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Foliar magnesium application: A new nutrient management strategy to enhance peanut yield in phosphorus-limited soils

Mingzhu Ma [a,1], Chunming Bai [b,1], Zhiyu Sun [a], Siwei Zhang [a], Huan Liu [a], Shaikh Amjad Salam [a], Jiayin Pang [c,d], Jean Wan Hong Yong [e,f], Yifei Liu [a,c,d,*], Hans Lambers [c,d], Kadambot HM. Siddique [c]

[a] *China-Australia Joint Laboratory for Plant Nutrition and Germplasm Resources Innovation, College of Land and Environment, National Engineering Research Center for Efficient Utilization of Soil and Fertilizer Resources, Northeast China Plant Nutrition and Fertilization Scientific Observation and Research Center for Ministry of Agriculture and Rural Affairs, Key Laboratory of Protected Horticulture of Education Ministry and Liaoning Province, Shenyang Agricultural University, Shenyang, China*
[b] *Seed Industry Innovation Research Institute, Liaoning Academy of Agricultural Sciences, Shenyang, China*
[c] *The UWA Institute of Agriculture, The University of Western Australia, Perth, WA, Australia*
[d] *School of Biological Sciences, The University of Western Australia, Perth, WA, Australia*
[e] *Future of Farming Institute, Faculty of Science and Engineering, Maastricht University, Venlo, Netherlands*
[f] *Department of Biosystems and Technology, Swedish University of Agricultural Sciences, Alnarp, Sweden*

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ABSTRACT

Sustainable peanut production, a critical source of edible oil and plant protein, is often constrained by phosphorus (P) deficiency in soils. Developing practical agronomic strategies to enhance crop resilience under such nutrient stress is vital for securing food production. This study aimed to evaluate the efficacy and physiological basis of foliar magnesium (Mg) application as a potential nutrient management strategy to improve peanut performance in P-limited environments. A two-year field study evaluated the effects of exogenous magnesium on growth and photosynthetic performance in two peanut varieties with contrasting photosynthetic P-use efficiency (PPUE) under limiting and adequate P availability conditions. The high-PPUE variety (ICG4750, “H”) and low-PPUE variety (ICG9249, “L”) were treated with either foliar-applied magnesium (M1) or no magnesium (M0). Physiological, biochemical, and agronomic parameters were measured. The results confirmed that phosphorus deficiency severely inhibited plant growth and final pod yield. Foliar Mg application effectively mitigated these adverse effects, restoring biomass and yield. Physiologically, Mg supplementation enhanced stomatal conductance and protected the photosynthetic apparatus from photoinhibition, which was associated with improved electron transport and increased ATP synthase activity. Moreover, the high-PPUE genotype (H) showed stronger growth and photosynthetic performance than the low-PPUE genotype (L), highlighting the role of genetic background in the effectiveness of nutrient management. These findings demonstrate that foliar Mg application is a viable agronomic practice to enhance peanut productivity in P-deficient soils. The interaction between Mg nutrition and varietal P efficiency offers a promising approach for integrated nutrient management, contributing to more sustainable peanut cultivation systems.

1. Introduction

Peanut (*Arachis hypogaea*), a major oilseed and food legume, holds substantial importance in global agriculture. Unlike non-leguminous crops, legumes engage in symbiotic nitrogen fixation with rhizobia, sequestering approximately 200 million tons of nitrogen annually [1]. This biological nitrogen fixation significantly contributes to sustainable agriculture and environmental conservation. However, the process is

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[*] Corresponding author. China-Australia Joint Laboratory for Plant Nutrition and Germplasm Resources Innovation, College of Land and Environment, National Engineering Research Center for Efficient Utilization of Soil and Fertilizer Resources, Northeast China Plant Nutrition and Fertilization Scientific Observation and Research Center for Ministry of Agriculture and Rural Affairs, Key Laboratory of Protected Horticulture of Education Ministry and Liaoning Province, Shenyang Agricultural University, Shenyang, China.

E-mail addresses: liuyifei@syau.edu.cn, yifeiliu6@hotmail.com (Y. Liu).

[1] Mingzhu Ma and Chunming Bai contributed equally to this work.

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energetically demanding, rendering peanut cultivation highly dependent on phosphorus (P) [2]. However, peanuts are predominantly grown in nutrient-poor soils with low plant-available P concentrations. Recent studies have identified P deficiency as a major constraint limiting peanut yield potential [3], underscoring the urgent need for optimized nutrient management strategies to enhance productivity under suboptimal soil conditions.

Phosphorus is an essential macronutrient that plays a central role in diverse physiological and biochemical processes, including enzyme activation, energy transfer, carbohydrate metabolism, nucleic acid synthesis, and intracellular signaling [4,5]. Globally, over one-third of arable land suffers from limited P availability, causing yield losses of up to 40% [6], with approximately 70% of the world's top 28 crops cultivated on P-deficient soils [7]. To meet increasing food demands and achieve higher yields, global P fertilizer use has surged [8,9]. However, phosphate rock—the primary resource for P fertilizer production—is facing depletion [1]. Between 1961 and 2020, global P fertilizer consumption increased nearly fivefold, with China alone recording a more than 60-fold rise during that period [10]. Despite such extensive application, plants absorb only 10–15% of the applied P [11], while the excess often contributes to environmental issues such as eutrophication [12]. Thus, improving both soil P acquisition and P use efficiency, particularly photosynthetic P use efficiency (PPUE, defined as the rate of photosynthesis per unit leaf P), is critical for reducing fertilizer dependency and promoting sustainable crop production [13].

Photosynthesis—the process through which vascular plants, algae, and photosynthetic bacteria convert light energy into organic matter—relies extensively on phosphorus-rich molecules such as ribosomal RNA, ATP, NADPH, and phospholipids [14,15]. P deficiency disrupts these fundamental processes, impairing stomatal regulation, ATP synthase activity, and the regeneration of ribulose-1,5-bisphosphate (RuBP), ultimately constraining carbon assimilation [16,17]. PPUE is determined by the interplay between the photosynthetic rate, leaf P concentration, and leaf mass per area (LMA). Under P-deficient conditions, plants often adopt a strategy of preferential P allocation to mesophyll cells to sustain photosynthetic capacity. This adaptive strategy has been well-documented in Proteaceae species growing in the P-impoverished soils of southwestern Australia [4,18]. Such efficient P allocation patterns may hold promise for enhancing P efficiency and tightening the P cycle in legume-based systems. However, the mechanisms of P partitioning in peanut leaves and the genotypic variations in PPUE remain poorly understood and warrant further investigation.

