https://doi.org/10.17221/35/2026-PSE

Synergistic root-photosynthesis responses to phosphorus rates optimise grain appearance quality in phosphorus-efficient rice cultivars

*Jing Cao, Li Wang, Qinyao Meng, Hao Cheng, Xihui Zhao, Guowei Xu**

College of Agriculture, Henan University of Science and Technology, Luoyang, Henan, P.R. China
Jing Cao and Li Wang contributed equally to this work.
**Corresponding author: gwxu2007@163.com*

Citation: Cao J., Wang L., Meng Q.Y., Cheng H., Zhao X.H., Xu G.W. (2026): Synergistic root-photosynthesis responses to phosphorus rates optimise grain appearance quality in phosphorus-efficient rice cultivars. Plant Soil Environ., 72: 211–227.

Abstract: Combining phosphorus management with phosphorus-efficient cultivars is an effective strategy for improving rice quality. To investigate their effects on root characteristics and photosynthetic traits, a pot experiment was conducted with two rice cultivars differing in phosphorus efficient: Liangeng 7 (weakly efficient) and Yongyou 2640 (highly efficient). Four phosphorus rates (0, 0.44, 0.88, and 1.32 g/pot, designated as P0, P1, P2, and P3, respectively) were applied. A significant cultivar-phosphorus interaction was observed. Most root traits (the length, dry weight, volume, total absorption area, active absorption area, oxidation activity, and acid phosphatase activity) and photosynthetic traits (photosynthetic rate, transpiration rate, and stomatal conductance) initially increased and then decreased with increasing phosphorus rates, while the leaf intercellular CO_2 concentration showed the opposite trend. Liangeng 7 performed optimally under P2, whereas Yongyou 2640 reached its peak under P1. Compared with Liangeng 7, Yongyou 2640 exhibited better appearance quality, root traits, and photosynthetic parameters. Correlation analysis showed that root length, root physiological activity and leaf photosynthetic parameters (except intercellular CO_2 concentration) were significantly negatively correlated with chalkiness degree. These findings demonstrate that matching phosphorus supply to cultivar-specific efficiency optimises root-photosynthesis synergy, leading to superior grain appearance quality with less phosphorus input.

Keywords: rice (*Oryza sativa* L.); appearance quality; root trait; photosynthesis; phosphorus management

As living standards advance, consumer demand for rice (*Oryza sativa* L.) has shifted from meeting basic dietary needs to pursuing superior quality. Consequently, enhancing rice grain quality has become increasingly pivotal alongside sustaining high grain yield (Hu et al. 2022). As a core rice quality trait, grain appearance directly shapes market price and milling efficiency, and ultimately determines the economic returns of farmers and the entire rice industry (Kanokwan et al. 2023). Phosphorus is an essential macronutrient that plays a critical role in plant growth and agricultural productivity. Phosphorus deficiency in rice inhibits plant growth, impairs nutrient acquisition, and ultimately diminishes rice quality (Deng et al. 2022, Prathap et al. 2023, Sun et al. 2024b, Zhang et al. 2025). Therefore, elucidating how phosphorus fertilisation management finely regulates rice appearance quality is essential for advancing sustainable agricultural development and catering to dynamic market demands.

Supported by the National Natural Science Foundation of China, Grant No. U1304316; by the Joint Research Fund for Science and Technology Development of Henan Province, Grant No. 242103810031; by the Science and Technology Research Project of Henan Province, Grant No. 242102110169; by the Open Foundation of the Key Laboratory of Cultivation and Physiology of Jiangsu Province, Grant No. 027388003K11009, and by the Doctoral Research Initiation Fund of Henan University of Science and Technology, Grant No. 13480108.

The root system, as the primary organ for water and nutrient acquisition and a key site for synthesising hormones and organic acids, is fundamental to crop performance. Consequently, root morphological and physiological traits are directly correlated with and collectively determine the quality of formation (Chiba et al. 2017, Xu et al. 2020, Vinarao et al. 2023, Li et al. 2024, Gong et al. 2025). While increasing phosphorus application generally promotes rice root growth – resulting in greater biomass and surface area that enhance nutrient uptake – it also intensifies photosynthate consumption. Conversely, reducing phosphorus application can increase the number, average length, and total length of lateral roots. Under phosphorus stress, the root-to-shoot ratio typically rises as plants allocate more carbohydrates to root growth to improve phosphorus acquisition and sustain overall development (Liu 2021, Ding et al. 2021, Gu et al. 2023, Zhang et al. 2023, Liu et al. 2024, Muhandiram et al. 2024, Srivastava et al. 2025). However, excessive phosphorus application fails to enhance root physiological activity significantly; instead, undissolved excess phosphorus can increase soil solution osmotic potential, inhibit root metabolism, and ultimately compromise overall crop performance (Prodhan et al. 2019, Cheng et al. 2023, Sinclair et al. 2024, Zulfiqar et al. 2025). Root traits vary considerably across crop species and among phosphorus-efficient cultivars within the same species. Previous studies indicate that under low-phosphorus stress, phosphorus-inefficient cultivars exhibit more pronounced changes in plant dry weight, root morphology, and physiological activity compared to phosphorus-efficient cultivars. These varietal differences tend to diminish as the external phosphorus supply increases (Wang et al. 2024, Liu et al. 2025). Although existing research has extensively examined crop root systems under low-phosphorus stress and varietal selection (Zulfiqar et al. 2021, Deng et al. 2022, Verbeeck et al. 2023, Lv et al. 2024, Mishra et al. 2025), it remains unclear how phosphorus-efficient rice cultivars dynamically adjust their root morphology and physiology in response to varying phosphorus levels throughout the growth cycle.

Phosphorus is an essential component of photosynthetic assimilation and photophosphorylation, playing a direct role in crop photosynthesis (Gao et al. 2023, Chen et al. 2024, Costa et al. 2025). Studies have shown that low soil phosphorus availability reduces the net photosynthetic rate, stomatal conductance, and intercellular CO_2 concentration in leaves, leading to stunted plant growth as well as shorter and narrower leaves. The application of phosphate fertiliser can mitigate these low-phosphorus-induced limitations by delaying leaf senescence and enhancing photosynthate production, ultimately improving rice quality (Veronica et al. 2017, Zhang et al. 2021, Oo et al. 2023, Sun et al. 2024b, Lu et al. 2025). It has been reported that phosphorus-efficient cultivars adapt to low-phosphorus stress by promoting chloroplast development, thereby preserving the structure and function of photosynthetic organs and mitigating the suppression of photosynthetic rate. In contrast, low-phosphorus-utilising cultivars exhibit a significant decline in photosynthetic capacity (Sun et al. 2024b, Zhang et al. 2025). However, evidence regarding the differences in leaf photosynthetic traits among phosphorus-efficient cultivars under varying phosphorus application rates remains limited.

Root systems serve as an underground "nutrient-signal hub," integrating aboveground photosynthetic functions as well as quality formation through their morphology and physiology (Zhang et al. 2017, Jiang et al. 2024, Ray and Dalal 2024, Camli-Saunders and Villouta 2025). Previous studies have shown that higher phosphorus application rates can reduce amylose content and improve the appearance and eating quality of rice, although these effects vary substantially among cultivars (Zhang et al. 2021, Oo et al. 2023). Nevertheless, it remains unclear how root and photosynthetic traits respond to varying phosphorus rates in cultivars with differing phosphorus efficiency, and how these responses collectively influence rice appearance quality.

This study aimed to test the hypothesis that combining different phosphorus applications with phosphorus-efficient cultivars synergistically optimised appearance quality by modulating root characteristics and photosynthetic traits. We systematically evaluated key rice root traits – including root length, root dry weight, root volume, root diameter, total and active root absorption areas, root oxidation activity, and root acid phosphatase activity – as well as photosynthetic parameters (photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration) and rice appearance quality traits (namely chalky kernel percentage, chalky area, and chalkiness degree). These findings provide a theoretical basis and technical support for developing cultivar-adapted phosphorus management strategies to optimise rice appearance quality.

https://doi.org/10.17221/35/2026-PSE

MATERIAL AND METHODS

Plant materials. The pot experiment was conducted at the research station of Henan University of Science and Technology in Henan Province, China (34°39'N, 112°26'E). Two rice cultivars commonly grown in the region, Liangeng 7 (weakly phosphorus-efficient) and Yongyou 2640 (highly phosphorus-efficient), were selected as test materials based on a previous experiment (Zhang et al. 2025). According to our previous research, compared with Liangeng 7, Yongyou 2640 exhibited a 53% increase in average yield under low P treatment (Zhang et al. 2025). The experiment was carried out during the rice growing seasons of 2021 and 2022. Seeds were sown in a seedling nursery on May 10, 2021, and May 11, 2022, with young seedlings transplanted into pots on June 10, 2021, and June 11, 2022, respectively. A 30-day seedling age is a standard practice for rice production in the region. The soil used in the pots was a clay loam [Typic fluvaquents, Entisols (US taxonomy)], which had the following properties in 2021 and 2022, respectively: alkali-hydrolysable nitrogen (alkali hydrolysis diffusion method), 102.8 and 105.1 mg/kg; available phosphorus (Olsen method), 4.9 and 5.2 mg/kg; available potassium (ammonium acetate extraction followed by flame photometry), 115.3 and 118.6 mg/kg; and organic matter (potassium dichromate oxidation method), 19.1 and 19.3 g/kg. Each pot (25 cm in diameter × 30 cm height) was filled with 15 kg of soil and planted with three hills, each containing two seedlings. Each treatment was replicated 25 times (25 pots). The main growth stages – mid-tillering, heading, and maturity – were recorded at 24–25, 76–78, and 124–126 days after transplanting, respectively.

Treatments. The experiment was a fully randomised block design. Four phosphorus (P) fertiliser rates were applied: 0, 0.44, 0.88, and 1.32 g P per pot, designated as P0, P1, P2, and P3, respectively, based on a previous experiment (Zhang et al. 2025). Total superphosphate (5.89% P) and potassium chloride (43% K) were applied as base fertilisers. However, superphosphate was omitted from the P0 treatment. Nitrogen and potassium fertiliser application rates were uniform across all treatments at 2.0 g N/pot and 0.83 g K/pot, respectively. Nitrogen fertiliser was applied in four splits: 30% as basal at pre-transplanting (1 day before transplanting), 30% at the recovering stage (7 days after transplanting, DAT), and 20% at spikelet-promoting (applied at the leaf age of remainder 3.5) and 20% at spikelet-preserving (applied at the leaf age of remainder 1.5). From transplanting to maturity, specific irrigation regimes were maintained. A shallow water layer of 2–3 cm was kept during the plant recovery stage. Thereafter, plants were re-irrigated to a 2–3 cm water depth when the soil water potential at 15 cm depth reached –20 kPa; this was continued until one week before final harvest, except for a drainage period during the late tillering stage (Li et al. 2025). Pots were covered with a removable rain shelter during rainfall. Soil water potential in each plot was monitored using soil moisture tension meters (Nanjing Institute of Soil Science, Chinese Academy of Sciences, China). Weeds were manually removed, and pesticides were applied as needed to control diseases and insect pests throughout the growing season in both years.

