Coexistence Desert Plants Respond to Soil Phosphorus Availability by Altering the Allocation Patterns of Foliar Phosphorus Fractions and Acquiring Different forms of Soil Phosphorus

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Abstract

Coexisting plants can enhance soil phosphorus (P) availability and plant-P acquisition. However, whether plants growing in P-impoverished desert ecosystems present flexible foliar-P allocation strategies and show discrepancies in their response to different chemical forms of soil-P in plant/plant mixed systems requires further exploration. Four sites with different soil-P availabilities were chosen and foliar-P fractions of legume *Alhagi sparsifolia* and non-legume *Karelinia caspia* in sole and mixed systems were determined. Correspondingly, soil P-fractions, alkaline phosphatase, β-glucosidase, and other soil properties were measured. Our results found *Alhagi sparsifolia* and *Karelinia caspia* were not complementary in mixed system. Compared to the sole *Karelinia caspia*, the dry leaf weight of mixed *Karelinia caspia* was increased by 16%, while mixed *Alhagi sparsifolia* was reduced by 30% relative to the sole *Alhagi sparsifolia*. In a mixed system, *Alhagi sparsifolia* allocated 34% foliar-P to nucleic acid-P, but *Karelinia caspia* allocated 35% foliar-P to metabolic-P and 32% foliar-P to structural-P, respectively. Moreover, compared to the sole system, soil active Pi in the mixed system was increased by 22%, but active organic-P (Po) was reduced by 14%. Furthermore, soil active Pi and Po were stronger determinants for the foliar-P fractions of mixed *Alhagi sparsifolia*, while active Pi and enzyme activity were stronger determinants for mixed *Karelinia caspia*. Overall, the flexible allocation of nucleic acid-P by mixed *Alhagi sparsifolia* and the different responses of foliar-P fractions in mixed systems to soil active Pi and Po indicated the P utilization and allocation strategies of two coexisting desert species to low-P environments.

Keywords Coexistence plant species · Complementarity effect · Desert ecosystems · Foliar-P fraction · Legume · Soil active P

Introduction

Phosphorus (P) is a crucial macronutrient in plant growth, but its availability is generally limited in the soils of most ecosystems (Xia et al. 2020). Due to this P deficiency, plants have evolved advanced strategies to improve P acquisition and P use efficiency (Ceulemans et al. 2017; Lambers et al. 2018). The processes that enhance soil P acquisition include increased desorption, solubilization, and mineralization of P from recalcitrant soil inorganic P (Pi) and organic P (Po) pools using root-secreted phosphatases, protons, and low-molecular-weight organic acids (Lambers et al. 2010; Yu et al. 2020). In addition, greater root surface area, root length, and optimized root structure make it possible for plants to improve soil P-acquisition (Shane et al. 2006). The processes that improve P use efficiency include reducing the

critical P requirement in plant growth, increasing growth per unit P uptake, and improving the reallocation capacity of internal P (Richardson et al. 2011).

Plants obtain soil P using various strategies, but the method used by different plant species and their abilities are inconsistent (Lambers et al. 2022). In P-acquisition systems, several legumes have developed P activation strategies to secrete greater amounts of protons, carboxylates, and organic acids to mobilize more recalcitrant soil P fractions than non-legumes (Shane and Lambers 2005). Moreover, plant–plant mixed systems are being increasingly recognized as a crucial element in strategies through which plants could promote P acquisition through complementarity effects among coexisting plants (Bennett 2021; Woods et al. 2021). Mixed planting between several legumes and non-legumes improved the P nutrition of non-legumes (Li et al. 2007). Liao et al. (2020) found that intercropped maize and faba bean could significantly improve the average aboveground P content of maize compared to sole maize. Unfortunately, the majority of previous reports only focused on the total P content of plants (Arunachalam et al. 2021; Richardson et al. 2011), and the foliar-P fractions have been insufficiently investigated in relation to different functions in plant/plant mixed systems.

Recently, foliar-P fractions allocation has become an important means of exploring the adaptation of plants to P deficiency environments (Hidaka and Kitayama 2011, 2013; Yan et al. 2019). Gao et al. (2022a) demonstrated that the legume *Alhagi sparsifolia* is tends to distribute higher proportion P to the nucleic acid-P fraction in the P deficiency condition. In addition, foliar-P fractions were found that to be affiliated with plant tolerance to chilling (Yan et al. 2021). These findings may be associated with the foliar-P fractions with different functions dominating physiological changes in leaves (Hayes et al. 2018). In foliar-P fractions, metabolic-P (namely ADP, ATP and inorganic-P [Pi]) is the active fraction in foliar metabolic activities, nucleic acid-P (components of RNA and DNA) dominates hydrolases and protein synthesis, and structural-P (components of membrane phospholipids) is primarily involved in leaf photosynthesis and cell structures, namely, cell membranes, whereas the function of residual-P (including phosphorylated proteins) is unknown (Ågren et al. 2012; Mo et al. 2019). Therefore, foliar-P fractions may be more suitable for exploring plant adaptability to low P environment than leaf total-P content in the plant/plant mixed systems.

Complementarity effects usually occur in nutrient uptake by coexistence plants according to different soil layers and different soil-P pools, such as the Po or Pi pool (Postma and Lynch 2012). Plants could absorb various chemical forms of P in soil solution (Turner 2008), including orthophosphate forms (Hinsinger 2001), which are directly absorbed by plant roots, as well as organic and recalcitrant soil-P, from which

the P must be released through the root exudates (Richardson et al. 2011). The mineralization of Po fractions may relate to the vital source of P for plants, particularly in a P-limited ecosystem (Rui 2012). Previous researchers have found that in a plant/plant mixed system, a sole maize system and a mixed maize and faba bean system depleted the NaOH-Pi and HCl-Po fractions, while a sole faba bean depleted the NaHCO$_3$-Po and NaOH-Po fractions (Liao et al., 2020). This evidence for the utilization of different soil-P fractions by the two plants in conditions of coexisting (i.e. P-resource partitioning) better explains the advantages of a mixed system of maize and faba in agricultural production.

P limitation frequently occurs in the desert ecosystem with the lower soil-P availability (Xia et al. 2020). Moreover, recent studies have found that the leaf total-P and the allocation pattern of foliar-P fractions of sole *Alhagi sparsifolia* are closely related to soil active P (Gao et al., 2022a). Therefore, the ways that coexisting desert plants obtain the limited soil-P resources and use leaf P efficiently in mixed systems can demonstrate P utilization strategies of desert plants in extremely P-deficient environments. Based on the above considerations, the foliar-P fractions, soil active Pi (sum of resin-P, NaHCO$_3$-Pi, NaOH-Pi) and Po (sum of NaHCO$_3$-Po, NaOH-Po) in sole and mixed *Alhagi sparsifolia* and *Karelinia caspia* were explored at sites with different soil-P availability. We aimed to (a) investigate whether a mixed system of *Alhagi sparsifolia* and *Karelinia caspia* has complementarity effects on leaf P status, (b) explore the allocation patterns of foliar-P fractions of sole and mixed *Alhagi sparsifolia* and *Karelinia caspia* at different soil-P availability sites, and (c) reveal the potential relationship between foliar-P fractions allocation and active P (Pi and Po) in soil and other soil properties in mixed systems.

Materials and Methods

Study Area Description

Fieldwork for this study was performed in 2020 at the juncture of the Qira oasis and the Taklimakan desert, which features dune movement threat and a hyper-arid climate. The extremely low annual precipitation (35 mm) accompanied by strong evaporation potential (2600 mm) lead to low vegetation coverage (less than 15%) and sparsely distributed phreatophyte plants (Table S1), i.e. *Alhagi sparsifolia*, *Karelinia caspia*, *Calligonum mongolicum* and *Tamarix ramosissima*, and so forth (Gao et al. 2022b; Zeng et al. 2013). Through field investigation and analysis of the properties of bare land at multiple naturally established sampling sites, four sites were chosen that had different soil-P availabilities. Moreover, the results of soil resin-P beneath sole or *Alhagi*

sparsifolia and *Karelinia caspia* mixed system showed a general growth from sites 1 to site 4 (Table S2). Each site is at least 2 km distant from the others. Three plots were designed per site, and the area of each plot was 100 m². The area of each site was about 2 hectares, and the distance between the plots within each site was more than 50 m. In each plot, sole *Alhagi sparsifolia*, sole *Karelinia caspia*, and *Alhagi sparsifolia*/*Karelinia caspia* mixed growth were found. All sites/plots have the similar plant densities and proportions between the two species and between the different communities types (sole/mixed) and are randomly arranged within each plot at each site.

Sample Collection

The plant samples were obtained in September 2020. Three representative sole *Alhagi sparsifolia*, sole *Karelinia capsica*, mixed *Alhagi sparsifolia* and mixed *Karelinia capsica* (*Alhagi sparsifolia/Karelinia capsica* mixed system) with a similar heights and crown widths were selected per plot, respectively. Thus, nine individuals per species (sole/mixed) were selected per site. At least 3.0 g young leaves (the most recent fully expanded) were collected from per individual (sole/mixed) at each plot under natural conditions. The collected leaves were put in resealable bags and were immediately put in a car refrigerator at 4 °C and then stored at − 80 °C to measure the foliar-P fraction content. The total time from collection to storage in a − 80 °C freezer was no more than 2 h. Moreover, all leaves were collected from each individual, and oven dried 48 h at 75 °C to obtain dry leaf weight, shattered and sieved (< 0.15 mm), and finally measured for total-P content.

