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Legume crops use a phosphorus-mobilising strategy to adapt to low plant-available phosphorus in acidic soil in southwest China

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Abstract: Phosphorus (P) deficiency significantly affects crop productivity, especially legume crops. Therefore, it is important to understand the P-acquisition strategies of different leguminous crops. In this study, we undertook a pot experiment with 11 legume crops (soybean, faba bean, pea, cowpea, common bean, lentil, adzuki bean, chickpea, grass pea, red kidney bean and common vetch) to investigate P-acquisition strategies related to root morphology, organic acid and acid phosphatase exudations, and arbuscular mycorrhizal fungi (AMF) colonisation under low (4.4 mg/kg) and optimal (40 mg/kg) P conditions. The results revealed that P deficiency significantly decreased biomass and P accumulation, root length (10.5%), and root surface area (7.9%), increased organic acid exudation (80.2%) and acid phosphatase activity (16.8%), and did not affect root diameter or root AMF colonisation rate. Principal component analysis revealed a positive correlation between organic acid exudation and acid phosphatase activity, while root length and root surface area negatively correlated with organic acid exudation, acid phosphatase activity and root AMF colonisation rate. P accumulation positively correlated with root length, surface area, and diameter but negatively correlated with organic acid exudation, acid phosphatase activity, and AMF colonisation rate. These findings confirmed the following: (1) legume crops use a P-mobilisation strategy related to organic acid exudation and acid phosphatase activity to acquire P under low soil P conditions; (2) organic acid exudation coincided with acid phosphatase activity to mobilise soil inorganic and organic P, improving P accumulation; (3) a trade-off exists between the P-scavenging strategy related to root morphology traits and mobilisation strategy.

Keywords: phosphorus deficiency; macronutrient; adaptability; root exudates; arbuscular mycorrhizal symbiosis

Phosphorus (P), an important component of nucleic acids, phospholipids, ATP, and other major functional substances, participates in plant protein synthesis, photosynthesis, and respiratory metabolism (Castagno et al. 2021). However, despite the high total P in soils (400–1 200 mg/kg), plant-available soil P is often limited due to forming insoluble complexes with iron and aluminium (Bhadouria et al. 2017).

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Organic P, accounting for 30–65% of total soil P, is typically less readily absorbed and used by crops (Castagno et al. 2021). Acidic soils, accounting for about one-fifth of China's arable land, pose additional challenges with low pH levels below 4.5 (Ling et al. 2023). In regions like Guizhou province, characterised by strong karst plateaus, mountainous areas, and human interference and destruction, soil fertility has significantly declined, particularly soil available P (He et al. 2019, Zhang et al. 2019). This scarcity of P is a major limiting factor for crop productivity (He et al. 2017, Yang et al. 2022), highlighting the need to understand crop P-acquisition strategies in these areas to improve agricultural output.

Legumes are important grain and oil crops in China, contributing significantly to human dietary protein. However, the low plant-available P impairs the legume crop yields and quality (Li et al. 2022b). Root traits have shown promise for improving P uptake (Lynch 2019), with shallow-rooted legume crops typically more tolerant to low P stress (Lynch 2019, Yi et al. 2022). Under P deficit, soybean (*Glycine max* (L.) Merr) produced high adventitious roots (Zhao et al. 2004), and common bean (*Phaseolus vulgaris* L.) exhibited a "topsoil foraging" strategy to increase P uptake (Lynch 2019, Yi et al. 2022). Moreover, legume crop roots can form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), enhancing P absorption (Tawaraya 2022). These fungi create extensive mycelium networks that extend the P-absorbing range from the immediate root zone (4 mm) to distances of 17 cm or more (Ye et al. 2013, Zhang et al. 2016). Root exudates play a critical role in plant root-soil rhizosphere microbial interactions and are considered a key mechanism for plants to adapt to low P environments (Li et al. 2022b). Low P stress induces the release of organic acids and acid phosphatase in lupin (*Lupinus micranthus* Guss), soybean, common bean, maise (*Zea mays* L.), wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), enhancing inorganic or organic P uptake (Alberto et al. 2019, Tian et al. 2019, Ding et al. 2020). However, previous studies have focused on limited crop species and specific root traits, with few investigations into P-acquisition strategies across diverse legume crop species. Understanding these P-acquisition strategies is essential for improving legume crop productivity under low P soil conditions.