Sampling and measurement

Root length, diameter, volume, and root weight. Root length, diameter, volume, and weight were measured at the mid-tillering, heading, and maturity stages. At each growth stage, the roots of rice plants from three pots per treatment (each pot as a replicate) were separated at the nodal base using a hydropneumatic elutriation system to wash off adhering soil. The fresh roots from each pot were arranged and floated in a shallow water tray (30 cm × 30 cm) to facilitate morphological analysis and minimise measurement error. Root length, diameter, and volume were scanned with an Epson Expression 1680 scanner (Seiko Epson Corp., Tokyo, Japan) and analysed using the WinRHIZO Root Analyser System (Regent Instruments Inc., Quebec, Canada). Subsequently, the roots were oven-dried at 75 °C until a constant weight was achieved, and the dry weight was recorded.

Root total absorption area, active absorption area, root oxidation activity and activities of acid phosphatase in roots. Root samples from three pots per treatment were collected at the mid-tillering, heading, and maturity stages. The total and active root absorption areas were determined using the methylene blue method (Wu et al. 2020). Root oxidation activity was quantified by the α-naphthylamine method (Ramasamy et al. 1997). Root acid phosphatase activity was measured according to the method of Popova and Deng (2010). Specifically, 0.2 g of root samples was homogenised in 0.8 mL of a modified buffer (pH 5.2) and 0.2 mL of 0.1 mol/L sodium p-nitrophenyl phosphate. The mixture was incubated in a water bath at 30 °C for 30 min. The enzymatic reaction was terminated by adding 0.2 mL of $CaCl_2$ and 0.8 mL of NaOH. The absorbance of the supernatant was then measured at 400 nm.

Photosynthetic characteristics. Photosynthetic parameters, including the photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration, were measured between 09:00 and 11:00 h using a Li-Cor 6800 portable photosynthesis system (Li-Cor Inc., Lincoln, USA). Measurements were taken on the uppermost fully expanded leaves from ten hills for each treatment when the photosynthetically active radiation above the canopy was 1 500 $\mu mol/m^2/s$.

Harvesting and evaluation of appearance quality. Rice plants were harvested on October 14, 2021, and October 15, 2022. Five pots per treatment were harvested to determine rice appearance quality.

The appearance quality of rice was evaluated according to the method of Xu et al. (2019). Briefly, chalkiness was determined by visually inspecting 100 head rice kernels. Chalky kernel percentage (CKP) was calculated as the proportion of chalky kernels among the total number inspected. Chalky area (CA) was defined as the proportion of the chalky region within an individual kernel's total area. Chalkiness degree (CD) was derived from the product of CKP and CA.

Data analysis. Statistical analysis was conducted by analysis of variance (ANOVA) using SPSS sta-

Table 1. Chalky kernel percentage, chalky area and chalkiness degree of Liangeng 7 and Yongyou 2640 under different phosphorus application rates

Year	Cultivar	Treatment	Chalky kernel percentage (%)	Chalky area (%)	Chalkiness degree (%)
2021	Liangeng 7	P0	27.7^{a}	15.5^{a}	4.2^{a}
		P1	25.3^{b}	13.1^{b}	3.2^{b}
		P2	20.7^{c}	9.7^{d}	2.1^{d}
		P3	25.3^{b}	12.0^{c}	3.2^{b}
	Yongyou 2640	P0	24.7^{b}	9.6^{d}	2.5^{c}
		P1	17.3^{d}	6.8^{f}	1.3^{g}
		P2	20.3^{c}	8.0^{e}	1.5^{f}
		P3	20.3^{c}	8.2^{e}	1.8^{e}
2022	Liangeng 7	P0	28.7^{a}	15.1^{a}	4.3^{a}
		P1	25.7^{b}	12.1^{b}	3.1^{b}
		P2	20.3^{c}	10.4^{c}	2.1^{cd}
		P3	24.0^{b}	12.1^{b}	2.9^{b}
	Yongyou 2640	P0	25.0^{b}	9.3^{cd}	2.3^{c}
		P1	17.7^{c}	6.8^{e}	1.2^{f}
		P2	19.0^{c}	7.4^{de}	1.5^{ef}
		P3	20.3^{c}	8.2^{d}	1.7^{de}
Analysis of variance					
Year (Y)			ns	ns	ns
Cultivar (C)			160.7^{**}	801.1^{**}	944.6^{**}
Phosphorus fertiliser rate (P)			71.6^{**}	90.1^{**}	197.9^{**}
Y × C			ns	ns	ns
Y × P			ns	ns	ns
C × P			20.9^{**}	27.7^{**}	45.4^{**}
Y × C × P			ns	ns	ns

P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient cultivar. Different letters donate statistical significance at $P < 0.05$ within a column in the same year. $^{*}P < 0.05$; $^{**}P < 0.01$; ns – not significant at $P = 0.05$

tistical analysis software (version 27.0; IBM Corp., Armonk, USA). Means were tested by the least significant difference (*LSD*) test at $P < 0.05$. Line and bar charts were generated with SigmaPlot software (Version 10.0, Systat Software Inc., San Jose, USA). The heatmap analysis was generated using Origin 2021 (OriginLab Corp., Northampton, USA).

RESULTS

Appearance quality. Chalky kernel percentage in both Liangeng 7 and Yongyou 2640 exhibited a U-shaped response to increasing phosphorus application rates, initially decreasing and then increasing. However, the specific P rate required to minimise the CKP differed markedly between the two cultivars (Table 1). Liangeng 7 achieved its minimum under the P2 treatment, averaging a 27.3% reduction compared to the no-phosphorus control (P0). In contrast, Yongyou 2640 reached its minimum CKP under the lower P1 treatment, with an average reduction of 29.6% relative to P0. At the same P application level, Yongyou 2640 consistently exhibited a lower CKP than Liangeng 7.

Similarly, chalky area and chalkiness degree also varied significantly with cultivar and P rate (Table 1).

Table 2. Root length and root diameter of Liangeng 7 and Yongyou 2640 under different phosphorus application rates of rice

Cultivar	Treatment	Root length (cm/hill)			Root diameter (mm)		
		mid-tillering	heading	maturity	mid-tillering	heading	maturity
2021							
Liangeng7	P0	9 781^{g}	19 863^{g}	16 907^{f}	0.43^{b}	0.40^{cd}	0.40^{cd}
	P1	13 131^{e}	21 667^{f}	19 180^{e}	0.44^{ab}	0.43^{b}	0.42^{ab}
	P2	15 580^{d}	30 014^{c}	26 416^{c}	0.45^{a}	0.52^{a}	0.43^{a}
	P3	14 810^{d}	23 059^{e}	19 564^{e}	0.41^{c}	0.42^{b}	0.40^{cd}
Yongyou 2640	P0	11 050^{f}	22 522^{ef}	21 540^{d}	0.40^{c}	0.41^{bc}	0.41^{bc}
	P1	23 710^{a}	37 524^{a}	32 946^{a}	0.45^{a}	0.42^{b}	0.42^{ab}
	P2	19 691^{b}	35 150^{b}	30 555^{b}	0.40^{c}	0.39^{d}	0.41^{bc}
	P3	18 210^{c}	24 263^{d}	22 934^{d}	0.36^{d}	0.39^{d}	0.39^{d}
2022							
Liangeng7	P0	9 249^{f}	17 737^{h}	15 427^{h}	0.38^{d}	0.44^{e}	0.42^{e}
	P1	14 465^{e}	20 036^{g}	17 455^{g}	0.46^{b}	0.46^{d}	0.46^{c}
	P2	21 861^{b}	31 312^{d}	26 425^{d}	0.48^{a}	0.51^{a}	0.50^{a}
	P3	17 559^{d}	29 787^{e}	24 227^{e}	0.47^{ab}	0.48^{b}	0.48^{b}
Yongyou 2640	P0	15 435^{e}	21 511^{f}	20 479^{f}	0.43^{c}	0.40^{g}	0.40^{f}
	P1	25 457^{a}	37 337^{a}	34 301^{a}	0.47^{ab}	0.47^{c}	0.47^{bc}
	P2	20 058^{c}	35 317^{b}	30 548^{b}	0.44^{c}	0.44^{e}	0.44^{d}
	P3	18 174^{d}	32 560^{c}	27 587^{c}	0.40^{d}	0.43^{f}	0.43^{d}
Analysis of variance							
Year (Y)			89.5**	13.9**	145.5**	261.9**	622.0**
Cultivar (C)			1 869**	1 031**	68.7**	288.5**	72.9**
Phosphorus rates (P)			1 186**	384.2**	80.4**	105.0**	105.3**
Y × C			6.0*	ns	ns	ns	61.9**
Y × P			186.3**	37.4**	20.0**	14.0**	46.4**
C × P			489.3**	171.0**	51.5**	117.2**	34.7**
Y × C × P			4.3*	3.0*	20.9**	31.0**	11.4**

P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient cultivar. Different letters donate statistical significance at $P < 0.05$ within a column in the same year. $^{*}P < 0.05$; $^{**}P < 0.01$; ns – not significant at $P = 0.05$

https://doi.org/10.17221/35/2026-PSE

Liangeng 7 reached its minimum CA and CD at 0.88 g P/pot (P2). In contrast, Yongyou 2640 reached its minimum at the lower rate of 0.44 g P/pot (P1). On average across all P treatments, Yongyou 2640 demonstrated 34.8% lower CA and 43.7% lower CD than Liangeng 7.

Root length, diameter, volume, and root weight. Root length followed a typical low-high-low trajectory during the growth cycle, peaking at the heading stage (Table 2). Liangeng 7 attained its maximum root length across all growth stages under the P2 treatment, with an average increase of 75.1% over the P0 control. In contrast, Yongyou 2640 consistently reached its maximum under the P1 treatment, averaging a 73.3% increase over P0. At the same P application level, Yongyou 2640 exhibited longer roots than Liangeng 7 at all stages, with average increases of 35.7% at mid-tillering, 27.2% at heading, and 33.0% at maturity in 2021, and corresponding increases of 24.4, 36.1, and 42.0% in 2022.

With increasing phosphorus application rate, the average root diameter first increased and then decreased for both Liangeng 7 and Yongyou 2640 (Table 2). Liangeng 7 achieved its maximum diameter at 0.88 g P/pot (P2) across all stages, whereas Yongyou 2640 peaked at 0.44 g P/pot (P1). In contrast to root length, the average root diameter of Yongyou 2640 was consistently smaller than that of Liangeng 7, with annual average reductions of 5.4% in 2021 and 7.0% in 2022.

