Plant Soil
https://doi.org/10.1007/s11104-026-08651-z

RESEARCH ARTICLE

Root traits and rhizosphere phosphorus dynamics regulate phosphorus uptake in peanut across contrasting soils

Carlos Felipe dos Santos Cordeiro · Anita Beltrame · Chad Penn · Ciro Antonio Rosolem

Received: 18 September 2025 / Accepted: 11 May 2026
© The Author(s) 2026, modified publication 2026

Abstract

Aims Peanut (*Arachis hypogaea* L.) efficiently explores soil phosphorus (P) through root plasticity and rhizosphere modifications. However, how root system adjustments vary across soils with contrasting P availability remains unclear. This study evaluated peanut root traits, P uptake, and bulk soil and rhizosphere P dynamics under contrasting soil types and P levels.

Methods Two peanut cultivars contrasting in growth cycle and root development were grown under greenhouse conditions in three soil-specific experiments (sandy loam, silt loam, and silty clay loam) adjusted to low, medium, and high P levels. Plant biomass, root morphological traits, and P uptake were quantified, together with changes in bulk soil and rhizosphere P fractions.

Results Plants with more extensive root systems exhibited greater P uptake under low P conditions. In silt loam, root growth sustained biomass production even at low P, with minimal response to additional fertilization. Rhizosphere soils had, on average, 0.4 units lower pH than bulk soil and showed marked depletion of labile phosphorus fractions near roots. The degree of P depletion correlated with P uptake, particularly for water-extractable P. Despite higher total P in the silt loam, its lower solubility limited plant availability compared with sandy loam and silty clay loam.

Conclusion Enhanced P uptake in low-P soils was primarily driven by greater carbon allocation to roots, increased root length, and a mild, localized rhizosphere acidification, enabling the solubilization of less labile P forms. These findings highlight the potential of breeding and selecting peanut cultivars with superior root systems to improve P use efficiency and reduce reliance on phosphate fertilizers.

Keywords Peanut *(Arachis hypogaea* L.) · Root traits · Phosphorus solubility · Soil texture · Rhizosphere P dynamics

Responsible Editor: Carla S. Santos.

C. F. d. S. Cordeiro (✉) · C. A. Rosolem
Department of Agronomy, São Paulo Western University, Raposo Tavares HWY, Km 572, Presidente Prudente, São Paulo 19067-175, Brazil
e-mail: cordeirocfs@gmail.com; carloscordeiro@unoeste.br

A. Beltrame · C. Penn
Department of Agronomy, Purdue University, West Lafayette, IN 47907, USA

C. Penn
United States Department of Agriculture-Agricultural Research Service, National Soil Erosion Research Laboratory, West Lafayette, IN 47907, USA

C. A. Rosolem
Department of Crop Sciences, School of Agricultural Sciences, São Paulo State University, Botucatu, São Paulo, Brazil

Published online: 22 May 2026

Introduction

Although soils often contain elevated total phosphorus (P), only a small fraction is available for plant uptake due to strong sorption to iron (Fe), aluminum (Al), calcium (Ca) oxides, and clay minerals (Hinsinger 2001). Agriculture is the dominant consumer of inorganic phosphate fertilizers globally, and to sustain high yields, intensive cropping systems have often relied on P fertilization at rates exceeding crop removal, accounting for approximately 8%–25% of global inorganic phosphate fertilizer use (Roy et al. 2016). This dependency highlights the urgent need to improve phosphorus use efficiency (PUE) in cropping systems. Improving PUE, however, depends not only on fertilizer management but also on a mechanistic understanding of how plants access soil P within the rhizosphere, where P availability is dynamically regulated (Cordeiro and Rosolem 2026).

Phosphorus use efficiency can be divided into two components: phosphorus utilization efficiency and phosphorus uptake efficiency. Phosphorus utilization efficiency refers to the yield produced per unit mass of P taken up by the plant, with more efficient genotypes producing higher yields with lower P uptake. Phosphorus uptake efficiency reflects the ability of plants to acquire phosphorus from the soil P pool as a whole, encompassing both readily available and less labile P forms. Root traits such as greater root length density, smaller root diameters, and higher carbon allocation to roots expand the soil volume explored and increase contact with P sources (Rosolem et al. 1999; Otani and Ae 1996). In addition, rhizosphere modifications, including organic acid exudation and phosphatase activity, can mobilize less labile P fractions (Almeida et al. 2020; Janegitz et al. 2017). Because orthophosphate concentrations in soil solution are typically low and rapidly depleted near the root surface, steep concentration gradients develop in the rhizosphere, making P supply to the root—rather than uptake kinetics—the primary limitation to P acquisition (Barber 1995). These processes are often accompanied by a localized and moderate decrease in rhizosphere pH, which can alter sorption–desorption equilibria and enhance P mobilization without inducing detrimental soil acidity (Hinsinger 2001). However, significant gaps remain regarding how these processes vary across soils with contrasting P pools and solubility.

Peanut (*Arachis hypogaea* L.) is recognized for its strong ability to mobilize P from poorly soluble forms, including Ca-bound P under alkaline conditions (Shibata and Yano 2003) and Fe/Al-bound P under acidic conditions through root exudates and microbial associations (Wissuwa and Ae 2001; Jiang et al. 2024). Despite reports of no differences in P uptake between Valencia and Spanish peanut types, regardless of differences in root length (Murabayashi et al. 1994), recent studies in tropical sandy soils showed that Virginia-type peanut cultivars with more extensive root systems exhibit higher P uptake efficiency under low-P conditions (Cordeiro et al. 2024), resulting in higher yields (Cordeiro et al. 2025). These findings suggest that variation in root traits is a major driver of P efficiency, yet it remains unclear whether these advantages persist across soils with different textures, desorption capacities (i.e., the ability of soils to release sorbed P from mineral surfaces into the soil solution), and inherent P pools.

In addition to genetic variation in root development, peanut cultivars differ in growth duration. Late-maturing cultivars generally allocate more carbon to roots over a longer period, potentially enhancing P uptake under low-P conditions (Cordeiro et al. 2024). In contrast, early-maturing cultivars tend to depend more strongly on readily available P (Cordeiro et al. 2025). Still, it is uncertain whether the superiority of late types can be attributed primarily to root system investment or merely to their longer life cycle.

We hypothesized that cultivars allocating more carbon to roots and developing longer root systems would explore and deplete soil P more effectively in the rhizosphere, enhance mobilization of less labile P fractions, and maintain higher P uptake under P-deficient conditions. To test this, we compared two peanut cultivars differing in growth cycle duration and root system size in three independent soil-specific experiments**,** conducted on sandy loam, silt loam, and silty clay loam soils adjusted to low, medium, and high P levels. Specifically, we expected that: (i) cultivars with greater carbon allocation to roots would exhibit superior P uptake in soils with limited labile P. (ii) rhizosphere P depletion and acidification would correlate directly with root length and P uptake. (iii) soil texture and P desorption capacity would modulate the relative advantage of extensive root systems. By explicitly linking root traits, rhizosphere P dynamics, and soil properties, this study provides a

mechanistic framework to improve PUE and reduce fertilizer dependence in peanut production systems.

Material and methods

Experimental design and setup

Two peanut cultivars contrasting in growth cycle and root development were selected: IAC OL3 (early-maturing, shorter cycle, reduced root system) and IAC 503 (late-maturing, longer cycle, greater carbon allocation to roots, and more extensive root length) (Cordeiro et al. 2024). This contrast allowed evaluation of how variation in root traits influences phosphorus (P) acquisition under contrasting soil conditions.

Three independent greenhouse experiments were conducted, each using a distinct soil texture: sandy loam (Typic Hapludult, Ultisol), silt loam (Typic Hapludalf, Alfisol), and silty clay loam (Typic Argiudoll, Mollisol). Within each soil-specific experiment, treatments were arranged in a 2×3 factorial design consisting of two cultivars (IAC OL3 and IAC 503) and three soil P levels (low, medium, and high), following a randomized complete block design with four replications.