Among the mineral nutrients involved in P metabolism, magnesium (Mg) plays a particularly critical role. Mg is not only the central atom of chlorophyll but also an essential activator of key photosynthetic enzymes, including ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) [19]. Mg deficiency directly suppresses Rubisco activation, reduces chloroplast abundance, and ultimately decreases photosynthetic capacity [20,21]. More importantly, Mg functions as a “bridge” in photosynthetic energy conversion by serving as an essential cofactor for ATP synthase–mediated ATP synthesis, thereby directly enabling the conversion of the thylakoid proton gradient into chemical energy [22]. This indicates that an adequate Mg supply is a prerequisite for the efficient utilization of limited P resources (e.g., ATP and NADPH) in carbohydrate synthesis. Consistently, the application of certain exogenous substances has been shown to directly stimulate the photosynthetic apparatus. For example, glucose seed priming has been reported to promote okra growth by enhancing net photosynthetic rate and the activities of key metabolic enzymes [23]. These findings suggest that directly enhancing photosynthetic carbon assimilation through exogenous regulation represents an effective strategy to mitigate abiotic stress and improve crop productivity. Previous studies have indicated that Mg may facilitate P uptake and translocation by enhancing the activity of phosphate transporters, thereby contributing to the maintenance of optimal intracellular P concentrations [21]. Furthermore, increasing attention has been paid to the synergistic interplay between P and Mg in crop physiological and mycorrhizal symbiosis processes [24]. For instance, elevated P supply has been shown to increase tissue Mg concentrations in several plant species [25]. Under high-Mg conditions, P-inefficient soybean genotypes exhibited a striking 284% increase in Mg concentration under P-deficient conditions, compared to a modest 94% increase in P-efficient genotypes. Notably, a strong positive correlation between shoot Mg content and the concentrations of P, potassium (K), and calcium (Ca) was observed exclusively in P-inefficient soybeans, suggesting that nutrient interactions involving Mg may be highly genotype-dependent [25]. Despite these findings, the physiological and molecular bases of Mg–P interactions in plants remain largely unexplored and warrant further investigation.

Collectively, these studies indicate that Mg theoretically possesses dual potential to enhance plant tolerance to P deficiency by sustaining photosynthetic efficiency and promoting P acquisition. However, whether this potential can be effectively realized under field production conditions—particularly in peanuts, a legume crop with a high P demand—and the underlying physiological mechanisms remain unclear. Moreover, the capacity to maintain photosynthetic function under P limitation varies among species and genotypes, with P productivity use efficiency (PPUE) exhibiting substantial inter- and intraspecific variation [18,26]. Nevertheless, the role of non-P mineral elements in shaping intraspecific PPUE variation remains poorly explored.

On this basis, the present study proposes the following hypotheses: (1) under soil Olsen-P deficiency, foliar Mg supplementation can directly enhance the functional integrity of the photosynthetic apparatus in peanut leaves; (2) this improvement is dependent on genotype; and (3) the underlying mechanism is primarily attributable to the direct protection of the photosynthetic apparatus by Mg rather than indirect effects mediated through enhanced P uptake and internal redistribution. To test these hypotheses, three research objectives were established and aligned with specific physiological and agronomic indicators: (1) to systematically evaluate the effects of foliar Mg application on growth, photosynthetic performance, and yield in two peanut genotypes contrasting in PPUE under low-P field conditions, with particular emphasis on agronomic traits (plant height, dry matter accumulation, and yield) and leaf photosynthetic characteristics (gas exchange and chlorophyll fluorescence); (2) to elucidate the key physiological mechanisms by which Mg alleviates P deficiency, focusing on its regulatory effects on photosystem I and II coordination, linear electron transport, ATP synthase activity, and the partitioning of thylakoid proton gradients (ΔpH and Δψ); and (3) to assess the genotypic dependency of Mg fertilizer efficacy, thereby providing a theoretical basis for developing an integrated “genotype selection–Mg nutrition management” strategy for peanut production.

2. Materials and methods

2.1. Experimental location

A field study was conducted between 2022 and 2023 at the Liaoning Academy of Agricultural Sciences' experimental farm in China (41°82′ N, 123°56′ E). The area has a temperate monsoon climate, with an average annual temperature of 9.1 °C and annual precipitation of 914 mm, primarily from June to September (Fig. S1). The soil type in the experimental field is classified as aeolian sand [27]. Prior to the experiment, the topsoil (0–20 cm) was sampled and analyzed for its physical and chemical properties, which were: 45.8 mg N kg^{-1} total nitrogen (N), 126 mg K kg^{-1} available K, 10.2 mg P kg^{-1} Olsen-P, 3.52 g Ca kg^{-1} exchangeable Ca, 204 mg Mg kg^{-1} exchangeable Mg, 13.4 g kg^{-1} organic matter (determined using the hydration heat potassium dichromate oxidation-colorimetric method), 1.48 g cm^{-3} bulk density and pH 6.7 (1:2.5, w/v) [28]. Furthermore, our previous work establishes a soil Olsen-P concentration below 12.7 mg kg^{-1} (corresponding to 0.41 mM in solution) as the threshold for low-P stress in peanuts [16].

2.2. Plant material and experimental design

The experiments were carried out from May 12 to October 3, 2022, and from May 5 to September 28, 2023. Two peanut (*Arachis hypogaea* L.) varieties were used: ICG4750 (H) with high PPUE (226 μmol $CO_2 \cdot g^{-1} \cdot P \cdot s^{-1}$) and ICG9249 (L) with low PPUE (41 μmol $CO_2 \cdot g^{-1} \cdot P \cdot s^{-1}$), according to screening experiments by our research group (unpublished data). There were two P levels: 0 (P0) and 52.4 kg P ha^{-1} (P1). Plants were sprayed with either water (M0) or 30 mM $MgSO_4$ (M1). The PPUE was calculated using the following equation:

$$\mathrm{PPUE} = \frac{\mathrm{Pn}}{\mathrm{LMA} \cdot [\mathrm{P}]} \tag{1}$$

Where: PPUE (μmol $CO_2 \cdot g^{-1} \cdot P \cdot s^{-1}$) represents photosynthetic phosphorus utilization efficiency; Pn (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) represents net photosynthetic rate (based on area); LMA ($g \cdot m^{-2}$) represents leaf mass per area; [P] ($mg \cdot g^{-1}$) represents the concentration of P in young fully expanded leaves.

The experiment was arranged in a split-plot design, with the P level as the main plot and the Mg level and peanut variety as subplots (Fig. S2). The design consisted of 24 plots with eight treatments (2 P levels × 2 Mg levels × 2 varieties), each replicated three times. Each plot measured 4.5 m^2 (3 m × 1.5 m), covering a total experimental area of 108 m^2. Peanuts were planted on ridges 3 m long and 50 cm apart, with a ridge surface width of 20 cm. A single row of peanuts was planted per ridge, with 30 cm between rows and 15 cm between planting holes. Each hole received two seeds, thinning seedlings to one plant per hole 15 days after sowing. Before ridging, the field was fertilized with 90 kg N ha^{-1} (urea), 52.4 kg P ha^{-1} (superphosphate, applied only in P1), and 100 kg K ha^{-1} potassium (KCl). All fertilizers are evenly applied before rotary tillage as a base fertilizer. The depth of rotary tillage is generally 10-15 cm. A Mg solution was applied evenly to the peanut leaves' upper and lower surfaces via foliar spray three times during the peanut growth period (30, 45, and 60 days after sowing). Parameters were measured three days after the final Mg treatment. Standard agricultural practices, including irrigation, weeding, and pest control, were employed throughout the growth period.