Table 3. Root volume and root weight of Liangeng 7 and Yongyou 2640 under different phosphorus application rates of rice

Cultivar	Treatment	Root volume (cm^3/hill)			Root weight (g/hill)		
		mid-tillering	heading	maturity	mid-tillering	heading	maturity
2021							
Liangeng7	P0	20.1^{f}	34.7^{f}	32.8^{h}	1.44^{f}	5.50^{e}	3.71^{f}
	P1	25.9^{e}	39.9^{e}	37.7^{f}	1.64^{de}	7.53^{c}	5.63^{e}
	P2	31.9^{cd}	48.0^{c}	44.5^{c}	1.80^{d}	8.56^{b}	6.65^{c}
	P3	30.8^{d}	38.9^{e}	35.0^{g}	1.52^{ef}	7.57^{c}	6.08^{d}
Yongyou 2640	P0	33.0^{c}	41.5^{e}	39.2^{e}	1.98^{c}	6.71^{d}	6.20^{d}
	P1	45.3^{a}	55.0^{a}	50.9^{a}	3.58^{a}	12.83^{a}	7.95^{a}
	P2	37.2^{b}	51.9^{b}	47.2^{b}	2.69^{b}	9.05^{b}	7.51^{b}
	P3	33.7^{c}	44.5^{d}	42.6^{d}	2.07^{c}	8.50^{b}	6.63^{c}
2022							
Liangeng7	P0	18.3^{g}	33.8^{f}	31.0^{g}	1.48^{e}	5.57^{f}	3.86^{e}
	P1	26.6^{f}	38.1^{e}	36.2^{f}	1.81^{d}	7.53^{c}	6.02^{c}
	P2	34.2^{d}	48.3^{c}	45.6^{c}	2.84^{b}	8.71^{b}	6.46^{b}
	P3	30.6^{e}	40.4^{d}	39.1^{d}	1.50^{e}	6.80^{d}	5.31^{d}
Yongyou 2640	P0	30.0^{e}	40.4^{d}	38.4^{e}	2.03^{c}	6.29^{e}	5.93^{c}
	P1	44.6^{a}	53.6^{a}	50.1^{a}	3.95^{a}	10.33^{a}	7.34^{a}
	P2	38.0^{b}	50.2^{b}	47.5^{b}	2.85^{b}	7.71^{c}	7.16^{a}
	P3	36.5^{c}	47.9^{c}	47.4^{b}	2.05^{c}	7.48^{c}	5.58^{d}
Analysis of variance							
Year (Y)		ns	ns	12.3^{**}	70.0^{**}	71.9^{**}	53.0^{**}
Cultivar (C)		$1\,656^{**}$	590.0^{**}	$1\,544^{**}$	$1\,129^{**}$	263.4^{**}	810.7^{**}
Phosphorus rates (P)		380.4^{**}	255.1^{**}	567.2^{**}	374.4^{**}	305.9^{**}	391.3^{**}
Y × C		ns	ns	ns	10.0^{**}	47.7^{**}	25.0^{**}
Y × P		13.3^{**}	7.9^{**}	48.0^{**}	27.7^{**}	7.0^{**}	17.7^{**}
C × P		196.1^{**}	66.5^{**}	141.0^{**}	203.6^{**}	116.5^{**}	89.0^{**}
Y × C × P		4.7^{**}	ns	ns	20.6^{**}	9.1^{**}	4.0^{*}

P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient cultivar. Different letters denote statistical significance at $P < 0.05$ within a column in the same year. $^{*}P < 0.05$; $^{**}P < 0.01$; ns – not significant at $P = 0.05$

https://doi.org/10.17221/35/2026-PSE

Root volume and weight showed trends similar to root length, increasing initially before declining and peaking at the heading stage (Table 3). However, the P requirements for maximising these traits differed between cultivars: Liangeng 7 required 0.88 g P/pot (P2), while Yongyou 2640 achieved its maxima at 0.44 g P/pot (P1). Compared with Liangeng 7, Yongyou 2640 consistently exhibited higher root volume and weight. Specifically, Yongyou 2640's root volume was greater by 41.3% (mid-tillering), 20.0% (heading), and 20.6% (maturity) in 2021, and 40.5, 20.7, and 21.9% in 2022. Similarly, its root weight was higher by 60.3, 27.6, and 32.6% in 2021, and 48.1, 12.2, and 22.9% in 2022.

Root absorption area, oxidation activity, and activities of acid phosphatase. The root total and active absorption areas fluctuated throughout the growth cycle, peaking at the heading stage (Figure 1). However, the optimal P rate under the present pot conditions and soil P status for maximising these areas differed between cultivars: Liangeng 7 reached its maximum under the P2 treatment, whereas Yongyou 2640 reached its maximum under the P1 treatment. Furthermore, Yongyou 2640 exhibited significantly larger total and active absorption areas than Liangeng 7. This consistent trend across both experimental years confirms that P application significantly influences root absorption area, and that the optimal P rate is cultivar-specific and dependent on P efficiency.

Root oxidation activity in both cultivars increased initially, then decreased with increasing P application rates (Figure 2). However, their optimal P levels under the present pot conditions and soil P status differed: Liangeng 7 achieved peak activity across all stages at 0.88 g/pot, while Yongyou 2640 did so at 0.44 g/pot. Furthermore, Yongyou 2640 demonstrated significantly higher root oxidation activity than Liangeng 7, with average increases of 14.0% at

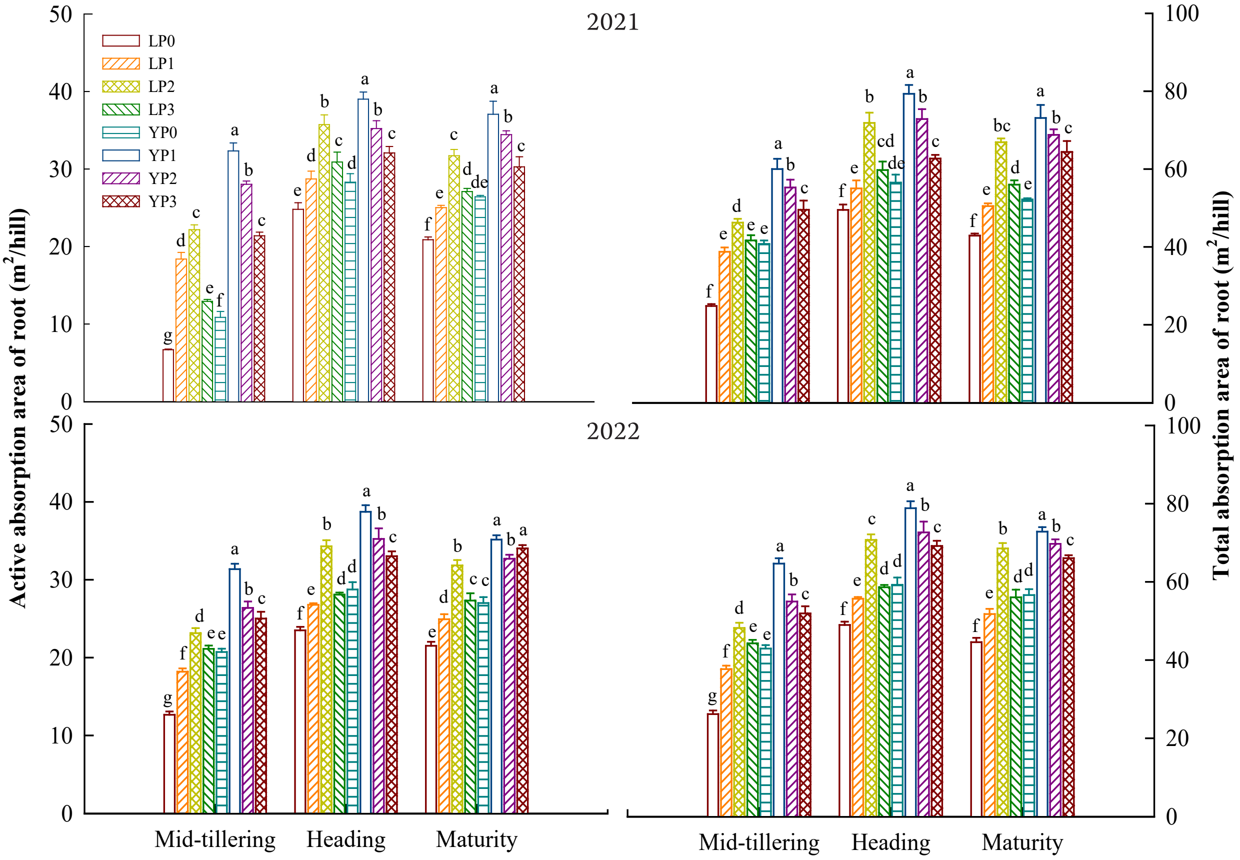

Figure 1. Changes in active and total absorption area of rice root with Liangeng 7 and Yongyou 2640 at mid-tillering, heading and maturity stage under different phosphorus fertiliser rates. P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient. Vertical bars represent ± standard error (SE) of the mean. The SE was calculated across three replications for each year. Different letters indicate statistical significance at $P < 0.05$ within the same stage