During the long evolution process, plants have developed diverse belowground strategies to enhance P uptake under P deficit (Lambers 2021). A P-mobilisation strategy related to carboxylate release has been reported in plants grown in P-impoverished soils in southwestern Australia (Lambers et al. 2018). Lupins, for instance, exhibit greater changes in root acid phosphatase activity than root morphology under low P stress (Wu et al. 2021), indicating that lupin uses a P-mobilisation strategy related to acid phosphatase release. Conversely, increasing root length and AMF colonisation rates, a P-scavenging strategy, can facilitate P uptake under low soil-available P conditions (Zhang et al. 2019, 2022). However, the specific P-acquisition strategies adopted across legume crop species remain poorly understood.

Consequently, this study investigated the P-acquisition strategies of 11 legume crop species under low soil P conditions to (1) compare their P-acquisition strategies and adaptability to low P stress; (2) investigate the contributions of root morphological traits, root exudates, and AMF colonisation rate to P accumulation in low P environments; (3) identify key root traits related to low P tolerance in legume crops.

MATERIAL AND METHODS

Experimental setup. A pot experiment was conducted at Guizhou University's West Campus (26°26'42"N, 106°39'28"E) in Guiyang city, Guizhou province, from April to June 2022. The study included 11 legume crop species: soybean (*Glycine max* L.), faba bean (*Vicia faba* L.), pea (*Pisum sativum* L.), cowpea (*Vigna unguiculata* L.), common bean (*Phaseolus vulgaris* L.), lentil (*Lens culinaris*), adzuki bean (*Vigna umbellate*), chickpea (*Cicer arietinum* L.), grass pea (*Lathyrus sativus* L.), red kidney bean (*Phaseolus vulgaris*) and common vetch (*Vicia sativa* L.). The pots were arranged in a completely randomised design, with five replicates for each species and treatment combination. Each pot (26 cm high and 17 cm diameter) contained 5 kg soil. After germination, four seeds were sown in each pot and later thinned to two. Fertilisation was applied 25 days after sowing at one of two P rates: optimal P (OP) received 40 mg P/kg (applied as KH_2PO_4) and 20 mg N/kg (applied as NH_4HCO_3), while low P (LP) received 4.4 mg P/kg and 20 mg N/kg. The amounts of KH_2PO_4 and NH_4HCO_3 required for 55 pots under OP were calculated and dissolved in 5.5 L water, with 100 mL/pot applied to each pot. The LP pots used the same method, but KCl was added to balance the K fertiliser application with that under OP. The soil was an orthic acrisol collected from 30–40 cm soil depth (26°6'32"N, 106°5'59"E) in Lian village, Jichang Town, Anshun city, Guizhou province. Soil parameters mentioned above were determined following the methods in Zhang et al. (2022b). Soil pH was determined by deionisation water extraction, t with a 2.5:1 deionisation water:to soil ratio. About 0.5 g of soil was digested with $K_2Cr_2O_7$-H_2SO_4 and titrated with $FeSO_4$ to determine soil organic carbon (Nelson and Sommers 1982). Soil-available P (Olsen-P) was extracted by 0.5 mol/L $NaHCO_3$, the molybdenum blue method was used to determine available P concentrations, total P was melted by NaOH, washed by concentrated sulfuric acid, and determined by molybdenum-stibium anti-spectrophotometry (Bao 2000). The basic soil physical and chemical properties were as follows: pH 5.26, 9.88 g/kg organic carbon, 0.38 g/kg total P, 1.26 g/kg total nitrogen, 5.25 g/kg total potassium, and 5.68 mg/kg available P.

Harvest and measurements. Plants were harvested at the flowering stage, 45~60 days after sowing. Eight root functional traits related to P acquisition were measured: root length, root surface area, root diameter, specific root length, root volume, organic acid exudation, acid phosphatase activity, and AMF colonisation rate. The shoot and root samples were oven-dried at 75 °C for 48 h to constant weight, weighed, and ground to a fine powder to determine P content using a molybdenum-antimony-scandium colour agent (Bao 2000). Phosphorus accumulation (mg/plant) was calculated by multiplying root and shoot biomass by P concentration.

Root morphological traits and root exudates. For exudate collection, roots were carefully removed and gently shaken to remove non-rhizosphere soil and then rinsed and soaked multiple times with deionised water to remove rhizosphere soil while minimising root damage. The entire root systems of each plant were placed in a collection bottle containing 50 mL of 0.02 mmol $CaCl_2$ solution (deionised water) and stored in the dark for 1 h. The collection solutions were filtered, shaken, transferred into two 10 mL tubes and stored at –20 °C for further analysis. Two to three drops of 0.05% thymol were added to inhibit microbial decomposition of root exudates (Zhang et al. 2016). The HPLC method in Ye et al. (2013) was used to determine seven organic acid components (oxalic acid, tartaric acid, malic acid, lactic acid, citric acid, fumaric acid, and succinic acid) using an Agilent 1260 Infinity II system (Agilent Technologies, Santa Clara, USA). Acid phosphatase activity was measured using the p-nitrophenol phosphate disodium (p-NPP) method, according to Wu et al. (2021).

