Fine-root traits are devoted to the allocation of foliar phosphorus fractions of desert species under water and phosphorus-poor environments

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Abstract:

• Leaf and fine root traits are expected to predicate the response and adaptation of plants to different environments. However, whether and how fine root traits are related to foliar phosphorus (P) fraction allocation of desert species under water and P-poor environments remains unclear.

• We exposed seedlings of *Alhagi sparsifolia* Shap. (*Alhagi*) treated with two water and four P-supply levels for three-years pot experiments, and measured foliar P fraction concentrations, leaf traits, and fine root traits.

• The allocation proportion of foliar nucleic-P and acid phosphatase (APase) activity of fine root was significantly increased by 45.94 and 53.3% under drought and no P-supply treatments, contrasted to the well-watered and high P-supply treatment, whereas foliar metabolic-P and structural-P were significantly reduced by 3.70 and 5.26%. The allocation proportions of foliar structural-P and residual-P were positively correlated with fine root P (FRP) concentration, but nucleic acid-P was negatively correlated with FRP concentration. Moreover, a trade-off association was found between the allocation proportion to all foliar P fractions with respect to FRP concentration, fine root APase activity, and foliar Mn concentration (indicate the released amounts of root carboxylates), followed by fine root morphological traits. Overall, drought condition enhances the requirement for *Alhagi'*s aboveground and underground link than well-watered condition.

• Changes the fine root traits and the allocation of P to foliar nucleic acid-P were two coupled strategies of *Alhagi* under low soil water and/or P-supply. Fine root APase activity and carboxylates amounts were better predictors of foliar P fraction allocation than root morphological traits. These results advance our understanding of foliar P allocation strategies via mediating fine root traits under drought and P-poor environments.

Keywords: plant functional traits, fine root, foliar P fraction, drought, P deficient, soil P fraction, desert vegetation, desert ecosystem

1. Introduction

Plant functional traits are crucial indices for predicating how plants respond and adapt to varied environments across levels of organization (He et al., 2020; Carmona al., 2021). Throughout the last few decades, plant adaptation and environmental response research has focused on the interactions among several traits as they are interconnected (Bruelheide et al., 2018; Ma et al., 2018). Although their prevalence, these attribute constellations typically alter among functional group of plant traits (e.g., leaf N concentration and root length) and situations (e.g., drought and nutrients-deficiency), giving important insights in a variety of scenarios (Osnas et al., 2018; He et al., 2020).

The balance between the fine roots (those with a diameter less than 2 millimeters corresponding to roots of order 1-3), which are the most importance plant organs to uptake water and nutrients, as well as leaves, which are the primarily responsible organs for photosynthetic processing, has always been a major ecological concern for researchers (Bergmann et al., 2020; Lamber et al., 2022). Indeed, fine roots are sometimes regarded as the belowground equivalent of leaves, as their primary purpose is to acquire nutrients and a closely relationship was found between fine foot and leaf traits (Shen et al., 2019). The plant economics spectrum hypothesis therefore postulates that leaf and fine root traits should exhibit a substantial amount of covariation (Carmona al., 2021). Prior studies have shown functionally comparable correlations between leaves and fine roots, such as a significant positive correlation between leaves N and root N and specific leaf area (SLA) and specific root length (SRL) (Díaz et al., 2016). However, other studies suggested that decoupling between root and leaf traits (Kramer-Walter et al., 2016). For example, Burton et al. (2020) observed plant root traits were unrelated to leaf traits in 57 species of undercanopy plants. It should be noted that earlier research focused mostly on morphological traits (Liu et al., 2016). Root physiological traits, including the secretion of root acid phosphatease (APase) and carboxylates, can gradually convert fixed and unavailable soil P that cannot be absorbed by plants into soil labile-P fractions, which are directly available for plants to absorb (Shi et al., 2020). In low-P soils, roots have a reduced capacity to capture P, despite the fact that root APase activity is enhanced in response to these conditions (Lugli et al., 2020; Lamber et al., 2022). Based on a study conducted by Ushio et al. (2015), fine root APase activity and leaf total P concentration in the tropical forest of Borneo were significantly negatively correlated in this area, with the correlation being stronger in poor-P soil.

The composition of foliar P fractions with distinct functions (metabolic, nucleic, structural, and residual) exhibits a stronger sensitivity to soil labile-P fractions than the soil total P (Yan et al., 2021). Among them, foliar metabolic-P is mainly substances for enzymes in glycolysis and the Calvin-Benson cycle (Veneklaas et al., 2012), nucleic acid-P make

up 40-60% organic P of leaves, with 85% into RNA (rRNA), structural-P are essential for plant growth and stress responses, and can substitute non-P lipids for phospholipids under nutrients-poor (Prodhanet al., 2019). Residual-P fraction that is not well characterized but is expected to include phosphorylated proteins (Veneklaas et al., 2012). Fabaceae species was found had higher nucleic acid-P concentrations and relatively lower metabolic-P concentrations than non-Fabaceae species in P-poor soils (Yan et al., 2019). It could be contributed to the high protein concentrations in Fabaceae species that need be supported by high nucleic acid-P concentrations. However, the low metabolic-P concentrations may difficult the activity of enzymes that use metabolites as substrates (Lamber et al., 2022). In addition, previous research has shown that leaf total P concentrations in Fabaceae species are often greater than the world average (Mori et al., 2016), however there are outliers, mostly from P-poor areas, with low leaf total P concentration (Guilherme et al., 2019). It suggests that in low-P scenarios, some Fabaceae species should invest a little amount of P at least in one of the foliar P fraction listed above. However, in order to determine if reducing the P allocation will result in the sacrifice of ideal traits and if it will be linked to changes in root traits, further research is still required.

In a water-limited desert environment, the coordination of desert species' leaf and root functional traits is of great ecological significance for their adaptation to water scarcity and nutrient deprivation, particularly during harsh drought conditions (Gao et al., 2023). The root system that extends to groundwater (mainly phreatophytes), high root crown ratio, small or evolved into distorted branches, and low N and P concentrations in leaves are all adaptive traits of desert species to cope with adverse conditions (Liu et al., 2016; Tariq et al., 2022a). In hyper-arid desert ecosystems, research has found that the concentration of soil labile-P and leaf total P in desert species are much lower than global levels (Gao et al., 2022a, b). To accommodate to the P-poor soils, desert species adopted flexible allocation strategies among distinct foliar P fractions, example as allocating more foliar P to the structural-P or nucleic-acid P (Gao et al., 2022a, Tariq et al., 2022b). Furthermore, changing the morphological traits of roots, increasing root APase activity and the release amount of carboxylates are strategies for roots reply low P in soils (Gao et al., 2023). However, there is currently insufficient evidence on how the combined effects of drought and P-deficient affect foliar P allocation and fine root traits in desert species at once, and whether the allocation patterns of foliar P fractions and fine root traits present some tradeoffs.

This study selected *Alhagi sparsifolia* as the researches object because it is a typical deep-rooted desert species that occurs widely distributed in the southern desert ecosystem of Taklamakan Desert. A three-year pot experiment with different water and P-supply levels was performed. The allocation patterns to distinct foliar P fractions, leaf traits and

fine root traits were determined at once, as well as the trade-off relationship between fine root traits and foliar P fractions were analyzed. We aimed to verify the three next hypotheses: (1) Variations of foliar P fractions and the fine root traits were more sensitive to the drought and/or low P conditions than well-watered and/or rich P conditions; (2) There is a trade-off relationship between the foliar P allocation and fine root traits, and four foliar P fractions differ from one another in the allocation patterns; (3) Physiological traits of fine root rather than morphological traits are closely related to the foliar P fraction allocation patterns.

2. Materials and Methods

2.1 Experiment design

The study area is located in the desert-oasis transition zone on the southern edge of Taklamakan Desert. The region has a warm temperate continental desert climate with sparse precipitation, hyper-arid climate, and strong seasonality. The annual average temperature, annual average precipitation, and maximum evaporation potential are 11.9 °C, 35 mm, and 2600 mm, respectively. The main type of soil is sandy soil, with low concentrations of available P and organic matter (Gao et al., 2022a). The vegetation is mainly composed of perennial herbs such as *Alhagi* (Fabaceae) and *Karelinia caspia* Pall. (Composite), shrub *Tamarix ramosissima* Ledeb. (Tamaricaceae) and *Calligonum caput-medusae* Schrenk (Polygonaceae), which are drought and salt tolerant. These perennial species together formed the protective forest around the desert-oasis transition zone.