After the leaves of each individual were collected, at the base of each sampled individual, 0–60 cm deep soil samples were sampled using a profile method. A soil profile with length, width and height of 60, 60 and 60 cm was excavated. After the floating soil on the profile was removed, soil samples were carefully collected evenly from below the profile. About 500 g harvested soil samples were immediately retained by the quartering method and then were divided into two parts and put in resealable bags, respectively. One was placed into a car refrigerator at 4 °C and brought to the laboratory, sieved through a 2 mm mesh, and then stored in a 4 °C refrigerator to measure soil enzyme activity, soil organic matter (SOM), microbial biomass phosphorous (MBP), NH_4^+-N, and NO_3^--N. The second was used to measure soil-P fractions, electrical conductivity (EC), pH, total N, and total P after natural air-drying. Thus, the unit of replication at each site was either nine individuals or nine soil samples.

Foliar Total-P and Foliar-P Fractions Analysis

Dry Leaf samples were used to determine the total-P content using an inductively coupled plasma optical emission spectrometer (ICP-OES) Model 5300DV (Perkin Elmer) after shattering and acid-digesting. Frozen leaf samples were used to determine the foliar-P fractions, including the metabolic-P (including Pi), structural-P, nucleic acid-P, and residual-P fraction. Briefly, 1.0 g leaf sample of freeze-dried were weighted, then chloroform–methanol-formic acid, chloroform–methanol-water, water-washed chloroform, methanol (85%), 5% trichloroacetic acid (TCA), and 2.5% TCA were added successively for analysis. Finally, each foliar-P fraction obtained was acid-digested as described earlier before quantifying the total-P. The detailed method for determination was presented by Gao et al. (2022c).

Soil P Fraction Analysis

Active Pi (resin-P, $NaHCO_3$-Pi, and NaOH-Pi), active Po ($NaHCO_3$-Po, and NaOH-Po), HCl-P, and residual-P in soil were measured using a sequential extraction method (Hedley et al. 1982). In brief, 1.0 g soil sample was sifted with a 2 mm sieve after air-drying, was weighed, and was placed in a 50 mL tube. Then deionized water, cation exchange resin, $NaHCO_3$, NaOH, and HCl solution were added successively for continuous extraction. Po was obtained by subtraction. Finally, the residual soil after continuous extraction was digested to obtain residual-P. The detailed methods of this determination could be referred to Gao et al. (2022b).

Soil Physicochemical Properties Analysis

Alkaline phosphatase (ALP) and β-glucosidase activity were determined according to the methods outlined by Tabatabai and Bremner (1969) and Eivazi and Tabatabai (1988), respectively. Soil microbial biomass phosphorous (MBP) was determined referencing for the method developed by Brookes et al. (1985). Soil Olsen-P and total-P concentration were determined using the molybdenum blue colorimetry method after using 0.5 M $NaHCO_3$ extraction and digesting (8 mL H_2SO_4 and 2 mL $HClO_4$), respectively (Olsen and Sommers 1982). Fresh soil was extracted with 2 M KCl and soil NH_4^+-N and NO_3^--N were measured using an AA3 auto analyzer (Bran-Luebbe, Hamburg, Germany). Soil total-N was extracted with 5 mL of concentrated H_2SO_4 at 360 °C and then distilled using a full-automatic Kjeldahl apparatus. SOM was determined using $K_2Cr_2O_7$ oxidation. Soil pH and EC were measured from a soil–water slurry (soil:water, 1:2.5) using a compound electrode (MP551, China).

Statistical Analyses

Analysis of variance (one-way, two-way, and three-way) was used to analyze the dry leaf weight, leaf total-P, and foliar-P fractions among plant species (P), cropping systems (C), sampling sites (S) and their interaction (C × S, C × P, S × P and C × S × P). Relative value totals (RVT) of the major parameters in a mixed system were calculated to examine whether over-yielding in terms of dry leaf weight, leaf total-P, and foliar-P fractions occurred at the community level. The relative value (RV) of individual species was calculated to examine the performance of specific species in mixed systems. For detailed calculation methods, see Hooper and Dukes (2004) and Sun et al. (2017). A relative value > 1 indicates that the mixed system has more value than the average sole system of the species constituting the mixed system. Foliar-P fractions, soil MBP, ALP, β-glucosidase, and soil-P fractions were plotted using GraphPad Prism 9.0. A correlation heat map and structural equation modeling (SEM) were used to analyze the potential relationships between foliar-P fractions, soil active P, and soil physical and biological properties for the two plant species in response to the sole and mixed systems. The SEM analyses were performed with IBM SPSS-Amos 26.0, and further details regarding SEM

analyses are given in Supplementary materials (Table S3). Statistical analyses were performed with the SPSS PASW statistics 21.0 and R project (R Development Core Team 2018).

Results

Leaf Dry Matter Accumulation and P Content

The total leaf P content and dry weight of *Alhagi sparsifolia* and *Karelinia caspia* showed different response to the sole and mixed systems under different levels of P availabilities in soil (Fig. 1). The leaf total-P content and dry weight of mixed *Karelinia caspia* were higher than the *Karelinia caspia* alone, the opposite relationship to that shown by *Alhagi sparsifolia* alone and mixed *Alhagi sparsifolia*. For instance, compared to the sole *Alhagi sparsifolia*, the dry leaf weight of mixed *Alhagi sparsifolia* was reduced by 39% at site 2, 42% at site 3, and 18% at site 4, respectively. In addition, the dry leaf weight and total-P content of sole or mixed systems gradually increased as the soil-P availability increased, with the exception of the total-P content of the leaf of *Karelinia caspia* at site 4.
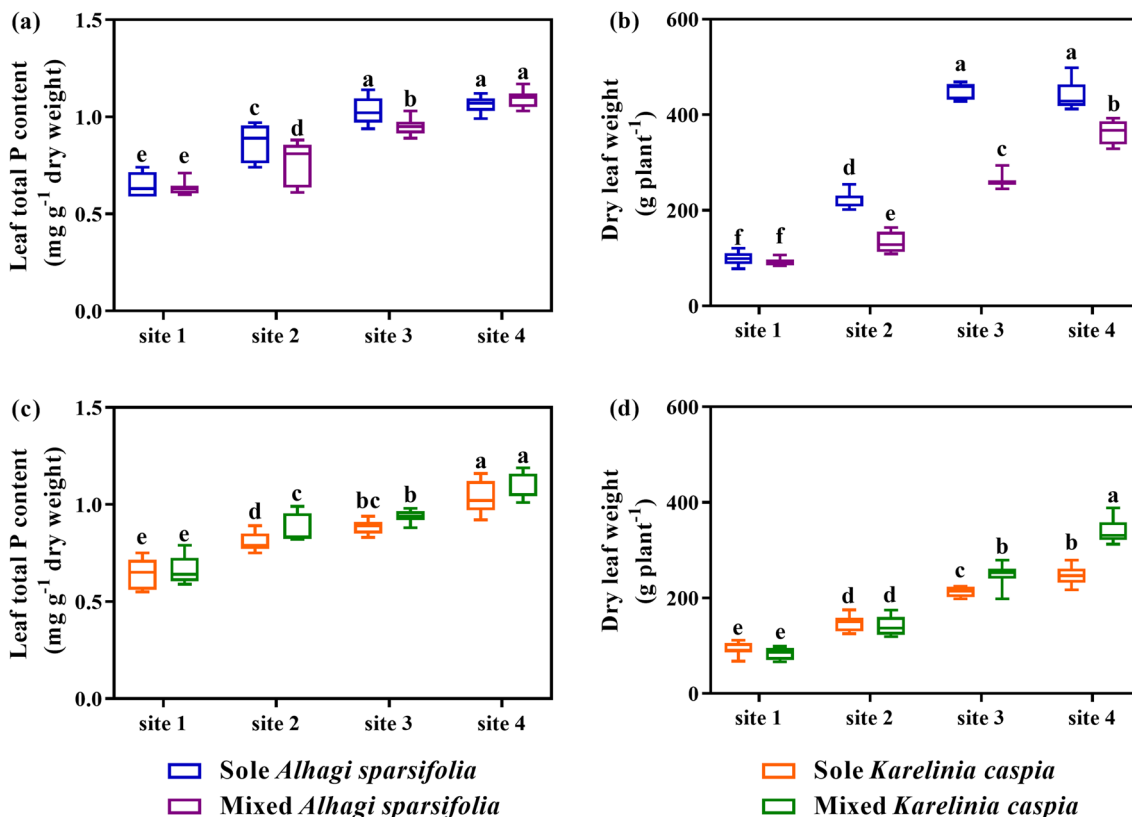

Fig. 1 Leaf total phosphorus content and dry weight of sole/mixed *Alhagi sparsifolia* and *Karelinia caspia* in different soil P availability sites. Lowercase letters above the bars indicate significant differences in different sampling sites (*P* < 0.05).

The relative value of the dry leaf weight and leaf total-P of *Alhagi sparsifolia* (RV_A) and *Karelinia caspia* (RV_K) indicated over-yielding in the mixed systems at the four sites, except for the dry leaf weight of RV_A at sites 2 and 3. The relative value totals (RVT_{A+K}) showed the same trend. Moreover, the RV_K was significantly higher across the four sites than RVT_{A+K} and RV_A (Fig. 2). Furthermore, dry leaf weight showed significant differences between different sites (S, $P < 0.001$), plant species (P, $P < 0.001$), and the interaction between cropping systems, sites and plant species ($C \times S \times P$, $P < 0.001$, Table 1). The leaf total-P presented significant differences at different sites ($P < 0.001$), and the interaction between cropping systems, sites, and plant species ($C \times S \times P$, $P < 0.05$).