After collecting the root exudates, the roots were scanned with an Epson PV850 Pro-scanner (Epson Inc., Long Beach, USA), and analysed using WinRhizo 2019 Pro (Régent Instruments, Inc., Quebec, Canada) to determine root length, surface area, diameter, and volume. Specific root lengths were obtained by dividing root length by root dry weight.

They estimated the AMF colonisation rate. Approximately 0.3–0.5 g lateral roots were randomly sampled and stored in glutaraldehyde and formaldehyde alcohol acetic acid fixatives for the mycorrhizal colonisation experiment. The trypan blue staining method used 30 randomly selected stained root segments on prepared glass slides to observe mycelia and vesicles, with five visual scopes randomly chosen in each small root segment. Infection rates were calculated as follows:

$$\text{AMF infection rates (\%)} = \frac{\text{N1}}{\text{N2} \times \text{N3}} \times 100\%$$

where: N1 – total number of observed fields with mycelium and vesicle infection; N2 – five visual fields observed randomly in each small root segment; N3 – 30 randomly selected stained root segments.

Data analysis. Data analysis was conducted using SPSS 26.0 software (IBM, Chicago, USA). The effects of species, P rate and their interactions on biomass, P accumulation, root morphological traits, root exudates, and mycorrhizal symbiosis were assessed by two-way analysis of variance (ANOVA). Pearson's correlation analysis examined correlations among root functional traits, P accumulation, and biomass. The least significant differences (*LSD*) were calculated at $P = 0.05$. Principal component analysis was performed with Origin 2022 (Origin Lab, Northampton, USA).

RESULTS

Biomass and P accumulation. Shoot and root dry weights and P accumulation ranged from 0.73~5.89 g/plant, 0.15~1.66 g/plant, and 4.17~22.34 mg/plant, respectively (Table 1). Without P supply, shoot and root dry weights and P accumulation significantly decreased by 16.9, 24.7 and 23.6%, respectively, with significant species P level interactions for each parameter (Table 1). Faba beans had the highest shoot and root dry weights and P accumulation, while lentils had the lowest values (Table 1).

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Table 1. Shoot and root dry weights and phosphorus (P) accumulation for 11 legume crops under optimal P (OP) and low P (LP) environments

Species	P level	Shoot dry weight	Root dry weight	P accumulation
		(g/plant)		(mg/plant)
Soybean	OP	1.67 ± 0.16^{a}	0.44 ± 0.04^{a}	8.0 ± 0.5^{a}
	LP	1.40 ± 0.14^{b}	0.44 ± 0.05^{a}	5.7 ± 0.1^{b}
Faba bean	OP	5.89 ± 0.38^{a}	1.66 ± 0.10^{a}	22.3 ± 0.3^{a}
	LP	4.14 ± 0.36^{b}	1.02 ± 0.09^{b}	18.3 ± 1.3^{b}
Pea	OP	2.41 ± 0.25^{a}	0.33 ± 0.07^{a}	10.5 ± 0.9^{a}
	LP	2.55 ± 0.11^{a}	0.31 ± 0.02^{a}	9.1 ± 0.3^{b}
Cowpea	OP	1.40 ± 0.17^{a}	0.45 ± 0.06^{a}	7.6 ± 0.3^{a}
	LP	1.08 ± 0.14^{b}	0.32 ± 0.02^{b}	6.1 ± 0.9^{b}
Common bean	OP	1.41 ± 0.12^{a}	0.37 ± 0.04^{a}	9.8 ± 0.5^{a}
	LP	0.84 ± 0.06^{b}	0.26 ± 0.02^{b}	6.5 ± 0.6^{b}
Lentil	OP	0.85 ± 0.12^{a}	0.21 ± 0.02^{a}	4.2 ± 0.3^{a}
	LP	0.73 ± 0.01^{a}	0.15 ± 0.01^{b}	4.2 ± 0.1^{a}
Adzuki bean	OP	1.72 ± 0.11^{a}	0.54 ± 0.03^{a}	15.4 ± 1.3^{a}
	LP	1.44 ± 0.17^{b}	0.36 ± 0.02^{b}	8.7 ± 0.3^{b}
Chickpea	OP	1.78 ± 0.06^{a}	0.47 ± 0.04^{a}	8.7 ± 0.4^{a}
	LP	1.50 ± 0.16^{b}	0.42 ± 0.02^{b}	6.1 ± 0.2^{b}
Grass pea	OP	2.15 ± 0.20^{a}	0.39 ± 0.06^{a}	11.2 ± 1.0^{a}
	LP	2.35 ± 0.10^{b}	0.36 ± 0.03^{a}	9.6 ± 1.1^{b}
Red kidney bean	OP	3.19 ± 0.28^{a}	0.52 ± 0.06^{a}	9.9 ± 0.2^{a}
	LP	2.69 ± 0.20^{b}	0.44 ± 0.02^{b}	8.5 ± 0.4^{b}
Common vetch	OP	1.66 ± 0.15^{a}	0.33 ± 0.03^{a}	8.5 ± 0.3^{a}
	LP	1.32 ± 0.10^{b}	0.22 ± 0.03^{b}	5.9 ± 0.3^{b}
Species		0.35***	0.09***	1.3***
P level		0.15***	0.04***	0.5***
Species × P level		0.50***	0.13**	1.8***