2.3. Plant sampling and measurements

2.3.1. Growth and yield parameters

After completing three rounds of foliar Mg application treatments (63 days after sowing), the length of the main stem from the cotyledonary node to the apical meristem was measured with a soft ruler as the plant height, and the stem diameter was assessed using a vernier caliper. The leaf area of the third fully-developed leaf was measured using a LI-3000C leaf area meter (LI-COR, Lincoln, USA). Plant P concentration was determined colorimetrically by the vanadate-molybdate yellow method after digestion with a mixture of H_2SO_4-H_2O_2. Peanut root and shoot samples were digested using a microwave system (Milestone Ethos one, Italy) with procedure Settings following the study by Sun et al [17]. The magnesium concentration of the sample was determined by flame atomic absorption spectrometry (AA-4002400304, PerkinElmer, Waltham, MA, USA).

Peanut harvests were conducted on October 3, 2022, and September 28, 2023. Samples were collected from the central one-third area of each plot to ensure accurate yield measurements. All pods were air-dried, weighed, and adjusted to an 8% moisture content to determine pod yield. Peanuts were shelled manually to determine grain yield. After data collection, plant samples, including roots, stems, and leaves were heated at 105 °C for 30 min, dried at 65 °C to a constant weight, and then weighed. The ratio of root dry weight to shoot dry weight was recorded as root-to-shoot ratio (R/S).

2.3.2. Leaf gas-exchange parameters and chlorophyll-fluorescence parameters

After three rounds of foliar Mg application treatments (63 days after sowing), gas-exchange parameters of the third fully-developed leaves were measured for three randomly selected peanut plants per treatment. Photosynthetic gas-exchange parameters, including net photosynthetic rate (Pn), stomatal conductance (g_s), atmospheric CO_2 concentration (C_a), transpiration rate (Tr), and intercellular CO_2 concentration (C_i), were measured using a GFS-3000 gas exchange system (Heinz Walz GmbH, Effeltrich, Germany). Measurements were carried out under controlled conditions: leaf cuvette temperature set at 25 °C, the relative humidity was kept at 60%, the ambient CO_2 concentration was set at 400 ± 5 μmol mol^{-1}, and the photosynthetic photon flux density (PPFD) was set at 1000 μmol quanta·m^{-2} s^{-1}, provided by an LED array. Data collection occurred between 8:30 and 10:30 a.m. on sunny days, following standard protocols with necessary modifications [27,29,30].

Chlorophyll fluorescence (PSII) and P700 (PSI) parameters were measured using the Dual-PAM 100 system (Heinz Walz, Effeltrich, Germany), controlled by Dual-PAM v1.19 software [31–33]. After 30 min of dark adjustment, the measuring light (faint light, <1 μmol quanta·$m^{-2} \cdot s^{-1}$) was turned on to fully open the PSII reaction centers, and the minimum fluorescence yield (Fo) was measured. A high-intensity saturation pulse (10,000 μmol quanta·$m^{-2} \cdot s^{-1}$) was applied to shut down the PSII reaction centers, and the maximum fluorescence yield (Fm) was measured. Actinic Light (282 μmol quanta·$m^{-2} \cdot s^{-1}$) was applied to induce photosynthesis. Saturating pulses were intermittently applied to open and close some PSII centers. The maximum fluorescence yield (Fm') and fluorescence yield (F) of the leaf were recorded during the transition from darkness to light. Finally, after turning off the measuring light and the actinic light, the minimum fluorescence yield (Fo') was determined. The maximum quantum yield of PSII (Fv/Fm), the actual quantum yield of PSII [Y(II)], the quantum yield of regulatory energy dissipation in PSII [Y(NPQ)], the quantum yield of non-regulatory energy dissipation in PSII [Y(NO)], the actual quantum yield of PSI [Y(I)], the quantum yield of non-photochemical energy dissipation due to donor-side restriction of PSI [Y(ND)], the quantum yield of non-photochemical energy dissipation due to acceptor side restriction of PSI [Y(NA)], relative electron transport rate of PSII [ETR(II)], and relative electron transport rate of PSI [ETR(I)] were calculated based on Klughammer and Schreiber [34].

Thylakoid membrane stability and ATPase function were evaluated using the P515/535 module of the Dual-PAM 100 system. After adequate dark adjustment (>1 h), a single-turnover saturating pulse stimulation method was used to observe changes in the P515 signal, assessing the integrity of the thylakoid membrane structure. During the dark adjustment phase, a slow decrease in the P515 signal after stabilization, along with a rapid decay of the P515 signal under actinic light conditions, both indicate the stability of the thylakoid membrane structure and high ATPase activity, reflecting the superior photosynthetic performance of the leaf. This pattern of signal changes can serve as a key indicator for assessing the efficiency of the photosynthetic system, where the slow decay of the signal after dark adjustment and the rapid decay of the signal under light work together to ensure efficient progression of the photosynthetic process.

The dark-light-dark response of the P515 double-wave 550 nm to 515 nm differential signal reveals the proton-motive force (PMF), including the proton gradient (ΔpH) and membrane potential (Δψ) across the thylakoid membrane. After 12 h of dark adjustment, PMF, ΔpH, and Δψ were evaluated under actinic light (531 μmol quantum $m^{-2}s^{-1}$) with 0 s on and 220 s off.

2.3.3. Leaf chlorophyll and flavonoid indices

The flavonoid index (FLAV) and chlorophyll index (CHL) of the third fully-developed leaf of peanut plants were determined using a portable ultraviolet-visible fluorescence spectrometer (FOSS-A, Multiplex Research, Nils Foss Allé, Denmark). The formula used for calculations is

[35]: CHL=FRF_R/RF_R; FLAV = log (FRF_R/FRF_{UV}), where FRF_R is far-infrared fluorescence induced by red light, RF_R is red light-induced infrared fluorescence, and FRF_{UV} is far-infrared fluorescence induced by ultraviolet light.

2.4. Data analyses

Microsoft Excel 2016 (Microsoft Corp., Redmond, WA, USA) and Origin Learning Edition 2023 (Origin Labs, Northampton, MA, USA) were used for statistical analyses and graph generation. The results are presented as the average of three biological replicates. Statistical analyses were conducted using IBM SPSS Statistics 19 software (IBM, Armonk, New York, USA). Duncan's new multiple range test was used to assess result significance, with a significance level of $P = 0.05$.