A pot experiment lasted for a total of three years relied on the long-term ecological experiment station (80°43′45″E, 37°00′57″N), located the oasis area on the southern edge of Taklimakan Desert, Xinjiang Province, China. According to the data information of the soil basic properties in this area (Table S1), and referring to the experimental treatment methods of other soil and climate conditions similar to area studies (Xia et al., 2020), conducted two water treatments: W1 (25–35% Maximum field capacity, MFC) and W2 (65–75% MFC), and four P-supply treatments: P0 (0 g P m^{-2} y^{-1}), P1 (1 g P m^{-2} y^{-1}), P2 (3 g P m^{-2} y^{-1}), and P3 (5 g P m^{-2} y^{-1}). A total of 8 treatments with 24 replicates (192 pots) for each treatment were executed. The P resource was ammonium dihydrogen phosphate (P 27%, N 12% in mass). The N brought in by P fertilizer is balanced by urea (N 46%).

The container used for planting is a corrugated pipe with a diameter of 30 cm and a height of 100 cm. The soil used was sourced from the 0–20 cm surface soil in desert natural habitats. In mid March 2021, pre-treated *Alhagi* seeds (soaked at 35 ℃ for 30 min, then soaked in water for 24 h until the embryo is exposed) were sown in corrugated pipes, with a

sowing depth of about 1–2 cm. The five seeds were scattered in each corrugated pipe, and then covered with soil and film. When the seedlings had 2–3 leaves, remove the film and manage them uniformly for 15 days (supplied same amount water). Then, based on the growth potential, remove the seedlings with significant differences in growth potential to ensure that one plant survives in each pipe. After the unified maintenance, water treatment will be started in mid April, 2021. A soil moisture tachometer was used to monitor the soil water content every day to ensure that the soil water content of W1 was 25–35% MFC and that of W2 was 65–75% MFC. The treatment time for P was mid April 2021, 2022 and 2023, and it was applied with water at once.

2.2 Sample collection

Sample collection was conducted in mid June 2021, 2022 and 2023, respectively. Firstly, a total of 40 undamaged fresh leaves for each replicate/pot were collected. Among them, 20 leaf samples were immediately measured for leaf traits; the other 20 leaves were stored in a -20 ℃ refrigerator for foliar P fraction concentration determination. Then, the entire aboveground was harvested for leaf total N and P concentrations, and dry weight determination. After collecting the aboveground samples, carefully cut the corrugated pipe longitudinally with a saw to expose the soil to collect soil samples (approximately 10 g per pipe), and then rinse with water to obtain the entire root system for root scanning. Approximately 4.0 g fresh samples of washed fine roots were stored in a refrigerator at 4 ℃ for the determination of root APase activity (within one week). The remaining samples were divided into coarse/fine root, dried to obtain dry weight, and then crushed to determine the N and P concentrations. It should be noted that there is a good linear relationship between the released amounts of root carboxylates and the concentration of foliar manganese (Mn) (Lambers et al., 2022). Therefore, foliar Mn concentration was used to replace the released amounts of root carboxylates in this study.

2.3 Determination of leaf traits

Cleaned the surface of the 20 fresh leaves taken back, performed a Vernier scale with an accuracy of 0.01mm to measure the total thickness of the 20 leaves, and divided the total thickness by the number of leaves to obtain the average leaf thickness (LD) of a single leaf. Then measured the blade thickness using a scanner and calculated the leaf area (SA) using Image J software. After scanning, put those leaves in a 75 ℃ oven to constant weight for obtaining the leaf dry weight (LDW). Finally, calculated the specific leaf area (SLA) and leaf tissue density (LTD) according to the following formula:

$$\text{Specific leaf area (SLA)} = \text{leaf area/leaf dry weight} \quad (1)$$

Leaf tissue density (LTD) = leaf dry weight/(leaf area × Leaf thickness) (2)

2.4 Determination of foliar P fraction concentrations, and of total N and P concentration of leaves and fine roots

The foliar P fractions were divided into metabolic-P (including inorganic phosphorus: Pi), nucleic acid-P, structural-P, and residual-P, and the detailed determination process was referred to Hidaka & Kitayama (2011) and Gao et al. (2022c). Briefly, first performed freeze-drying on the sample before measurement (MM400, Retsch, Haan, Germany). Then, we weighed 1.0 g of freeze-dried sample and sequentially added 2 ml solution containing chloroform, methanol and formic acid (12:6:1, v/v/v), 2.5 ml solution containing chloroform, methanol and water (1:2:0.8, v/v/v), 4 ml washed chloroform, 5 ml methanol (85%, v/v), 2 ml 5% trichloroacetic acid (TCA), and 2 ml 2.5% TCA to obtain the extract solution of four foliar P fractions. Among them, the pellet was separated from the extractant by applying centrifuged (15 min, 5000 rpm). Finally, added HNO_3: H_2SO_4 (3:1, v/v) to digest the above supernatant, determined the concentration of four foliar P fractions using a full band spectrophotometer at 620 nm. Leaves and fine roots samples were dried to constant weight at 75 ℃, then weighed, crushed, ground and digested in a solution containing concentrated HNO_3, $HClO_4$ and H_2SO_4 (7:2:1, v/v/v), and finally N, P and Mn concentration in leaves, and P concentration in fine roots were measured using an elemental analyzer (ICP-ABS Hitachi Z-5000, Japan).

2.5 Determination of acid phosphatase activity

The activity of root acid phosphatase (APase) was determined according to the method of Tabatabai & Bremner (1969). Briefly, a fresh root sample of 1.0 g was weighed, added 8 ml buffer solutions containing 0.2 M sodium acetate (pH 5.8), ground in an ice-environment, purified, and centrifuged for 15 min at 12 000 r min^{-1}. Then, in a newly prepared 15 ml centrifuge tube, transferred 1 mL supernatant solution, added 2 mL of 0.05 M *p*-nitrophenyl phosphate (*p*NPP), and maintained in darkness at 37 °C for 30 min. To halt the reaction after culture, we added 2 ml of 0.5 M $CaCl_2$ and 2 ml of 2 M NaOH. Centrifuge at 2500 r min^{-1} for 5 min. Transferred the subsequent into another newly prepared 15 ml centrifuge tube and centrifuged for 5 min at 4000 r min^{-1}. Ultimately, the APase activity of 5 ml aliquots was measured in a 410 nm spectrophotometer, which was expressed as μ mol *p*NP per gram per minute (μ mol *p*NP g^{-1} min^{-1}).

2.6 Determination of root morphology traits

Employing root analysis software (WinRhizo Pro 2004b software, Quebec, QC, Canada) on the complete root sample images of *Alhagi* obtained on the Expression 1600 Pro scanner (Model EU-35, Epson, Tokyo, Japan), the root volume (RV, cm^3), root length (RL, cm), and surface area (SA, cm^2) of fine roots were determined. Then, by drying the sample

191 in an oven (at 75 ℃, 48 h) and weighing the sample, the respective dry weight of fine roots was obtained. The specific
192 root length (SRL, cm mg^{-1}), specific root surface area (SRSA, cm^2 mg^{-2}), and root tissue density (RTD, mg cm^{-3}) were
193 computed using the dry weight of fine roots.
194
195 **2.7 Determination of soil Hedley P fraction**
196 The soil Hedley-P fractionation method divided soil P into nine components: resin P, sodium bicarbonate Pi
197 ($NaHCO_3$-Pi), sodium hydroxide Pi (NaOH-Pi), dilute hydrochloric acid Pi (conc. HCl-Pi), concentrated hydrochloric
198 acid Pi (1 M HCl-Pi), and residual-P. The sodium bicarbonate Po ($NaHCO_3$-Po), sodium hydroxide Po (NaOH-Po), and
199 dilute hydrochloric acid Po (conc. HCl-Po) were obtained from the difference value between total P ($NaHCO_3$-P,
200 NaOH-P and conc. HCl-P) and Pi ($NaHCO_3$-Pi, NaOH-Pi, and conc. HCl-Pi). Among them, Pi fractions were obtained
201 by sequentially adding resin, 0.5 M $NaHCO_3$, 0.1 M NaOH, 0.1 M HCl and 1 M HCl, followed by H_2SO_4-H_2O_2
202 digestion of the residual. Refer to Gao et al. (2022b) for detailed extraction and determine processes.
203
204 **2.8 Data analysis**
205 To investigate the effect of different water conditions, P-supply levels, and their interactions on leaf traits, foliar P
206 fraction concentrations and allocation proportions, and fine root traits, we applied a two-way factorial ANOVA testing
207 using the IBM SPSS 22.0 (Statistical Graphics Crop, Princeton, NJ, USA). The association between leaf traits, leaf N
208 and P concentrations, and leaf and fine root dry weight was assessed using simple linear regression. Mantel's and
209 Pearson's correlations, together with the accompanying heatmap, were used to evaluate the relationships between fine
210 root traits and foliar P fraction concentrations and allocation proportions. After that, a statistical pattern of high
211 matching was established using structural equation modeling (SEM), which was then utilized to investigate the causal
212 links between four foliar P fractions vis-à-vis the fine root traits, respectively. Step-by-step fitting of the SEM allowed
213 for the retention of only significant coefficient-containing paths. R 4.0.4 (R Core Team, 2021) and Graphpad Prism 9.0
214 (GraphPad Software, San Diego, CA, USA) were used to generate all of the figures.
215
216 **3. Result**
217 **3.1 Soil Hedley P fraction**
218 Significant interactions between water and P-supply treatments were observed on soil resin-P and $NaHCO_3$-Pi
219 concentrations (Fig. 1, $p < 0.001$). Compared to the well-watered and high P-supply treatment, soil resin-P and
220 $NaHCO_3$-Pi concentrations were significantly lower by 87.03 and 93.22% in drought and no P-supply treatment.