Data are mean ± standard error (SE, $n = 3$). Different letters indicate significant differences between two P levels within a legume crop cultivar. $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$; ns – not significant at $P = 0.05$

Root morphology traits. Genetic variations in root length, surface area, diameter, volume, and specific root length were evident among the 11 legume species. The interaction between species × P levels interaction significantly affected root length, surface area, volume, and specific root length (Figure 1). P deficit significantly decreased root length (10.5%, $P < 0.05$) and surface area (7.9%, $P < 0.05$; Figure 1A, B). Under both P levels, the faba bean had the greatest root length and surface area, while the cowpea had the lowest values (Figure 1A, B). Root diameter did not respond to the P deficit, and the faba bean had the largest root diameter under both P levels (Figure 1C). P deficit did not affect specific root lengths across all legume crop species, but the specific root lengths of soybean, common bean, and grass pea significantly increased under low P conditions (Figure 1D).

Root exudates, acid phosphatase and root AMF colonised rate. Genetic variations existed for root-exudated organic acid content and acid phosphatase activity, with significant species × P level interactions (Figure 2). Total organic acids ranged from 162.3~6 003.3 μmol/g root dry weight (RDW) under low P and 142.2~3 516.6 μmol/g RDW under optimal P (Figure 2A). P deficit significantly increased organic acid (from 681.7 to 1 228.7 μmol/g RDW) and acid phosphatase (from 13.6 to 15.9 μg/h/g RDW) exudation (Figure 2A). Grass peas had the lowest organic acids under both P levels,while common beans had the highest values. Faba beans had the lowest acid

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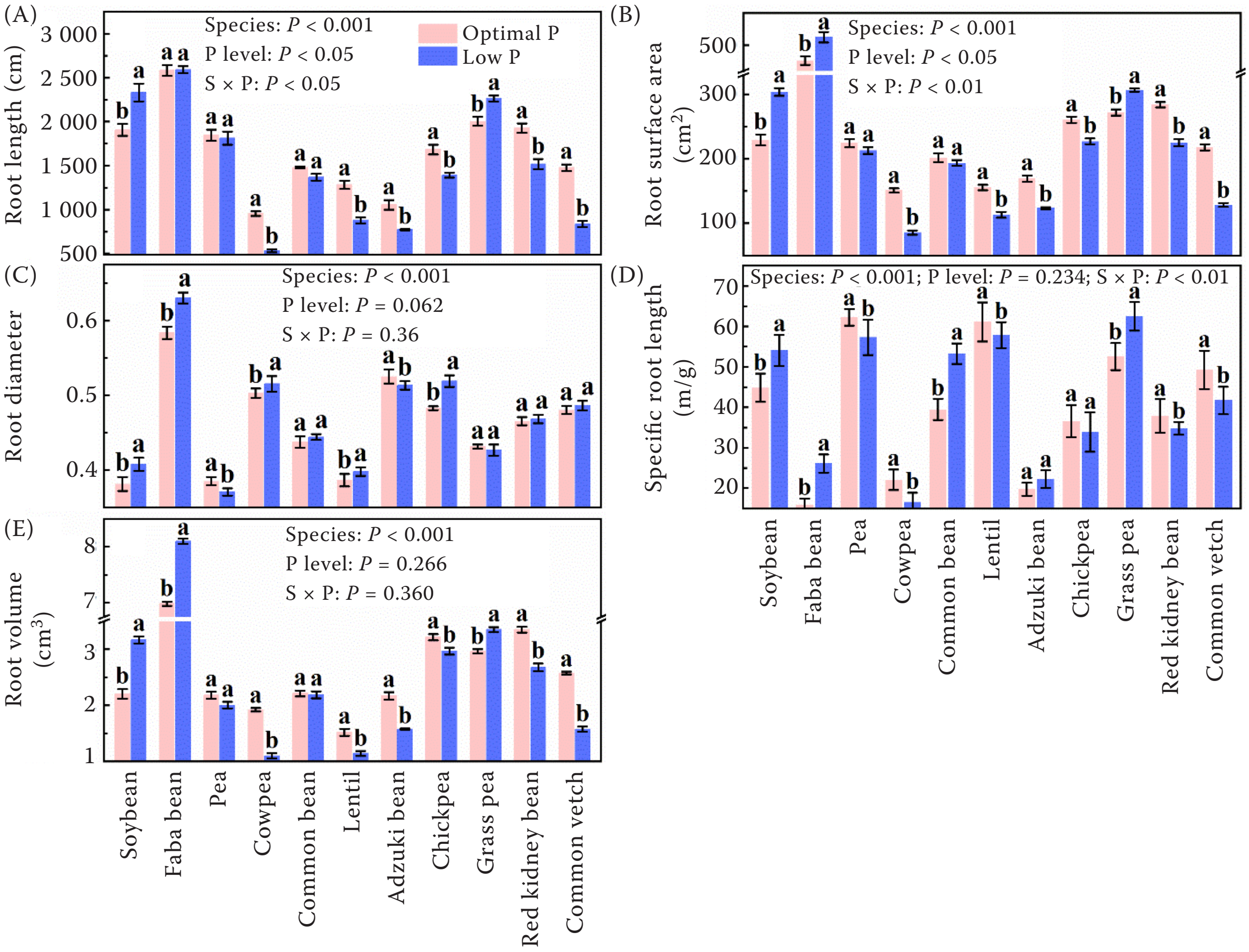