3. Results

3.1. Effect of foliar Mg application on peanut growth and yield

The two peanut varieties, ICG4750 (H, high PPUE) and ICG9249 (L, low PPUE), differed in plant height, dry matter accumulation, leaf area, and root-to-shoot ratio (Table 1). Data from both growing seasons showed consistent trends: compared with the P0 treatment, P application (P1) significantly promoted peanut growth, resulting in average increases of approximately 19.5% in plant height, 26.0% in dry matter accumulation, and 15.5% in leaf area ($P < 0.05$). These results indicate that P availability is a key factor limiting peanut vegetative growth. Concurrently, the FLAV and CHL significantly increased under the P1 treatment (Fig. 1), suggesting that adequate P availability contributes to the maintenance of leaf photosynthetic structure and function. The root-to-shoot ratio was highest under the P0M0 treatment, followed by the P0M1, P1M0, and P1M1 treatments (Table 1).

The P0M1 treatment significantly increased 100-pod weight, 100-kernel weight, and yield compared with P0M0 (Table 3). The P1M0 and P1M1 treatments further boost peanut yield and its components. Spraying Mg increased the 100-pod weight (4% in 2022 and 7% in 2023), 100-kernel weight (6% in 2022 and 7% in 2023), and yield (4% in 2022 and 4% in 2023) compared with water spray. Additionally, the high-PPUE variety (H) exhibited significantly higher yield and yield components than the low-PPUE variety (L).

3.2. Effect of foliar Mg application on leaf gas exchange parameters

Phosphorus and Mg significantly influenced leaf gas exchange parameters in peanut (Fig. 2). Pn, g_s, and Tr increased significantly with increasing levels of P and Mg, whereas Ci values demonstrated a decreasing trend. Under low-P conditions, foliar Mg application (P0M1) significantly enhanced leaf gas exchange performance. Across the two growing seasons, foliar Mg application increased Pn, g_s, and Tr by approximately 13%, 17%, and 10.5% on average, respectively ($P < 0.05$), while significantly decreasing Ci. This pattern of a synchronous increase in Pn and gs accompanied by a decrease in Ci indicates that Mg application initially alleviated low-P–induced stomatal limitation, thereby directly contributing to the enhancement of photosynthetic rate.

3.3. Effect of foliar Mg application on leaf photosystem activity

We assessed the impacts of P and Mg treatments on the fluorescence parameters of peanut leaves (Fig. 3). The P0M0 treatment resulted in lower Fv/Fm than the P0M1 treatment did, while P1M1 gave similar Fv/Fm values to those of P1M0 (Fig. 3A). Notably, variety × P, variety × M, and variety × P × M interactions did not significantly affect Fv/Fm (Table 2). P deficiency induced photoinhibitory stress, which was partially alleviated by Mg application. Under low-P conditions, the actual quantum yield of PSI [Y(I)] decreased, whereas the non-photochemical quantum yields of its donor and acceptor sides, Y(ND)

Table 1
Effects of foliar Mg application on growth and development of peanuts with different PPUE genotypes under low-P stress.

Variety	Treatment	2022					2023				
		Plant height	Stem diameter	DMA	Leaf area	R/S	Plant height	Stem diameter	DMA	Leaf area	R/S
L	P0M0	10.3 ± 0.5e	4.7 ± 0.1c	5.8 ± 0.2f	106 ± 1.9e	0.30 ± 0.01a	11.1 ± 0.5f	4.8 ± 0.1d	5.7 ± 0.2e	109 ± 3.5e	0.31 ± 0.01a
	P0M1	12.9 ± 0.4d	5.0 ± 0.1bc	6.9 ± 0.2e	127 ± 2.8c	0.28 ± 0.01a	13.4 ± 0.5e	5.1 ± 0.1c	6.7 ± 0.3d	128 ± 2.2c	0.27 ± 0.01b
	P1M0	14.3 ± 0.5d	5.2 ± 0.2bc	7.1 ± 0.3e	129 ± 1.8c	0.21 ± 0.02c	14.7 ± 0.3de	5.3 ± 0.2bc	7.2 ± 0.2d	129 ± 1.4c	0.20 ± 0.01d
	P1M1	16.2 ± 0.5c	5.3 ± 0.2b	8.5 ± 0.4cd	132 ± 1.4c	0.17 ± 0.01d	16.3 ± 0.6cd	5.4 ± 0.2bc	8.6 ± 0.3c	135 ± 1.7bc	0.17 ± 0.01e
H	P0M0	17.2 ± 0.5c	4.7 ± 0.1c	7.9 ± 0.1de	119 ± 2.5d	0.24 ± 0.01b	17.2 ± 0.5c	4.7 ± 0.1d	7.5 ± 0.3d	120 ± 2.6d	0.25 ± 0.01bc
	P0M1	19.4 ± 0.8b	5.3 ± 0.1b	9.2 ± 0.3bc	132 ± 1.6c	0.23 ± 0.02bc	19.6 ± 0.4b	5.3 ± 0.2bc	9.0 ± 0.4c	133 ± 2.2c	0.23 ± 0.01c
	P1M0	19.6 ± 0.8b	5.4 ± 0.2b	10 ± 0.5b	142 ± 1.5b	0.14 ± 0.01e	19.6 ± 0.5b	5.4 ± 0.1b	10.2 ± 0.3b	141 ± 0.9b	0.14 ± 0.01f
	P1M1	21.6 ± 0.6a	5.8 ± 0.1a	11.4 ± 0.4a	158 ± 1.2a	0.13 ± 0.01e	21.9 ± 0.7a	5.8 ± 0.1a	11.6 ± 0.4a	154 ± 3.4a	0.14 ± 0.01f

Notes: DMA: dry matter accumulation ($g \cdot plant^{-1}$); R/S: root to shoot ratio.

Table 2
Significance of sources of variability for peanut growth and yield parameters.

	Plant height	Stem diameter	DMA	Leaf area	R/S	Pn	g_s	Tr	Ci	Fv/Fm	PMF	Δψ	ΔpH
Variety (V)	***	*	***	***	***	***	***	***	**	NS	***	***	***
Phosphorus (P)	***	***	***	***	***	***	***	***	***	***	NS	***	***
Magnesium (M)	***	**	***	***	NS	***	***	***	NS	***	NS	***	***
V × P	NS	NS	NS	*	NS	**	NS	***	NS	NS	NS	NS	NS
V × M	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	***	***	***
P × M	NS	NS	NS	NS	NS	**	NS	***	NS	*	**	**	NS
V × P × M	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Significant differences at * 0.05, ** 0.01, and *** 0.001 probability levels; NS, no significant difference.
Notes: DMA: dry matter accumulation, R/S: root to shoot ratio, Pn: net photosynthetic rate, g_s: stomatal conductance, Tr: transpiration rate, Ci: intercellular CO_2 concentration, Fv/Fm: maximum quantum yield of PSII, PMF: proton motive force, ΔpH: proton gradient, Δψ: membrane potential.

