits of roots, AM hyphal biomass and *phoD* community related to P acquisition

For the *phoD* harboured bacterial communities, the co-occurrence network analysis indicated that the networks of females and males were similar under well-watered conditions, while under water deficiency, the network of females was more complex than that of males, with a higher degrees of connectivity between OTUs (Figure 3A–D). One-way ANOVAs were also conducted to analyse the network parameters, including degree, betweenness, closeness and eigenvector, and the results showed that females under drought had a significantly higher degree, closeness and eigenvector than the other three groups, whereas betweenness was significantly lower (Figure 3E–H).

Root morphology traits (SRL, RTD), physiological traits (pH, foliar Mn^{2+} and acid phosphatase activity) and AM hyphal biomass (16:1ω5c PLFA and 16:1ω5c NLFA) explained almost 50% of the variation in the *phoD* community at the OTU level (Figure 4A). Furthermore, the VPA analysis revealed that root morphology traits explained 0.32% of the variation in the *phoD* community, root physiology traits explained 5.20% and AM hyphal biomass explained 2.32% of the variation (Figure 4B). In addition, the co-interpretation of root morphology and physiology traits was 0.50%, morphology and AM hyphal biomass was 4.62%, physiology and AMF AM hyphal biomass was 1.61%, and the co-interpretation rate of all these three interactions was 4.12% (Figure 4B).

There were many correlations between root morphology, physiology and *phoD* community. The Spearman correlation analysis showed that SRL was positively correlated with pH, acid phosphatase activities and AMF hyphal biomass ($p < 0.05$; Figure S3a–c). Acid phosphatase activities were positively correlated with rhizosphere pH, Shannon diversity of *phoD* community and AM hyphal biomass ($p < 0.05$; Figure S3d–f). However, foliar Mn^{2+} concentrations did not show significant correlations with any of these indicators ($p > 0.05$).

The SEM model fit well the significance criteria ($p = 0.08$, $\chi^2 = 3.06$, df = 1, GFI = 0.955) (Figure 5). Root physiology traits (rhizosphere pH, foliar Mn^{2+} and acid phosphatase activity) positively impacted *phoD* communities, AM hyphal biomass and P acquisition of *P. euphratica* females and males. In addition, the diversity and composition of the *phoD* community had a strong positive effect on P acquisition, and the root morphology traits significantly influenced the root physiology traits. However, the effects of root morphology traits on P acquisition, the diversity and composition of the *phoD* community and AM hyphal biomass were not significant (Figure 5).

4 | DISCUSSION

Our study systematically compared sex-specific strategies in P acquisition in *P. euphratica* under different soil water availability conditions. It showed a strong trade-off between increased foliar P accumulation under well-watered conditions and the ability to withstand low P under water deficiency. We observed distinct patterns: males enhance root exudation and depend on stronger mycorrhizal associations, and maintain the community stability of PSB to tolerate drought. In contrast, females showed more effective root morphological proliferation for enhanced P acquisition under well-watered conditions (Figure 6). Another important finding was that physiological traits (foliar Mn^{2+}, rhizosphere pH and acid phosphatase activity) were more important than morphological traits for P acquisition in *P. euphratica* in an arid region. They directly affected the dissolution of inorganic P and organic P mineralization, and regulated the diversity and composition of PSB communities.

Below-ground processes related to P acquisition are mediated by external environmental conditions and/or the internal P status of plants (Honvault, Houben, Firmin, et al., 2021). The performance of desert plants is generally limited by P and worsened by drought stress (Luo et al., 2020; Vitousek et al., 2010; Yuan & Chen, 2015). Our study showed increased levels of available P in soil under well-watered conditions (Table S1). However, there were sex-specific variations in the P acquisition depending on water availability. Furthermore, under well-watered conditions, the foliar and root P concentrations of females were greater than those of males (Figure 1). Therefore, females were more dependent on adequate soil water for P acquisition. In humid (favourable) conditions, female individuals had higher sex-related costs associated with greater nutrient requirements compared to males (Hultine et al., 2016; Nowak et al., 2021; Xia, He, Yu, Lv, et al., 2020). By contrast, in dry (unfavourable) conditions, males and females did not differ in leaf mineral nutrients (Dawson & Ehleringer, 1993). Similarly, our results suggested that there were no sex-specific differences in leaf and root P concentrations under water deficiency.