Among them, drought treatment significantly reduced soil resin-P concentration by 48.7% and $NaHCO_3$-Pi concentration by 67.96%, but increased conc. HCl-Pi concentration by 3.4% compared to the well-watered treatment. P-supply treatment was related to higher soil labile and moderately labile-P fraction (resin-P, $NaHCO_3$-P and NaOH-P) concentrations by 37.69–89.86% with respect to no P-supply treatment.

3.2 Leaf traits and the dry weight and concentration of N and P in leaves and fine roots

The SLA was significantly increased by 13.74% in well-watered and high P-supply treatment relative to the drought and no P-supply treatment (Table 1, Fig. S1, $p < 0.05$). However, the LTD was increased by 44.44% in drought and no P-supply treatment when compared to the well-watered and high P-supply treatment. In addition, leaf and fine root P (FRP) concentrations and leaf dry weight were remarkably decreased by 19.87, 4.96 and 65.32% in drought and no P-supply treatment when compared to the well-watered and high P-supply treatment (Fig. 2, $p < 0.001$). There is a significantly positive relationship between the FRP and leaf total P concentrations, fine root and leaf dry weight, whereas a significantly negative relation between the FRP concentration and leaf N:P ratio ($p < 0.001$). Furthermore, the proportion of leaf dry weight in whole plant was significantly reduced in drought and no P-supply when compared to the well-watered and high P-supply treatment ($p < 0.05$), and drought significantly increased the proportion of fine root dry weight in whole plant relative to the well-watered treatment (Fig. S2).

3.3 Foliar P fraction concentration and allocation proportion

Compared to the well-watered and high P-supply treatment, foliar nucleic acid-P concentration and its allocation proportion were significantly increased by 36.27 and 45.94% in drought and no P-supply treatment ($p < 0.01$), but foliar metabolic-P and structural-P allocation proportion were significantly reduced by 3.70 and 5.26% (Fig. 3, $p < 0.05$). Foliar residual-P concentration and proportion were also reduced by 36.79 and 32.39% in drought and no P-supply treatment related to the well-watered and high P-supply treatment ($p > 0.05$). Among them, metabolic-P and structural-P concentration and allocation proportion were increased by 1.61 and 1.45, 3.03 and 2.50% in well-watered treatment when compared to the drought treatment (Table S2, $p < 0.05$). Compared to the high-P supply, foliar nucleic acid-P allocation proportion was rose by 40.94% in no P-supply treatment ($p < 0.05$).

3.4 Fine root morphological and physiological traits

Water treatment significantly affected the fine root traits, except for the RTD (Fig. 4, Table S3). Compared to the drought treatment, the RL, SA, RV, SRL and SRSA of fine root were significantly increased by 296.86%, 132.32%,

48.71%, 208.52% and 51.08% in well-watered treatment ($p < 0.05$). However, the APase activity of fine root and foliar Mn concentration under drought treatment were 13.32 and 14.67% higher than in well-watered treatment ($p < 0.05$). The APase activity, SA and foliar Mn concentration under no P-supply treatment were 52.53, 27.89 and 38.22% greater than under high P-supply treatment ($p < 0.05$). Only the APase activity in all fine root traits was substantially elevated by 53.30% in drought and no P-supply treatments compared to the well-watered and high P-supply treatments ($p < 0.05$).

3.5 Relationship between foliar P fractions and leaf and fine root traits

There are strong positive correlations among the foliar metabolic-P, structural-P and residual-P with respect to LA and LT, whereas negative correlations were observed among them and LTD (Figs. S3, S4, $p < 0.001$). In contrast, foliar nucleic acid-P was negatively correlated with the LA, LT and SLA, while was positively correlated with the LTD ($p < 0.01$). Moreover, fine root traits mainly affected the foliar P fraction allocation proportions (excluding nucleic acid-P), especially in the presence of drought conditions (Fig. 5). Under the drought treatment, nucleic acid-P allocation proportion was mainly negatively affected by FRP concentration, and significantly positively affected by RL, SA, SRL, SRSA, APase activity, and foliar Mn concentrations (Figs. 5a, b). However, the structural-P and residual-P allocation proportions were reverse. The correlation between fine root traits and the allocation proportion and concentration of foliar P fractions in well-watered conditions was similar to drought conditions, but more strongly correlated in drought conditions (Figs. 5c, d, Fig. S5). Overall, foliar P fraction allocation was primarily determined by the concentration of FRP, APase activity, and foliar Mn concentration.

3.6 SEM analysis on the correlation between the allocation of foliar P fractions and fine root traits

The SEM analysis indicated that the trade-offs between the FRP concentration and foliar metabolic-P and nucleic acid-P allocation proportions were different from that of other foliar P fractions, respectively (Figs. 6, 7). A convergence in the balance relationship between structural-P and residual-P allocation proportions and fine root traits was found. Under drought treatment, metabolic-P allocation proportion was mainly affected by the direct effects of APase activity, nucleic acid-P was affected by both the direct and indirect effects of foliar Mn concentration, as well as the direct effects of FRP concentration, structural-P was affected by both the direct and indirect effects of APase activity, as well as the direct effects of FRP concentration, and residual-P was affected by the direct effects of FRP concentration (Figs. 6A, 7A). Under well-watered treatment, metabolic-P allocation proportion was mainly affected by the direct effects of APase activity, nucleic acid-P was affected by direct effects of FRP concentration, structural-P was affected by the direct

effects of FRP concentration and SRL's direct and indirect effects, and residual-P was affected by direct effects of FRP concentration (Figs. 6B, 7B).

In general, accompanied by a decrease in FRP concentration, a trade-off occured between the reduced structural-P and residual-P allocation proportions and the increased nucleic acid-P allocation proportion and foliar Mn concentration under drought or well-watered conditions. Among them, there was a substantial negative correlation between foliar Mn concentration and nucleic acid-P under drought conditions, whereas it was significantly positively related to the structural-P allocation proportion. Noteably, the root APase activity was most important factor for the metabolic-P, whether under drought or well-watered conditions, but well-watered eliminated the effects of root APase activity on the other three foliar P fractions.

4 Discussions

4.1 Foliar P fraction allocation and the adaptability of fine root traits to drought and P-deficient conditions

The behavior of foliar P allocation often provides a possible adaptation mechanism that enables plant to adapt to P-deficient environments (Lambers et al., 2022). Compared to well-watered and high P-supply conditions, *Alhagi* reduced foliar metabolic-P, structural-P and residual-P allocation proportions in drought and no P-supply conditions. This result was consistent with the results on foliar P fraction of Verbenaceae (*Clerodendrum cyrtophyllum* Turcz.) and Proteaceae (RBr) in P-limited tropical forests (Mo et al., 2019). Nevertheless, it is important to be aware that the concentration of metabolic-P and structural-P in this study were lower than those of Verbenaceae. This may be due to a lower soil $NaHCO_3$-P in this study (approximately 17.9 mg kg^{-1}), whereas proximately 74.1 mg kg^{-1} in P-limited tropical forests. Besides, the drought condition in this study was about 25% MFC, while the study of Mo et al. (2019) was located in the Tropical monsoon climate region with sufficient water. Therefore, we speculated that this is highly likely attributed to lower water and P concentrations in soils resulting in lower metabolic-P concentrations of *Alhagi* in leaves. In addition, drought and no P-supply significantly increased nucleic acid-P concentration and allocation proportion in *Alhagi* leaves. This may be due to the insufficient of soil water and P leading to the tendency of *Alhagi* leaves allocating a higher proportion of foliar P towards the esseential fractions DNA and RNA (especifically rRNA). This allocation pattern is crucial for maintaining vital life functions, such as the preservation of genetic information and the synthesis of proteins necessary for survival (Caio et al., 2018). For example such we have observed in other studies under drought and/or P deficiency plants tends to synthesize more secondary metabolites to stress defense (Sulpice et al., 2014). To activate these pathways it is necessary to increase the concentration of the enzymes involved in those