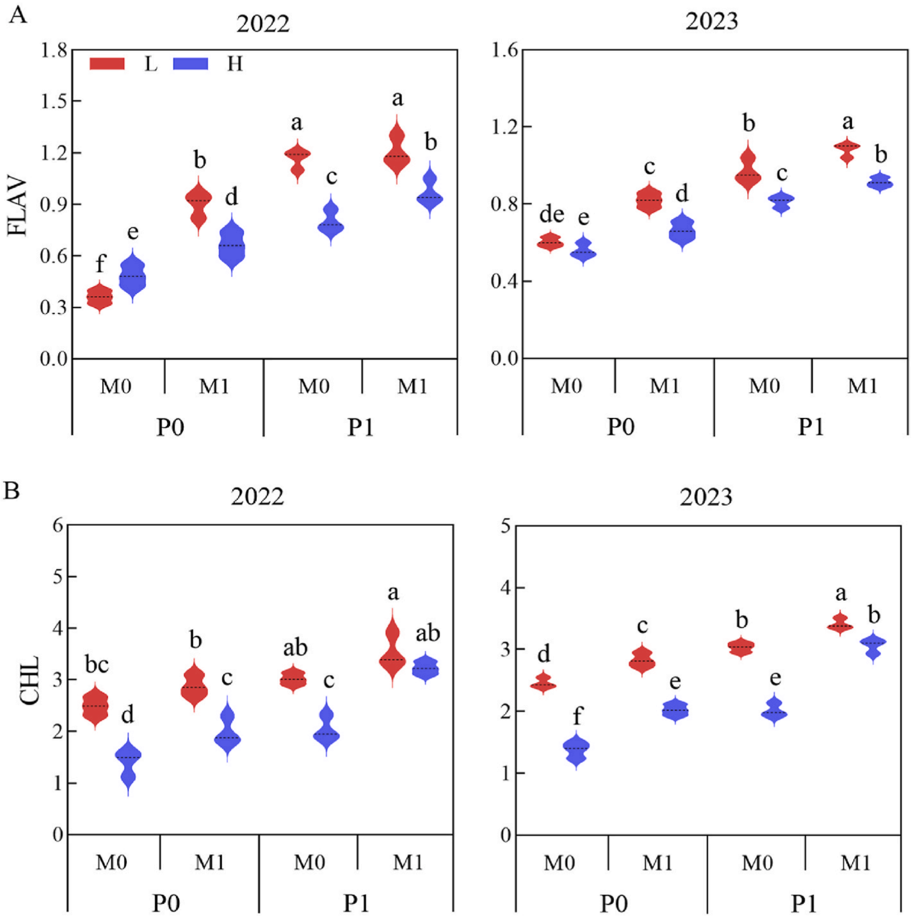

Fig. 1. Effects of foliar Mg application on (A) flavonol index (FLAV) and (B) chlorophyll index (CHL) of peanuts with different PPUE genotypes under low-P stress.

Table 3
Effects of foliar Mg application on 100-pod weight, 100-kernel weight, and yield of peanuts with different PPUE genotypes under low-P stress.

Variety	Treatment	2022				2023			
		100-pod weight (g)	100-kernel weight (g)	Yield (kg·ha^{-1})	Percentage increase in yield (%)	100-pod weight (g)	100-kernel weight (g)	Yield (kg·ha^{-1})	Percentage increase in yield (%)
L	P0M0	165 ± 5.2f	61.5 ± 2.0e	3350 ± 30g	0	163 ± 7.6e	62.7 ± 3.0e	3382 ± 32g	0
	P0M1	174 ± 5.2ef	65.7 ± 1.9d	3519 ± 18f	5.0	174 ± 6.0de	67.9 ± 2.4d	3549 ± 18f	4.9
	P1M0	179 ± 3.7de	69.3 ± 2.0dc	3617 ± 16e	8.0	182 ± 4.2cd	70.8 ± 1.6cd	3647 ± 14e	7.8
	P1M1	184 ± 5.0cd	71.3 ± 2.4c	3673 ± 12d	9.6	189 ± 5.7c	73.8 ± 2.2c	3703 ± 12d	9.5
H	P0M0	191 ± 5.3c	72.1 ± 3.0c	3648 ± 15d	0	187 ± 8.2c	74.9 ± 3.3c	3680 ± 14d	0
	P0M1	199 ± 5.6b	81.3 ± 2.2b	3933 ± 13c	7.8	210 ± 5.5b	83.9 ± 2.2b	3954 ± 12c	7.4
	P1M0	204 ± 3.1 ab	83.7 ± 2.5 ab	4015 ± 14b	10.1	213 ± 5.8 ab	85.4 ± 2.3 ab	4046 ± 13b	9.9
	P1M1	211 ± 3.9a	85.8 ± 1.4a	4135 ± 17a	13.3	224 ± 5.8a	89.3 ± 2.1a	4166 ± 17a	13.0

Notes: Percentage increase in yield (%): Yield increase ratio of each variety relative to its P0M0 treatment.