Plants are able to modify root morphology to adapt to variable soil environments (Lambers, 2022). Under water deficiency, SRL of males and females increased significantly, while irrigation allowed them to reduce SRL in fine roots. It was discovered that female SRL was much larger, irrespective of water availability (Figure 2). A large contact area between roots and soil is expected to enhance water and P acquisition. Previous studies have found that plants with a greater SRL could increase nutritional exploration under favourable conditions. (Hodge, 2004; Xia, He, Yu, Miao, et al., 2020). Hence, the greater SRL of females compared to males suggested that females

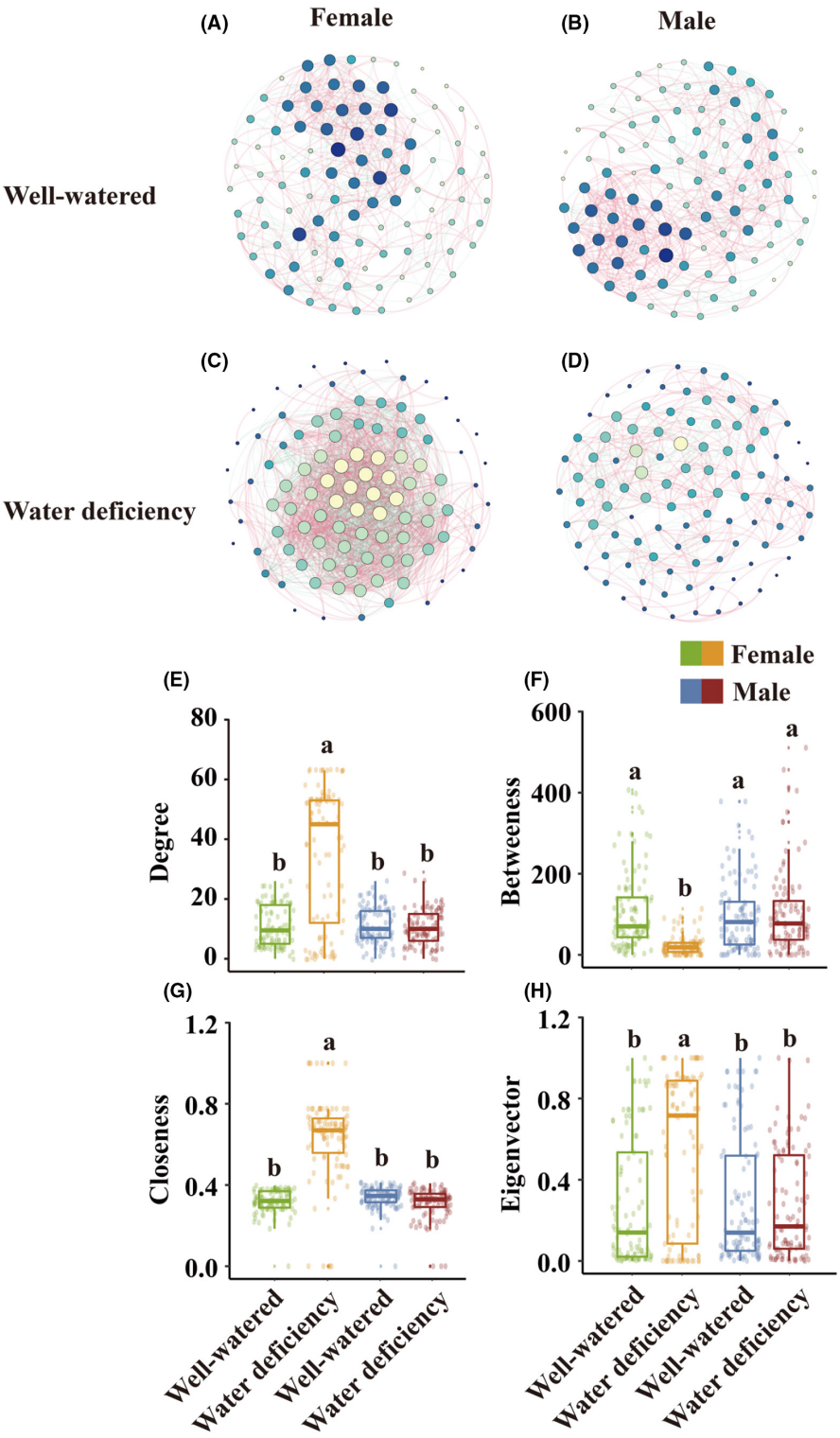

FIGURE 3 The co-occurrence networks at the OTU level of *Populus euphratica* females and males under well-watered (A, B) and water deficiency conditions (C, D). Pink and green lines represent positive and negative correlations among nodes respectively. The degree (E), betweenness centrality (F), closeness centrality (G) and eigenvector centrality (H) of four groups. Different letters indicate significant differences among treatments at $p < 0.05$, ANOVA with Tukey's honestly significant difference test.

probably had more absorptive roots, which may facilitate P acquisition under well-watered conditions.

Although leaf and root P concentrations of males showed a slightly lower increase, they were less impacted by drought compared to females (Figure 1). In addition to modifications in root morphology, the release of P-mobilizing exudates, colonization with AMF and maintenance of PSB are potentially an effective strategy to promote P acquisition under water deficiency. The male SRL was smaller than that of females under water deficiency in resource exploration regions (Figure 2). However, when the water shortage and photosynthetic products are limited, this conservative strategy may reduce the long-term cost (McCormack et al., 2012). Roots with such features tend to have long life spans and they are suitable for a relatively slow root growth rate, and they have potentially a more outstanding defence against pathogens. This may be beneficial for adapting to resource shortage habitats (Freschet et al., 2018). The