Foliar-P Fraction Content

The RV_A and RV_K of the four foliar-P fractions implied that the mixed system has more foliar-P fractions than the species' average sole system average (Fig. 2). Among them, the metabolic-P and structural-P of RV_K were higher than RVT_{A+K} and RV_A. However, the Nucleic acid-P of RV_A was higher than RV_A and then than RVT_{A+K}. The residual-P

implied that RVT_{A+K} was higher than RV_A and RV_K. Additionally, the nucleic acid-P, structural-P, and residual-P contents of the two desert species showed significant interaction differences between cropping systems, sites, and plant species, respectively ($P < 0.01$; Table 1). *Alhagi sparsifolia/Karelinia caspia* mixed system significantly reduced the contents of metabolic-P and structural-P of mixed *Alhagi sparsifolia* compared to sole *Alhagi sparsifolia* (Fig. 3). However, the nucleic acid-P of mixed *Alhagi sparsifolia* was higher than the sole *Alhagi sparsifolia*. Conversely, the mixed system increased the contents of metabolic-P and structural-P of mixed *Karelinia caspia*, with the exception of structural-P at site 4, but it decreased the nucleic acid-P, and residual-P content of mixed *Karelinia caspia*.

Foliar-P Fraction Allocation

Mixed planting changed the allocation proportion of *Alhagi sparsifolia* and *Karelinia caspia* (Fig. 4). The metabolic-P and structural-P proportions of mixed *Alhagi sparsifolia* were significantly lower than sole *Alhagi sparsifolia*, but nucleic acid-P was increased, particularly in site 1, which had the lowest soil available P
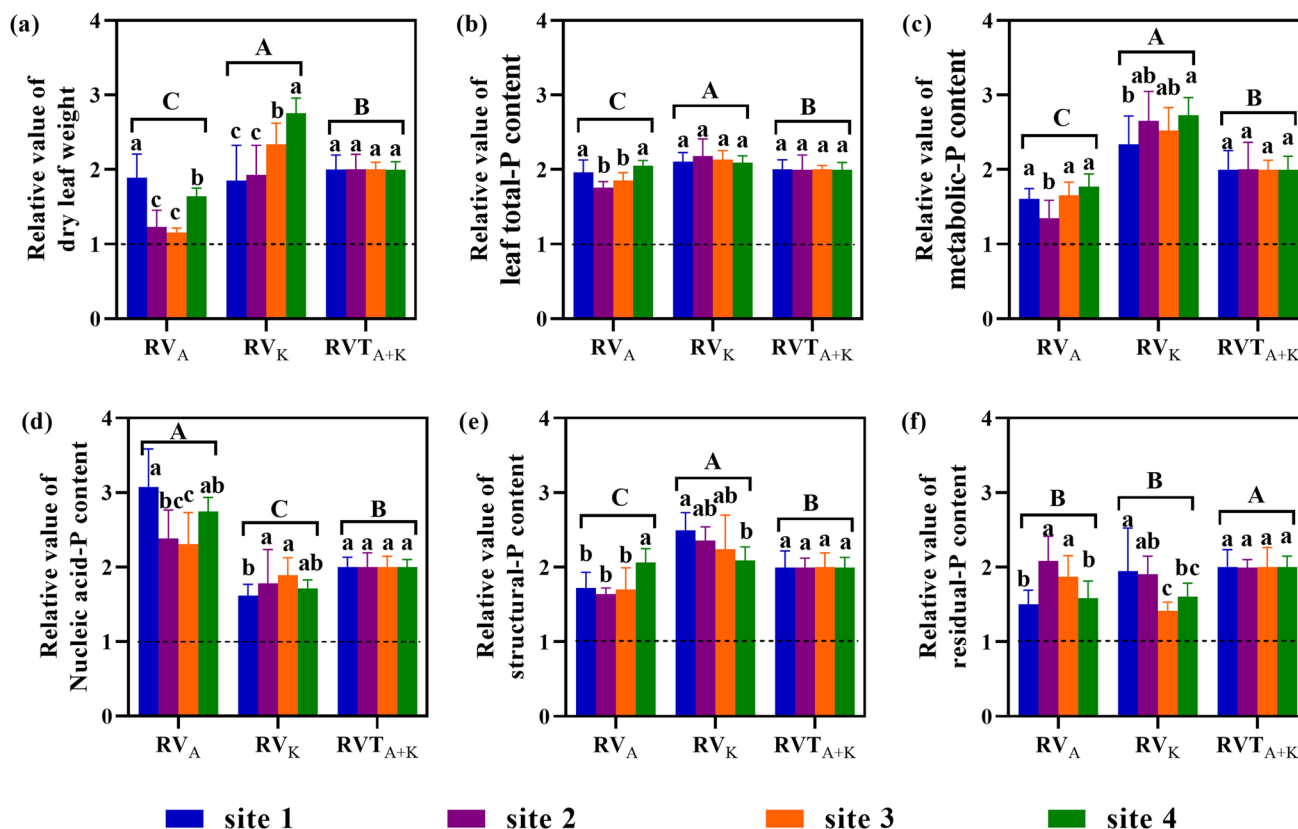

Fig. 2 The relative values of dry leaf weight, leaf total-P and foliar-P fractions at the community level (RVT) and individual species level (RV) in the mixed system. Lowercase letters above the bars indicate significant differences in different sampling sites ($P < 0.05$); uppercase letters indicate significant differences in different individual species and community levels ($P < 0.05$).

Table 1 ANOVA results for dry leaf weight, leaf total-P, and foliar-P fractions as affected by cropping systems (C), four sampling sites (S), plant species (P), and their interactions

	Dry leaf weight (g plant⁻¹)	Leaf total-P (mg g⁻¹)	Metabolic-P		Nucleic acid-P		Structural-P		Residual-P	
			Content (mg g⁻¹)	Proportion (%)	Content (mg g⁻¹)	Proportion (%)	Content (mg g⁻¹)	Proportion (%)	Content (mg g⁻¹)	Proportion (%)
F										
C	2.47	0.02	0.04	0.02	1.24	2.81	0.08	0.02	5.69	5.86
S	121.97	224.70	45.34	4.31	60.44	0.16	71.18	6.15	11.55	0.11
P	12.70	0.26	0.72	0.20	0.09	0.70	24.83	131.68	233.53	509.90
C×S	5.82	8.47	8.54	3.46	8.48	4.67	8.48	4.40	8.51	2.47
C×P	10.17	2.71	39.20	114.37	25.51	229.42	10.86	18.21	0.57	0.49
S×P	16.07	6.66	6.88	10.42	7.18	3.16	7.19	5.33	7.02	1.62
C×S×P	64.33	2.79	2.43	1.58	4.03	5.30	5.04	4.90	6.42	16.29
P										
C	0.118	0.882	0.845	0.879	0.268	0.096	0.78	0.896	0.019	0.017
S	<0.001	<0.001	<0.001	0.006	<0.001	0.924	<0.001	0.001	<0.001	0.957
P	<0.001	0.614	0.398	0.66	0.761	0.404	<0.001	<0.001	<0.001	<0.001
C×S	0.001	<0.001	<0.001	0.018	<0.001	0.004	<0.001	0.004	<0.001	0.064
C×P	0.002	0.102	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	0.452	0.485
S×P	<0.001	<0.001	<0.001	<0.001	<0.001	0.027	<0.001	0.002	<0.001	0.186
C×S×P	<0.001	0.043	0.069	0.197	0.009	0.002	0.002	0.003	<0.001	<0.001

$DF_C = 1$, $DF_S = 3$, $DF_P = 1$, $DF_{C×S} = 3$, $DF_{C×P} = 1$, $DF_{S×P} = 3$, $DF_{C×D×P} = 3$
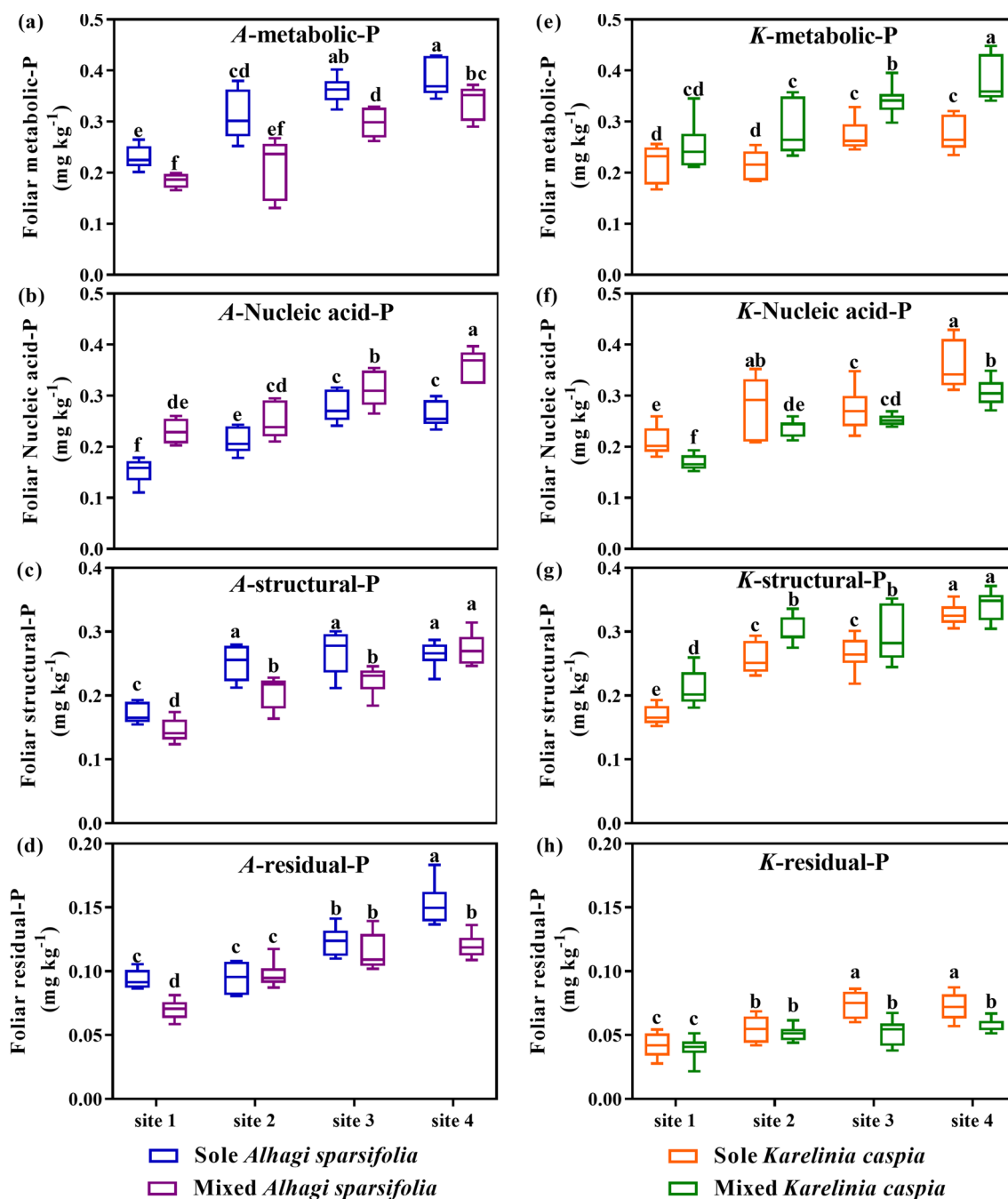
Fig. 3 Foliar-P fraction content of sole/mixed *Alhagi sparsifolia* and *Karelinia caspia* in different soil-P availability sites. Lowercase letters above the bars indicate significant differences in different sampling sites ($P < 0.05$).