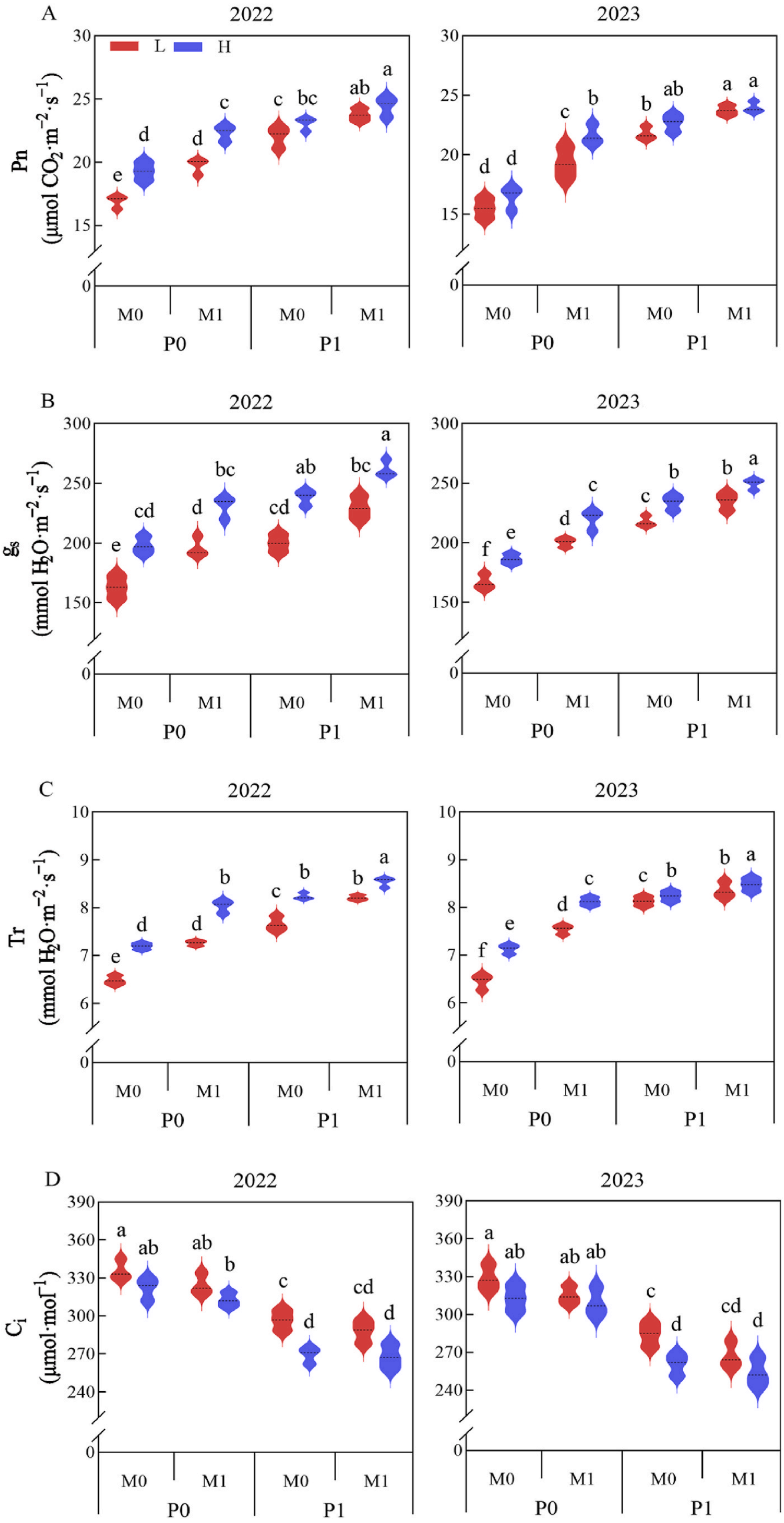

Fig. 2. Effects of foliar Mg application on gas-exchange parameters of peanuts with different PPUE genotypes under low-P stress.

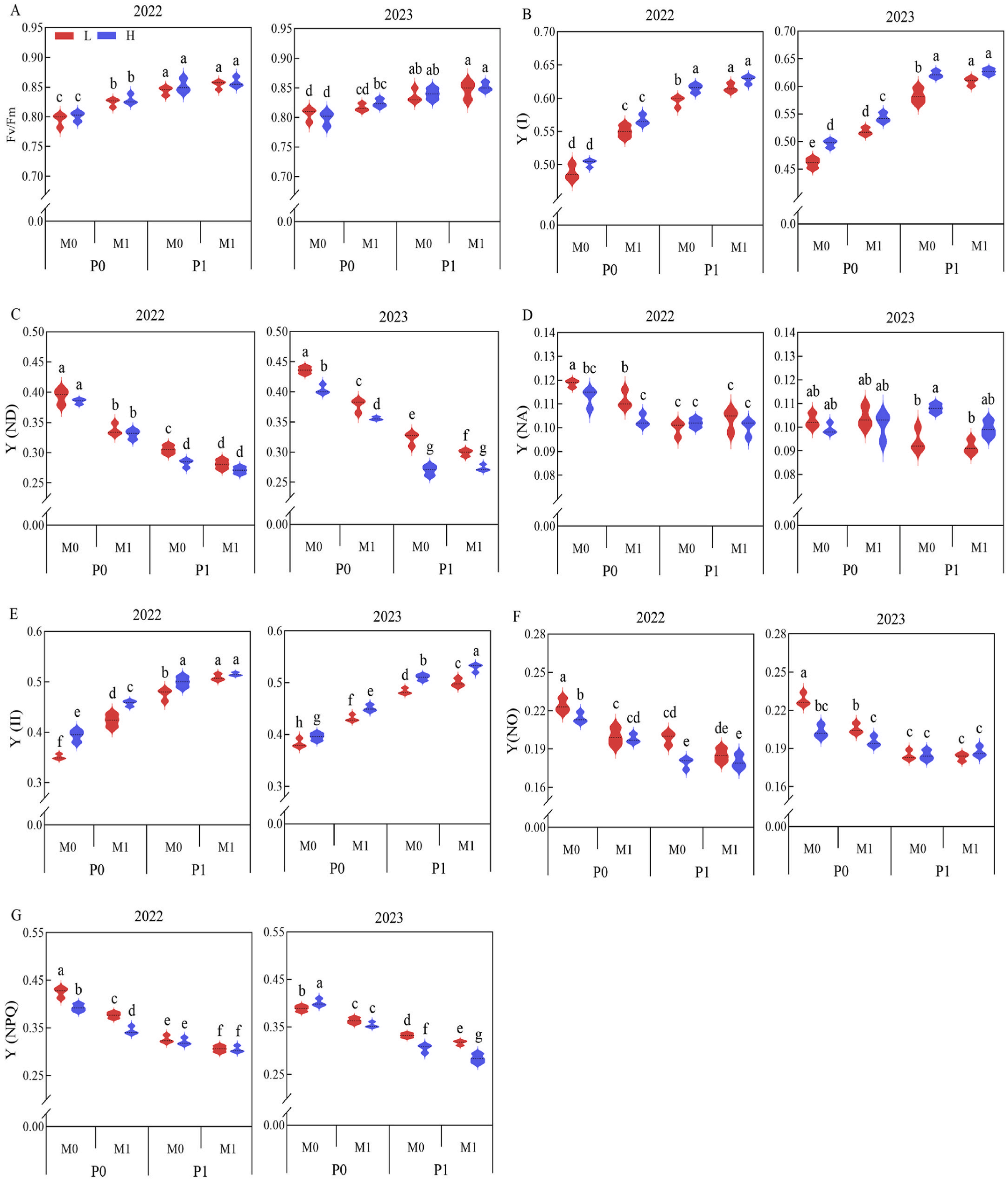

Fig. 3. Effects of foliar Mg application on chlorophyll fluorescence parameters of peanuts with different PPUE genotypes under low-P stress.

and Y(NA), increased (Fig. 3B–D). Following Mg application, Y(I) in the P0M1 treatment recovered to more than 88% of the level observed in the P1M0 treatment ($P < 0.05$). Under the P0M0 treatment, the actual quantum yield of PSII [Y(II)] was significantly reduced (Fig. 3E), primarily due to a marked increase in non-photochemical quenching for heat dissipation, Y(NPQ) (Fig. 3F). Furthermore, in the L cultivar, an increase in Y(NO) indicated that excess excitation energy in PSII was not fully dissipated, resulting in photochemical damage. The P0M1 treatment alleviated PSII photoinhibition by reducing Y(NPQ) and Y (NO), thereby restoring Y(II) (Fig. 4A). Collectively, these results demonstrate that low-P stress simultaneously inhibited the activities of both PSII and PSI while activating protective thermal dissipation mechanisms. Foliar Mg application systematically enhanced the operational efficiency of both photosystems by improving photochemical efficiency and reducing excess excitation energy.