https://doi.org/10.17221/35/2026-PSE

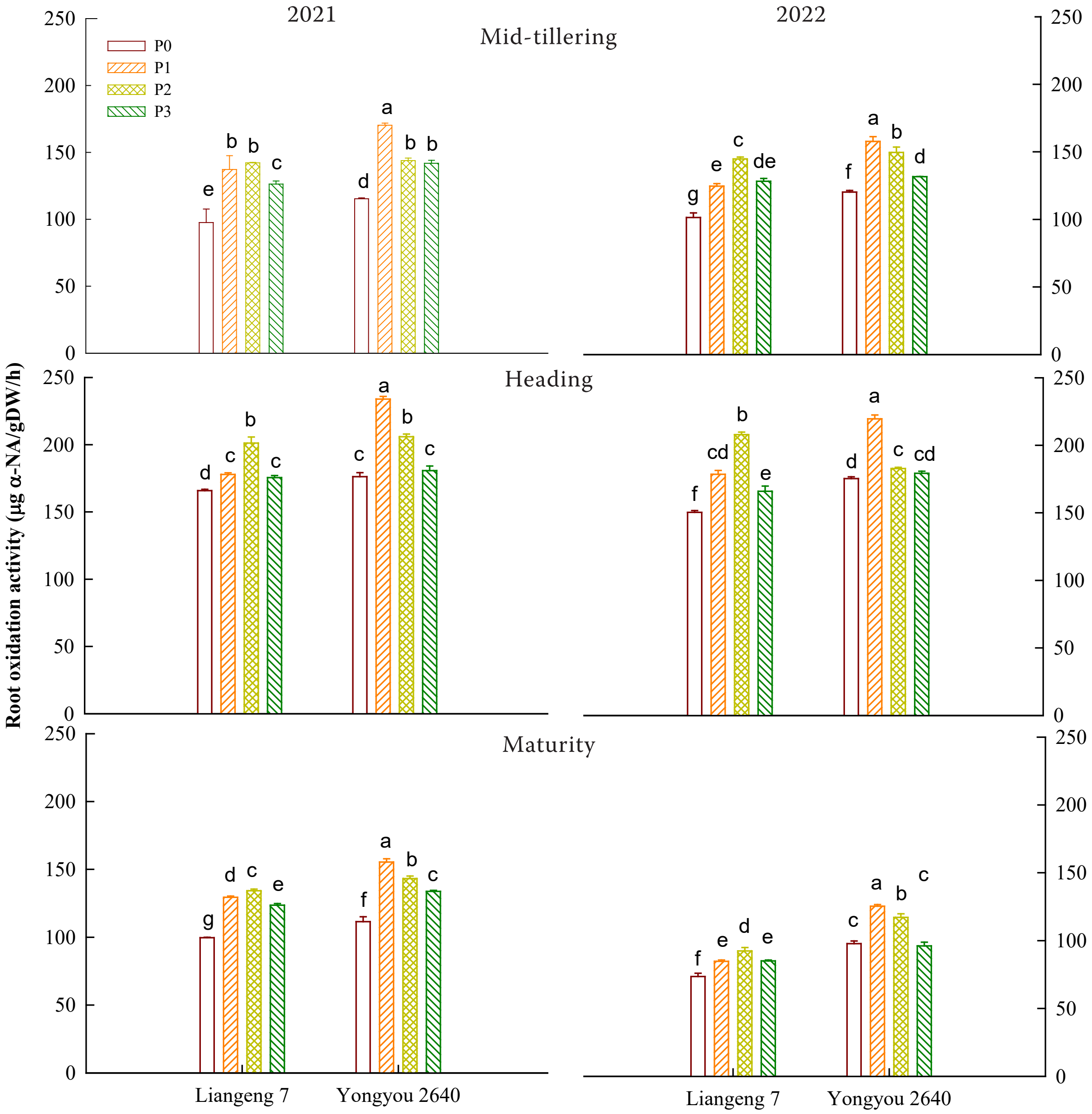

Figure 2. Changes in root oxidation activity with Liangeng 7 and Yongyou 2640 at mid-tillering, heading and maturity stage under different phosphorus fertiliser rates. P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient. Vertical bars represent ± standard error (SE) of the mean. The SE was calculated across three replications for each year. Different letters indicate statistical significance at $P < 0.05$ within the same stage. DW – dry weight

mid-tillering, 10.8% at heading, and 11.7% at maturity in 2021; the corresponding increases were 12.8, 8.9, and 30.1% in 2022.

Root acid phosphatase (APase) activity showed a unimodal response to increasing P rates, also peaking at the heading stage (Figure 3). The two cultivars differed markedly in the P input required for maximum APase activity. Liangeng 7 achieved its highest activity under the P2 treatment, with average increases of 76.2% (2021) and 111.8% (2022) over P0. In contrast, Yongyou 2640 peaked at the P1 treatment, showing average increases of 27.3% (2021) and 50.0% (2022) over P0. At the same P level, Yongyou 2640 maintained significantly higher APase activity than Liangeng 7, with increases of 53.8% in 2021 and 33.3% in 2022.

Photosynthetic characteristics of leaves. The net photosynthetic rate (P_n) and transpiration rate (T_r) in rice declined throughout the growth cycle (Figure 4). Both parameters exhibited a unimodal response to

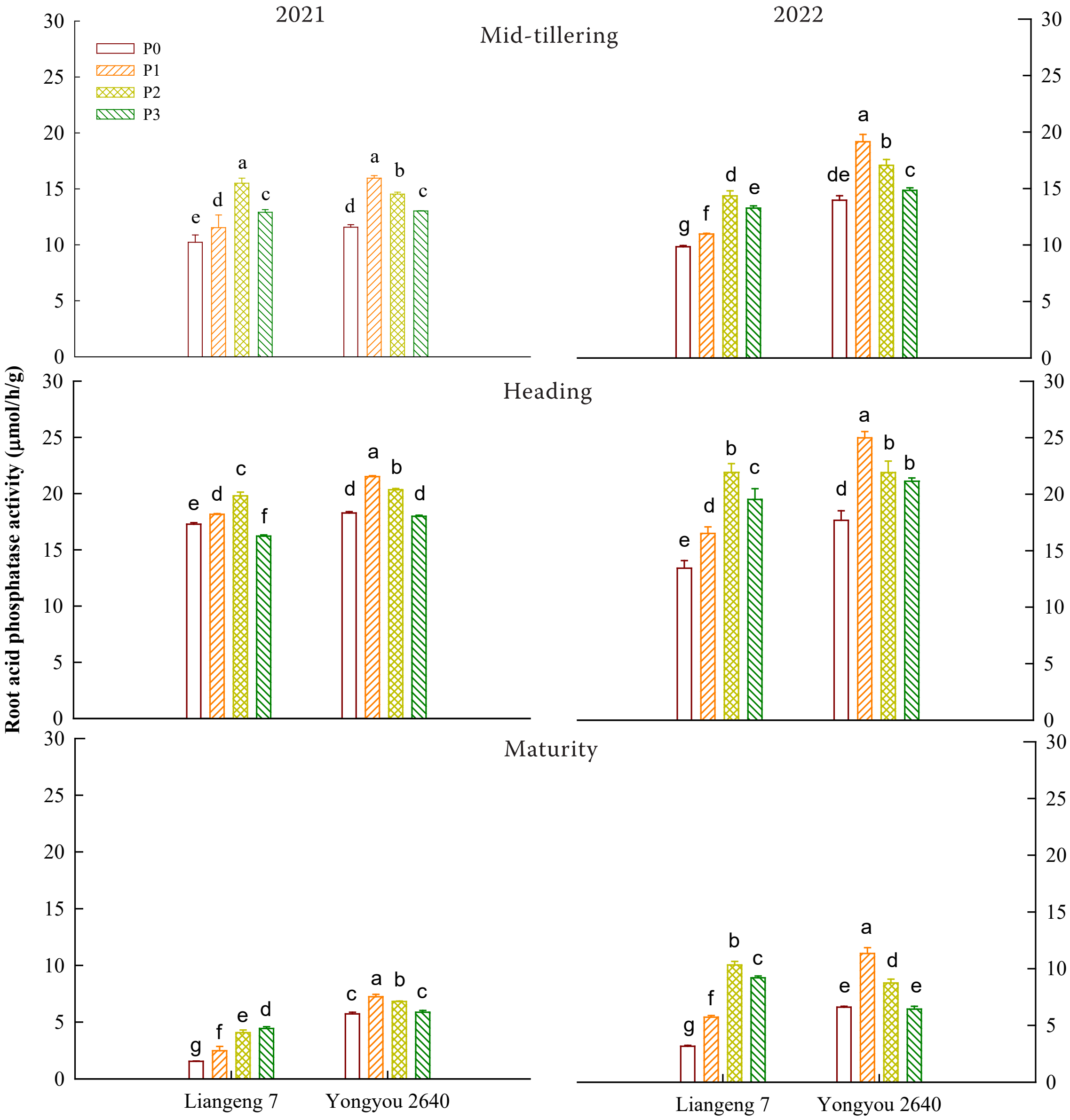

Figure 3. Changes in root acid phosphatase activity with Liangeng 7 and Yongyou 2640 at mid-tillering, heading and maturity stage under different phosphorus fertiliser rates. P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient. Vertical bars represent ± standard error (SE) of the mean. The SE was calculated across three replications for each year. Different letters indicate statistical significance at $P < 0.05$ within the same stage

P application, increasing initially before declining. The optimal P rate under the present pot conditions and soil P status for maximising P_n and T_r across all growth stages was 0.88 g/pot for Liangeng 7, but only 0.44 g/pot for the high phosphorus-efficient cultivar Yongyou 2640. Notably, Yongyou 2640 consistently demonstrated superior P_n and T_r compared to Liangeng 7. This trend, consistent over both study years, confirms that phosphorus application significantly influences P_n and T_r, with the optimal rate being cultivar-specific. The higher photosynthetic capacity of the high phosphorus-efficient cultivar facilitates greater production of photosynthetic assimilates.

Similar to leaf P_n and T_r, stomatal conductance (g_s) in both cultivars also exhibited an initial increase followed by a decrease as P application rates increased (Figure 5). However, the optimal P level under the present pot conditions and soil P status for maximum g_s differed: Liangeng 7 attained its highest g_s under the P2 treatment, with average increases of