Soils with low labile P content were collected in November 2023 from the 0.00–0.20 m layer. Sandy loam and silt loam soils were sampled in Indiana (40°20′56.0″N, 82°45′37.5″W; 40°20′43.1″N, 87°03′27.2″W), and the silty clay loam soil was sampled in Ohio (40°28′17.6″N, 86°59′52.2″W), USA. All sites had been under soybean and maize production in recent years. Initial soil chemical and physical properties, including pH, are presented in Table 1. M3: Mehlich-3. pH: water

Within each experiment, three P levels were established based on target Mehlich-3 P concentrations of 17, 35, and 70 mg kg^{-1}, corresponding to low, medium, and high P levels, respectively. The original soils served as the low-P treatment, while medium- and high-P treatments were obtained through P fertilization as described below.

Soil incubation and soil preparation

A preliminary incubation study was conducted to calibrate P additions required to achieve the target medium and high soil P levels. For this purpose, 200 g of each soil were placed in individual containers and amended with increasing amounts of a concentrated KH_2PO_4 solution, corresponding to discrete P additions ranging from 0 to 176 mg kg^{-1}. These stepped P additions were used solely to establish the relationship between applied P and soil-test P.

Each P solution was diluted in 100 mL of deionized water and applied to the soil, bringing moisture content to approximately 50% of field capacity. Soils were incubated at ~28 °C for four days, air-dried for two days, and re-incubated for an additional four days after the addition of 100 mL of water. This 8-day wet–dry cycle was used to accelerate equilibration of added P with soil constituents. However, it is acknowledged that this relatively short incubation period may not have been sufficient to achieve full equilibrium between applied phosphorus and soil fractions.

Table 1 Selected soil characteristics before the experiment

Soil type	pH	P	Al	S	Ca	Mg	K	–
		M3 extractable						
		μg g^{-1}	mg kg^{-1}					
Sandy loam	5.81	17.3	587.6	41.0	953.3	218.4	152.5	–
Silt loam	6.22	15.8	798.1	85.8	2230.0	440.1	131.1	–
Silty clay loam	6.35	15.0	698.8	109.5	2926.3	768.9	187.4	–
	B	Cu	Zn	Mn	Fe	Clay	Sandy	Silt
	μg^{-1}					%		
Sandy loam	0.20	1.20	2.00	109.2	156.1	11.3	58.7	30.0
Silt loam	0.40	2.70	1.60	170.3	131.2	18.8	23.0	58.3
Silty clay loam	0.40	2.90	1.90	67.0	150.9	28.5	14.1	57.4

M3 Mehlich-3, *pH* water

After equilibration, soils were air-dried and analyzed for Mehlich-3 extractable P using the Mehlich-3 chemical extractant (Mehlich 1978), a multi-element solution commonly used to estimate plant-available P. Linear response curves relating applied P to equilibrated Mehlich-3 P were generated for each soil and used to calculate the P rates required to achieve the target medium and high P levels.

For large-scale incubation, soils were amended following the same procedure using 20 L buckets containing 15 kg of soil and 7.5 L of solution. Potassium chloride was applied to balance K inputs associated with the P treatments. Due to low Ca and S availability in the sandy loam soil, 280 mg kg^{-1} of $CaSO_4$ was added. After equilibration, soils were placed in 4 L pots containing 3 kg of soil.

In this study, different phosphorus fractions were used to represent P pools with contrasting lability and potential availability. Water-extractable P represents the most readily available phosphorus in soil solution. Resin- and Mehlich-3–extractable P represent labile and plant-available P pools. Ammonium citrate–extractable P represents moderately labile P associated with mineral surfaces, whereas ammonium oxalate–extractable P reflects P bound to amorphous Fe and Al oxides. Soil P was characterized using these extractants to assess inherent soil P pools rather than treatment effects.

Greenhouse conditions and plant growth

The experiments were conducted under greenhouse conditions with a 14 h photoperiod, maximum daytime temperature of 30, and minimum nighttime temperature of 22 °C. Four peanut seeds were planted per pot on February 16, 2024, and full emergence occurred eight days later. Ten days after emergence, seedlings were thinned to one plant per pot.

Fifteen days after emergence, 90 mg kg^{-1} of N was applied as urea. Soil moisture was maintained at 60%–70% of water-holding capacity and monitored using tensiometers. Plants were harvested on May 2, 2024, 67 days after emergence, when the late-maturing cultivar had reached the R4 (full pod) stage and the early-maturing cultivar had reached R5 (beginning seed).

Sample collection and analysis

At harvest, plants were separated into leaves, stems, gynophores, and pods. Samples were washed, oven-dried at 65 °C for 72 h, ground to pass a 0.50 mm sieve, and digested using strong acid and peroxide (Zarcinas et al. 1987). Phosphorus concentrations were determined by inductively coupled plasma atomic emission spectroscopy (ICP-AES; Optima 8300, Thermo Fisher Scientific).

Roots were carefully separated, and 10–15 g of rhizosphere soil was collected by gently shaking the roots to remove loosely adhering soil, followed by the collection of soil remaining attached to the root surface using tweezers, corresponding approximately to a thickness of 1–2 mm around the roots. Roots were washed, stored at 10 °C, and scanned in a water-filled tray using an Epson LA2400 scanner. Root traits, including total root length, root volume, and average root diameter, were analyzed using WinRhizo software (Regent Instruments). Root length density was calculated as the ratio of total root length to the total soil volume of the pot.

Root samples were oven-dried, weighed, ground, and analyzed for P concentration. Total plant P uptake was calculated based on dry matter production of all plant components and their respective P concentrations.

Soil samples were analyzed for pH in a 1:5 soil-to-water ratio (Thomas, 1996) and for Mehlich-3 P. Ammonium citrate, anion exchange resin, ammonium oxalate, and total P extractions were performed following established protocols, and P, Fe, and Al concentrations were measured by ICP-AES. The degree of P saturation (DPS) was calculated as the molar ratio of oxalate-extractable P to Al + Fe.

In uncultivated soils, P desorption was evaluated under flowing water conditions following Penn et al. (2022). Briefly, deionized water was passed through 5 g of soil at 0.14 mL min^{-1} using a peristaltic pump connected to a constant-head Mariotte bottle (Fig. 1). Leachates were collected every 60 min and analyzed for dissolved P to generate desorption kinetics.

Statistical analysis

Within each soil-specific experiment, data were analyzed using a 2 × 3 factorial design (cultivar × P level) in a randomized complete block design with four replications. Cultivar and P level were treated as fixed