concentration. Conversely, the allocation proportion of metabolic-P of mixed *Karelinia caspia* was considerably higher than *Karelinia caspia* alone, and its nucleic acid-P and residual-P were lower than *Karelinia caspia* alone. Furthermore, we also found that residual-P proportion was significantly associated with cropping systems (Table 1; $P < 0.05$). Only the allocation proportion of metabolic-P

and residual-P were closely related to the sites with different soil available P concentrations. The allocation proportions of nucleic acid-P, structural-P, and residual-P of the two desert species had significant interaction differences between cropping systems, sites, and plant species, respectively ($P < 0.01$).
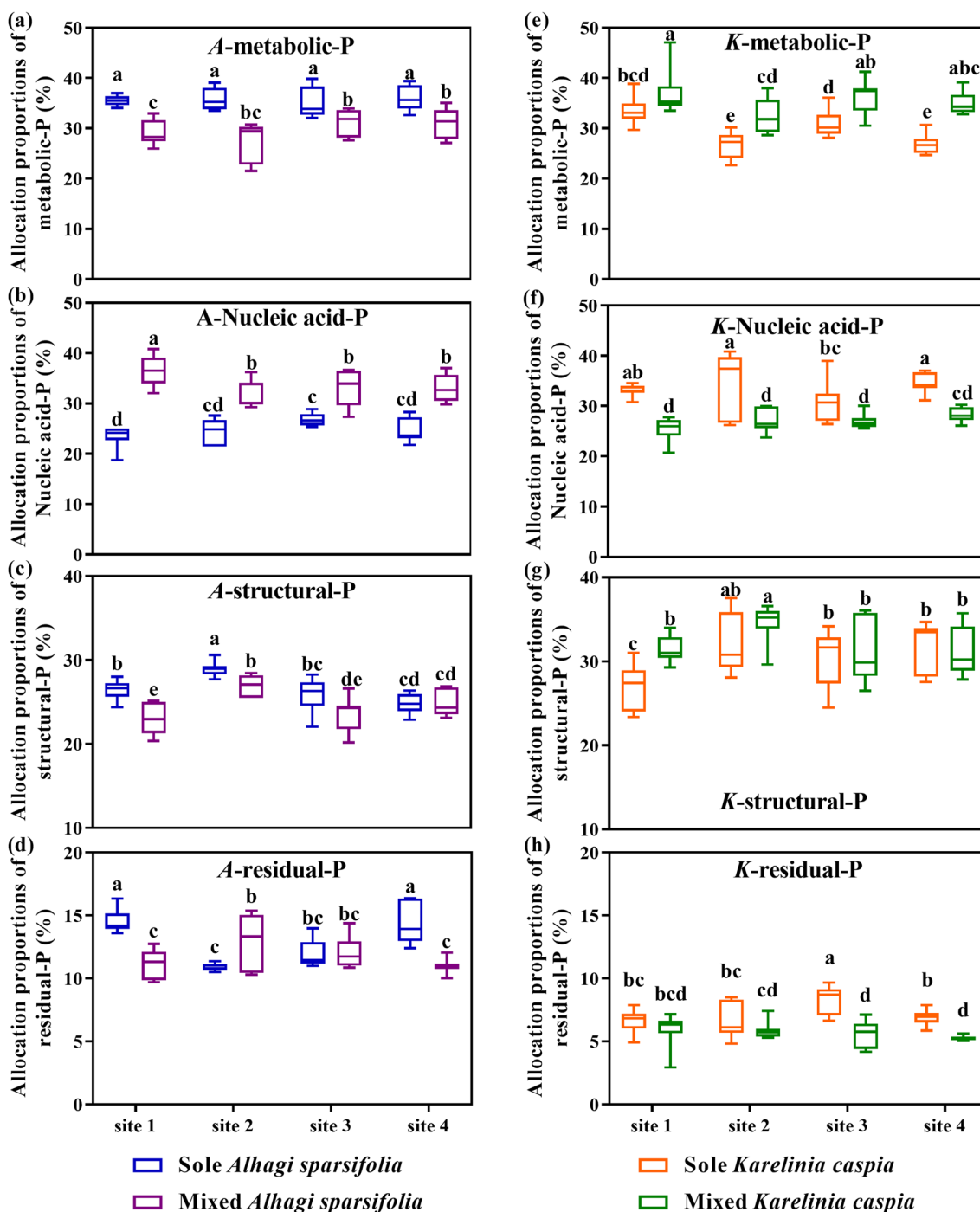
Fig. 4 Allocation proportions of foliar-P fractions of sole/mixed *Alhagi sparsifolia* and *Karelinia caspia* in different soil P availability sites. Lowercase letters above the bars indicate significant differences in different sampling sites ($P < 0.05$).

Soil-P Fractions

Soil resin-P increased from sites 1 to site 4 across sole and *Alhagi sparsifolia/Karelinia caspia* mixed systems, except for the resin-P beneath sole *Alhagi sparsifolia* at site 4 (Table S2). However, other soil-P fractions did not show

regular changes from site 1 to site 4. In addition, the soil resin-P of site 1 and site 2 and $NaHCO_3$-P and NaOH-Pi of site 3 and site 4 were significantly higher in the mixed system than the sole system at site 1. Moreover, soil active Pi (sum of resin-P, $NaHCO_3$-Pi, NaOH-Pi) was significantly higher in the mixed system than sole *Alhagi sparsifolia* or

Karelinia caspia (Table 2). On the contrary, active Po in soil (sum of $NaHCO_3$-Po, NaOH-Po) was lower in the mixed system than in *Alhagi sparsifolia* or *Karelinia caspia* alone, and the highest active Po was at site 1 (Table 2).

Soil Physical and Biological Properties

Soil ALP and β-glucosidase activities showed significant differences in site 1, with the lowest soil P availability (Fig. 5). Soil ALP activity in the *Alhagi sparsifolia/Karelinia caspia* mixed system increased by 193% and 186% relative to that in the sole *Alhagi sparsifolia* and *Karelinia caspia* at site 1, respectively. At site 1, β-glucosidase activity in soil was 12% higher in the mixed system than in the *Alhagi sparsifolia* alone. However, soil MBP in the mixed system was significantly higher than sole *Alhagi sparsifolia* at sites 2, 3, and 4. For *Karelinia Caspia* alone, the mixed system increased the concentrations of soil NH_4^+-N and SOM and decreased soil EC in sites 1 to 4 (Fig. 6). On the contrary, the mixed system reduced soil NH_4^+-N of sites 3 and 4, SOM of sites 1 and 2, and EC of sites 1, 3 and 4, but increased soil NO_3^--N from sites 1 to 4 compared to *Alhagi sparsifolia* alone.

Relationship Between Foliar-P Fractions, Soil Active P, and Physical and Biological Properties

Foliar-P fractions of mixed *Alhagi sparsifolia* and *Karelinia caspia* were generally more affected by active Pi and active Po in soil than in the plantings with either species alone (Figs. 7, 8). For instance, the foliar-P fractions of mixed *Karelinia caspia* and *Alhagi sparsifolia* were significantly positively related to the active Pi in soil, and foliar-P fractions of mixed *Alhagi sparsifolia* were also significantly negatively correlated with active Po in soil (Fig. 7). However, only the metabolic-P and residual-P of mixed *Karelinia caspia* were negatively related to active Po in soil. In addition, the foliar-P fractions of sole and mixed *Alhagi sparsifolia* and *Karelinia caspia* were basically negatively correlated with soil enzyme activity and other soil properties. However, soil MBP was significantly positively correlated with foliar-P fractions of sole *Karelinia caspia*, except for metabolic-P fraction.