3.4. Effect of foliar Mg application on photosynthetic electron transport

The photosynthetic electron transport rate of both peanut varieties progressively rose as the light intensity was increased (Fig. 4B). The P0M0 treatment produced the lowest ETR(I) and ETR(II) in both peanut varieties, with P1M1 the highest. Compared with P0M0, the P0M1 treatment significantly enhanced ETR(I) and ETR(II), achieving similar levels to those observed in the P1M0 treatment under high light intensity. Under highlight intensity, the H variety had faster electron transfer rates than the L variety, indicating greater tolerance to strong light in the high-PPUE variety.

3.5. Effect of foliar Mg application on thylakoid membrane integrity, ATP synthase activity, and proton-motive force

Photosynthetic electron transfer processes depend on the generation of a transmembrane potential by PSII and PSI charge separation and the Q cycle on the Cyt b_6/f complex. ATP synthase (ATPase) facilitates proton transport from the thylakoid lumen to the membrane exterior, reducing the transmembrane potential. The P515 signal variation

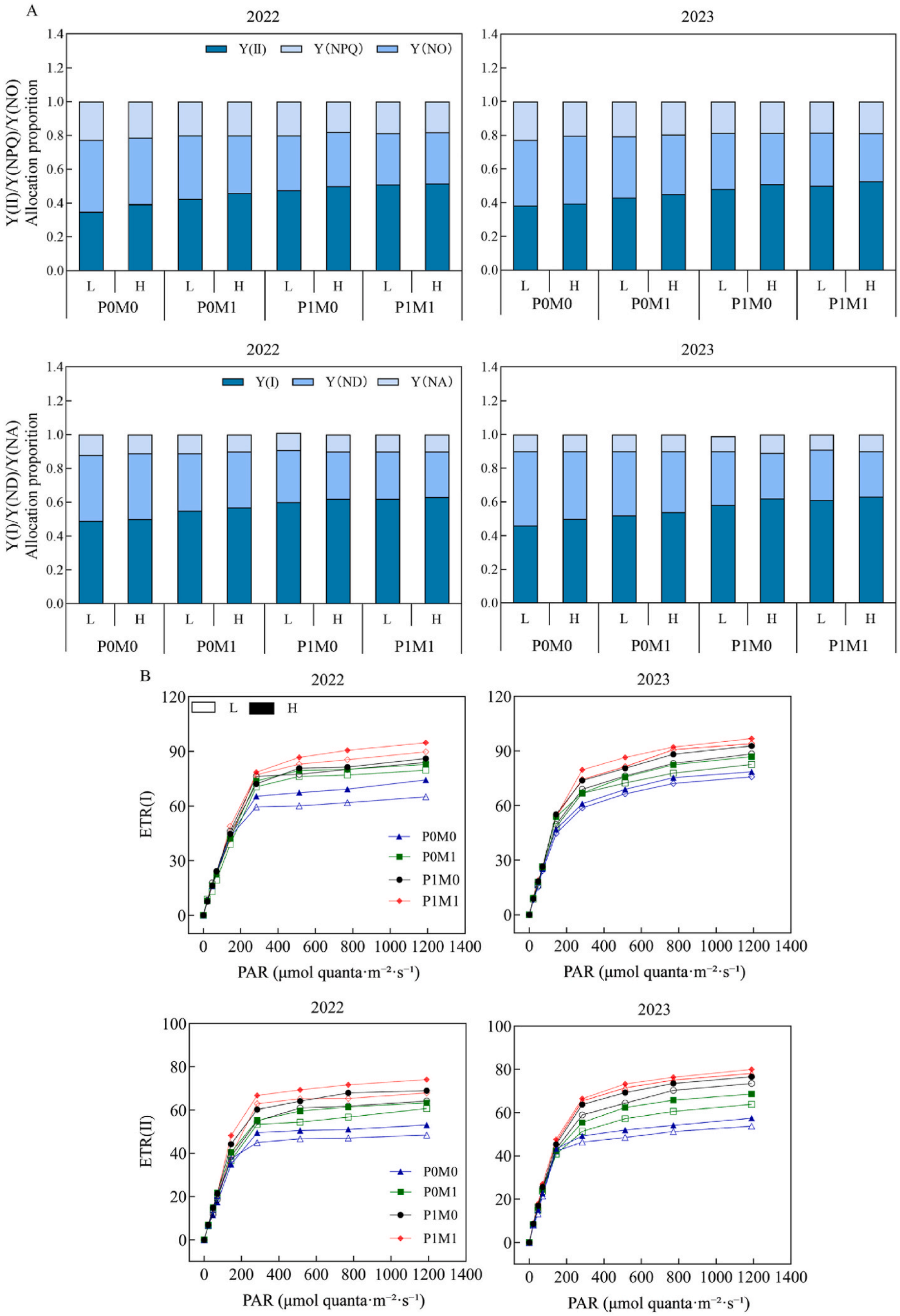

Fig. 4. Effects of foliar Mg application on the (A) distribution ratio of fluorescence parameters in photosystem and (B) relative electron transfer rate of PSI and PSII of peanuts with different PPUE genotypes under low-P stress.

provides insight into the functional state of the photosynthetic apparatus. With complete functionality, the P515 induction curve typically showed the following characteristics: following dark adjustment, a gradual decline in the P515 signal indicates robust thylakoid membrane integrity (Fig. 5A; before AL). After pre-illumination with actinic light, we observed a swift decline in the P515 signal reflecting high ATPase activity (Fig. 5A; after AL). In the P0M0 treatment, the rapid decay of the P515 signal after dark adjustment indicates compromised thylakoid membrane integrity, and a slower decay post-illumination suggests reduced ATPase activity. However, Mg application (P0M1) improved thylakoid membrane integrity and ATPase activity in both peanut varieties. Despite these improvements, these parameters remained lower than those in the P1M0 treatment, indicating that foliar Mg application only partially mitigated the damage caused by low-P availability.