Figure 1. Effect of optimal phosphorus (P) and low P on (A) total root length; (B) root surface area; (C) root diameter; (D) specific root length, and (E) root volume of 11 legume crops. Bars showed as ± standard error (SE, $n = 5$). Different letters indicate significant differences between two P levels within a legume crop variety at $P = 0.05$

phosphatase activity under both P levels,while lentils had the highest values (Figure 2).

Variations in root AMF colonisation rates existed between species. However, the P deficit did not significantly affect the AMF colonisation rate (Figure 3). The AMF colonisation rate ranged from 64.0~99.6% under optimal P and 47.8~97.6% under low P, which significantly increased in pea, chickpea, and adzuki bean but decreased in soybean and lentil under P deficit (Figure 3).

Correlation and principal component analyses. The correlation analysis revealed positive correlations between P accumulation and shoot ($r = 0.85$, $P < 0.001$) and root ($r = 0.84$, $P < 0.001$) biomass (Figure 4). P accumulation positively correlated with root length ($r = 0.56$, $P < 0.001$), root surface area ($r = 0.74$, $P < 0.001$), root volume ($r = 0.80$, $P < 0.001$), and root diameter ($r = 0.59$, $P < 0.001$) but negatively correlated with specific root length ($r = –0.43$, $P < 0.001$), organic acid exudation ($r = –0.22$, $P < 0.05$), acid phosphatase activity ($r = –0.62$, $P < 0.001$), and AMF colonisation rate ($r = –0.33$, $P < 0.001$; Figure 4). Acid phosphatase activity positively correlated with specific root length ($r = 0.54$, $P < 0.001$) but negatively correlated with root diameter ($r = –0.26$, $P < 0.01$; Figure 4). Root morphological parameters negatively correlated with organic acid exudation, acid phosphatase activity, and AMF colonisation rate (Figure 4).

The principal component analysis based on seven root functional traits of 11 legume crops explained 71.8% of the variation in the first two components (Figure 5). PC1 represented 45.2% of the variance and primarily comprised root surface area, organic acid exudation, acid phosphatase activity, and AMF colonisation rate. In contrast, PC2 represented 26.6% of the variability and primarily comprised root length, specific root length, and root diameter (Figure 5).