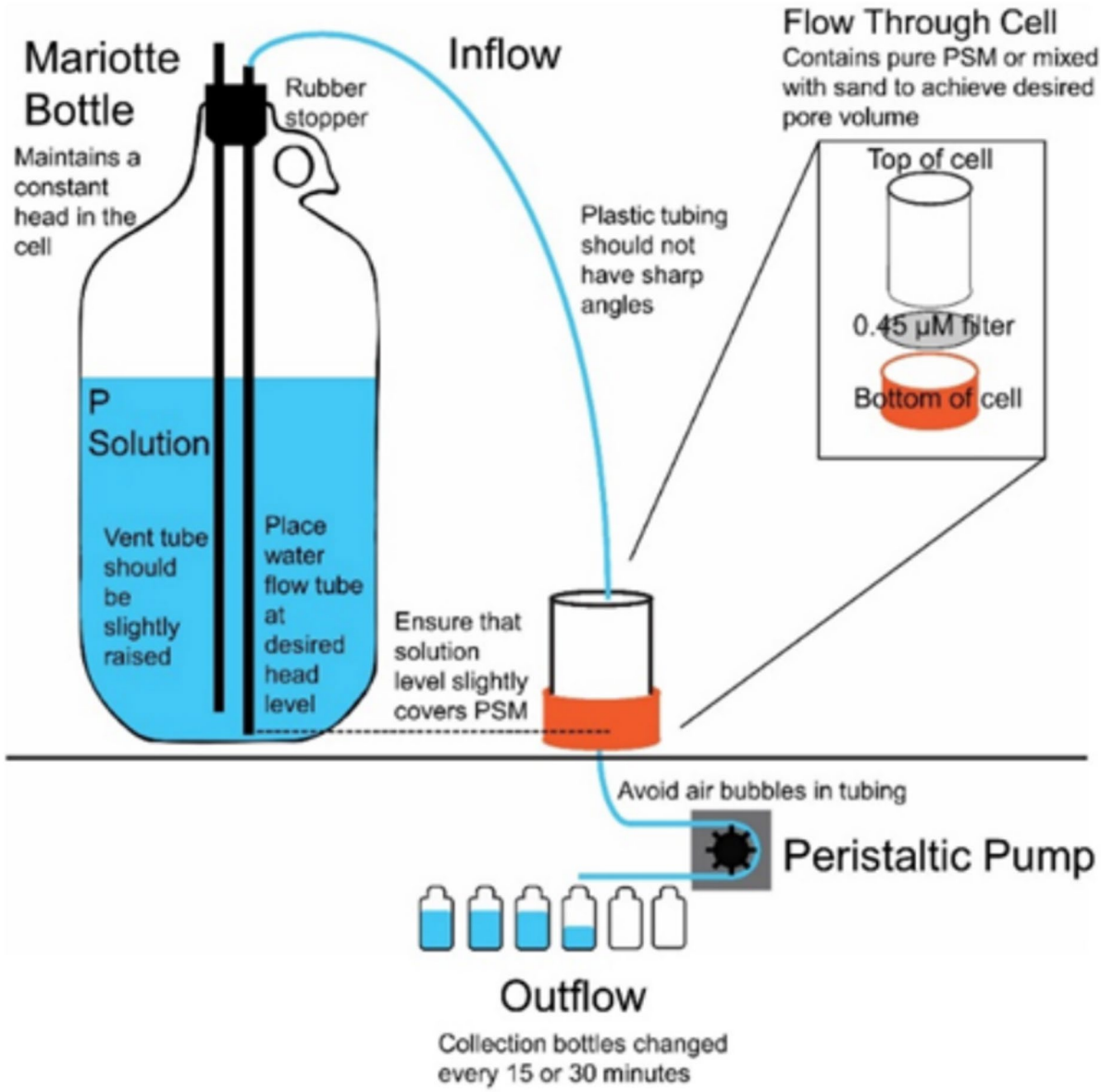


Fig. 1 Diagram showing the components of the flow-through system for studying phosphorus desorption under flowing conditions

effects and block as a random effect. Analyses were conducted using generalized linear mixed models in SAS GLIMMIX (version 9.4 M3). When significant effects were detected, means were compared using the least significant difference (LSD) test at $p < 0.05$. Regression analyses were performed to evaluate relationships between P uptake, root length, biomass production, and changes in rhizosphere P relative to bulk soil.

Results

Biomass yield

Peanut biomass production responded to P supply in a soil-dependent manner (Table 2). In the sandy loam and silty clay loam soils, total biomass increased from low to medium P, with no further gains at high P, regardless of cultivar. In contrast,

Table 2 Vegetative and reproductive growth of two peanut cultivars grown under three P levels in three soil-specific experiments. Within each soil texture, different lowercase letters indicate significant differences among P levels for a given cultivar, whereas ** indicates significant differences between cultivars within the same P level. *Ns* denotes non-significant differences. Means were compared using the LSD test ($p < 0.05$)

Sandy loam		Leaf		Stem		Pods	
	Cultivar	Early cv	Late cv	Early cv	Late cv	Early cv	Late cv
		g plant^{-1}					
	P levels						
	Low P	9.5 a	9.6 b^{ns}	5.7 b	8.7 b**	4.6 c	3.7 b**
	Medium P	12.4 a	13.2 a^{ns}	8.6 a	9.9 a**	7.1 a	4.1 a**
	High P	12.5 a	11.3 ab^{ns}	8.0 a	8.6 b^{ns}	6.1 b	3.1 b**
		Roots		Shoot		Total biomass	
		g plant^{-1}					
	Low P	3.1 c	4.1 ab**	19.8 b	22.4 b^{ns}	22.9 b	26.2 b^{ns}
	Medium P	3.7 b	4.5 a**	28.1 a	27.2 a^{ns}	31.8 a	31.7 a^{ns}
	High P	4.3 a	3.8 b^{ns}	26.5 a	22.9 b**	30.8 a	26.7 b**
		Shoot: root		Pods		Gynophores	
		ratio		number			
	Low P	6.4 b	5.4 b**	16.5 a	7.0 a**	39.2 c	33.5 b^{ns}
	Medium P	7.4 a	6.1 a**	19.5 a	8.2 a**	51.0 b	50.0 a^{ns}
	High P	6.3 b	6.0 a^{ns}	15.0 a	11.3 a^{ns}	65.5 a	32.5 b**
Silt loam		Leaf		Stem		Pods	
	Cultivar	Early cv	Late cv	Early cv	Late cv	Early cv	Late cv
		g plant^{-1}					
	P levels						
	Low P	11.2 b	11.7 a^{ns}	9.0 b	8.8 b^{ns}	2.4 b	2.7 a^{ns}
	Medium P	14.1 a	12.9 a^{ns}	10.1 ab	11.1 a^{ns}	4.6 a	2.4 a**
	High P	14.6 a	13.7 a^{ns}	11.4 a	11.2 a^{ns}	3.1 b	2.7 a^{ns}
		Roots		Shoot		Total biomass	
		g plant^{-1}					
	Low P	3.1 b	3.8 a**	22.6 b	23.1 a^{ns}	25.7 b	27.1 a^{ns}
	Medium P	4.1 a	4.2 a^{ns}	28.7 a	26.4 a^{ns}	32.8 a	30.5 a^{ns}
	High P	4.3 a	4.2 a^{ns}	29.1 a	27.2 a^{ns}	33.4 a	31.3 a^{ns}
		Shoot: root		Pods		Gynophores	
		ratio		number			
	Low P	7.2 a	6.1 a**	14.3 a	6.8 a**	56.8 a	35.0 a**
	Medium P	7.0 a	6.4 a^{ns}	16.5 a	4.0 a**	50.5 a	33.0 a**
	High P	6.7 a	6.6 a^{ns}	9.2 a	4.5 a^{ns}	53.0 a	34.0 a**
		Leaf		Stem		Pods	

Table 2 (continued)

Silty clay loam	Cultivar	Early cv	Late cv	Early cv	Late cv	Early cv	Late cv
		g plant^{-1}					
	P levels						
	Low P	9.5 b	9.6 b^{ns}	5.7 b	8.7 b**	4.6 c	3.7 a**
	Medium P	12.4 a	13.2 a^{ns}	8.6 a	9.6 a**	7.0 a	4.0 a**
	High P	12.4 a	11.3 ab^{ns}	8.0 a	8.6 b^{ns}	6.1 b	3.1 b**
		Roots		Shoot		Total biomass	
		g plant^{-1}					
	Low P	3.1 b	4.2 ab**	19.8 b	22.1 b**	22.9 b	26.1 b**
	Medium P	3.8 b	4.5 a**	28.1 a	27.2 a^{ns}	31.8 a	31.7 a^{ns}
	High P	4.3 a	3.8 b^{ns}	26.5 a	22.2 b**	30.8 a	26.7 b**
		Shoot: root		Pods		Gynophores	
		ratio		number			
	Low P	6.4 b	5.4 b**	16.5 a	7.0 a**	39.2 c	33.5 b^{ns}
	Medium P	7.4 a	6.1 a**	19.5 a	8.3 a**	51.0 b	50.0 a^{ns}
	High P	6.3 b	6.0 a^{ns}	15.0 a	11.3 a^{ns}	65.5 a	32.5 b**

in the silt loam soil, the late-maturing cultivar (IAC 503) did not respond to P fertilization, whereas the early-maturing cultivar showed an increase in biomass from low to medium P, with no further gains at high P. These results indicate reduced responsiveness to increasing soil P availability in this soil. Under low P conditions, the late-maturing cultivar (IAC 503) allocated more biomass to roots, resulting in a lower shoot:root ratio and greater investment in belowground growth under P limitation, whereas the early-maturing cultivar (IAC OL3) produced a greater number of gynophores under high P availability (Table 2).