The SEM analysis further indicated that soil properties and enzyme activity were the strongest determinant for the foliar-P fractions of *Alhagi sparsifolia* alone (Fig. 8). Soil

Table 2 Soil active Pi and Po in different cropping systems at four sites with different soil-P availabilities

Soil P	Cropping systems	site 1	site 2	site 3	site 4
Active Pi	Sole *Alhagi sparsifolia*	9.20 ± 0.68^b	8.47 ± 1.46^c	11.37 ± 0.67^b	10.09 ± 2.56^c
	Sole *Karelinia caspia*	12.75 ± 0.49^a	10.89 ± 0.67^b	11.13 ± 0.85^b	11.84 ± 0.72^b
	Alhagi sparsifolia/Karelinia caspia mixed	11.87 ± 2.31^a	12.13 ± 1.17^a	12.28 ± 0.50^a	16.24 ± 1.67^a
Active Po	Sole *Alhagi sparsifolia*	32.11 ± 3.95^a	24.18 ± 4.15^b	18.62 ± 2.44^a	28.20 ± 3.38^b
	Sole *Karelinia caspia*	32.83 ± 6.14^a	26.27 ± 5.19^a	17.65 ± 2.30^b	31.60 ± 2.09^a
	Alhagi sparsifolia/Karelinia caspia mixed	26.87 ± 1.27^b	24.61 ± 1.14^b	16.07 ± 2.22^c	23.84 ± 2.13^c

Lowercase letters indicate significant differences in same soil active P form between different sites ($P < 0.05$). Active Pi (sun of resin-P, $NaHCO_3$-Pi, and NaOH-Pi), Active Po (sum of $NaHCO_3$-Po and NaOH-Po)
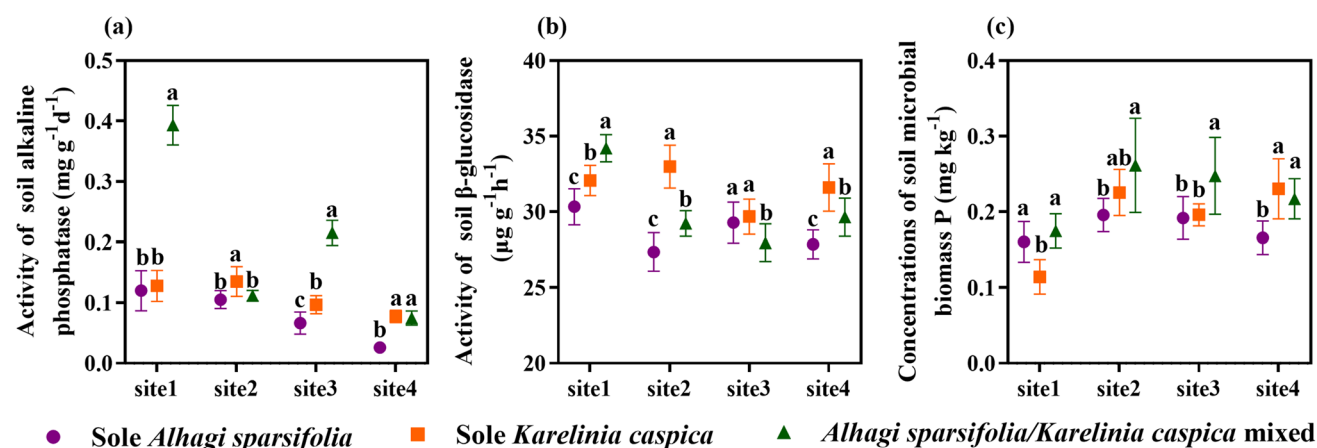

Fig. 5 Alkaline phosphatase and β-glucosidase activities and soil microbial biomass phosphorus concentration in different cropping systems. Lowercase letters above the bars indicate significant differences in different cropping systems in the same sampling site ($P < 0.05$).
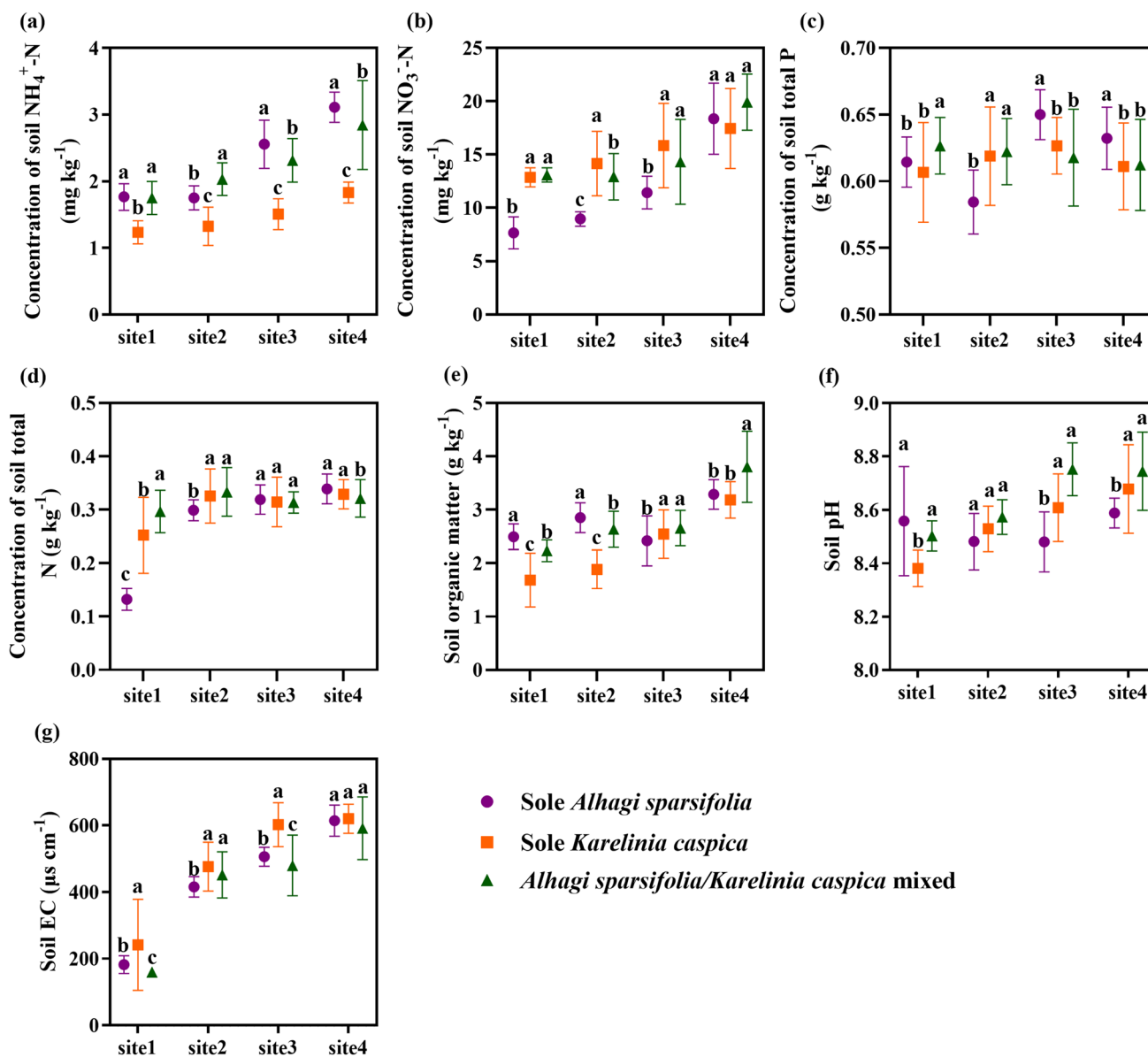
Fig. 6 Soil characteristics of four sites in different cropping systems. Lowercase letters above the bars indicate significant differences in different cropping systems in the same sampling site ($P < 0.05$).

active Pi, Po, and ALP activity were the three direct factors that determined the foliar-P fraction of mixed *Alhagi sparsifolia*. However, the foliar-P fractions of sole *Karelinia caspia* were only regulated by soil MBP. Active Pi and enzyme activity in soil were the two strongest determinants for the foliar-P fractions of mixed *Karelinia caspia*. In summary, soil active Pi, soil properties, ALP and β-glucosidase activity determined the foliar-P fraction of *Alhagi sparsifolia* and soil active Pi, ALP and MBP determined the foliar-P fraction of *Karelinia caspia*.