pathways, thus it becomes essential to preserve a appropriate capacity of protein synthesis and thus of the different rich-P RNAs. An additional potential mechanism to be taken into consideration is that the increase in nucleic acid-P levels observed during periods of drought and/or low P conditions could be attributed to a decline in metabolic-P. This decline in metabolic-P may result in a reduction in the activity of overall metabolic pathways, which can serve as an adaptive mechanism to counterbalance the need to allocate more sources to the production of the most enzymes linnked to the pathways involved in stress tolerance (Rizvi et al., 2019). This research further shown that a reduction in soil P availablity is associated with a decrease in structural-P allocation proportion. Structural P is mostly found inside phospholipids, which serve as a vital component of plasmalemma and organelle membranes involved in the formation of cell membranes (Mo et al., 2019). These cell membranes are the primary location for photosynthesis in plants. Thus, our study implied that inadequate P conditions may be have a substantial inhibitory effect on *Alhagi* photosynthesis. This inhibition is accompanied by the substitution of sulfates and galactolipids for foliar structural-P, leading to a reduced concentration of foliar structural-P. It may be another adaptation strategy for *Alhagi* in poor-P conditions.

Morphological traits of the root system typically determine the roots' adaptability and ability to acquire restricted resources (Aslam et al., 2022). This study indicated that the SRL and SRSA of *Alhagi* fine roots under three P-supply levels were lower than under no P-supply conditions. It may be attributed to the higher SRL and SRSA of *Alhagi* fine roots occurred at low P conditions can enhance their ability to explore more efficient P-uptake. Numerous species exhibited higher RTD in low P or drought conditions, which is regarded as a significant adaptive strategy for coping with soil P shortage or adverse environment conditions (Laliberté et al., 2015; Wurzburger & Wright, 2015). The findings of this study suggested that an increased RTD may have a decelerating effect on root development and enhance the capacity of plants to extend their tissues and defend against nutrient insufficiency, namely P deficiency. Hence, the presence of high RTD in poor P or adversity environments might potentially facilitate the development of fine roots, thereby augmenting their capacity to acquire water and limiting nutrients. Besides, prior studies have widely reported that a negative association between soil P concentration and both root APase activity and carboxylate secretion in plant roots (Lugli et al., 2020). It was consistent with the results in this study that drought and/or low P conditions increased APase activity of *Alhagi* fine root and foliar Mn concentration indicating the released amounts of root carboxylates. A possible reasonable speculation is that the APase of *Alhagi* fine root catalyze the hydrolysis of -C-O-P bonds liberating P from organic matter and the effectively carboxylates can by changing soil pH desorbs P occluded (adsorbed) on minerals (Shi et al., 2020; Lambers et al., 2022). Therefore, *Alhagi* can activate soil P-availability to obtain more P by fine root in the environment lacking P. Those results verified our first hypotheses that the variations of *Alhagi* fine root

traits and foliar P fractions are more sensitive to drought and/or low P condition than well-watered and/or high P condition.

4.2 The trade-off between foliar P fraction allocation proportions and fine root traits

As the two most important organs for nutrient absorption and utilization, leaves and fine roots jointly participate in and regulate plant growth and various physiological and chemical processes (Roumet et al., 2016). The findings of this research indicated that the leaf and fine root traits of *Alhagi* were not decoupled. Foliar P fraction allocation proportion was mainly driven by the FRP concentration and the root physiological traits related to P activation in the root system, among which the balance between foliar P fraction allocation proportions and fine root traits was more closely related under drought treatment. As more optimal were the conditions (more water and/or P-supply) for plant production, more P was allocated to metabolic activity and to create a more strong and great leaf structure to be able to capture more light, then more P is proportionally allocated to metabolic, structural and residual fractions, whereas diminishing the nucleic acid-P percentage respect to total foliar P. This also coincided with higher FRP concentrations in a general situation of more favorable conditions for plant P-uptake. In this situation, allocation to increase fine root traits related to soil resource uptake was reduced. This was reversed as the soil conditions (less water and/or P supply) were harsher. However, Yu et al. (2022) indicated that no significant relationship between leaf N and root N in 12 plant species studied in semi-arid regions. The possible explanation for this difference was attributed to the differences in plant species, whereby plant physical traits, including size, woodiness, and longevity, exhibit significant heterogeneity between various species. Several studies have shown that herbaceous plants exhibiting elevated SRL and N concentrations in their roots, as well as elevated SLA and N concentrations in their leaves, may have comprehensive nutrient acquisition strategies (Tjoelker et al., 2005; Freschet et al., 2018). In the study conducted by Weemstra et al., (2016), it was observed that the traits of woody species exhibited a contrasting pattern when compared to herbaceous species. However, this study suggested that growth forms have the potential to concurrently influence variations in leaf and fine root traits. *Alhagi* is a typical Fabaceae herbaceous widely distributed in hyper-arid and P-impoverished desert ecosystem, with a relatively high demand for P. Thus, this may be an important reason for the significant correlation between the foliar P fractions and fine root traits, as well as the differences with other research results.

Among the four foliar P fractions, structural-P can characterize the size of plant photosynthetic capacity, and higher concentrations of structural-P indicate sufficient P nutrients and increased photosynthetic capacity (Caio et al., 2018; Mo et al., 2019). The findings of this study suggested that the foliar structural-P was mainly positively driven by FRP

concentration, which means that good root nutrient absorption can conducive to the allocation of foliar P to the structural-P that dominates photosynthesis. Under drought treatment, the allocation proportion of structural-P was also significantly negatively driven by fine root APase activity. This also proved that lower soil available P and FRP concentrations under drought treatment induce more phosphatase release from roots. On the contrary, foliar nucleic acid-P allocation proportion was mainly driven by the negative direction of FRP concentration, it indicated that lower P concentrations in fine roots can induce plant leaves to allocate more foliar P to the nucleic acid-P fractions involved in enzyme and protein synthesis, in order to activate and release a portion of P present in vacuoles for current plant needs. However, when more optimal were the conditions (more water and/or P-supply), *Alhagi* roots absorb more P to supply it to leaves, while foliar P is preferentially allocated to other P-fractions. In addition, it is important to highlight that the foliar metabolic-P allocation proportion was mainly driven negatively by the activity of APase in fine roots rather than FRP concentration. We speculate that this may be attributed to metabolic-P existing in cytoplasm is the most active fraction in the four P fractions, participating in various physiological and biochemical reactions of leaves thus may be greatly influenced by factors other than root P concentration.

In water and nutrient limited environments, compared to the physiological traits of plant roots, morphological traits are often the most variable, significant, and studied (Freschet et al., 2018; Ros et al., 2018). Under P poor condition, plants often either/neither expand the distribution of root systems (mainly fine roots) to explore more intensely P patches in the soil or release some active P substances into the rhizosphere environment to increase the bioavailability of P (Shahidi et al., 2017). However, the strategy of expand root systems always requires plants to invest a large amount of C (Ushio et al., 2015). Moreover, compared to morphological traits of fine root, there are stronger correlation between physiological traits and FRP concentration, especially the carboxylates concentration. This may be attributed to the synthesis and release of phosphatase is a process that requires higher energy investment compared to the release of carboxylates (Lugli et al., 2020). Therefore, for the absorption and distribution of P nutrients, root physiological traits (especially the carboxylates) related to P activation may be more important than morphological traits. The results of this study also supported the theory that foliar P fraction allocation in *Alhagi* was mainly driven by the concentration of FRP, root APase activity, and carboxylates secretion compared to the morphological traits of fine roots. Furthermore, this research also indicated that the trade-off between foliar P fraction allocation and fine root traits under drought treatment was stronger than that under well-watered treatment. This implied that good water conditions may reduce the correlation between aboveground and underground traits, while drought will increase the need of connection between aboveground and underground plants. Overall, our second and third hypotheses were verified.

5 Conclusions

This study found that the foliar P fraction allocation patterns and the fine root traits were significantly affected by the drought and/or low P conditions in soils. A correlation was observed between the foliar P fraction allocation of in *Alhagi* leaves and fine root traits, indicating a trade-off connection, and that this correlation in form of trade-off is more intense under low soil P availability. As example, metabolic-P, structural-P, and residual-P allocation proportions exhibited a reduction as the concentration of fine root P declined. Conversely, there was a rise in nucleic acid-P with decreasing concentration of fine root P. It indicated that good nutrient acquisition of fine root P is linked with more P in leaves mainly allocated to active metabolism, and to increase the capacity of light capturing.