P uptake

Phosphorus uptake increased with increasing Mehlich-3 P levels for both cultivars, although the response from medium to high P differed between cultivars and soils (Fig. 2). The early-maturing cultivar showed increased P uptake from medium to high P in all three soils. In contrast, the late-maturing cultivar showed a further increase from medium to high P only in the silt loam soil, whereas no additional increase was observed in the sandy loam and silty clay loam soils. Under low P conditions, the late-maturing cultivar consistently showed greater P uptake than the early-maturing cultivar across all soils, with increases of 16%, 23%, and 29% in sandy loam, silt loam, and silty clay loam, respectively (Fig. 2). This cultivar-specific response suggests that soil properties modulated the benefit of additional P supply, particularly for the late-maturing cultivar.

Root growth

Root traits responded strongly to P availability and cultivar differences (Table 3). Under low P conditions, the late-maturing cultivar exhibited greater total root length across all soils. Root length and root length density generally increased from low to medium P, with smaller or no increases from medium to high P, while average root diameter showed only minor variation.

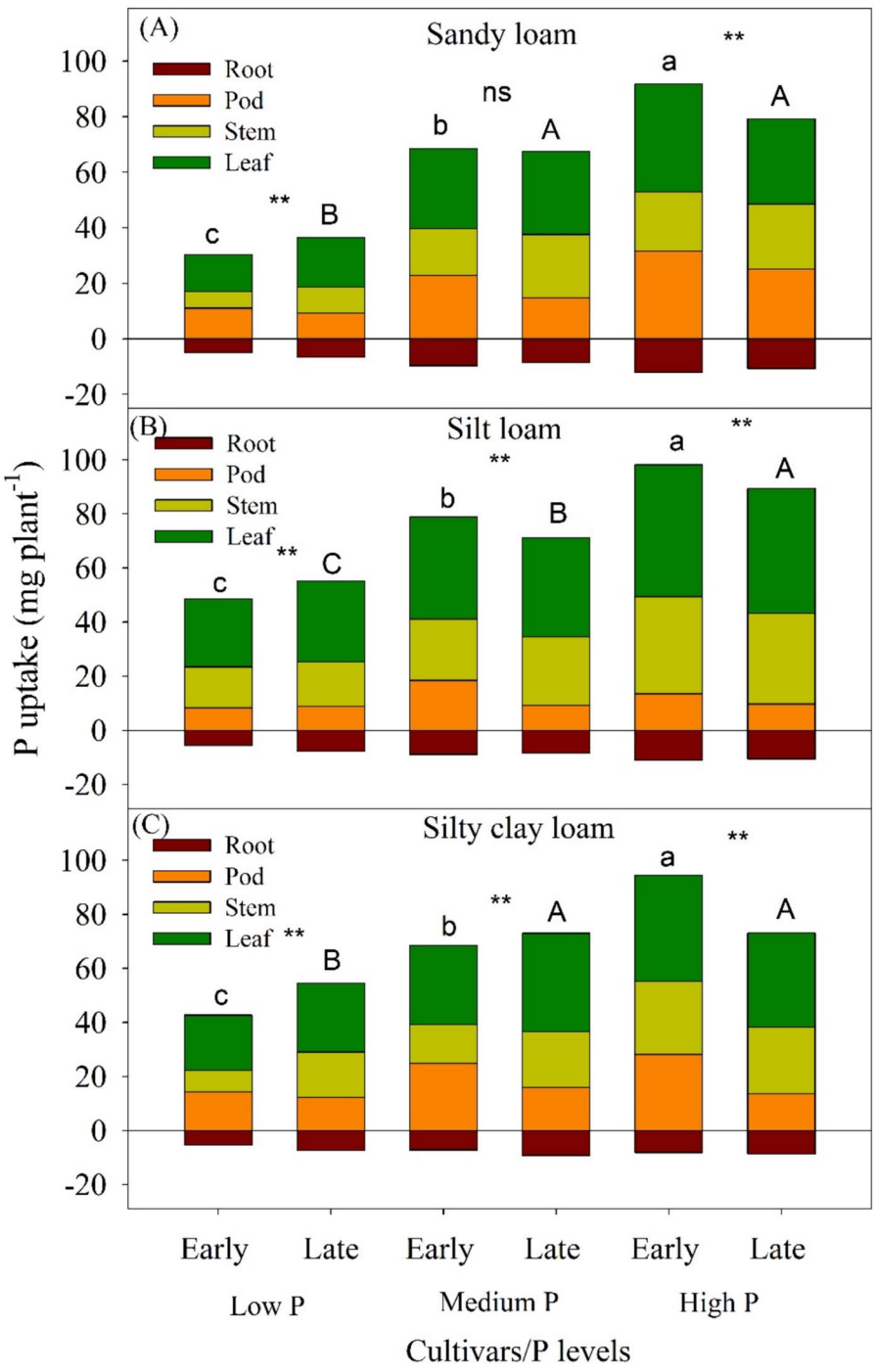


Fig. 2 Phosphorus (P) uptake by two peanut cultivars grown under three soil P levels in three soil-specific experiments. Within each soil texture, different lowercase and uppercase letters indicate significant differences among P levels for the early- and late-maturing cultivars, respectively. ** indicates significant differences between cultivars within the same soil texture and P level, whereas ns denotes non-significant differences ($p < 0.05$)

Phosphorus uptake increased with total root length and biomass in the sandy loam and silt loam soils, whereas a plateau response was observed in the silty clay loam soil (Fig. 3), indicating that in soils with higher clay content, increases in root development beyond a threshold do not proportionally enhance P uptake.

Table 3 Root growth traits of two peanut cultivars grown under three P levels in three soil-specific experiments. Within each soil texture, different lowercase letters indicate significant differences among P levels for a given cultivar, whereas ** indicates significant differences between cultivars within the same P level. Ns denotes non-significant differences. Means were compared using the LSD test ($p < 0.05$)

Sandy loam	P levels	Root length		Root density		Average root diameter	
		m plant^{-1}		m m^{-3}		mm	
	Cultivar	Early cv	Late cv	Early cv	Late cv	Early cv	Late cv
	Low P	74.2 b	89.9 b**	30.7 b	28.3 b^{ns}	0.615 a	0.652 a^{ns}
	Medium P	144.9 a	150.1 a^{ns}	45.8 a	42.6 a^{ns}	0.485 a	0.547 a^{ns}
	High P	141.7 a	146.9 a^{ns}	40.5 ab	48.9 a^{ns}	0.620 a	0.495 b^{ns}
Silt loam		Root length		Root density		Average root diameter	
		m plant^{-1}		m m^{-3}		mm	
	Cultivar	Early cv	Late cv	Early cv	Late cv	Early cv	Late cv
	Low P	102.5 c	118.5 c**	45.8 b	35.2 b^{ns}	0.415 a	0.472 a**
	Medium P	148.4 b	143.9 b^{ns}	52.8 ab	47.1 and	0.407 a	0.405 b^{ns}
	High P	176.2 a	170.4 a^{ns}	58.7 a	50.9 a^{ns}	0.417 a	0.412 b^{ns}
Silty clay loam		Root length		Root density		Average root diameter	
		m plant^{-1}		m m^{-3}		mm	
	Cultivar	Early cv	Late cv	Early cv	Late cv	Early cv	Late cv
	Low P	90.5 b	102.5 c**	39.5 a	32.1 b^{ns}	0.470 a	0.527 a^{ns}
	Medium P	146.5 a	178.6 a**	48.8 a	49.5 a^{ns}	0.447 a	0.502 ab^{ns}
	High P	146.9 a	140.1 b^{ns}	45.5 a	46.7 a^{ns}	0.475 a	0.432 b^{ns}