strong physiological ability of males can effectively alleviate the P shortage caused by drought. Strengthening root exudation is an important mechanism by which males adapt to soil P deficiency. The release of P-mobilizing exudates (e.g. soil acid phosphatases) represents a P-mining strategy, enhancing soil P availability through ligand exchange or chelating cations from precipitated phosphates (Ding et al., 2021; Ryan et al., 2001). Males significantly maintained the release of acid phosphatases and mineralized P under drought. Foliar Mn^{2+} can be used as a symptom of organic acid release from roots (Lambers et al., 2021). More Mn^{2+} accumulated, indicating more organic acids being released to activate P. During drought, foliar Mn^{2+} increased significantly in males, suggesting more available P displaced in the rhizosphere. This strategy was particularly effective in males: little P was in the soil solution and most P was strongly absorbed onto soil particles, and chemically protected soil P pools with a low availability were used (see, Wang & Lambers, 2020).

Moreover, males may acquire P also through mycorrhizal hyphae in a complementary fashion. Depending on the root diameter, there may be 'do it yourself' and 'outsourcing' P acquisition strategies, and the trade-offs depend on environmental conditions (Xia, He, Yu, Lv, et al., 2020). Certain species have a higher SRL (Chen et al., 2016; Li, Ma, et al., 2013; Li, Yu, et al., 2013), which allows a greater P uptake with a lower carbon investment. In comparison, plants with thick roots form stronger associations with AM, increasing P acquisition (Eissenstat et al., 2015; Liu et al., 2015). In addition, PSB recycles the available P by decomposing litter and root exudates, which are vital processes that link plant and soil P nutrition (Adnan et al., 2020). Drought significantly reduced the alpha diversity and network stability of the female PSB community but it did not affect males (Figures 2 and 3). These results indicated that compared with females, males could effectively maintain the stability of the PSB community and form a closer cooperative relationship with PSB in the rhizosphere.