The correlation between the allocation proportion of foliar P fractions and fine root physiological traits related to P activation was shown to be more pronounced than the correlation with morphological traits. It implied that fine root physiological traits are better predictors of foliar P fraction allocation than morphological traits, especially the release of carboxylates.

Drought conditions enhanced the trade-off relationship between foliar P fraction allocation patterns and fine root traits, which implied drought will increase the demand of connection between aboveground and underground plants. Conversely, good water conditions weakened this connection.

Generally, this indicated that when the amount of P obtained from soil was reduced under drought and/or low P conditions, *Alhagi* not only can improve their ability to obtain P by changing the fine traits, but also can allocate more P to the most basic and necessary function where P participate in protein synthesis, which means having sufficient enzymes to maintain the primary and defensive operations. This study greatly supplements the research gap on the trade-off between foliar P fraction and fine root traits of desert species, and is conducive to strengthening the understanding of P nutrient cycling, absorption, and efficient utilization strategies in desert ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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Author contributions

FJZ, AT and YJG planned and designed the research; YJG performed the research and wrote the paper, AT, FJZ, XYL, JS and JP provided critical suggestions on the manuscript, and all authors revised the manuscript.

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Table 1 Leaf traits were affected by water and phosphorus treatments and the overall effects of water and P supplies and their interactions on leaf traits

	Leaf area LA (cm^2)	Leaf thickness LT (cm)	Specific leaf area SLA ($cm^2\ g^{-1}$)	Leaf tissue density LTD ($g\ cm^{-3}$)
Water treatment (W)				
Drought	11.42±3.17	0.52±0.11	41.52±14.66	0.06±0.03
Well-watered	13.35±3.92	0.51±0.10	45.74±16.46	0.05±0.02
P supply treatment (P)				
No P supply	9.57±2.07c	0.45±0.08b	42.14±18.72b	**0.07±0.03a**
Low P	11.43±2.73b	0.52±0.11a	41.02±16.37b	0.06±0.02b
Intermediate P	12.84±4.14a	0.55±0.11a	41.97±10.69b	0.05±0.02bc
High P	14.71±4.13a	0.55±0.11a	**49.39±14.90a**	0.04±0.01c
Fixed effect				
W	0.001	0.658	0.063	0.114
P	< 0.001	< 0.001	0.031	< 0.001
W * P	0.418	0.506	**0.020**	**0.009**

Note: Means with different lower-case letters are significantly different ($p < 0.05$).Values are means ± standard deviation, n = 96 for water treatment, n = 48 for P supply treatment.

Figure captions

Fig. 1 Soil phosphorus fraction concentration under different water and phosphorus treatments

Note: The data set consists of 24 observations, with the mean value reported as the mean ± standard deviation (SD). The bars in the graph depict the mean standard deviation values. Values shown by distinct letters indicate a statistically significant difference among the various treatments involving water and phosphorus supply ($p < 0.05$). W indicates water treatment, P indicates P supply treatment, W*P indicates the interactions with water and P supply treatment.

Fig. 2 Phosphorus concentration and dry weight of leaves and fine roots under different water and phosphorus treatments

Note: The data set consists of 24 observations, with the mean value reported as the mean ± standard deviation (SD). The bars in the graph depict the mean standard deviation values. Values shown by distinct letters indicate a statistically significant difference among the various treatments involving water and phosphorus supply ($p < 0.05$). Each point represents an individual data. R^2 and p values for linear trend lines are shown on each plot. ***$p < 0.001$. W indicates water treatment, P indicates P supply treatment, W*P indicates the interactions with water and P supply treatment.

Fig. 3 The concentration and allocation proportion of foliar phosphorus fractions under different under different water and phosphorus treatments

Note: The data set consists of 24 observations, with the mean value reported as the mean ± standard deviation (SD). The bars in the graph depict the mean standard deviation values. Values shown by distinct letters indicate a statistically significant difference among the various treatments involving water and phosphorus supply ($p < 0.05$). W indicates water treatment, P indicates P supply treatment, W*P indicates the interactions with water and P supply treatment.

Fig. 4 Fine root morphology and physiological traits under different water and phosphorus levels

Note: The data set consists of 24 observations, with the mean value reported as the mean ± standard deviation (SD). The bars in the graph depict the mean standard deviation values. Values shown by distinct letters indicate a statistically significant difference among the various treatments involving water and phosphorus supply ($p < 0.05$). W indicates water treatment, P indicates P supply treatment, W*P indicates the interactions with water and P supply treatment.

Fig. 5 Correlation analysis between the allocation proportion of foliar phosphorus fractions and fine root traits

Note: The magnitude of the Pearson correlation coefficient is shown by the intensity of color. The strength of the association increases as the value approaches ± 1. As the value approaches zero, the strength of the link diminishes. Statistical significance is shown only if $p < 0.05$. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. FRP, fine root phosphorus

concentration; RL, root length; SA, root surface area; RV, root volume, SRL, specific root length; SRSA, specific root surface area; RTD. Root tissue density; APase, root acid phosphatase; Mn, indicating the amount of carboxylic acid secreted.

Fig. 6 Structural equation models of the allocation proportion of foliar phosphorus fractions and fine root traits

Note: The blue lines serve to represent positive relationships, while the green lines are used to signify negative relationships. The solid lines in the diagram depict associations that are statistically significant, whereas the dashed lines show relationships that are not statistically significant. The asterisks serve as indicators of statistical significance. * not present, $p > 0.05$; otherwise *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The standardized regression coefficients for each path are provided, and results of model fit tests are shown below each figure. FRP, fine root P concentration; RL, root length; SRL, specific root length; SA, surface area; MP, metabolic-P; NP, nucleic acid-P; SP, structural-P; RP, residual-P.

Fig. 7 Structural equation models of showing the direct and indirect effects of the foliar phosphorus fraction allocation and fine root traits in drought (A) and well-watered treatment (B).

Note: The standardized total effects may be calculated by summing the standardized direct impacts and the standardized indirect effects.