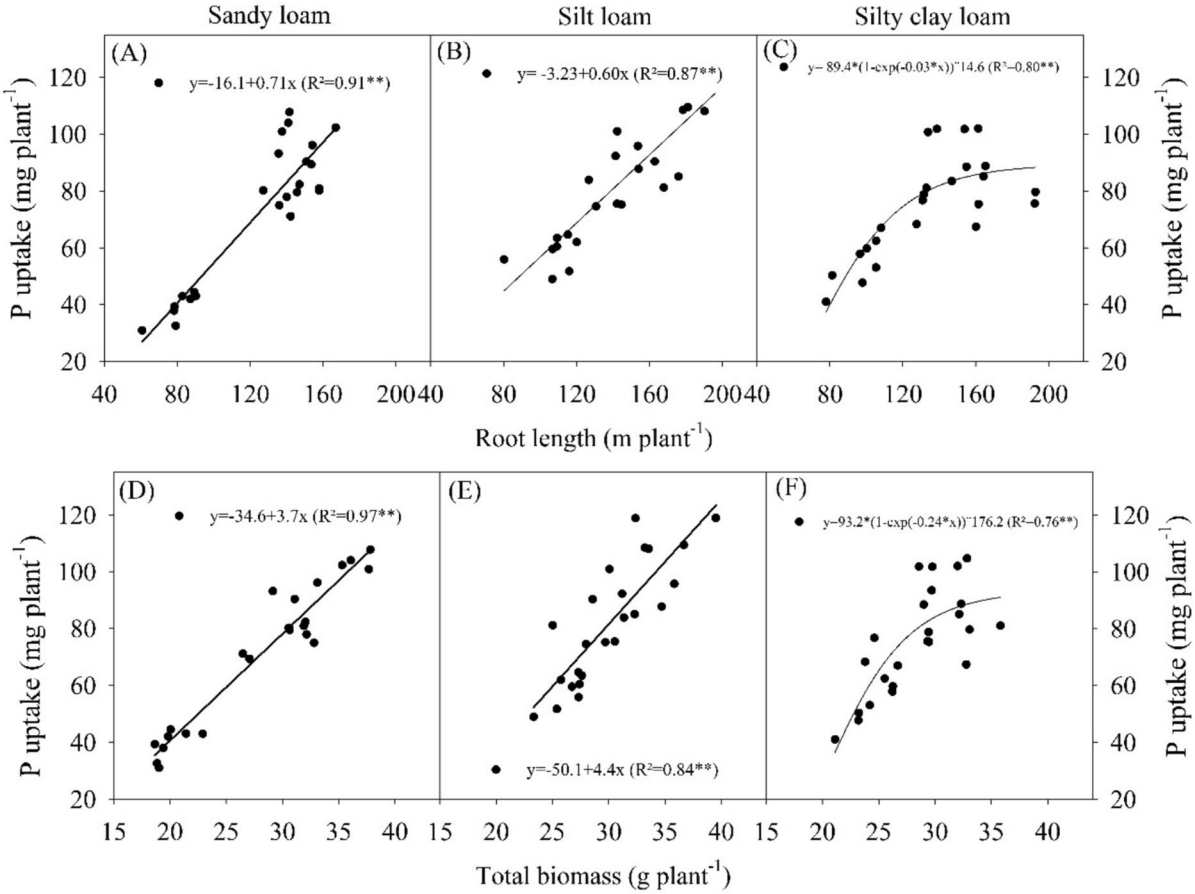


Fig. 3 Relationships P uptake and total root length (**A**–**C**) and total plant biomass (**D**–**F**) for peanut grown in three soil-specific experiments. Panels **A** and **D** correspond to sandy loam, **B** and **E** to silt loam, and **C** and **F** to silty clay loam soils. Asterisks (*, **) indicate significant regression coefficients at $p \leq 0.05$ and $p \leq 0.01$, respectively. Each point represents an individual experimental unit (pot)

Soil P dynamics

Fertilizer application increased Mehlich-3 P, water-extractable P, resin P, ammonium citrate P, ammonium oxalate P, and total soil P but did not affect soil pH (Table 4). In the flow-cell P desorption test, P desorption increased linearly across all soils and P levels.

After 24 h, maximum P desorption reached 4.8, 5.3, and 6.1 mg kg^{-1} in the silt loam, sandy loam, and silty clay loam, respectively. The slope of the fitted lines represents the P desorption rate and highlights clear differences among soil textures (Fig. 4).

All three low P soils showed the lowest desorption rates. Notably, the medium P silt loam exhibited a desorption rate more similar to the low P than to the high P soils, indicating a lower P release capacity. These results suggest that the sandy loam and the silty clay loam released P more readily than the silt loam, and that the high and medium P soils desorbed P at a faster rate than the low P soils (Fig. 4).

Rhizosphere phosphorus dynamics

There was minimal interaction cultivar, P level, and soil type for soil pH and P, so these factors were analyzed separately (Table 5). Increasing labile P levels reduced water pH by 0.4 only in the silty clay loam. While soil P levels had little impact on bulk soil pH, rhizosphere soil pH was, on average, 0.4 lower than bulk soil pH (Table 5), indicating a consistent rhizosphere acidification across soils.

Table 4 Soil pH and P fractions determined by different extractants in three soil textures adjusted to three P levels prior to peanut cultivation. Extractants represent P pools with contrasting lability. DPS denotes the degree of P saturation determined by ammonium oxalate extraction

		pH	P water	P resin	Mehlich-3	Ammonium Citrate
	P levels	water	mg kg^{-1}			
Sandy loam	Low P	8.0	0.47	1.41	17.3	1.04
	Medium P	7.8	0.78	5.93	35.9	4.35
	High P	8.3	5.4	21.7	72.1	13.96
		pH	P water	P resin	Mehlich-3	Ammonium Citrate
	P levels	water	mg kg^{-1}			
Silt loam	Low P	7.9	0.30	2.10	15.8	0.22
	Medium P	7.6	0.58	7.73	31.1	3.16
	High P	7.4	3.06	25.1	71.2	15.3
		pH	P water	P resin	Mehlich-3	Ammonium Citrate
	P levels	water	mg kg^{-1}			
Silty clay loam	Low P	7.8	0.41	2.85	15.0	0.25
	Medium P	7.4	0.81	9.00	27.7	2.44
	High P	7.9	3.62	29.9	64.5	12.65
		P-oxalate	Al—oxalate	Fe-oxalate	DPS	Total P
	P levels	mg kg^{-1}			ratio	mg kg^{-1}
Sandy loam	Low P	100.3	661.2	213.9	0.052	299.7
	Medium P	128.4	666.6	215.1	0.066	312.6
	High P	154.5	668.8	219.6	0.081	356.1
		P-oxalate	Al—oxalate	Fe-oxalate	DPS	Total P
	P levels	mg kg^{-1}			ratio	mg kg^{-1}
Silt loam	Low P	166.7	1069.9	386.7	0.040	405.3
	Medium P	194.9	1057.7	377.7	0.048	427.1
	High P	243.9	1043.8	364.3	0.061	548.3
		P-oxalate	Al—oxalate	Fe-oxalate	DPS	Total P
	P levels	mg kg^{-1}			ratio	mg kg^{-1}
Silty clay loam	Low P	106.0	778.6	708.5	0.044	272.4
	Medium P	127.6	824.9	698.3	0.050	283.2
	High P	168.4	902.1	739.7	0.064	323.3

Water-extractable P was higher in rhizosphere soil than in bulk soil for sandy loam and silt loam. However, resin P and Mehlich-3 P were consistently lower in rhizosphere soil, resulting in a depletion zone in the peanut rhizosphere. This depletion pattern was specific to labile P fractions, and was not observed for ammonium citrate P and ammonium oxalate P.

The depletion (i.e. original non-cultivated soil P concentration minus rhizosphere P concentration) of water-extractable P in the rhizosphere correlated linearly with P uptake across all soil types. However, for Mehlich-3 P, the response followed a plateau. Ammonium oxalate P depletion correlated with P uptake only in the silty clay loam (Fig. 5). The highest depletion of water-extractable P (3–4 mg kg^{-1}) was observed in the sandy loam and the silty clay loam. For the remaining P fractions, differences between bulk and rhizosphere soils were small, suggesting limited depletion of these P pools (Fig. 5). No significant relationship was found between total soil P changes and P uptake (data not shown).