Discussion

Effects of Plant Coexistence on Leaf P Nutrients and Foliar-P Fractions

In the system of mixed growth of multiple plants, the phenomenon that one species of two plants improves, restrains, or neutralities the nutrition of the other species exhibits a certain universality (Li et al., 2007; Richardson et al. 2011). Previous studies have found that the total
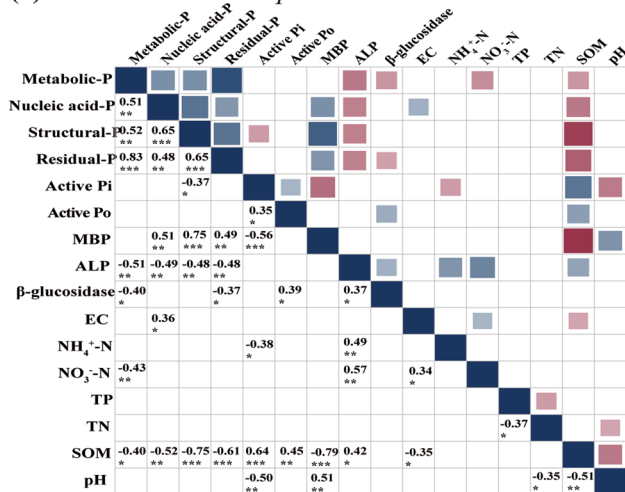
(a) Sole *Alhagi sparsifolia*
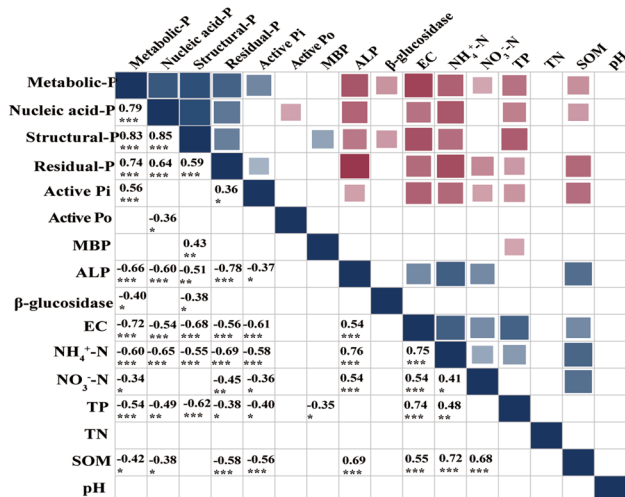
(b) Mixed *Alhagi sparsifolia*
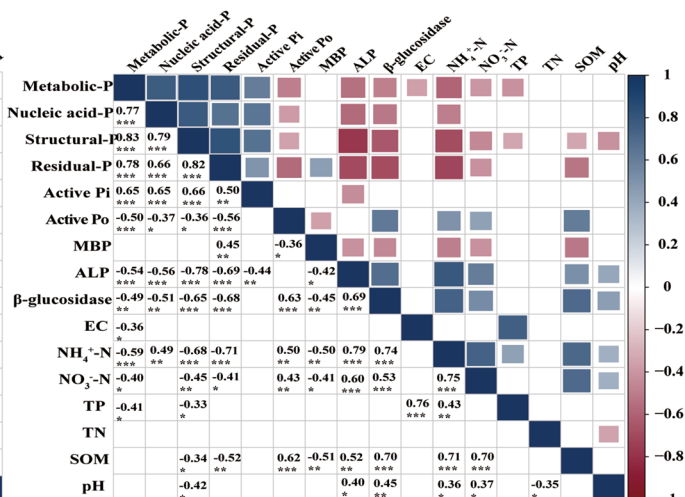
(c) Sole *Karelinia caspia*

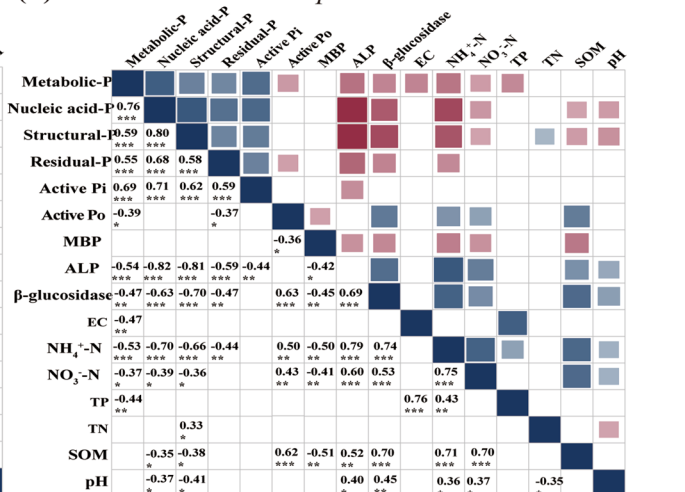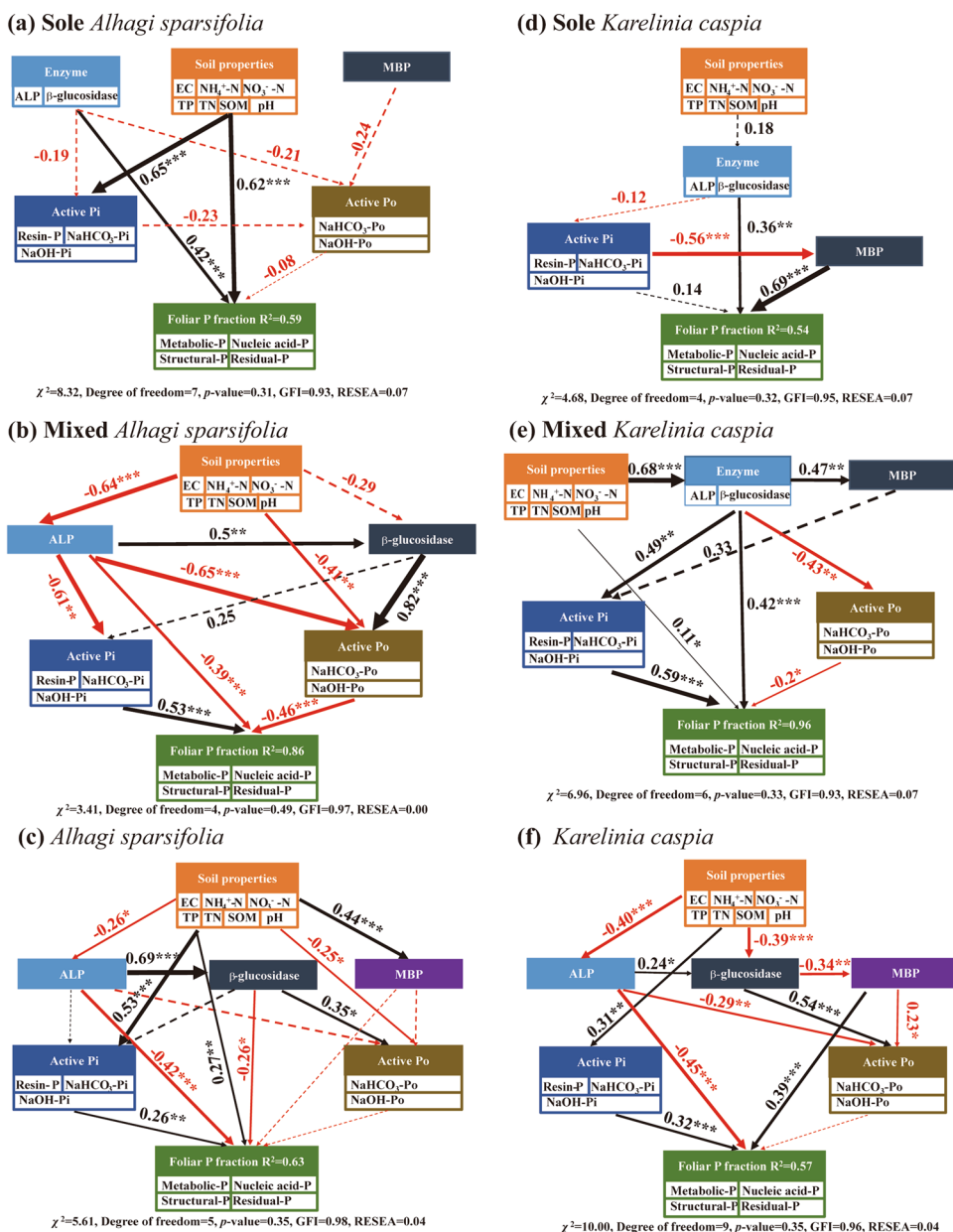**(d) Mixed** *Karelinia caspia*

Fig. 7 The relationship between foliar-P fraction and physical–chemical properties. Gradient color indicates the size of the Pearson correlation coefficient, ranging from − 1 to 1. Each square represents the correlation between the two parameters of transverse and longitudinal. Squares that only reach a significant level are retained. Asterisks represent the level of significance. No*, $P > 0.05$; *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$. The Arabic numerals above the asterisk refer to the corresponding Pearson correlation coefficient. *Pi* inorganic P; *Po* organic P; *MBP* microbial biomass P; *ALP* alkaline phosphatase; *TP* total P; *TN* total N; *SOM* soil organic matter.

nutrient uptake of N and P obtained by intercropping certain species is often higher than the uptake obtained by mono-cropping (Li et al. 2007; Liao et al. 2020). Unfortunately, although *Alhagi sparsifolia/Karelinia caspia* mixed improved the leaf total-P and foliar-P fractions contents of mixed *Karelinia caspia* at some sites, the results of mixed *Alhagi sparsifolia* in the present study were not expected. Therefore, the mixed *Alhagi sparsifolia/Karelinia caspia* system showed no complementary effect on P nutrients in leaf.

The possible reason is that mixed *Karelinia caspia* obtains more P from the root zone of mixed systems than mixed *Alhagi sparsifolia*. Previous research found that the root diameter and respiration rate of 1–4 root orders of *Karelinia caspia* were higher than those of *Alhagi sparsifolia* (Liu et al. 2016). The higher activity of fine roots may also be the evidence that the *Karelinia caspia* in *Alhagi sparsifolia/Karelinia caspia* mixed system could out-compete *Alhagi sparsifolia* for available P in soil. In addition, *Alhagi sparsifolia*, a typical deep-rooted plant, can obtain water not only from the soil but also from groundwater (Zeng et al. 2013). Therefore, *Alhagi sparsifoli/Karelinia caspia* mixed system could increase the possibility that *Karelinia caspia* would obtain water. Furthermore, the soil salinity of mixed system generally decreased compared to that of the *Karelinia caspia* alone (Fig. 6). Due to the

Fig. 8 Direct and indirect effects of soil properties, enzyme activities, active phosphorus, and microbial biomass phosphorus on the foliar-P fractions. Black solid lines indicate positive and significant; red solid lines indicate negative and significant; dashed lines indicate non-significant relationships. Multiple-layer rectangles indicate the PC1 from the principal component analysis performed for the foliar-P fraction, enzyme, and soil properties. Standardized regression coefficients for each path are given, and results for goodness-of-fit tests are also reported underneath each plot ($P > 0.05$ indicates a good fit).

adverse effect of salinity on soil P availability and plant roots on P absorption, the reduced soil salinity concentration relative to the case of *Karelinia caspia* alone may enable mixed *Karelinia caspia* to uptake P nutrients to a greater degree (Gong et al. 2017).