Plant investments in tissue construction will provide a return for an investment in resource acquisition (Ryan et al., 2012; Wen et al., 2019). Here, we found trade-offs and covariations among strategies related to P acquisition. When SRL was lower, the acid

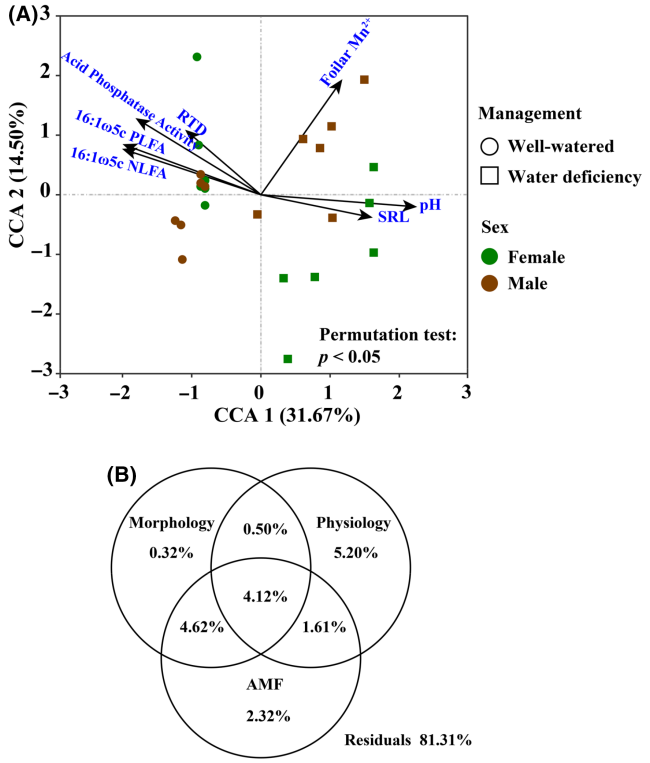

FIGURE 4 Canonical correspondence analysis of *phoD* bacterial OTUs constrained by morphological and physiological traits of roots and AM hyphal biomass across all experimental units (A), and variation in these three kinds of parameters explaining *phoD* community OTUs (B). The blue arrows are root trait and AM hyphal biomass indicators.