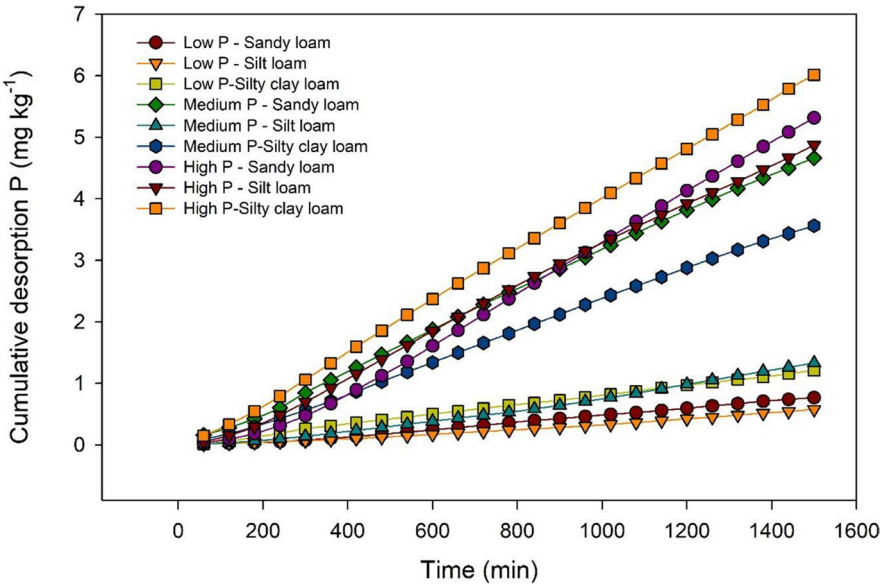


Fig. 4 Cumulative phosphorus (P) desorbed with water under flowing conditions as a function of time for the three soil textures used in the experiments, adjusted to three P levels prior to peanut cultivation. Data were obtained from the flow-cell assay shown in Fig. 1. The slope of each line represents the P desorption rate

Discussion

An increased root length and biomass with greater carbon allocation resulted in a superior adaptability of the late-maturing cultivar to soils with low labile P compared to the cultivar with smaller root development. This enhanced P uptake in P-deficient soils reduces reliance on P fertilizers in soils where there is an appreciable P pool (i.e. total and oxalate-extractable P), but limited solubility/lability (i.e. water-extractable P, Mehlich-3 P, resin-P). For example, the cultivar with greater root investment showed no response to increased labile P, even in soil with an initially poor P solubility. Soil clay and silt content, along with P levels, are key factors influencing P adsorption and desorption (Penn et al. 2022; Zhang et al. 2019). The P desorption rate determines P availability and diffusion, particularly for plants with a limited root absorption zone (Smolders et al. 2021), and under P deficiency peanuts modify the root morphology to enhance uptake (Otani and Ae 1996). Our findings suggest that this adaptation also depends on soil P desorption ability and total P content.

A central finding of this study is the prominent role of rhizosphere P dynamics in regulating peanut P uptake across soils with contrasting textures and P desorption capacities. Independent of soil type, peanut roots consistently induced localized depletion of labile P fractions in the rhizosphere, particularly water-, resin-, and Mehlich-3–extractable P. This depletion was directly associated with P uptake and root length, indicating that the rhizosphere acted as an active zone of phosphorus mobilization rather than a passive reflection of bulk soil properties. The moderate reduction in rhizosphere pH relative to bulk soil further supports the role of root-induced processes in altering P solubility and desorption–adsorption equilibria, especially in soils containing substantial pools of Fe-, Al-, and Ca-bound phosphorus. Together, these findings demonstrate that peanut phosphorus acquisition is governed not only by root system size but also by the capacity of roots to modify the chemical environment of the rhizosphere, thereby accessing less labile soil P pools.

In soils with lower clay content, greater root length was associated with higher P uptake. However, in clay soils, the relationship followed a plateau (Fig. 3). Silty clay loam exhibited the greatest cumulative P desorption and desorption rate with water, especially for the highest P treatment (Fig. 4). This suggests that in soils with high P desorption capacity, an extensive root system is not essential for maximizing P uptake. Notably, the cultivar with smaller root development showed the greatest P uptake at the highest labile P level across all soils. In contrast, for the cultivar with more extensive roots, there was no difference in P uptake between medium- and high-P soils, suggesting that greater root allocation enhanced P uptake efficiency, rendering additional soil P lability unnecessary. Recent studies indicate that various peanut

Table 5 Rhizosphere and bulk soil pH and P fractions determined by different extractants for two peanut cultivars grown under three P levels in three soil-specific experiments. Within each soil texture, different lowercase letters indicate significant differences ($p < 0.05$) between rhizosphere and bulk soil or among P levels. Means were compared using the LSD test. DPS denotes the degree of P saturation determined by ammonium oxalate extraction

	pH (water)			P water (mg kg^{-1})		
	Sandy loam	Silt loam	Silty clay loam	Sandy loam	Silt loam	Silty clay loam
Cultivars (C)						
Early	6.2 a	6.4 a	7.0 a	0.79 a	0.74 a	1.02 a
Late	6.1 a	6.4 a	7.0 a	0.71 a	0.72 a	0.98 a
P levels (P)						
Low P	6.1 a	6.4 a	7.2 a	0.44 b	0.30 c	0.72 c
Medium P	6.2 a	6.4 a	7.0 b	0.51 b	0.51 b	0.87 b
High P	6.2 a	6.5 a	6.9 b	1.30 a	1.36 a	1.40 a
Soil type (S)						
Rhizospheric soil	5.9 b	6.3 b	6.9 b	0.81 a	0.85 a	0.95 a
Bulk soil	6.3 a	6.6 a	7.2 a	0.68 b	0.60 b	1.04 a
	Mehlich-3 (mg kg^{-1})			Resin (mg kg^{-1})		
Cultivars (C)						
Early	21.4 a	23.2 a	21.4 a	6.6 a	7.6 a	6.8 a
Late	22.2 a	24.0 a	22.2 a	5.8 a	7.4 a	5.5 b
P levels (P)						
Low P	10.9 c	10.6 c	10.9 c	0.87 c	1.35 c	1.7 c
Medium P	17.2 b	19.3 b	17.2 b	4.99 b	5.9 b	4.9 b
High P	37.3 a	40.9 a	37.3 a	12.7 a	15.1 a	11.9 a
Soil type (S)						
Rhizospheric soil	20.4 b	21.1 b	20.4 b	5.31 b	6.5 b	5.6 b
Bulk soil	23.2 a	26.1 a	23.3 a	7.12 a	8.4 a	6.7 a
	Ammonium citrate (mg kg^{-1})			Ammonium oxalate (mg kg^{-1})		
Cultivars (C)						
Early	2.8 a	2.9 a	2.8 b	110.8 a	164.9 a	114.2 a
Late	2.3 a	3.4 a	3.3 a	108.1 a	160.2 a	108.1 b
P levels (P)						
Low P	0.41 c	0.24 c	1.55 b	90.5 c	131.9 c	93.4 c
Medium P	1.55 b	1.21 b	1.82 b	102.7 b	153.8 b	107.8 b
High P	5.68 a	7.8 a	5.5 a	134.1 a	201.9 a	135.2 a
Soil type (S)						
Rhizospheric soil	2.7 a	3.4 a	2.8 a	106.8 a	164.4 a	110.7 a
Bulk soil	2.2 a	2.8 a	3.1 a	111.4 a	160.8 a	113.6 a
	DPS			Total P (mg kg^{-1})		
Cultivars (C)						
Early	0.055 a	0.044 a	0.042 a	267.2 a	441.1 a	252.9 a
Late	0.056 a	0.045 a	0.044 a	252.2 b	446.2 a	259.6 a
P levels (P)						
Low P	0.045 c	0.036 c	0.035 c	234.8 c	393.9 c	238.5 c
Medium P	0.053 b	0.041 b	0.042 b	255.8 b	434.2 b	249.8 b
High P	0.070 a	0.056 a	0.053 a	288.5 a	502.8 a	280.5 a
Soil type (S)						
Rhizospheric soil	0.054 a	0.043 b	0.043 a	257.9 a	436.9 b	254.1 a
Bulk soil	0.055 a	0.047 a	0.042 a	261.6 a	450.3 a	258.5 a