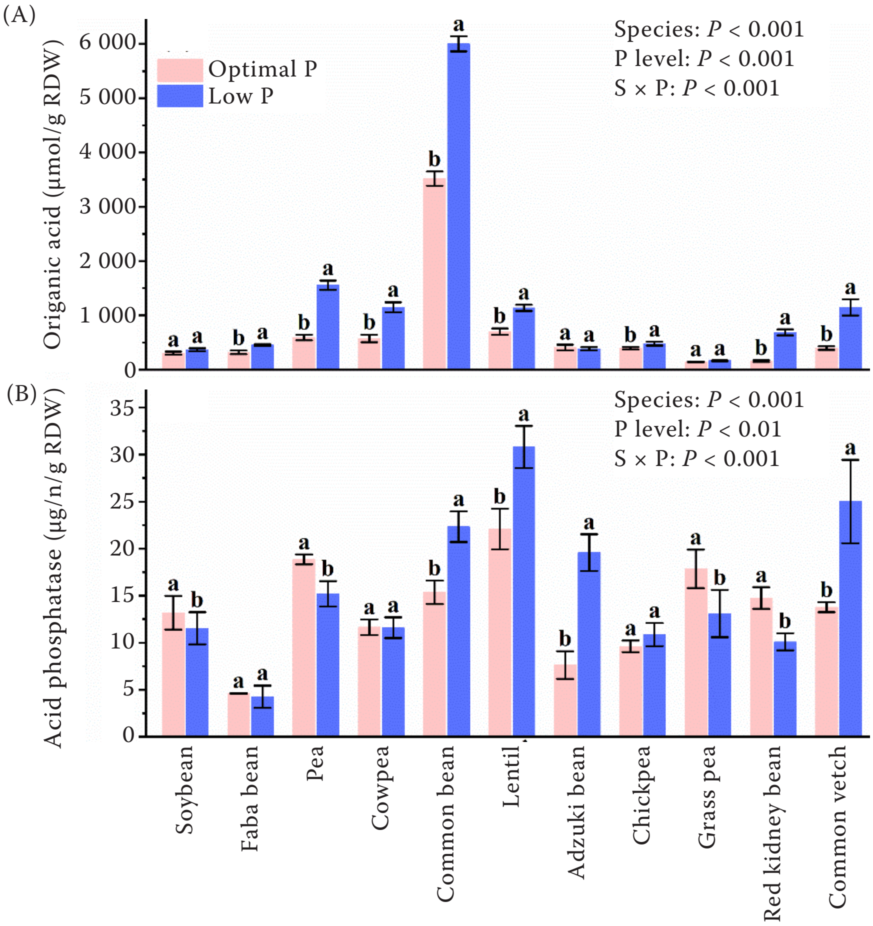

Figure 2. (A) Organic acid content and (B) acid phosphatase activity secreted by roots under optimal and low phosphorus (P) conditions for 11 legume crops. Data are mean ± standard error (SE, *n* = 3). Different letters indicate significant differences between two P levels within a legume crop variety at *P* = 0.05; RDW – root dry weight

Response of root morphological characteristic, carboxylates and mycorrhizal symbiosis to P deficit. This study highlighted the dynamic responses of root carboxylates and acid phosphatase to P deficiency, exhibiting greater plasticity than root morphology traits such as root length, root surface area, and root diameter in the 11 legume crops. Root plasticity is a crucial adaptation mechanism for efficient resource capture, including P acquisition from edaphic soil (Schnerider and Lynch 2020, He et al. 2021). The observed genetic variations and diverse responses of root morphology traits to P

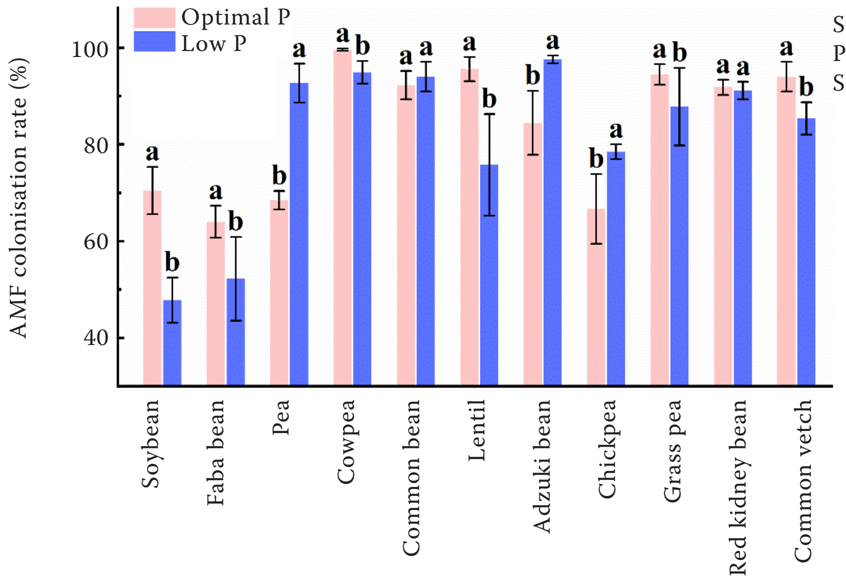

Figure 3. Arbuscular mycorrhizal fungi (AMF) colonisation rates of 11 legume crops under optimal phosphorus (P) or low P. Data are mean ± standard error (SE, *n* = 3). Different letters indicate significant differences between two P levels within a legume crop variety at *P* = 0.05