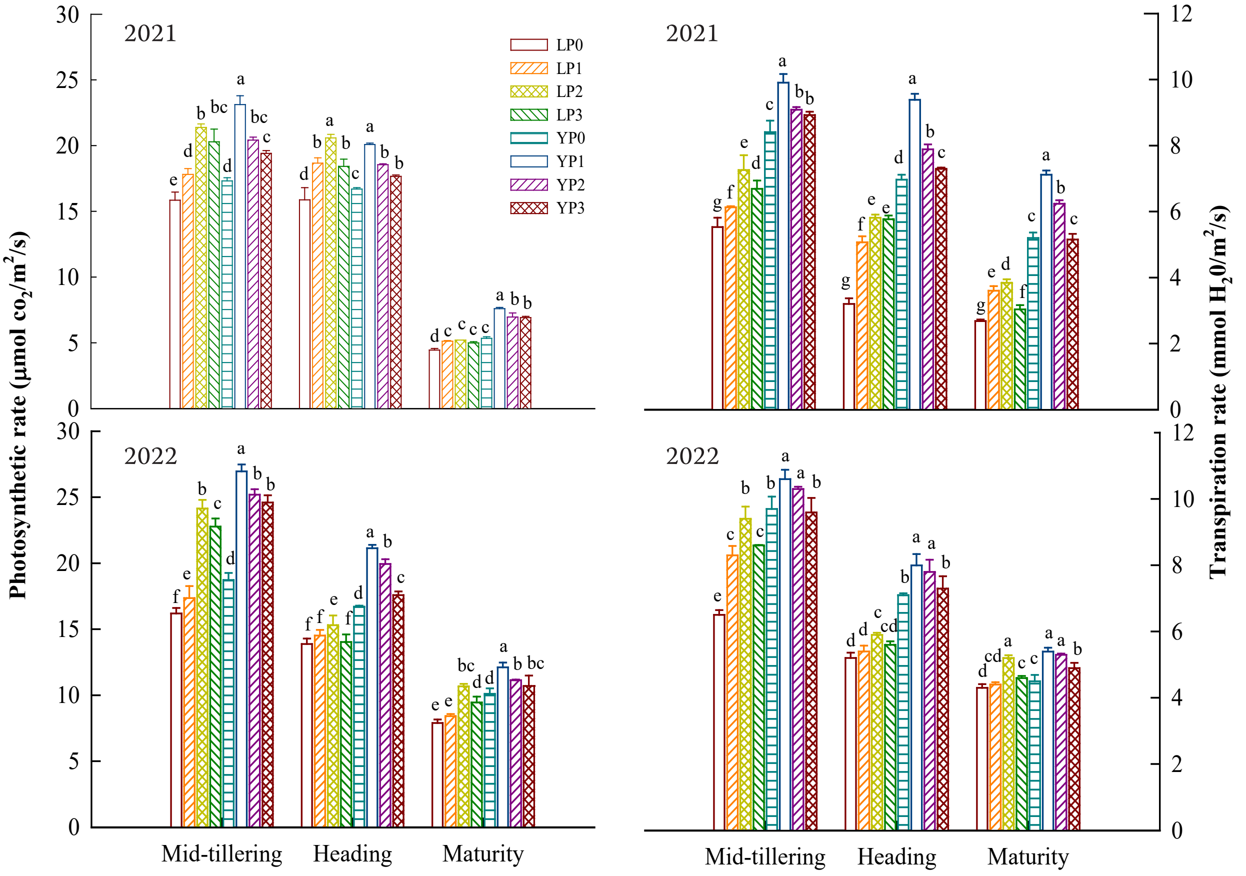

Figure 4. Photosynthetic rate and transpiration rate of leaves with Liangeng 7 and Yongyou 2640 at mid-tillering, heading and maturity stage under different phosphorus fertiliser rates. P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient. Vertical bars represent ± standard error (SE) of the mean. The SE was calculated across three replications for each year. Different letters indicate statistical significance at $P < 0.05$ within the same stage

21.3% in 2021 and 38.2% in 2022 compared to P0. In contrast, Yongyou 2640 peaked under the P1 treatment, showing average increases of 25.0% and 33.2% relative to P0 in 2021 and 2022, respectively. At the same P application level, Yongyou 2640 exhibited significantly higher g_s than Liangeng 7, by 63.9% in 2021 and 62.0% in 2022.

In contrast to leaf P_n and T_r, the intercellular CO_2 concentration (C_i) in both cultivars showed a distinct V-shaped response to increasing P application, declining initially before rising (Figure 5). The P application rate that minimised C_i across all growth stages was 0.88 g/pot for Liangeng 7, but only 0.44 g/pot for Yongyou 2640. Furthermore, Yongyou 2640 consistently maintained a lower C_i than Liangeng 7 at the mid-tillering and heading stages. This consistent trend over two study years confirms that P application significantly influences C_i, and that the optimal rate is cultivar-specific.

Correlation analysis among root characteristics, leaf photosynthetic traits and appearance quality in rice. Correlation analysis showed that root length, root dry weight, root volume, root oxidation activity, root acid phosphatase activity, and active root absorption area, as well as total root absorption area, were extremely significantly positively correlated with P_n, T_r, and g_s in both years, while they were extremely significantly negatively correlated with C_i (Figure 6). Additionally, root morphological and physiological indices, including root length, root weight, root volume, root total and active absorption area, root oxidation activity, root acid phosphatase activity, and photosynthetic parameters, including P_n, T_r, and g_s, were significantly or extremely significantly negatively correlated with chalky kernel percentage, chalky area and chalkiness degree in both years. But C_i was extremely significantly positively correlated with chalkiness indicators (Figure 7).

https://doi.org/10.17221/35/2026-PSE

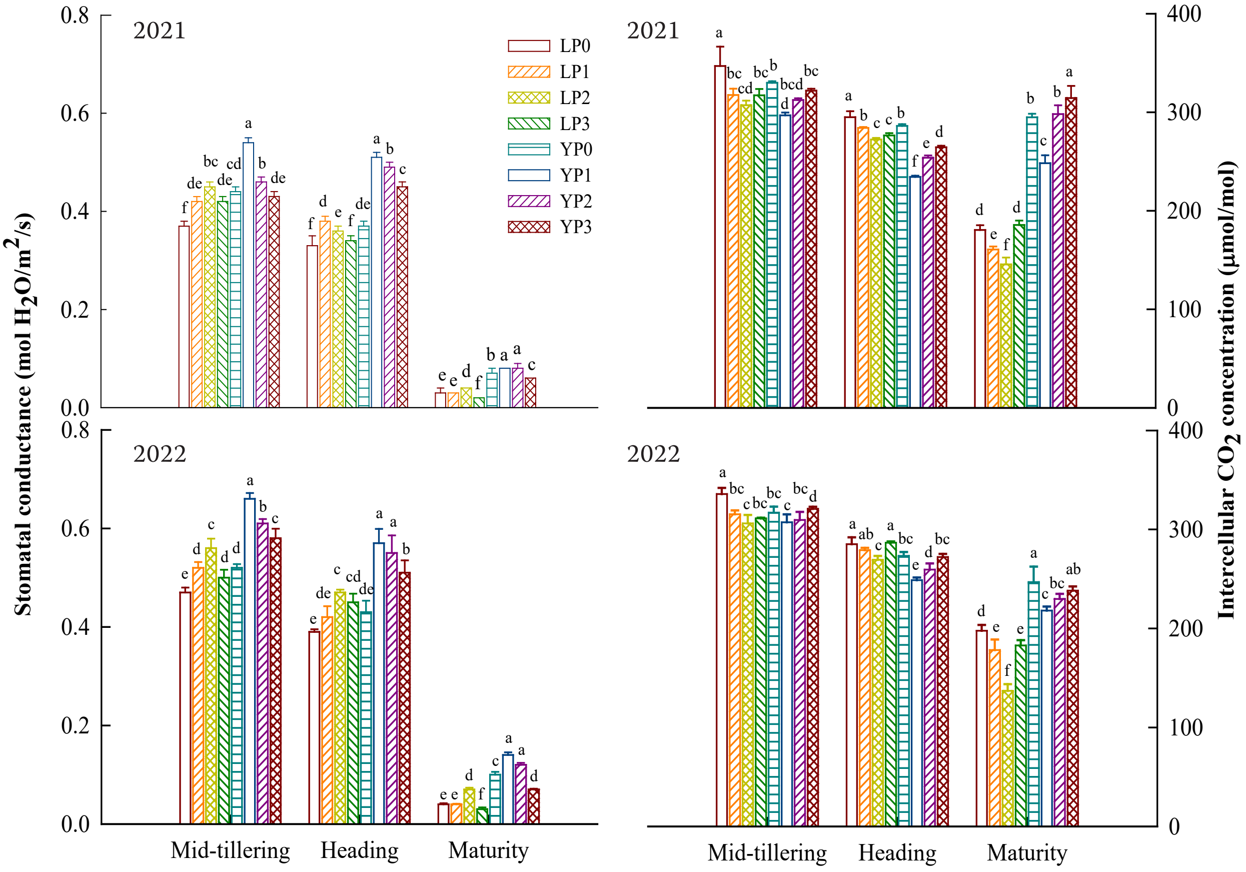

Figure 5. Changes in stomatal conductance and intercellular CO_2 concentration of leaves with Liangeng 7 and Yongyou 2640 at mid-tillering, heading and maturity stage under different phosphorus fertiliser rates. P0 – no phosphorus fertiliser application; P1 – 0.44 g/pot; P2 – 0.88 g/pot; P3 – 1.32 g/pot; Liangeng 7 – weakly phosphorus-efficient cultivar; Yongyou 2640 – highly phosphorus-efficient. Vertical bars represent ± standard error (SE) of the mean. The SE was calculated across three replications for each year. Different letters indicate statistical significance at $P < 0.05$ within the same stage

DISCUSSION

Effect of phosphorus application rates on root characteristics of different phosphorus-efficient rice cultivars. Root system functionality, determined by its morphological and physiological traits, is fundamental to crop growth, yield, and quality formation (Xu et al. 2020, Vinarao et al. 2023, Wei et al. 2024, Camli-Saunders and Villouta 2025, Kohli et al. 2025). Under low-phosphorus stress, rice modulates its root architecture by increasing root length, volume, and surface area while reducing root diameter – morphological adaptations that enhance soil phosphorus foraging. In contrast, application of an appropriate phosphorus rate can promote rice root system growth, enhance root physiological activity, and improve nutrient absorption, thereby establishing a solid foundation for supplying nutrients to the shoots (Zhang et al. 2021, Gu et al. 2023, Muhandiram et al. 2024, Srivastava et al. 2025). In the present study, key root traits – including length, weight, volume, oxidation activity, and acid phosphatase activity – displayed a unimodal response to increasing phosphorus rates, rising initially before declining (Tables 2–3; Figures 1–3). This unimodal response contrasts with the findings of Ding et al. (2021), who observed a monotonic decrease in these traits with increasing phosphorus. The initial suppression of root growth in this experiment is attributable to the low soil-available phosphorus levels (4.9 mg/kg in 2021 and 5.2 mg/kg in 2022). While moderate phosphorus application alleviated this limitation, excessive phosphorus failed to enhance physiological activity and even became inhibitory (Tables 2–3, Figures 1–3). This suppression under high phosphorus aligns with the results of Zhang et al. (2021) in