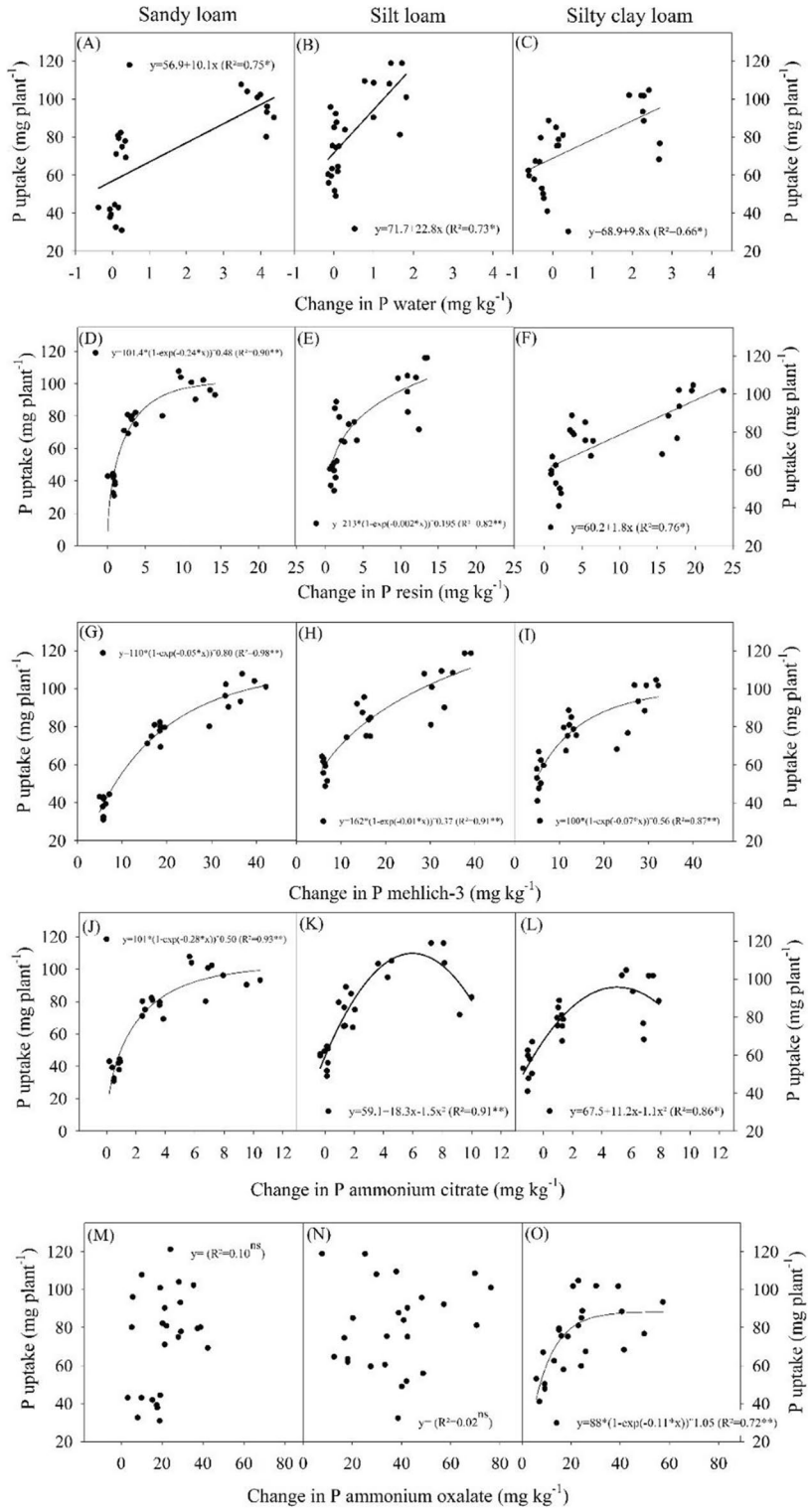


Fig. 5 Relationships P uptake and changes in rhizosphere P concentration relative to bulk soil (pre-plant – rhizosphere) for peanut grown in three soil-specific experiments. Panels show water-extractable P (A–C), resin-extractable P (D–F), Mehlich-3 P (G–I), ammonium citrate–extractable P (J–L), and ammonium oxalate–extractable P (M–O). Asterisks (*, **) indicate significant regression coefficients at $p \leq 0.05$ and $p \leq 0.01$, respectively, while ns denotes non-significant relationships. Each point represents an individual experimental unit (pot)

cultivars utilize less labile P forms through modifications in root architecture and root hair development (Cordeiro et al. 2024). This study adds a new perspective for peanut: rhizosphere pH alterations associated with root-driven P acquisition strategies. Across all soils, rhizosphere pH was lower than bulk soil (Table 5), likely due to organic acid exudation by peanut roots, which can facilitate Al-, Fe-, and Ca-bound P solubilization (Li et al. 2024) and enhance P uptake (Barrow 2017). While phosphatase enzymes also contribute to P acquisition, their role is linked to mineralization of organic P rather than acidification. Peanuts are known to release organic acids that reduce P adsorption and improve uptake efficiency (Janegitz et al. 2017). However, under P deficiency, up to 30% of plant carbon may be released as root exudates, potentially reducing yields by intensifying competition for carbohydrates between roots and reproductive organs (Mitra et al. 2022). Our findings show that Mehlich-3 P and resin-extractable P — both labile fractions— were, on average, 17% and 27% lower in the rhizosphere soil, respectively, indicating a P depletion zone. This depletion typically extends 1–4 mm from roots, with root-induced pH reduction intensifying P depletion (Gahoonia and Nielsen 1992; Schwerdtner and Spohn 2022). P depletion in the rhizosphere is typically greater in crops with high P demand (Rubio et al. 2012). Further evidence for root-induced changes in soil P solubility is found in the fact that ammonium citrate-extractable P actually increased in the rhizosphere relative to bulk soil concentrations in silty clay loam, despite P uptake in the depletion zone.

Phosphorus uptake by peanuts reduced all P fractions in the rhizosphere (Fig. 5). P uptake correlated linearly with water-extractable P in the rhizosphere. Water, the weakest P extractor used in this study, represents the form of P that is directly taken up by plants. However, plants depend on soil processes to replenish the solution P pool (Barber 1995). Previous research suggests that water-extractable P may be a useful indicator of available P, but only when a minimum P threshold is met in the soil (Sorn-Srivichai et al. 1988). The reduction in oxalate-extractable P in the rhizosphere relative to pre-planted soils, observed only in soils with higher clay content, could be attributed to increased P desorption (Fig. 3). The plateau trend in P uptake as a function of the change in rhizosphere P for other extractors suggests that extensive rhizosphere modifications do not always enhance uptake efficiency, particularly in soils with high P availability.

Although high labile P levels did not enhance peanut biomass yields, they contributed to increased soil P saturation, particularly in soils with lower clay content (Table 5). High P saturation poses environmental risks, increasing P losses via erosion, leaching, and water contamination (Van Doorn et al. 2024). Soil P saturation often correlates more strongly with crop productivity compared to total soil P content (Gu et al. 2024), as it accounts for P reversibly bound to Al and Fe oxides (Schoumans and Chardon 2015). Given that peanuts efficiently exploit moderately labile P forms (Cordeiro et al. 2024), selecting cultivars with more extensive root systems and greater carbon allocation to roots could enable high productivity in moderately P-saturated soils while minimizing environmental risks.

A potential limitation of this study is that only two cultivars were evaluated. However, these cultivars were not arbitrarily selected but rather based on a previous screening study (Cordeiro et al. 2024) that assessed a broader set of peanut genotypes. From that larger dataset, the two cultivars chosen here represented contrasting strategies of root development and carbon allocation, allowing us to test the functional role of root traits under different soil conditions. Therefore, while the findings should not be generalized to maturity groups as a whole, they provide robust evidence that variation in root traits—previously identified across a wider genetic pool—directly influences P uptake and rhizosphere P dynamics across soils with contrasting P availability. The novelty of this study lies in linking these root system contrasts with soil texture and desorption capacity, offering new insights into strategies for improving P use efficiency.