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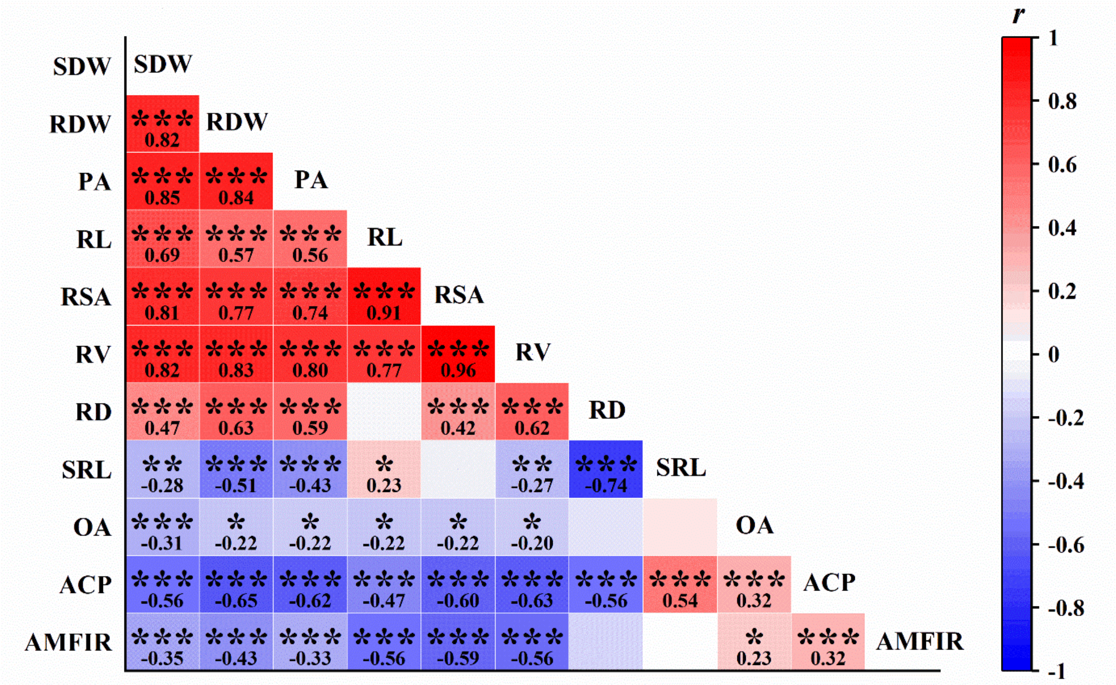

Figure 4. Pearson's correlation coefficients for root functional traits, phosphorus (P) accumulation, and biomass in 11 legume crops. SDW – shoot dry weight (DW); RDW – root DW; PA – P accumulation; RL – root length; RSA – root surface area; RV – root volume; RD – root diameter; SRL – specific root length; OA – organic acid exudation; ACP – acid phosphatase activity; AMFIR – arbuscular mycorrhizal fungi (AMF) infection rate. Data are mean correlation coefficients; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$