Fig. 1

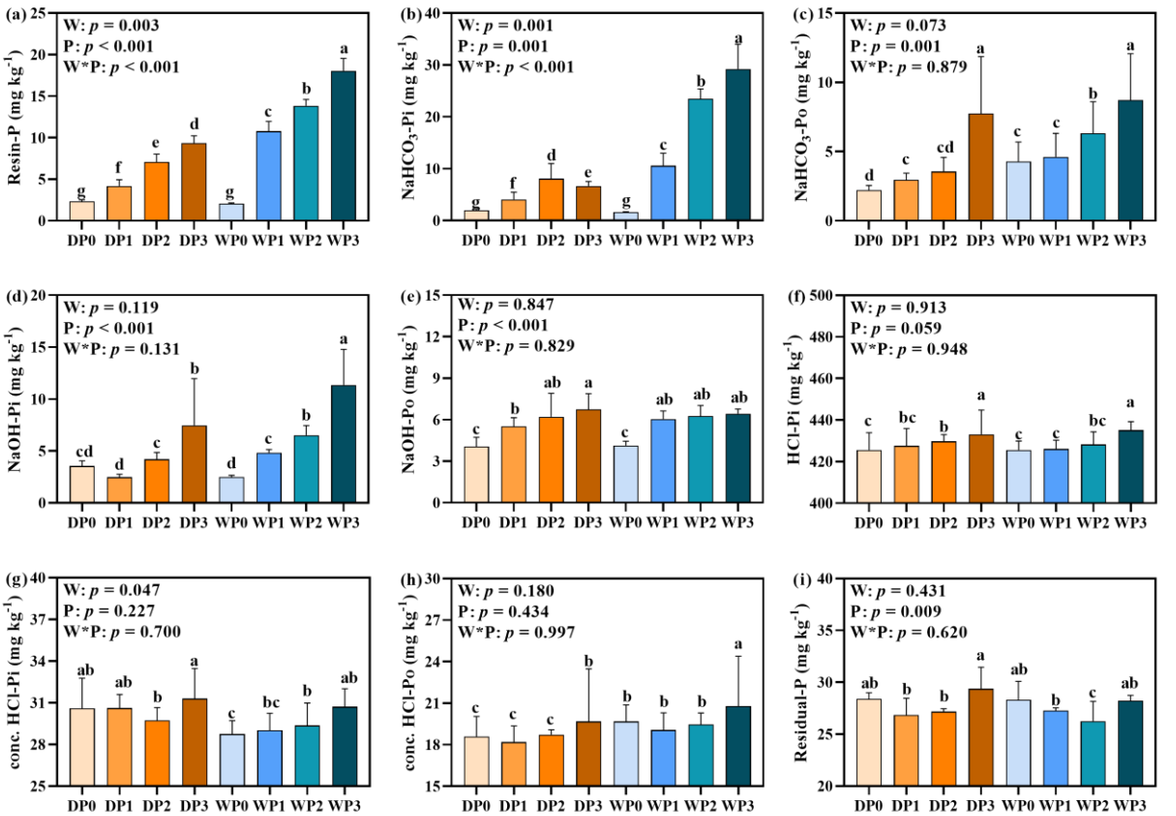

(a)
W: p = 0.003
P: p < 0.001
W*P: p < 0.001
Resin-P (mg kg-1)
(b)
W: p = 0.001
P: p = 0.001
W*P: p < 0.001
NaHCO3-Pi (mg kg-1)
(c)
W: p = 0.073
P: p = 0.001
W*P: p = 0.879
NaHCO3-Po (mg kg-1)
(d)
W: p = 0.119
P: p < 0.001
W*P: p = 0.131
NaOH-Pi (mg kg-1)
(e)
W: p = 0.847
P: p < 0.001
W*P: p = 0.829
NaOH-Po (mg kg-1)
(f)
W: p = 0.913
P: p = 0.059
W*P: p = 0.948
HCl-Pi (mg kg-1)
(g)
W: p = 0.047
P: p = 0.227
W*P: p = 0.700
conc. HCl-Pi (mg kg-1)
(h)
W: p = 0.180
P: p = 0.434
W*P: p = 0.997
conc. HCl-Po (mg kg-1)
(i)
W: p = 0.431
P: p = 0.009
W*P: p = 0.620
Residual-P (mg kg-1)
DP0 DP1 DP2 DP3 WP0 WP1 WP2 WP3

Fig. 2

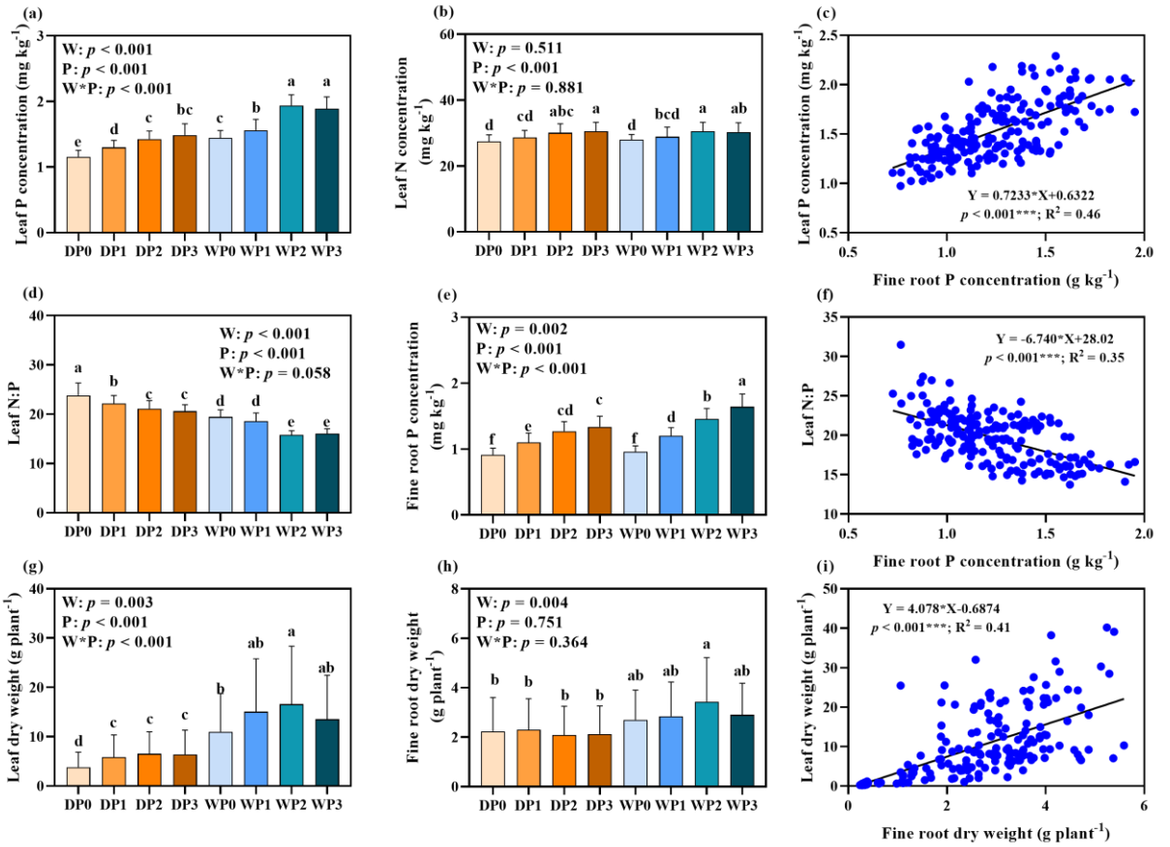
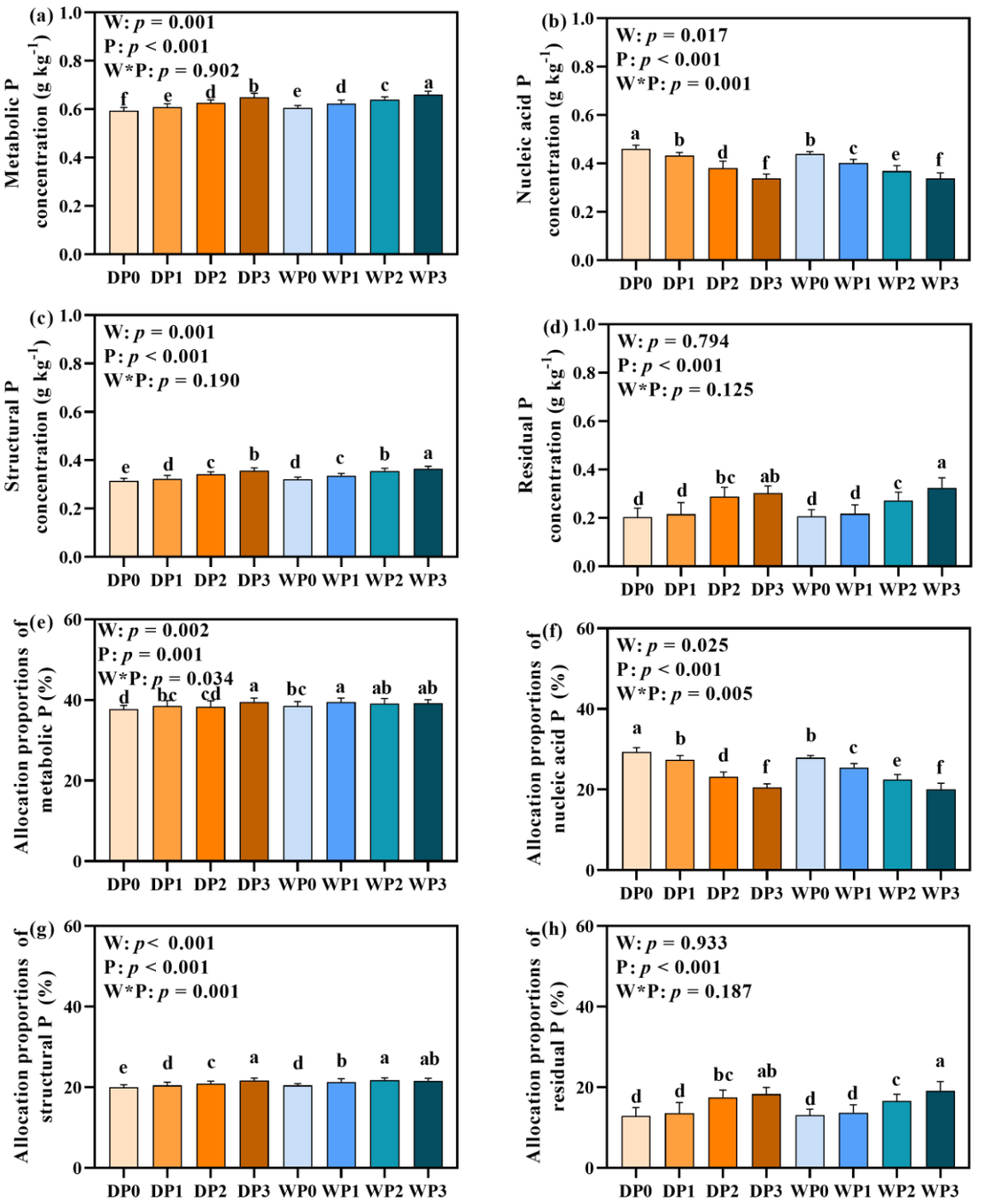