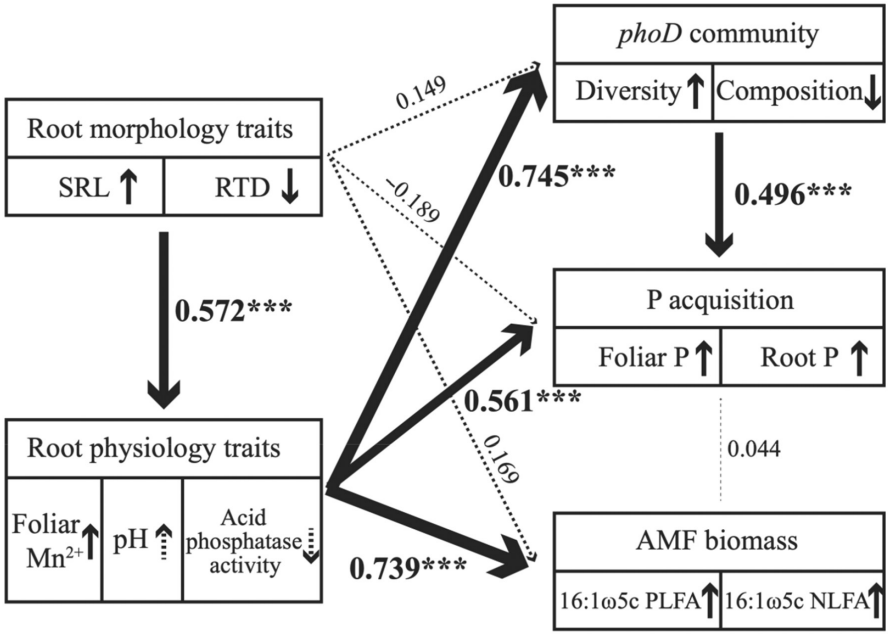

FIGURE 5 Structure equation modelling depicting direct and indirect regulatory pathways of root morphology and physiology with soil micro-organisms that affect P acquisition of *Populus euphratica*. Arrows represent significant (solid) or nonsignificant (dashed) path coefficients. Arrow width is proportional to the strength of the relationship. Numbers on the arrows are standardized direct path coefficients. Double-layered rectangles represent the first component of PCA conducted for morphological and physiological traits of roots, *phoD* communities, P acquisition and AMF biomass. The dark solid '↑' and dashed '⇣' symbols indicate a positive or negative relationship between the variables respectively. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

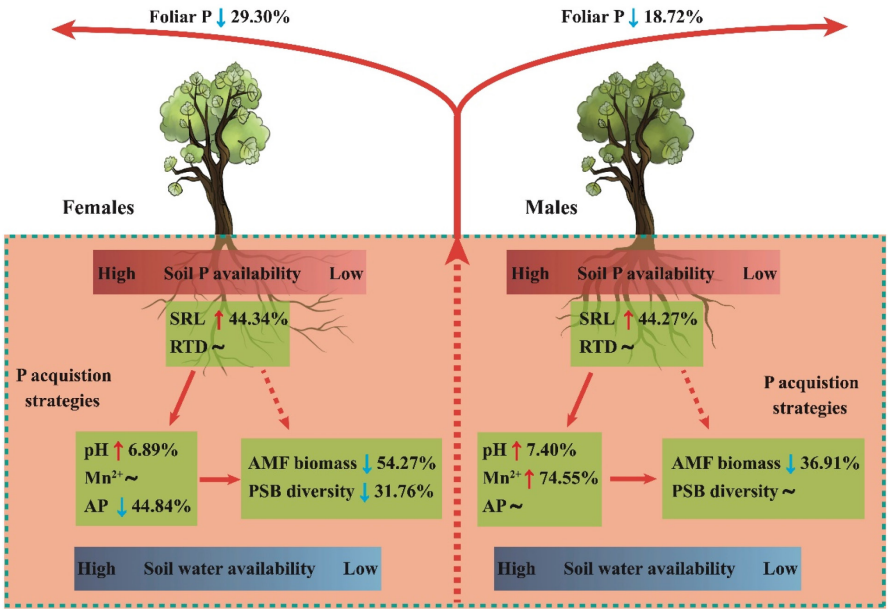

FIGURE 6 A simplified conceptual framework for P acquisition strategies of *Populus euphratica* females and males at low soil P availability gradient induced by water deficiency. Small arrows represent the variables' increase (red ones) and decrease (blue ones), and black wavy lines represent no significant change.

phosphatase level was higher and more associated with AM symbiosis (Figure 4 and Figure S3). Larger SRL means that the root diameter is smaller and it is crucial to explore the soil region more widely in order to get more nutrient absorption. In contrast, when SRL is small, the root diameter is slightly larger, and the cortex is thicker, which enhances the infection by AM fungi (Ma et al., 2018), followed by more effective hyphal proliferation to compensate for relatively limited root morphological exploration (Chen et al., 2016). Similar trade-offs in nutrient-foraging strategies between absorptive fine roots (root morphology) and the degree of colonization of associated AMF have been observed among tree species (Chen et al., 2016; Eissenstat et al., 2015; Liu et al., 2015). We firstly found that within *P. euphratica* populations, the diversification of resource-acquisition strategies resulting from trade-offs among root morphology and AM traits may be common, especially under resource (water and P)-limited habitats.