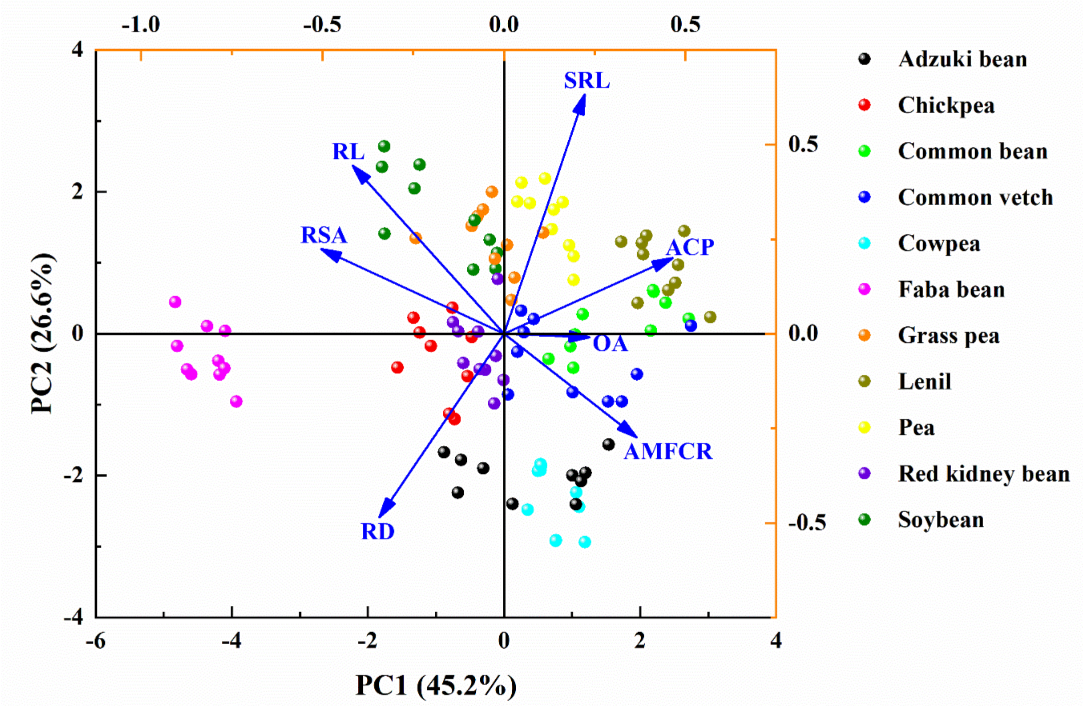

Figure 5. Principal component analysis of root length (RL), root surface area (RSA), root diameter (RD), specific root length (SRL), organic acid exudation (OA), acid phosphatase activity (ACP) and arbuscular mycorrhizal fungi (AMF) infection rate (AMFIR) for 11 legume crops

deficit underscored the significance of these traits in P accumulation under conditions of P deficit. This correlation between root morphology traits and P accumulation indicates that legume crops have varying P uptake abilities based on their root morphology (Li et al. 2022a, b). For instance, faba bean, with the highest P accumulation, had the most extensive root length, surface area, and volume, while lentil, with the lowest P accumulation, had the smallest of these traits. These findings imply results suggest that root length, surface area, and volume are primary drivers of P uptake, with variations in P accumulation largely attributed to differences in root morphology traits in legume crops (He et al. 2017, 2019, 2021). Longer root lengths, larger root surface areas, and greater root volumes enhance P accumulation by improving soil exploration, an efficient strategy for P accumulation under P deficit (Gamuyao et al. 2012, He et al. 2019). One possible explanation is that crops are grown in relatively P-rich agricultural soils than natural soils.

Root traits and P-acquisition strategy in legume crops. Plant roots play a crucial role in water and nutrient uptake, with different crops using various P-acquisition strategies in agroecosystems with uneven and low P availability (He et al. 2017, Zhang et al. 2019). These strategies are closely linked to a combination of root functional traits, explaining the diversity of P acquisition among crops (Yang et al. 2022). In this study, we observed contrasting P-acquisition strategies among legume crops (Figure 5). For instance, faba beans relied more on root morphology traits for P uptake, while lentils relied more on acid phosphatase activity and root AMF colonisation (Figure 5). The positive correlations between P accumulation and root morphological characteristics such as root length, surface area, and diameter, and negative correlations between P accumulation and root carboxylates, acid phosphatase, and root AM colonisation indicate that root morphology traits play more significant roles in P uptake than root carboxylates, acid phosphatase and root AMF colonisation. The positive correlation between carboxylate exudation and acid phosphatase activity suggests a coordinated action between these traits to release insoluble inorganic and organic P from the soil (Lambers 2021). The trade-off between different root functional traits involved in P acquisition explains the diversity in P-acquisition strategies, as each strategy varies in cost (Raven et al. 2018). Furthermore, this study confirmed that legume crops with different P-acquisition strategies exhibit distinct P accumulation abilities, highlighting their capacity to mobilise soil P by combining different root functional traits (Figure 5). Moreover, the negative correlation between P accumulation and root carboxylates could be attributed to roots not immediately taking up soil P released by root exudates, with the released P reabsorbed by soil particles (Lambers 2021). Another possible explanation is that soil microbes use the P mobilised by root carboxylates (Raymond et al. 2021), which requires further investigation. These findings also suggest that root carboxylates may have additional roles, such as recruiting beneficial root microorganisms (Pang et al. 2021).

In conclusion, this study revealed a trade-off between root morphological traits, root exudates, and mycorrhizal symbiosis, contributing to the multidirectional P-acquisition strategies of legume crop species with varying abilities to accumulate P. Legume crops adapt to P-deficit environments primarily by increasing root carboxylates and acid phosphatase. Future research should aim to verify the effect of soil microbes using root carboxylates on mobilised P.

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