(a)
Leaf P concentration (mg kg-1)
W: p < 0.001
P: p < 0.001
W*P: p < 0.001
(b)
Leaf N concentration (mg kg-1)
W: p = 0.511
P: p < 0.001
W*P: p = 0.881
(c)
Leaf P concentration (mg kg-1)
Y = 0.7233*X+0.6322
p < 0.001***; R2 = 0.46
Fine root P concentration (g kg-1)
(d)
Leaf N:P
W: p < 0.001
P: p < 0.001
W*P: p = 0.058
(e)
Fine root P concentration (mg kg-1)
W: p = 0.002
P: p < 0.001
W*P: p < 0.001
(f)
Leaf N:P
Y = -6.740*X+28.02
p < 0.001***; R2 = 0.35
Fine root P concentration (g kg-1)
(g)
Leaf dry weight (g plant-1)
W: p = 0.003
P: p < 0.001
W*P: p < 0.001
(h)
Fine root dry weight (g plant-1)
W: p = 0.004
P: p = 0.751
W*P: p = 0.364
(i)
Leaf dry weight (g plant-1)
Y = 4.078*X-0.6874
p < 0.001***; R2 = 0.41
Fine root dry weight (g plant-1)
DP0 DP1 DP2 DP3 WP0 WP1 WP2 WP3

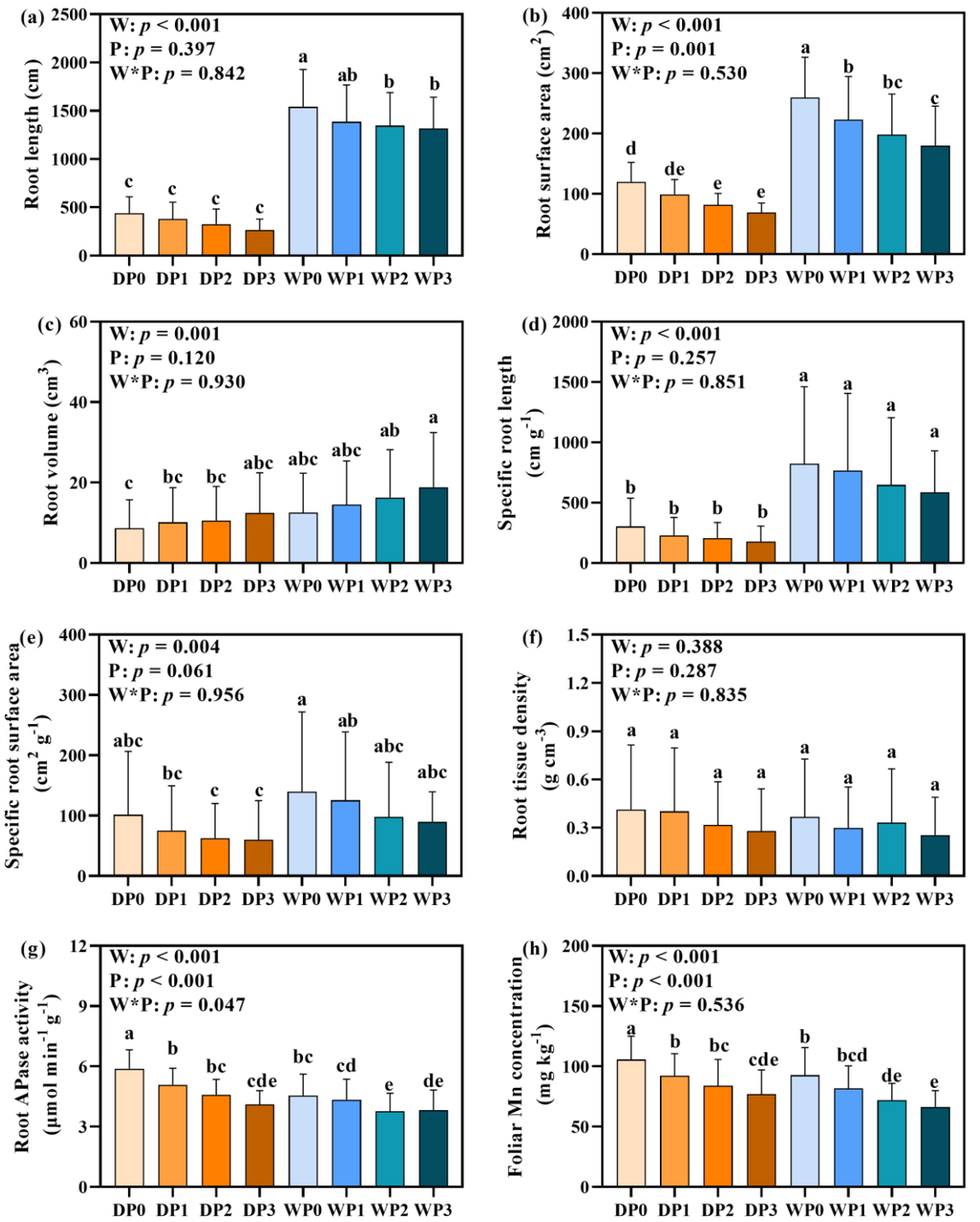
Fig. 3


(a)
W: p = 0.001
P: p < 0.001
W*P: p = 0.902
Metabolic P concentration (g kg-1)
(b)
W: p = 0.017
P: p < 0.001
W*P: p = 0.001
Nucleic acid P concentration (g kg-1)
(c)
W: p = 0.001
P: p < 0.001
W*P: p = 0.190
Structural P concentration (g kg-1)
(d)
W: p = 0.794
P: p < 0.001
W*P: p = 0.125
Residual P concentration (g kg-1)
(e)
W: p = 0.002
P: p = 0.001
W*P: p = 0.034
Allocation proportions of metabolic P (%)
(f)
W: p = 0.025
P: p < 0.001
W*P: p = 0.005
Allocation proportions of nucleic acid P (%)
(g)
W: p< 0.001
P: p < 0.001
W*P: p = 0.001
Allocation proportions of structural P (%)
(h)
W: p = 0.933
P: p < 0.001
W*P: p = 0.187
Allocation proportions of residual P (%)
DP0 DP1 DP2 DP3 WP0 WP1 WP2 WP3