Legumes generally exhibit higher P content because legumes roots can obtain more soil available P by secreting P-mobilizing substances to the rhizosphere (Dissanayaka et al. 2015). Those available P in the legume rhizosphere is likely to be obtained by another non-legume in a mixed growth system (Li et al. 2007). The results of this study also support this view because the mixed system significantly decreased soil NH_4^+-N and resin-P concentration relative to the values found for *Alhagi sparsifolia* alone,

but it also increased soil ALP and β-glucosidase activities. Mixed *Karelinia caspia* could compete for N and P available in the rhizosphere with mixed *Alhagi sparsifolia*, resulting in a decreased concentration of N and P available in the rhizosphere, promoting N fixation and the secretion of P-mobilizing substances of *Alhagi sparsifolia* and finally inducing the mixed system to obtain more P (Liao et al. 2020). In addition, because legumes have a more rapid litter decomposition rate, the SOM concentration increased when *Alhagi sparsifolia* and *Karelinia caspia* coexisted (Hassan et al. 2012; Liao et al. 2020). Relative to sole *Karelinia caspia*, the higher SOM in the mixed system may also be a crucial aspect for promoting improved

growth for mixed *Karelinia caspia*, and this could lead to more available P in soil were removed.

Although there is no complementary effect of leaf P nutrients in *Alhagi sparsifolia* and *Karelinia caspia* mixed system, a fascinating result showed that mixed *Alhagi sparsifolia* allocated more foliar-P to nucleic acid-P, particularly at site 1, which had the lowest P availability, but mixed *Karelinia caspia* allocated more foliar-P to metabolic-P and structural-P in the mixed system (Fig. 4). It was speculated that the desert species in the coexistence system preferentially allocated P to foliar-P fractions involved in enzyme synthesis and the metabolism of active cells, possibly to enhance their metabolic capacity and further strengthen photosynthetic P-use efficiency to adapt to the extreme P barren habitat in the study area (Gao et al. 2022a; Guilherme et al. 2018).

Predictors of Foliar-P Fraction in Plant Coexistence Systems

The differentiation of utilization of different chemical forms of P sources by plants could be used to reduce the competition of P in the rhizosphere, resulting in complementarity effects for plant–plant coexistence (Li et al. 2007). In this study, SEM analysis presented that soil active Pi and enzyme activity were the strongest determining factors for the foliar-P fractions of mixed *Karelinia caspia*, but active Pi and active Po in soil were the two direct factors that determined the foliar-P fraction of mixed *Alhagi sparsifolia* (Fig. 8). This implied that active Pi in soil remained the major P form in plant–plant mixed system, but active Po was more closely related to legumes (Hassan et al. 2012; Liao et al. 2020). This result is inconsistent with earlier research results, which showed that soil resin-P and $NaHCO_3$-Pi were the main plant-available P fractions in *Alhagi sparsifolia* planted alone (Gao et al. 2022a). However, we also note that a relationship between foliar-P fractions of mixed *Karelinia caspia* and active Pi in soil was stronger than that between mixed *Alhagi sparsifolia* and soil active Pi. This is probably because *Alhagi sparsifolia* formed *arbuscular mycorrhizal*, which could enhance root access to organic and, in particular, Pi sources outside the interaction root zone (Koide et al. 2000).

In the coexistence system between legume and non-legume, active Po in soil generally had a higher contribution to the P nutrients of legumes than non-legumes (Liao et al. 2020). The metabolic-P and residual-P of mixed *Karelinia caspia* had a significant negative correlation to active Po in soil. However, active Po in soil was extremely related to the four foliar-P fractions of mixed *Alhagi sparsifolia*. These results seemingly implied that mixed *Alhagi sparsifolia* was more affected by soil active Po than mixed *Karelinia caspia*. We speculate that this may have been attributable to the bio-N fixation of *Alhagi sparsifolia*, which improved available N in soil in the mixed system (Fig. 6), which may have urged the mixed *Karelinia caspia* to uptake more active Pi in soil to maintain elemental homeostasis (Li et al. 2021). However, the reduced concentration of active Pi in soil stimulated the mineralization of organic materials and associated Po (Richardson et al. 2011; Vance et al. 2003). Finally, soil active Po was reduced in the mixed systems (Table 2). Another better explanation was the root nodules of *Alhagi sparsifolia* could enhance the ability to absorb more active Po from soil (Fig. S1), but the active Po was reduced in the root zone of the interaction due to Po mineralization (Zhang et al. 2018). Finally, the contents of leaf total-P, foliar metabolic-P, and structural-P in mixed *Alhagi sparsifolia* were lower than in the mixed *Karelinia caspia* system.

Implications for Vegetation Restoration

The juncture of the Qira oasis and the Taklimakan desert is an extremely fragile desert ecosystem (Zeng et al. 2013). Recently, the desertification of the desert ecosystem has been aggravated due to global warming and human activities (Rasmusse et al. 2018). It is an important ecological strategy to use the dominant desert vegetation in this region to slow desertification (Gao et al. 2022b). Legumes can be planted mixed with other plants to improve the nutrient status (e.g. of N and P) in nutrient-poor ecosystem soils due to legumes' bio-N fixation ability (Li et al. 2007; Liao et al. 2020). However, our results show that the mixed planting of the desert legume *Alhagi sparsifolia* and non-legume *Karelinia caspia* may not be a good choice for vegetation restoration. Specifically, although the mixed system with *Alhagi sparsifolia* and *Karelinia caspia* increased the leaf P status of mixed *Karelinia caspia*, this study did not obtain key evidence on the improvement of P nutrients in mixed *Alhagi sparsifolia* plantings. That is, the mixed system of *Alhagi sparsifolia* and *Karelinia caspia* was not complementary regarding P nutrients to the mixed *Alhagi sparsifolia* system. In addition, our study also found that the mixed system significantly reduced the leaf biomass of *Alhagi sparsifolia*. Therefore, we suggest that the mixed planting of *Alhagi sparsifolia* and *Karelinia caspia* should be avoided in the process of the restoration of vegetation, and other possible mechanisms of promoting mixed growth for these two species in the natural ecosystem should be considered. This is crucial for biodiversity protection, vegetation restoration, and land degradation prevention of fragile desert ecosystems.

Conclusions

When *Alhagi sparsifolia* and *Karelinia caspia* coexist, the roots of the two plants compete for active Pi in soil. Unlike the case of sole growth, mixed *Karelinia caspia* plantings

have a better soil nutrient environment, so the mixed *Karelinia caspia* can obtain more soil active Pi than mixed *Alhagi sparsifolia*. The deprivation of soil active Pi would further accelerate the mineralization of active Po in soil that can be used by *Alhagi sparsifolia* in the soil. In addition, facing the competition of active P in soil, *Alhagi sparsifolia* allocated leaf P to nucleic acid P fraction involved in enzyme synthesis, to promote the efficient utilization of leaf P. Therefore, we conclude that in a mixed system, reducing the P requirement and the flexible allocation of foliar-P fractions of *Alhagi sparsifolia* may be the only reliable strategy for it to survive in the competitive environment of limited P resources. Furthermore, mixed *Alhagi sparsifolia*, which has better access to active Po, may be another, wise strategy to reply the competition of active Pi in the mixed system.

Author Contributions FZ and YG conceived and designed the experiments. YG, ZZ and XC performed the experiments. YG, YD, YZ and YL performed the data analysis, and YG wrote the manuscript. FZ and WI revised and edited the manuscript. All authors read and approved the final manuscript.

Declarations

Competing Interests 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.

References

Ågren GI, Wetterstedt JAM, Billberger MFK (2012) Nutrient limitation on terrestrial plant growth-modeling the interaction between nitrogen and phosphorus. New Phytol 194:953–960. https://doi.org/10.1111/j.1469-8137.2012.04116.x

Arunachalam V, Vaingankar JD, Kevat N (2021) Foliar traits in papaya plants intercropped in coconut. Natl Acad Sci Lett 44:267–270. https://doi.org/10.1007/s40009-020-00981-5

Bennett T (2021) Plant-plant interactions. Plant, Cell Environ 44:995–996. https://doi.org/10.1111/pce.14030

Brookes PC, Landman A, Pruden G, Jenkinson DS (1985) Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method for measuring microbial biomass nitrogen in soil. Soil Biol Biochem 6:837–842. https://doi.org/10.1016/0038-0717(85)90143-9

Ceulemans T, Samuel B, Jessica B, Stanley H, Kristin C, Gerrit P, Kasper VA, Erik S, Pascal B, Olivier H (2017) Phosphorus resource partitioning shapes phosphorus acquisition and plant species abundance in grasslands. Nat Plants 3:16224. https://doi.org/10.1038/nplants.2016.224

Dissanayaka DMSB, Maruyama H, Masuda G, Wasaki J (2015) Interspecific facilitation of P acquisition in intercropping of maize with white lupin in two contrasting soils as influenced by different rates and forms of P supply. Plant Soil 390:223–236. https://doi.org/10.1007/s11104-015-2392-x

Eivazi F, Tabatabai MA (1988) Glucosidases and galactosidases in soil. Soil Biol Biochem 20:601–606. https://doi.org/10.1016/0038-0717(88)90141-1

Gao YJ, Akash T, Zeng FJ, Corina G, Zhang ZH, Jordi S, Josep P (2022a) Allocation of foliar-P fractions of *Alhagi sparsifolia* and its relationship with soil-P fractions and soil properties in a hyperarid desert ecosystem. Geoderma 407:115546. https://doi.org/10.1016/j.geoderma.2021.115546