https://doi.org/10.17221/35/2026-PSE

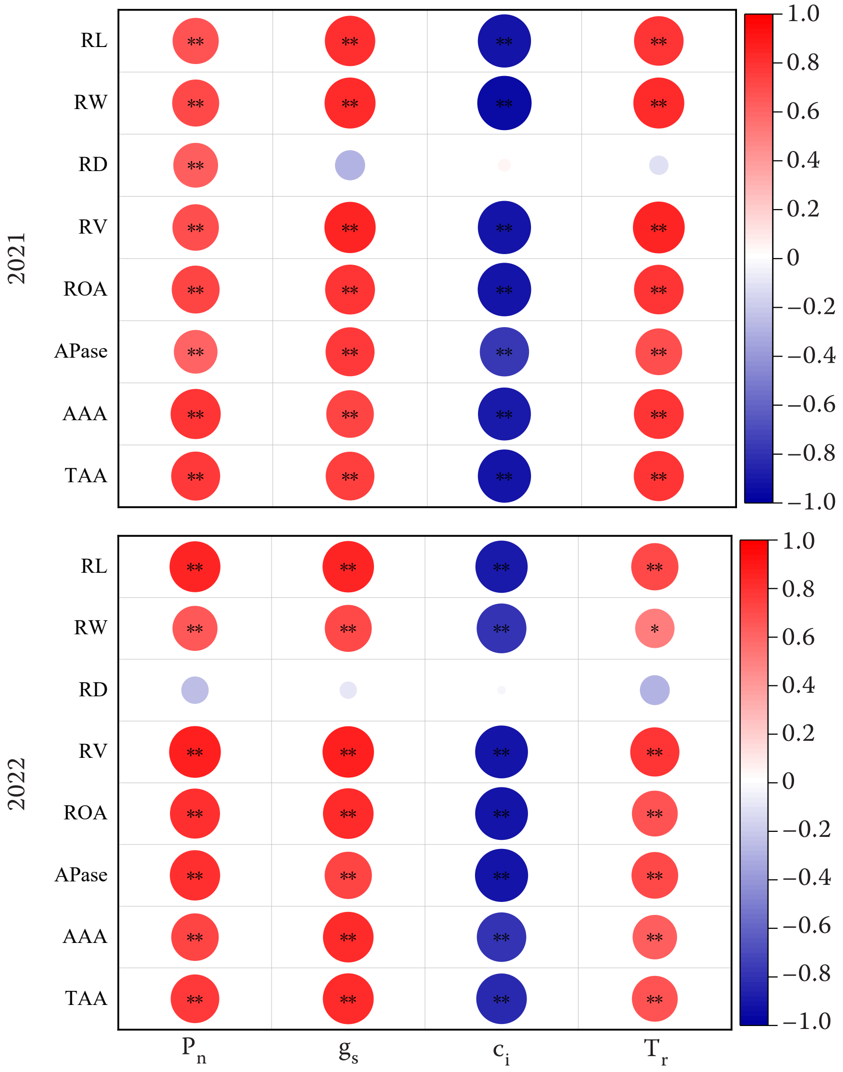

Figure 6. Correlation analysis between root morphological and physiological indices and photosynthetic parameters of Liangeng 7 and Yongyou 2640 under different phosphorus fertiliser rates. RL – root length; RW – root dry weight; RD – root diameter; RV – root volume; ROA – root oxidation activity; APase – root acid phosphatase activity; AAA – root active absorption areas; TAA – root total absorption areas; P_n – net photosynthetic rate; g_s – stomatal conductance; c_i – intercellular CO_2 concentration; T_r – transpiration rate. $^*P < 0.05$ and $^{**}P < 0.01$ indicate significance difference of *F*-values. Red and blue means positive and negative correlation, respectively

hydroponic systems. A plausible mechanism is that undissolved excess phosphorus fertiliser elevates the osmotic potential of the soil solution, thereby inhibiting root metabolism and function (Prodhan et al. 2019, Cheng et al. 2023, Sinclair et al. 2024, Zulfiqar et al. 2025).

The present results showed that Yongyou 2640 generally exhibited superior root morphological and physiological traits – including root length, root volume, root weight, root absorption area, root oxidation capacity, and root acid phosphatase activity – compared to those of Liangeng 7 (Tables 2–3, Figures 1–3). This advantage can be attributed to the enhanced allocation of carbohydrates to the roots of the high-phosphorus-efficient cultivar Yongyou 2640 under low-phosphorus stress. This provides energy in the form of respiratory ATP for cell division and elongation, as well as structural precursors for cell walls and membranes, thereby directly facilitating increases in root length and volume (Deng et al. 2022, Verbeeck et al. 2023, Li et al. 2024, Mishra et al. 2025). In contrast, both shoot and root growth of the weak phosphorus-efficient cultivar (Liangeng 7) were significantly inhibited under the same phosphorus-limited conditions (Deng et al. 2022, Verbeeck et al. 2023, Mishra et al. 2025). Furthermore, the high phosphorus-efficient cultivar optimises its root system architecture, developing a more extensive system that is highly efficient at exploring a larger soil volume and capturing heterogeneous resources (Deng et al. 2022, Vinarao et al. 2023, Sun et al. 2024b, Kohli et al. 2025). Consequently, Liangeng 7 requires a higher phosphorus input to achieve comparable growth. Additionally, Yongyou 2640 secretes greater amounts of acid phosphatase, which enhances root-mediated phosphorus mobilisation and uptake from the soil. This, in turn, promotes shoot growth and development, ultimately contributing to higher

https://doi.org/10.17221/35/2026-PSE

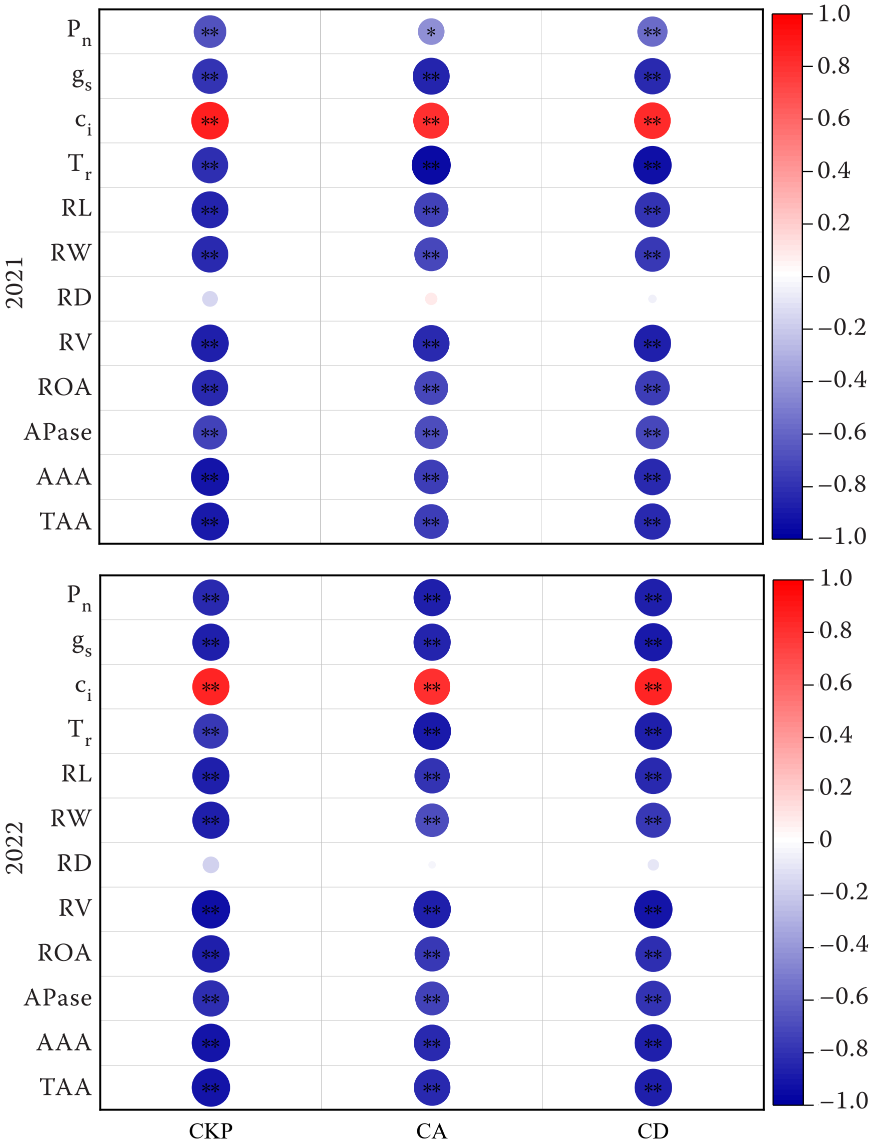

Figure 7. Correlation analysis between root morphological and physiological indices, photosynthetic parameters and chalky kernel percentage, chalky area, and chalkiness degree of Liangeng 7 and Yongyou 2640 under different phosphorus fertiliser rates. P_n – net photosynthetic rate; g_s – stomatal conductance; c_i – intercellular CO_2 concentration; T_r – transpiration rate; RL – root length; RW – root dry weight; RD – root diameter; RV – root volume; ROA – root oxidation activity; APase – root acid phosphatase activity; AAA – root active absorption areas; TAA – root total absorption areas; CKP – chalky kernel percentage; CA – chalky area; CD – chalkiness degree. *$P < 0.05$ and **$P < 0.01$ indicate significance difference of *F*-values. Red and blue mean positive and negative correlation, respectively

yield formation (Deng et al. 2022, Wang et al. 2024, Liu et al. 2025).

These results demonstrate that the weakly and highly phosphorus-efficient cultivars, Liangeng 7 and Yongyou 2640, achieved optimal root physiological activity and growth only at their respective phosphorus application rates (0.88 and 0.44 g/pot, respectively). This enhancement in root function subsequently improved nutrient uptake and photosynthate accumulation, which ultimately supported grain filling and optimised rice appearance quality. Therefore, phosphorus fertiliser application should be tailored to the specific requirements of cultivars with differing phosphorus efficiency.

Effect of phosphorus application rates on photosynthetic traits of different phosphorus-efficient rice cultivars. Photosynthesis is the most critical physiological process in crop development, accounting for over 90% of rice yield (Xu et al. 2018, Wu et al. 2022, Ray and Dalal 2024, Cui et al. 2025). As an essential component of photosynthetic assimilation and photophosphorylation, phosphorus plays a direct role in this process (Veronica et al. 2017, Chen et al. 2024, Linger and Long 2025). This study demonstrated that the optimal phosphorus rate under the present pot conditions and soil P status for maximising photosynthetic performance was 0.88 g/pot for Liangeng 7 and 0.44 g/pot for Yongyou 2640 (Figures 4–5). At these optimal rates, both cultivars achieved their highest net photosynthetic rate, stomatal conductance, and transpiration rate, coupled with the lowest intercellular CO_2 concentration. A key mechanism is that phosphorus fertilisation enhances the net photosynthetic rate primarily by boosting the photosynthetic activity of mesophyll cells (Shu et al. 2023, Chen et al. 2024). Given the low phosphorus availability in the experimental soil, phosphorus supplementation was essential to promote photosynthesis. Moreover, appropriate phosphorus application can mitigate the suppression of photosynthetic activity associated with elevated intercellular CO_2 concentrations. Conversely, excessive phosphorus application (1.32 g/pot) reduced stomatal conductance, transpiration rate, and overall photosynthetic performance (Figures 4–5). This decline can be attributed to an induced nutrient imbalance, particularly a reduction in iron (Fe) content, which ultimately impairs photosynthetic efficiency (dos Santos et al. 2020).