669

670

671 **Fig. 4**



672

673

Fig. 5

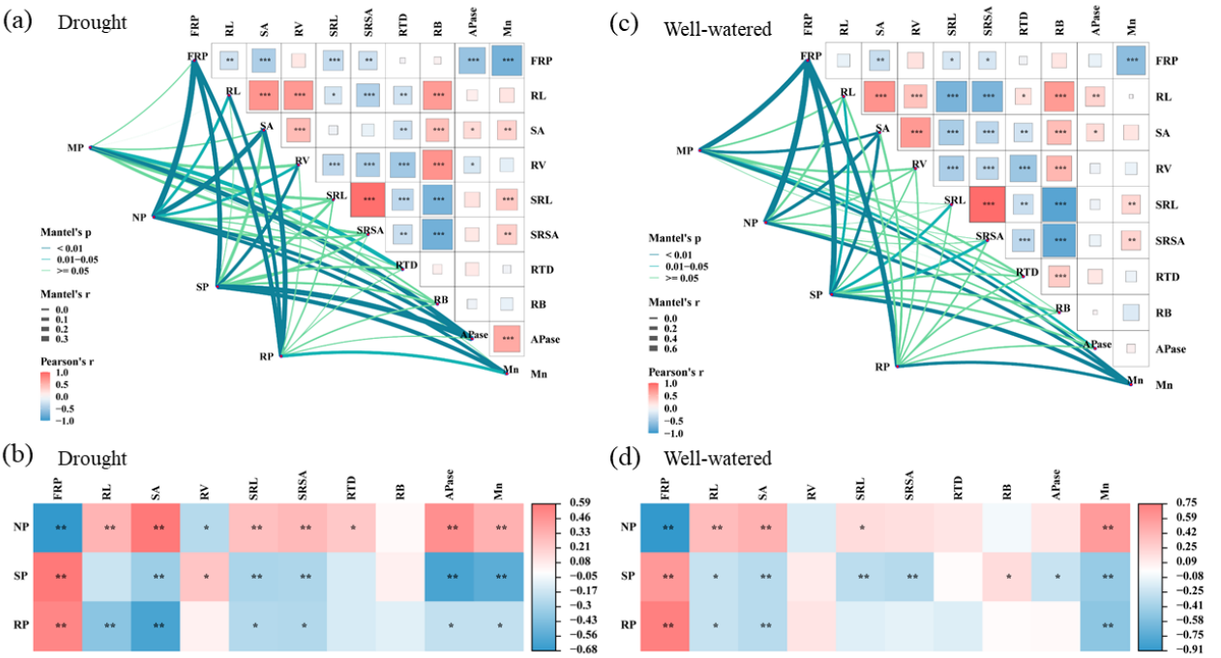
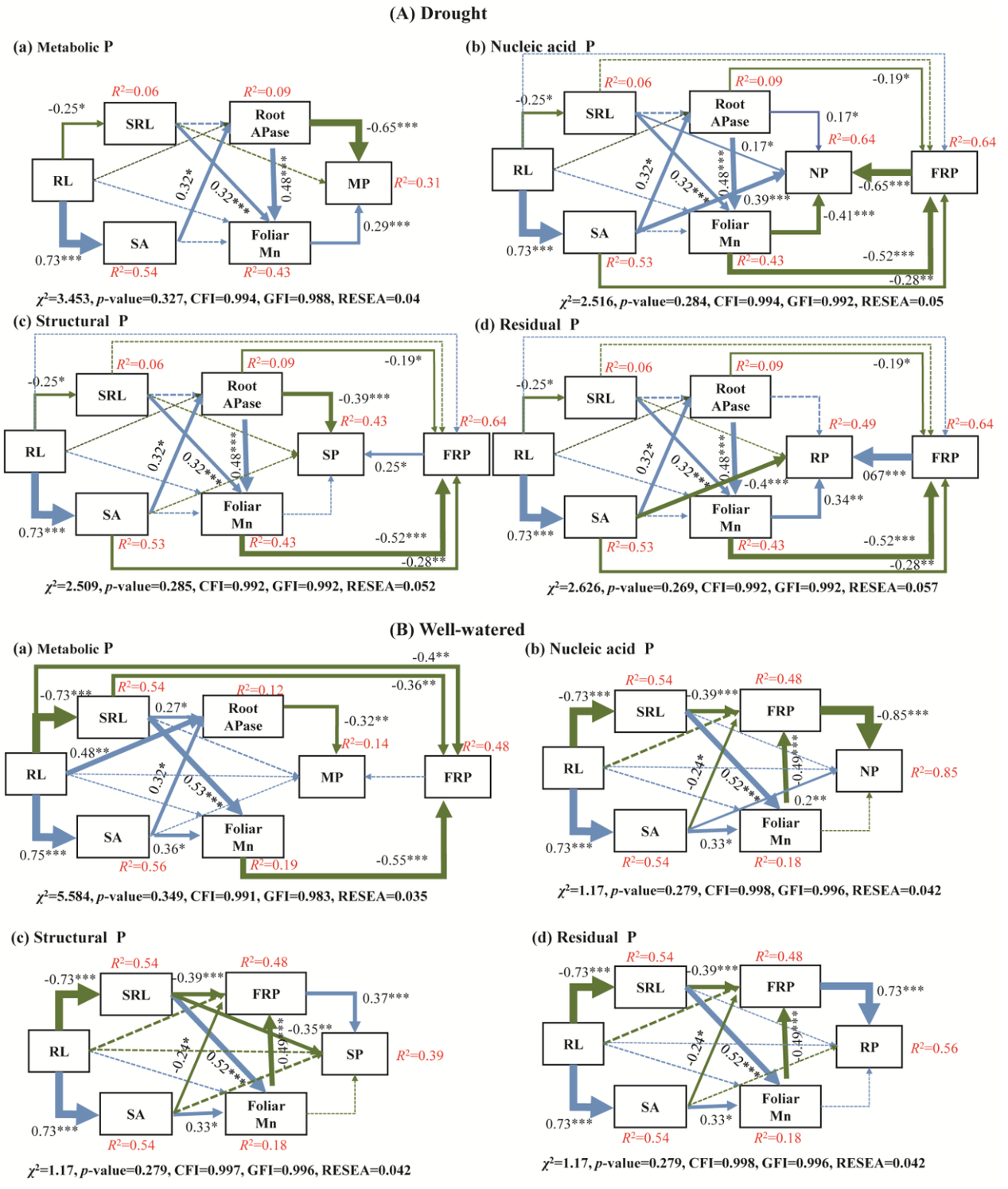

(a) Drought
(c) Well-watered
(b) Drought
(d) Well-watered
FRP
RL
SA
RV
SRL
SRSA
RTD
RB
APase
Mn
MP
NP
SP
RP
Mantel's p
< 0.01
0.01−0.05
>= 0.05
Mantel's r
Pearson's r

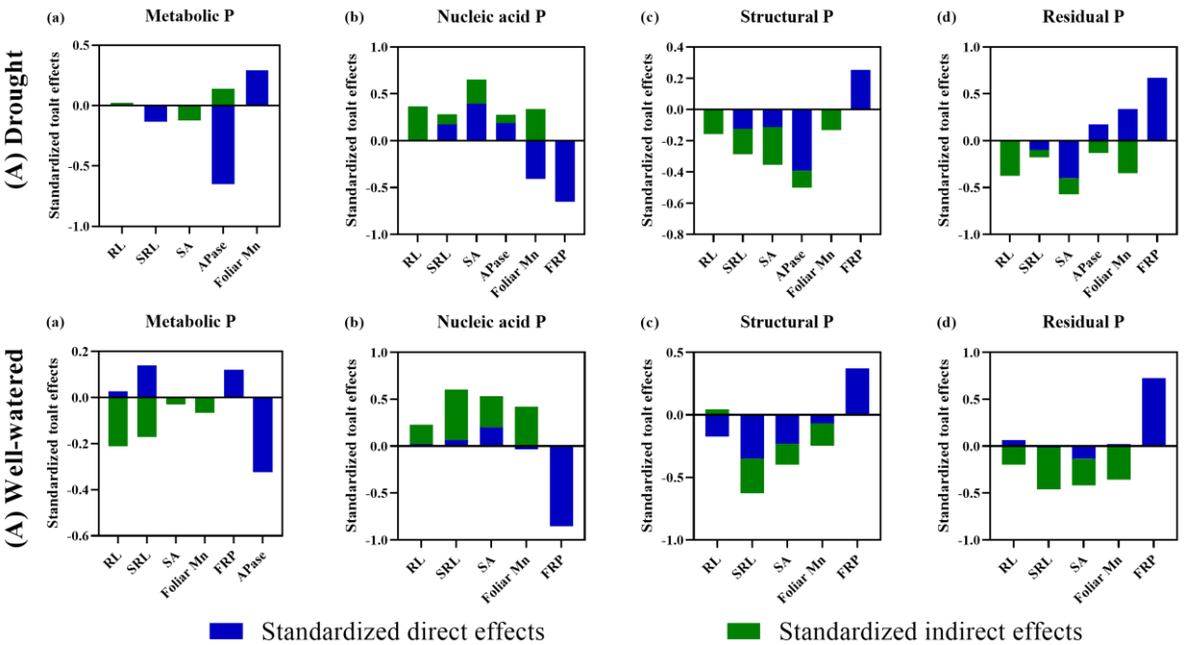
Fig. 6


(A) Drought
(a) Metabolic P
SRL
Root APase
RL
MP
SA
Foliar Mn
(b) Nucleic acid P
NP
FRP
(c) Structural P
SP
(d) Residual P
RP
χ²=3.453, p-value=0.327, CFI=0.994, GFI=0.988, RESEA=0.04
χ²=2.516, p-value=0.284, CFI=0.994, GFI=0.992, RESEA=0.05
χ²=2.509, p-value=0.285, CFI=0.992, GFI=0.992, RESEA=0.052
χ²=2.626, p-value=0.269, CFI=0.992, GFI=0.992, RESEA=0.057
(B) Well-watered
χ²=5.584, p-value=0.349, CFI=0.991, GFI=0.983, RESEA=0.035
χ²=1.17, p-value=0.279, CFI=0.998, GFI=0.996, RESEA=0.042
χ²=1.17, p-value=0.279, CFI=0.997, GFI=0.996, RESEA=0.042
χ²=1.17, p-value=0.279, CFI=0.998, GFI=0.996, RESEA=0.042

698

699

700 **Fig. 7**



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