Gao YJ, Akash T, Zeng FJ, Jordi S, Josep P, Zhang ZH, Waqar I, Xu MQ (2022b) "Fertile islands" beneath three desert vegetation on soil phosphorus fractions, enzymatic activities, and microbial biomass in the desert-oasis transition zone. CATENA 212:106090. https://doi.org/10.1016/j.catena.2022.106090

Gao YJ, Zhang ZH, Zhang B, Yin H, Chai XT, Xu MQ, Akash T, Zeng FJ (2022c) Foliar P-fractions allocation of *Karelinia caspia* and *Tamarix ramosissima* are driven by soil and groundwater properties in a hyper-arid desert ecosystem. Front Plant Sci 13:833869. https://doi.org/10.3389/fpls.2022.833869

Gong YM, Lv GH, Guo ZJ, Chen Y, Cao J (2017) Influence of aridity and salinity on plant nutrients scales up from species to community level in a desert ecosystem. Sci Rep 7:6811. https://doi.org/10.1038/s41598-017-07240-6

Guilherme PC, Clode PL, Oliveira RS, Lambers H (2018) Eudicots from severely phosphorus-impoverished environments preferentially allocate phosphorus to their mesophyll. New Phytol 218:959–973. https://doi.org/10.1111/nph.15043

Hassan H, Marschner P, McNeill A, Tang C (2012) Growth, P uptake in grain legumes and changes in rhizosphere soil P pools. Biol Fert Soils 48:151–159. https://doi.org/10.1007/s00374-011-0612-y

Hayes PE, Clode PL, Oliveira RS, Lambers H (2018) Proteaceae from phosphorus impoverished habitats preferentially allocate phosphorus to photosynthetic cells: an adaptation improving phosphorus-use efficiency. Plant, Cell Environ 41:605–619. https://doi.org/10.1111/pce.13124

Hedley MJ, Stewart JWB, Chauhan BS (1982) Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. Soil Sci Soc Am J 46:970–976. https://doi.org/10.2136/sssaj1982.03615995004600050017x

Hidaka A, Kitayama K (2011) Allocation of foliar phosphorus fractions and leaf traits of tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu. Borneo J Ecol 99:849–857. https://doi.org/10.1111/j.1365-2745.2011.01805.x

Hidaka A, Kitayama K (2013) Relationship between photosynthetic phosphorus use efficiency and foliar phosphorus fractions in tropical tree species. Ecol Evol 3:4872–4880. https://doi.org/10.1002/ece3.861

Hinsinger P (2001) Bioavailability of soil Pi in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237:173–195. https://doi.org/10.1023/A:1013351617532

Hooper DU, Dukes JS (2004) Overyielding among plant functional groups in a long-term experiment. Ecol Lett 7:95–105. https://doi.org/10.1046/j.1461-0248.2003.00555.x

Koide RT, Kabir Z (2000) Extraradical hyphae of the mycorrhizal fungus Glomus intraradices can hydrolyse organic phosphate. New Phytol 148:511–517. https://doi.org/10.1046/J.1469-8137.2000.00776.X

Lambers H (2022) Phosphorus acquisition and utilization in plants. Annu Rev Plant Biol. https://doi.org/10.1146/annurev-arplant-102720-125738

Lambers H, Brundrett M, Raven J, Hopper S (2010) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile

soils is linked to functional diversity for nutritional strategies. Plant Soil 334:11–31. https://doi.org/10.1007/s11104-011-0977-6

Lambers H, Albornoz F, Kotula L, Laliberte E, Ranathunge K, Teste F, Zemunik G (2018) How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus impoverished hyperdiverse ecosystems. Plant Soil 424:11–33. https://doi.org/10.1007/s11104-017-3427-2

Li L, Li SM, Sun JH, Zhou LL, Bao XG, Zhang HG, Zhang FS (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. PNAS 104:11192–11196. https://doi.org/10.1073/pnas.0704591104

Li MM, Petrie M, Tariq A, Zeng FJ (2021) Response of nodulation, nitrogen fixation to salt stress in a desert legume *Alhagi sparsifolia*. Environ Exp Bot 183:104348. https://doi.org/10.1016/j.envexpbot.2020.104348

Liao D, Zhang C, Li H, Lambers H, Zhang F (2020) Changes in soil phosphorus fractions following sole cropped and intercropped maize and faba bean grown on calcareous soil. Plant Soil 448:587–601. https://doi.org/10.1007/s11104-020-04460-0

Liu B, He J, Zeng FJ, Lei JQ, Arndt SK (2016) Life span and structure of ephemeral root modules of different functional groups from a desert system. New Phytol 211:103–112. https://doi.org/10.1111/nph.13880

Mo QF, Li ZA, Sayer EJ, Lambers H, Li YW, Zou B, Tang JW, Heskel M, Ding YZ, Wang FM (2019) Foliar phosphorus fractions reveal how tropical plants maintain photosynthetic rates despite low soil phosphorus availability. Funct Ecol 33:503–513. https://doi.org/10.1111/1365-2435.13252

Olsen R, Sommer L (1982) Phosphorus. In: Page AL, Miller RH, Keeney DR (eds) Methods of Soil Analysis (Part 2). American Society of Agronomy, Madison, pp 15–72

Postma JA, Lynch JP (2012) Complementarity in root architecture for nutrient uptake in ancient maize/bean and maize/bean/squash polycultures. Ann Bot 110:521–534. https://doi.org/10.1093/aob/mcs082

Rasmussen K, Brandt M, Tong XY, Hiernaux P, Diouf AA, Assouma MH, Tucker CJ, Fensholt R (2018) Does grazing cause land degradation? Evidence from the sandy Ferlo in northern Senegal. Land Degrad Dev 29:4337–4347. https://doi.org/10.1002/ldr.3170

Richardson AE, Lynch JP, Ryan PR, Delhaize E, Smith FA, Smith SE, Harvey PR, Ryan MH, Veneklaas EJ, Lambers H, Oberson A, Culvenor RA, Simpson RJ (2011) Plant and microbial strategies to improve the phosphorus efficiency of agriculture. Plant Soil 349:121–156. https://doi.org/10.1007/s11104-011-0950-4

Rui YC, Wang YF, Chen CR, Zhou XQ, Wang SP, Xu ZH, Duan JC, Kang XM, Lu SB, Luo CY (2012) Warming and grazing increase mineralization of organic P in an alpine meadow ecosystem of Qinghai-Tibet Plateau, China. Plant Soil 357:73–87. https://doi.org/10.1007/s11104-012-1132-8

Shane MW, Lambers H (2005) Cluster roots: a curiosity in context. Plant Soil 274:101–125. https://doi.org/10.1007/s11104-004-2725-7

Shane MW, Cawthray GR, Cramer MD, Kuo J, Lambers H (2006) Specialized 'dauciform' roots of Cyperaceae are structurally distinct, but functionally analogous with 'cluster' roots. Plant Cell Environ 29:1989–1999. https://doi.org/10.1111/j.1365-3040.2006.01574.x

Sun ZK, Liu XJ, Schmid B, Bruelheide H, Bu WS, Ma KP (2017) Positive effects of tree species richness on fine-root production in a subtropical forest in SE-China. J Plant Ecol 10:146–157. https://doi.org/10.1093/jpe/rtw094

Tabatabai MA, Bremner JM (1969) Use of p-Nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biol Biochem 1:301–307. https://doi.org/10.1016/0038-0717(69)90012-1

Team RC (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Turner BL (2008) Resource partitioning for soil phosphorus: a hypothesis. J Ecol 96:698–702. https://doi.org/10.1111/j.1365-2745.2008.01384.x

Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol 157:423–447. https://doi.org/10.1046/j.1469-8137.2003.00695.x

Woods CL, Maleta K, Ortmann K (2021) Plant-plant interactions change during succession on nurse logs in a northern temperate rainforest. Ecol Evol 11:9631–9641. https://doi.org/10.1002/ECE3.7786

Xia ZC, He Y, Yu L, Lv RB, Helena K, Li CY (2020) Sex-specific strategies of phosphorus (P) acquisition in *Populus cathayana* as affected by soil P availability and distribution. New Phytol 225:782–792. https://doi.org/10.1038/s41467-020-14492-w

Yan L, Zhang XH, Han ZM, Pang JY, Lambers H, Finnegan P (2019) Responses of foliar phosphorus fractions to soil age are diverse along a two-million-year dune chronosequence. New Phytol 223:1621–1633. https://doi.org/10.1111/nph.15910

Yan L, Sunoj VS, Short AW, Lambers H, Elsheery NI, Kajita TK, Wee AKS, Cao KF (2021) Correlations between allocation to foliar phosphorus fractions and maintenance of photosynthetic integrity in six mangrove populations as affected by chilling. New Phytol 232:2267–2282. https://doi.org/10.1111/NPH.17770

Yu RP, Li XX, Xiao ZH, Lambers H, Li L (2020) Phosphorus facilitation and covariation of root traits in steppe species. New Phytol 226:1285–1298. https://doi.org/10.1111/nph.16499

Zeng FJ, Song C, Guo HF, Liu B, Luo WC, Gui DW, Arndt SK, Guo DL (2013) Responses of root growth of *Alhagi sparsifolia* Shap. (Fabaceae) to different simulated groundwater depths in the southern fringe of the Taklimakan Desert. China J Arid Land 5:220–232. https://doi.org/10.1038/s41598-020-64045-w

Zhang L, Feng G, Declerck S (2018) Signal beyond nutrient, fructose, exuded by an *arbuscular mycorrhizal* fungus triggers phytate mineralization by a phosphate solubilizing bacterium. ISME J 12:2339–2351. https://doi.org/10.1038/s41396-018-0171-4