Both modifications in root morphology and in the association with AM are P-scavenging strategies, and they act in a complementary manner to increase the exploration of soil for P (Lambers, Raven, et al., 2008; Shen et al., 2011). Synergic response strategies between these physiological traits are common, such as soil acid phosphatase activity, organic acid release and rhizosphere pH regulation (Lambers, 2022). However, we did not find associations between Mn^{2+} and soil acid phosphatases (Figure 4). While P-mining trait expressions are a key to P acquisition, their cost in a given environment still determines how plants express and mix other functional traits (Honvault, Houben, Nobile, et al., 2021; Wen et al., 2021). Known adjustments in root morphological traits in response to drought are correlated with plant–microbe interactions in grassland ecosystems (Lozano et al., 2021). In contrast, we found that compared with the morphological adjustment of roots, root physiological response strategies have a greater effect on the PSB community in the rhizosphere of *P. euphratica* (Figure 5). Moreover, these physiological characteristics of roots could directly affect dissolved and mineralized P, and indirectly regulate P uptake by PSB.

A fundamental principle of sex ratio theory is that Fisherian forces balance uneven sex ratios (Fisher, 1930). However, the rate of change in sex ratios due to increased drought may exceed the rebalancing effect of Fisherian sex-ratio selection (de Jong & Klinkhamer, 2002). For long-lived dioecious *P. euphratica*, sex ratios may be highly susceptible to rapid climatic changes because their long generation turnover time limits the rate of adaptation to rapid climatic changes (Hultine et al., 2016). Petzold et al. (2013) found that *P. euphratica* showed a male biased sex ratio in Xinjiang, China. In addition, *P. euphratica* males tended to be more common at relatively drier and less fertile sites (Yu et al., 2022; Zhou et al., 2018). One way to assess potential sex ratio patterns and predict whether extreme sex ratio deviations are likely to occur under future climatic change context is to evaluate potential adaptive strategies associated with growth-related secondary sex characters and their plasticity. Our synthesis based on analyses on the functional traits of *P. euphratica* suggested that the morphological and physiological traits of female and male roots, and associated micro-organisms related to P uptake are differentially adjusted to water deficiency, which may lead to a greater stress tolerance in males than in females. These patterns amplify male-biased sex ratios and alter the population structure in *P. euphratica* in the context of climate change and drought tolerance. The imbalance in sex ratios is often accompanied by the loss of sexual reproduction and the predominance of clonal reproduction, which will lead to a reduction in genetic diversity and profound impact on the adaptation and evolution of *P. euphratica* populations.

5 | CONCLUSIONS

Sex-specific P acquisition strategies of *P. euphratica* were investigated by exploring morphological and physiological traits, and functional micro-organisms involved in P acquisition under different

water availability conditions. Males regulate physiological processes, establish AM associations and maintain PSB stability in the rhizosphere. The mixed strategy to acquire different pools in the soil can maximize P acquisition under water deficiency (Figure 6). In contrast, females have more acquisitive root systems with larger SRL, thus increasing the foraging region of roots and P acquisition with more P accumulation in leaves under irrigation. Moreover, we find that root physiological traits are strongly linked with the diversity and community composition of PSB in the rhizosphere, which is essential for P acquisition. Overall, our study uncovers the complex and potentially overlapping relationships between root traits and functional micro-organisms, and interprets these traits' trade-offs and their relative importance in P acquisition in dioecious *P. euphratica*. We provide the scientific basis for predicting the impact of climate change on *P. euphratica*, and developing management and restoration guidelines that consider gender differentiation.

AUTHOR CONTRIBUTIONS

Zhichao Xia was involved in conceptualization, data curation, formal analysis, investigation, methodology, software, visualization and writing—original draft. Yue He was involved in data curation and formal analysis. Zhu Zuodong was involved in investigation. Helena Korpelainen was involved in writing—review and editing. Chunyang Li was involved in funding acquisition, resources, project administration, supervision, validation, and writing—review and editing.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Date are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.3bk3j9kns. All bacterial data produced in this study are available at the National Center for Biotechnology Information under BioProject ID: PRJNA880504.

FIELDWORK PERMITS

We did not need permission for fieldwork.

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SUPPORTING INFORMATION

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