Conclusion

The use of peanut cultivars with greater carbon allocation to roots and longer root systems reduced dependence on labile soil P, but this advantage was strongly soil-dependent. Root-driven improvements in P uptake were modulated by soil texture, total P content, and particularly by ammonium oxalate-extractable P, which reflects soil P pools subject to

desorption processes. Phosphorus uptake was closely associated with rhizosphere P depletion, evidenced by consistent reductions in water-extractable P, resin P, Mehlich-3 P, and ammonium citrate P near the root surface. These results highlight the central role of root-induced rhizosphere processes, rather than bulk soil properties alone, in regulating P availability. Superior performance under P deficiency resulted from the combined effects of greater soil exploration, enhanced P desorption capacity, moderate rhizosphere acidification, and shifts among soil P forms. Incorporating peanut cultivars with more extensive root systems into production systems can therefore improve phosphorus use efficiency and reduce reliance on phosphate fertilizers, particularly in soils with appreciable total P but limited labile P availability.

Acknowledgements We thank São Paulo Research Foundation (FAPESP) for their support with the Ph.D scholarship for the first author, funding grant number (2023/06072-5 and 2020/14810-8).

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Almeida DS, Delai LB, Sawaya CHF, Rosolem CA (2020) Exudation of organic acid anions by tropical grasses in response to low phosphorus availability. Sci Rep 10:16955. https://doi.org/10.1038/s41598-020-73398-1

Barber SA (1995) Soil nutrient bioavailability: a mechanistic approach. John Wiley & Sons

Barrow NJ (2017) The effects of pH on phosphate uptake from the soil. Plant Soil 410:401–410. https://doi.org/10.1007/s11104-016-3008-9

Cordeiro CFDS, Rosolem CA (2026) Management strategies to improve phosphorus use efficiency under an uncertain climate: a review. Front Agron 7:1630934. https://doi.org/10.3389/fagro.2025.1630934

Cordeiro CFDS, Echer FR, Rosolem CA (2024) Root systems of peanut cultivars respond differently to soil P availability to improve P uptake. J Soil Sci Plant Nutr 187:484–493. https://doi.org/10.1002/jpln.202300144

Cordeiro CFS, Andrade MGP, Galdi LV, Echer FR, Rosolem CA (2025) Optimizing phosphorus rates for peanut: the role of soil P, water availability, and cultivar. Field Crops Res 333:110086. https://doi.org/10.1016/j.fcr.2025.110086

Gahoonia TS, Nielsen NE (1992) The effects of root-induced pH changes on the depletion of inorganic and organic phosphorus in the rhizosphere. Plant Soil 143:185–191. https://doi.org/10.1007/BF00007872

Gu Y, Ros GH, Zhu Q, van Doorn M, Shen J, Cai Z, Vries W (2024) Potential use of phosphorus saturation degree as combined indicator for crop yield and leaching risks at regional scale. Eur J Agron 161:127347. https://doi.org/10.1016/j.eja.2024.127347

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

Janegitz MC, Martins ARH, Rosolem CA (2017) Cover crops and soil phosphorus availability. Commun Soil Sci Plant Anal 48:1240–1246. https://doi.org/10.1080/00103624.2017.1341918

Jiang HJ, Zhang XY, Ma CY, Sun K, Xie, XG, Zhang W, Dai CC (2024) Endophytic colonization of Phomopsis liquidambaris recruits rhizospheric Ralstonia by inducing acetic acid secretion to facilitate phosphorus uptake by *Arachis hypogaea* L. in continuously cropped soil. Plant and Soil 1-20. https://doi.org/10.1007/s11104-024-06800-w

Li C, Ma X, Wang Y, Sun Q, Chen M, Zhang C, Dai Z (2024) Root-mediated acidification, phosphatase activity and the phosphorus-cycling microbial community enhance phosphorus mobilization in the rhizosphere of wetland plants. Water Res 255:121548. https://doi.org/10.1016/j.watres.2024.121548

Mehlich A (1978) Influence of fluoride, sulfate and acidity on extractable phosphorus, calcium, magnesium and potassium. Commun Soil Sci Plant Anal 9:455–476. https://doi.org/10.1080/00103627809366823

Mitra R, Yadav P, Usha K, Singh B (2022) Regulatory role of organic acids and phytochelators in influencing the rhizospheric availability of phosphorus and iron and their uptake by plants. Plant Physiol 27:193–206. https://doi.org/10.1007/s40502-022-00650-3

Murabayashi O, Rosolem CA, Zanotto MD (1994) Root system of peanuts as affected by phosphorus fertilization. Pesqui Agropecu Bras 29:1669–1673

Otani T, Ae N (1996) Sensitivity of phosphorus uptake to changes in root length and soil volume. Agron J

88:371–375. https://doi.org/10.2134/agronj1996.00021962008800030002x

Penn CJ, Williams MR, Camberato J, Wenos N, Wason H (2022) Desorption kinetics of legacy soil phosphorus: implications for non-point transport and plant uptake. Soil Syst 6:1–6. https://doi.org/10.3390/soilsystems6010006

Rosolem CA, Witacker JPT, Vanzolini S, Ramos VJ (1999) The significance of root growth on cotton nutrition in an acidic low-P soil. Plant Soil 222:183–188. https://doi.org/10.1023/A:1004623130548

Roy ED, Richards PD, Martinelli LA, Coletta LD, Lins SRM, Vazquez FF, Porder S (2016) The phosphorus cost of agricultural intensification in the tropics. Nat Plants 2:1–6. https://doi.org/10.1038/nplants.2016.43

Rubio G, Faggioli V, Scheiner JD, Gutiérrez-Boem FH (2012) Rhizosphere phosphorus depletion by three crops differing in their phosphorus critical levels. J Soil Sci Plant Nutr 175:810–871. https://doi.org/10.1002/jpln.201200307

Schoumans OF, Chardon WJ (2015) Phosphate saturation degree and accumulation of phosphate in various soil types in The Netherlands. Geoderma 237:325–335. https://doi.org/10.1016/j.geoderma.2014.08.015

Schwerdtner U, Spohn M (2022) Plant species interactions in the rhizosphere increase maize N and P acquisition and maize yields in intercropping. J Soil Sci Plant Nutr 22(3):3868–3884. https://doi.org/10.1007/s42729-022-00936-3

Shibata R, Yano K (2003) Phosphorus acquisition from non-labile sources in peanut and pigeonpea with mycorrhizal interaction. Appl Soil Ecol 24:133–141. https://doi.org/10.1016/S0929-1393(03)00093-3

Smolders E, Nawara S, De Cooman E, Merckx R, Martens S, Elsen A, Amery F (2021) The phosphate desorption rate in soil limits phosphorus bioavailability to crops. Eur J Soil Sci 72:221–233. https://doi.org/10.1111/ejss.12978

Sorn-Srivichai P, Syers JK, Tillman RW, Cornforth IS (1988) An evaluation of water extraction as a soil-testing procedure for phosphorus I. Glasshouse assessment of plant-available phosphorus. Fertil Res 15:211–223. https://doi.org/10.1007/BF01051343

Van Doorn M, van Rotterdam D, Ros G, Koopmans GF, Smolders E, de Vries W (2024) The phosphorus saturation degree as a universal agronomic and environmental soil P test. Crit Rev Environ Sci Technol 54:385–404. https://doi.org/10.1080/10643389.2023.2240211

Wissuwa M, Ae N (2001) Genotypic differences in the presence of hairs on roots and gynophores of peanuts (*Arachis hypogaea* L.) and their significance for phosphorus uptake. J Exp Bot 52:1703–1710. https://doi.org/10.1093/jexbot/52.361.1703

Zarcinas BA, Cartwright B, Spouncer LR (1987) Nitric acid digestion and multi-element analysis of plant material by inductively coupled plasma spectrometry. Commun Soil Sci Plant Anal 18:131–146. https://doi.org/10.1080/00103628709367806

Zhang Y, Huang S, Guo D, Zhang S, Song X, Yue K, Bao D (2019) Phosphorus adsorption and desorption characteristics of different textural fluvo-aquic soils under long-term fertilization. J Soils Sediments 19:1306–1318. https://doi.org/10.1007/s11368-018-2122-0

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.