Previous studies have shown that phosphorus-efficient cultivars can maintain a stable net photosynthetic rate under low-phosphorus stress, attributed to their ability to preserve the structural integrity and functional stability of photosynthetic organs, thereby mitigating the inhibitory effects of phosphorus deficiency (Deng et al. 2022, Sun et al. 2024b). Consistent with this, our study showed that under the same phosphorus application rate, the highly phosphorus-efficient cultivar Yongyou 2640 exhibited significantly higher photosynthetic rate, stomatal conductance, and transpiration rate, along with a lower intercellular CO_2 concentration, compared to the weak phosphorus-efficient Liangeng 7 (Figures 4–5). This superiority may be due to several factors. First, phosphorus-efficient cultivars exhibit greater chloroplast stability and higher light absorption and energy conversion efficiency, providing a structural basis for enhanced photosynthesis (Chen et al. 2024). Second, they prioritise maintaining the activity of key phosphorus-containing or phosphorus-activated enzymes essential for the dark reactions of photosynthesis (Furbank et al. 2023). Furthermore, by optimising internal phosphorus allocation to facilitate the synthesis and transport of photosynthetic products, these cultivars improve overall photosynthetic efficiency (Deng et al. 2022, Sun et al. 2024b). In contrast, the weakly phosphorus-efficient Liangeng 7 showed a significant reduction in photosynthetic rate under phosphorus deficiency (Figures 4–5), likely due to an impaired ability to remobilise phosphorus from photorespiratory glycolate to sustain photosynthetic metabolism (Yao et al. 2022, Furbank et al. 2023).

This study demonstrates that highly phosphorus-efficient cultivars utilise phosphorus more efficiently and maintain higher photosynthetic rates under phosphorus stress. Consequently, the adoption of such cultivars represents a viable strategy for reducing phosphate fertiliser application while enhancing photosynthetic efficiency, thereby contributing to the dual objectives of high crop productivity and agricultural sustainability.

Effect of phosphorus application rates on appearance quality of different phosphorus-efficient rice cultivars. Rice quality is influenced by a combination of factors, including genetic differences among cultivars, as well as environmental and agronomic conditions such as light, temperature, and cultivation practices (Zhang et al. 2021, Oo et al. 2023, Ray and Dalal 2024, Li et al. 2025). Zhang et al. (2021) reported that increased phosphorus fertilisation rates significantly raised the chalkiness degree in the cultivar Zhonghan 3, thereby deteriorating its appearance quality. However, our findings reveal a more nuanced relationship. We demonstrate that increasing phosphorus application improved the appearance quality of rice, but that supra-optimal phosphorus rates exert detrimental effects (Table 1). Suboptimal phosphorus application (either deficient or excessive) impairs rice quality by altering grain-filling dynamics, endosperm development, and bran thickness. These physiological alterations lead to a higher incidence of chalky grains and increased chalky area, which collectively compromise the milling quality and rice grain appearance quality (Oo et al. 2023, Zhang et al. 2025, Li et al. 2025). Notably, the appearance quality of Liangeng 7 attained its optimum at 0.88 g/pot, while that of Yongyou 2640 required only 0.44 g/pot (Table 1). The proposed mechanism involves optimised root morphology and activity, which synchronise shoot-root signal transduction to secure a sufficient supply of carbohydrates and minerals for grain development and high-quality starch biosynthesis (Zhang et al. 2017). Simultaneously, a strengthened photosynthetic source provides abundant assimilates, preventing chalkiness formation that arises from nutrient deficits during mid-grain filling (Oo et al. 2023, Ray and Dalal 2024). Our earlier research further demonstrated that appropriate phosphorus application delays leaf senescence – thus securing complete grain filling – and enhances the activity of starch metabolic enzymes, leading to more efficient starch synthesis and a more regular arrangement of starch granules (Li et al. 2025, Zhang et al. 2025). Collectively, these responses improve rice appearance quality, highlighting the importance of tailored phosphorus management – based on varietal phosphorus efficiency – for its enhancement.

https://doi.org/10.17221/35/2026-PSE

The relationship between root characteristics, leaf photosynthetic traits, and appearance quality in rice. Previous studies have established that enhancing photosynthetic potential, root vigour, and leaf nitrogen transport is essential for synergistically improving rice yield and quality (Sun et al. 2024a, Zhu et al. 2024). Consistent with this understanding, our results show that the highly phosphorus-efficient cultivar Yongyou 2640 achieves optimal appearance quality under a relatively low phosphorus supply (0.44 g/pot). This improvement is associated with enhanced photosynthetic productivity, resulting from the concurrent optimisation of both root morphology and physiology (Tables 1–3; Figures 1–5). Correlation analysis further supports these relationships. The observed improvements in root growth and photosynthesis contributed to reduced rice chalkiness, as evidenced by significant negative correlations among root morphophysiological indices, photosynthetic parameters, and chalkiness traits (Figures 6–7). Therefore, a synergistic management strategy that fine-tunes root architecture by promoting root growth while boosting physiological activity may enhance both nutrient acquisition and canopy photosynthesis, thereby contributing to superior grain appearance. However, this study also has certain limitations. Given that this study was conducted under pot conditions with low available phosphorus soil, the optimal phosphorus rate identified under these conditions should be validated in future field studies to determine appropriate application rates for practical agricultural production.

Acknowledgements. This work was supported by the National Natural Science Foundation of China, Grant No. U1304316; by the Joint Research Fund for Science and Technology Development of Henan Province, Grant No. 242103810031; by the Science and Technology Research Project of Henan Province, Grant No. 242102110169; by the Open Foundation of the Key Laboratory of Cultivation and Physiology of Jiangsu Province, Grant No. 027388003K11009, and by the Doctoral Research Initiation Fund of Henan University of Science and Technology, Grant No. 13480108.

REFERENCES

Camli-Saunders D., Villouta C. (2025): Root exudates in controlled environment agriculture: composition, function, and future directions. Frontiers in Plant Science, 16: 1567707.

Chen G., Ran Q.X., Wang C., Pang J.Y., Ren M.J., Wang Z.Y., He J., Lambers H. (2024): Enhancing photosynthetic phosphorus use efficiency through coordination of leaf phosphorus fractions, allocation, and anatomy during soybean domestication. Journal of Experimental Botany, 76: 1446–1457.

Cheng Y.Y., Narayanan M., Shi X.J., Chen X.P., Li Z.L., Ma Y. (2023): Phosphate-solubilizing bacteria: their agroecological function and optimistic application for enhancing agro-productivity. Science and Total Environment, 901: 166468.

Chiba M., Terao T., Watanabe H., Matsumura O., Takahashi Y. (2017): Improvement in rice grain quality by deep-flood irrigation and its underlying mechanisms. Jaro-japan Agricultural Research Quarterly, 51: 107–116.

Costa N.B., Benzerra G.D., de Moraes M.G., de Filippi M.C.C., Carvalho M.D.S., Bhosale R.A., de Castro A.P., Lanna A.C. (2025): Beneficial bacteria mitigate combined water and phosphorus deficit effects on upland rice. Plant and Soil, 512: 1457–1474.

Cui Y.M., Ma W.D., Yang C.N., Bai R.X., Xia T.Z., Wei C.Z., Zhang X.J., Zhou G.W. (2025): Subsurface drip irrigation combined with ammonium enhances root growth in rice (*Oryza sativa* L.), leading to improved N uptake and higher yield formation. Plants, 14: 891.

Deng Y.P., Men C., Qiao S.F., Wang W.J., Gu J.F., Liu L.J., Zhang Z.J., Zhang H., Wang Z.Q., Yang J.C. (2022): Tolerance to low phosphorus in rice varieties is conferred by regulation of root growth. The Crop Journal, 8: 534–547.

Ding Y., Wang Z.G., Mo S.R., Liu J., Xing Y., Wang Y.P., Ge C.L., Wang Y.L. (2021): Mechanism of low phosphorus inducing the main root lengthening of rice. Journal of Plant Growth Regulation, 40: 1032–1043.

Dos Santos M.S., Sanglard L.M.V.P., Barbosa M.L., Namorato F.A., de Melo D.C., Franco W.C.G., Pérez-Molina J.P., Martins S.C.V., DaMatta F.M. (2020): Silicon nutrition mitigates the negative impacts of iron toxicity on rice photosynthesis and grain yield. Ecotoxicology and Environmental Safety, 189: 110008.

Furbank R., Kelly S., von Caennerer S. (2023): Photosynthesis and food security: the evolving story of C_4 rice. Photosynthesis Research, 158: 121–130.

Gao D.P., Ran C., Dang K., Wang X.L., Zhang Y.H., Geng Y.Q., Liu S.Y., Guan Z.W., Guo L.Y., Shao X.W. (2023): Effect of phosphorus, iron, zinc, and their combined deficiencies on photosynthetic characteristics of rice (*Oryza sativa* L.) seedlings. Agronomy, 13: 1657.

Gong W.L., Vinarao R., Proud C., Wood S., Snell P., Fukai S., Mitchell J. (2025): Genomic regions and molecular markers associated with deeper rooting to improve grain yield in aerobic rice (*Oryza sativa* L.) production systems. Rice, 18: 124.

Gu P.Y., Tao W.Q., Tao J.Y., Sun H.W., Hu R.P., Wang D.J., Zong G.X.A., Xie X.A., Ruan W.Y., Xu G.H., Yi K.K., Zhang Y.L. (2023): The D14-SDEL1-SPX4 cascade integrates the strigolactone and phosphate signalling networks in rice. New Phytologist, 239: 673–686.

Hu X.Q., Zhang W.X., Lu L., Shao Y.F., Chen M.X., Zhu Z.W., Mou R.X. (2022): Comparison of quality of appearance, cooking quality, and protein content of green-labelled rice and conventional rice. Cereal Chemistry, 4: 873–883.

Jiang H., Xu X.T., Sun A.R., Bai C.Y., Li Y.Z., Nuo M., Shen X.R., Li W.C., Wang D.C., Tian P., Wei X.S., Wang G., Yang M.Y., Wu Z.H. (2024): Silicon nutrition improves the quality and yield of rice under dry cultivation. Journal of the Science of Food and Agriculture, 104: 1897–1908.

Kanokwan K., Tongmark K., Chakhonkaen S., Sangarwut N., Wasinanon T., Panyawut N., Ditthab K., Sikawetung K., Qi Y.B., Dapha S., Panya A., Phonsatta N., Muangprom A. (2023): Development of new aromatic rice lines with high eating and cooking qualities. Journal of Integrative Agriculture, 22: 679–690.

Kohli P.S., Donde R., Sirohi U., Singh B., Anantha M.S., Bhadana V.P., Sundaram R.M., Mangrauthia S.K., Giri J. (2025): Physiological and genetic basis of superior phosphate uptake and utilization efficiency in the rice landrace Wazuhophek. Journal of Experimental Botany, 228: 331.

Li G.H., Zhang Y., Zhou C., Xu J.W., Zhu C.J., Ni C., Huo Z.Y., Dai Q.G., Xu K. (2024): Agronomic and physiological characteristics of high yield and nitrogen use efficient varieties of rice: comparison between two near-isogenic lines. Food and Energy Security, 13: e539.

Li H.J., Li H.R., Zhang D.K., Jiang M.M., Cao J., Xu G.W. (2025): Irrigation methods and nitrogen-form interactions regulate starch-metabolising enzyme activity to improve rice yield and quality. Plant, Soil and Environment, 71: 185–201.

Linger E., Long W.X. (2025): Phosphorus limitation constrains global forest productivity directly and indirectly *via* forest community structural attributes: meta-analysis. Global Ecology and Biogeography, 34: e70048.

Liu D. (2021): Root developmental responses to phosphorus nutrition. Journal of Integrative Plant Biology, 63: 1065–1090.

Liu M.Y., Mooleki S.P., Li Y.L., Schneider D., Kochian L.V., Helgason B.L. (2025): Phosphorus fertilizer responsive bacteria and fungi in canola (*Brassica napus* L.) roots are correlated with plant performance. Plant and Soil, 513: 1927–1948.

Liu Y., Gao J.P., Zhao Y.Z., Fu Y.C., Yan B.C., Wan X., Cheng G.Q., Zhang W.Z. (2024): Effects of different phosphorus and potassium supply on the root architecture, phosphorus and potassium uptake, and utilization efficiency of hydroponic rice. Scientific Reports, 14: 21178.

Lu S.S., Xu X.M., Wu Y.Z., Ye J., Wu L.Y., Nie M.M., Sun S.B., Jing W., Cho H.K., Rouached H., Zheng L.Q. (2025): Unravelling OsPHT2;1 function in chloroplast phosphorus homeostasis and photosynthetic efficiency under low phosphorus stress in rice. Physiologia Plantarum, 177: e70082.

Lv X.M., Li Q.C., Deng X., Ding S.T., Sun R.B., Chen S.Q., Yun W.J., Dai C.R., Luo B.B. (2024): Fulvic acid application increases rice seedlings performance under low phosphorus stress. BMC Plant Biology, 24: 703.

Mishra A., Barik S.R., Lenka D., Pandit E., Behera L., Dash S.K., Sangeeta S., Das S., Pradhan S.K. (2025): Transfer of deeper rooting and phosphorus uptake QTL into the popular rice variety ‘maudamani’ *via* marker-assisted backcross breeding. Scientific Reports, 15: 25418.

Muhandiram K.C.L.S., Kikuta M., Nagaoka T. (2024): Shoot and root responses to low phosphorus and their genotypic variability in selected cultivars of Japanese core collections of maize and soybean. Soil Science of Plant Nutrition, 70: 100–113.

Oo A.Z., Asai H., Kawamura K., Marui J., Nakahara K., Takai T., Saito H., Win K.T., Pariasca-Tanaka J. (2023): Optimizing phosphorus management to increase grain yield and nutritional quality while reducing phytic acid concentration in black rice (*Oryza sativa* L.). Frontiers in Sustainable Food Systems, 7: 1200453.

Popova I.E., Deng S. (2010): A high throughput microplate assay for simultaneous colorimetric quantification of multiple enzyme activities in soil. Applied Soil Ecology, 45: 315–318.

Prathap V., Suresh K., Tyagi A. (2023): Comparative proteome analysis of phosphorus-responsive genotypes reveals the proteins differentially expressed under phosphorous starvation stress in rice. International Journal of Biological Macromolecules, 234: 123760.

Prodhan M.A., Finnegan P.M., Lambers H. (2019): How does evolution in phosphorus-impoverished landscapes impact plant nitrogen and sulfur assimilation? Trends in Plant Science, 24: 69–82.

Ramasamy S., Ten Berge H.F.M., Purushothaman S. (1997): Yield formation in rice in response to drainage and nitrogen application. Field Crops Research, 51: 65–82.

Ray A., Dalal V.K. (2024): Proteomics response of photosynthetic machinery to abiotic stresses: a review. Current Proteomics, 21: 626–638.

Shu Y., Huang G.J., Zhang Q.Q., Peng S.B., Li Y. (2023): Reduction of photosynthesis under P deficiency is mainly caused by the decreased CO_2 diffusional capacities in wheat (*Triticum aestivum* L.). Plant Physiology and Biochemistry, 198: 107680.

Sinclair T.R., Jafarikouhini N., Pradhan D. (2024): Unexpectedly, triple super phosphate fertilizer induces maize drought resilience. Journal of Plant Nutrition, 47: 1906–1915.

Srivastava A., Gupta A., Bishi S.K., Akhila P., Latha P.C., Subrahmanyam D., Brajendra P., Anantha M.S., Ch S.R., Sakhare A.S. (2025): Tolerance of *Oryza sativa* to low phosphate is associated with adaptive changes in root architecture and metabolic exudates. Plant Science, 252: 112415.

Sun Y.J., Xing M.W., He Z.T., Sun Y.Y., Deng Y.Q., Luo Y.H., Chen X.F., Cao Y., Xiong W.B., Huang X.H., Deng P.X., Luo M., Yang Z.Y., Chen Z.K., Ma J. (2024a): Effects of urea topdressing time on yield, nitrogen utilization, and quality of mechanical direct-seeding hybrid indica rice under slow-mixed fertilizer base application. Frontiers in Plant Science, 15: 1400146.

Sun Z.W., Qiao S.F., Xu Y.J., Ji D.L., Zhang W.Y., Gu J.F., Zhu K.Y., Wang Z.Q., Zhang J.H., Yang J.C. (2024b): Agronomic and physi ological performance of the indica rice varieties differing in tolerance to low phosphorus. Agronomy, 14: 41.

Verbeeck M., Houben E., De Bauw P., Rakotoson T., Merckx R., Smolders E. (2023): Root biomass explains genotypic differences in phosphorus uptake of rainfed rice subjected to water and phosphorus stresses. Plant and Soil, 486: 253–271.

Veronica N., Subrahmanyam D., Kiran T.V., Yugandhar P., Bhadana V.P., Padma V., Jayasree G., Voleti S.R. (2017): Influence of low phosphorus concentration on leaf photosynthetic characteristics and antioxidant response of rice genotypes. Photosynthetica, 55: 285–293.

Vinarao R., Proud C., Snell P., Fukai S., Mitchell J. (2023): Narrow root cone angle promotes deeper rooting, cooler canopy temperatures and higher grain yield in a rice (*Oryza sativa* L.) recombinant inbred line population grown under different water availabilities in aerobic production systems. Field Crops Research, 299: 108989.

Wang S.L., Ruan Y.H., Du M.X., Sun W., Zhang Y.L., Wang Y.C., Guo J.M., Shao R.X., Yang Q.H., Wang H. (2024): Optimization of phosphate fertilizer application strategies to improve phosphorus availability and utilization in maize. Agronomy Journal, 116: 453–464.

Wei P., Shi F., Wang X.X., Peng S.Y., Chai R.S., Zhang L.L., Zhang C.C., Luo L.C., Siddique K.H.M. (2024): Optimizing rice yield and phosphorus use efficiency through root morphology and soil phosphorus management in agricultural soils. Annals of Agricultural Sciences, 69: 53–66.

Wu F., Fang F.R., Wu N., Li L., Tang M. (2020): Nitrate transporter gene expression and kinetics of nitrate uptake by *Populus* × *canadensis* 'Neva' in relation to arbuscular mycorrhizal fungi and nitrogen availability. Frontiers in Microbiology, 11: 1–10.

Wu Q.X., Du B., Jiang S.C., Zhang H.W., Zhu J.Q. (2022): Side deep fertilizing of machine-transplanted rice to guarantee rice yield in conservation tillage. Agriculture, 12: 528.

Xu G.W., Jiang M.M., Lu D.K., Wang H.Z., Chen M.C. (2020): Nitrogen forms affect the root characteristic, photosynthesis, grain yield, and nitrogen use efficiency of rice under different irrigation regimes. Crop Science, 60: 2594–2610.

Xu G.W., Lu D.K., Wang H.Z., Li Y.J. (2018): Morphological and physiological traits of rice roots and their relationships to yield and nitrogen utilization as influenced by irrigation regime and nitrogen rate. Agricultural Water Management, 203: 385–394.

Xu Y.J., Gu D.J., Li K., Zhang W.Y., Zhang H., Wang Z.Q., Yang J.C. (2019): Response of grain quality to alternate wetting and moderate soil drying irrigation in rice. Crop Science, 59: 1261–1272.

Yao Z., Rao Z.L., Hou S.W., Tian C.W., Liu C.Y., Yang X.L., Zhu G.C. (2022): The appropriate expression and coordination of glycolate oxidase and catalase are vital to the successful construction of the photorespiratory metabolic pathway. Frontiers in Plant Science, 13: 999757.

Zhang B., Wang Y., Liu H., Yang X., Yuan P., Wang C., Shi L. (2023): Optimal phosphorus management strategies to enhance crop productivity and soil phosphorus fertility in rapeseed-rice rotation. Chemosphere, 337: 139392.

Zhang D.K., Li Y.Y., Li H.R., Li H.J., Zhao X.H., Cao J., Xu G.W. (2025): Phosphorus application rates affect the grain yields of different phosphorus-tolerant rice cultivars by regulating grain filling and leaf senescence characteristics. Plant, Soil and Environment, 71: 363–380.

Zhang Y.J., Zhang W., Wu M., Liu G.S., Zhang Z.J., Yang J.C. (2021): Effects of irrigation schedules and phosphorus fertilizer rates on grain yield and quality of upland rice and paddy rice. Environmental and Experimental Botany, 186: 104465.

Zhang Z.C., Gu T., Zhao B.H., Yang X., Peng Q., Li Y.F., Bai L.Y. (2017): Effects of common *Echinochloa* varieties on grain yield and grain quality of rice. Field Crops Research, 203: 163–172.

Zhu H.J., Nie L.L., He X., Wang X.H., Long P., Chen H.Y. (2024): Water and fertilizer management is an important way to synergistically enhance the yield, rice quality and lodging resistance of hybrid rice. Plant, 13: 2518.

Zulfiqar S., Gu R., Liu Y., Zhang Y.W. (2025): From genes to traits: maximizing phosphorus utilization efficiency in crop plants. Frontiers in Plant Science, 16: 1527547.

Zulfiqar A., Azhar B., Aroosa Z., Zeenat A., Aman S. (2021): Screening of rice varieties based on remodeling of root architecture linked to enhanced phosphorus transporters and ethylene signaling for better phosphorous acquisition under limiting conditions. Sains Malaysiana, 50: 1621–1638.

Received: January 21, 2026
Accepted: March 21, 2026