Furthermore, the P0 treatment decreased PMF and Δψ while elevating the proton gradient (ΔpH) in the thylakoid lumen, signifying

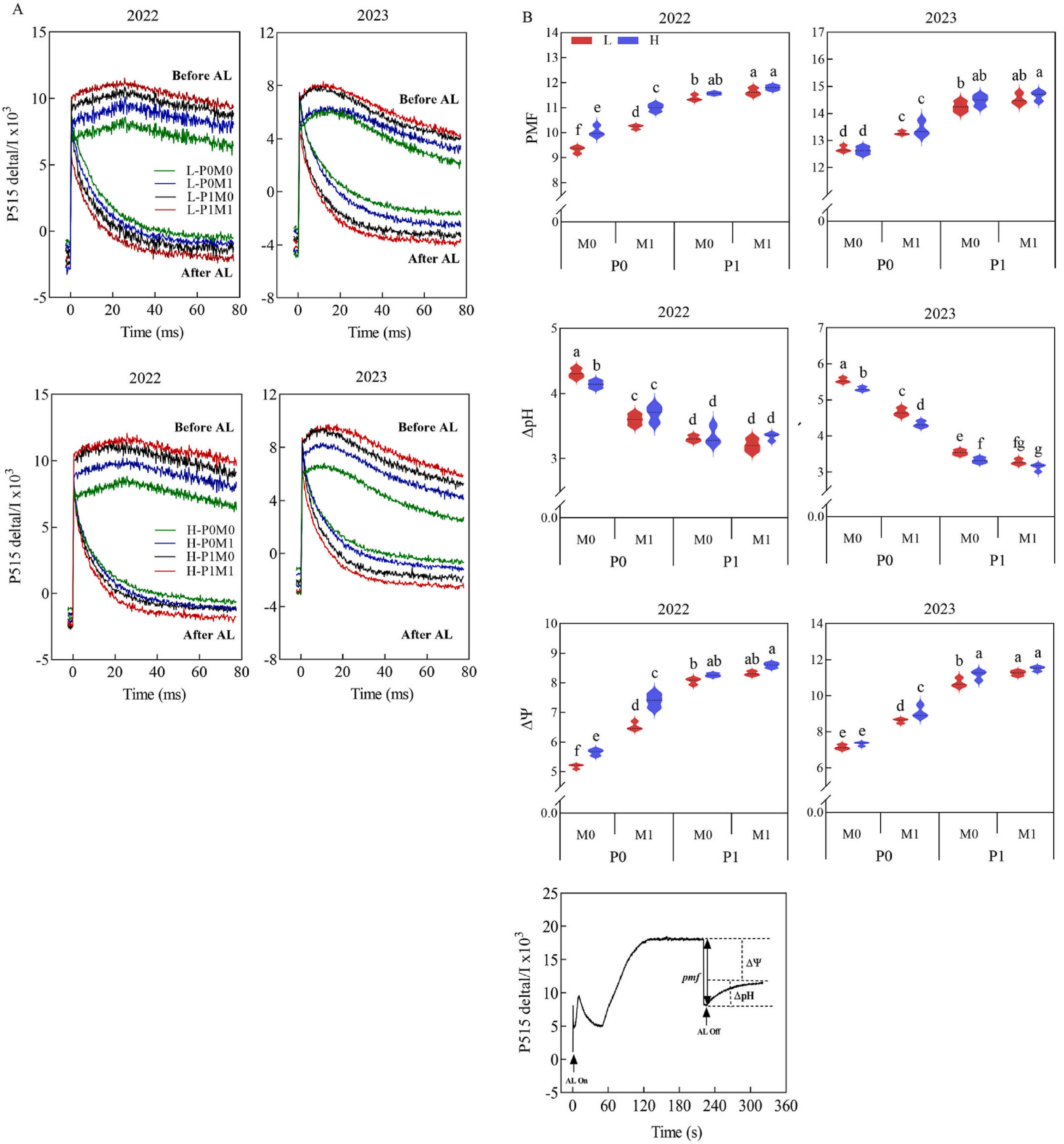

Fig. 5. Effects of foliar Mg application on (A) leaf thylakoid membrane integrity [before actinic light (AL)], ATP-synthase activity (after AL), and (B) proton-motive force (PMF) of peanuts with different PPUE genotypes under low-P stress.

decreasing proton efflux (Fig. 5B). The application of Mg increased PMF and $\Delta\psi$ while reducing ΔpH (Fig. 5B), especially in the P0 treatment. These results indicate that Mg application facilitated the accumulation of PMF under low-P conditions, thereby providing a stronger energetic basis for subsequent ATP synthesis.

4. Discussion

Phosphorus is essential for crop growth and development, and any deficiency will ultimately reduce yield. Our study revealed that low-P availability reduced plant height and dry matter accumulation (Table 1). When P is limited, plants typically increase their root-to-shoot ratio to facilitate greater P uptake. This involves a marked increase in root length, branching, and root hair density. These changes expand the root system's surface area and upregulate high-affinity P transporter expression, enhancing soil P mobilization and uptake efficiency [36]. Nevertheless, excessive resource allocation to the root system often restricts above-ground growth, reducing functional leaf area and carbon assimilation capacity. This implies that research on low-P tolerance should also focus on above-ground photosynthetic performance. Our 30 mM Mg^{2+} application increased peanut plant height, dry matter accumulation, and yield under low-P conditions (Tables 1 and 3). Additionally, Mg fertilization improves agronomic efficiency and crop yields [37,38]. Beyond its role as a fertilizer, Mg is a stress alleviator, aiding plants in managing various abiotic stresses [20,39]. Based on the results of this study, we propose that Mg plays a dual core role in alleviating P deficiency stress in peanuts, functioning as both a “photosynthetic engine” and a “P cycling catalyst.” First, Mg ensures the continuous and efficient generation of photosynthetic energy (ATP and reducing power) by directly stabilizing the photosynthetic apparatus and optimizing the coordination and electron transfer efficiency between photosystems. This enhanced energy supply subsequently provides the driving force for active P acquisition by the root system and for the reactivation and long-distance transport of P within the plant. This mechanism explains why Mg application simultaneously improved plant P nutritional status and photosynthetic carbon assimilation capacity. Collectively, Mg may initiate a positive feedback loop of “photosynthetic drive–P cycling,” in which efficient photosynthetic energy flow promotes P uptake and redistribution, while improved P nutrition, in turn, supports the development and functional maintenance of photosynthetic organs, ultimately contributing to yield formation. This conceptual framework provides a mechanistic hypothesis for the Mg–P synergistic effects observed both in this study and in previous reports.

Photosynthesis is particularly sensitive to P stress. Limiting P availability significantly impairs overall photosynthetic efficiency (Fig. 2). Our findings indicate that Mg application significantly increased Pn, g_s, and Tr (Fig. 2), alleviating stomatal restrictions and enhancing photosynthetic electron flow (Fig. 4B) Moreover, P deficiency reduces sink activity and obstructs carbohydrate transport, causing photosynthetic feedback inhibition and impeding plant growth and development [40]. Similarly, in the early stages of Mg deficiency, the obstruction of assimilate transport precedes the reduction in photosynthesis and the development of leaf chlorosis [41,42]. Hence, an adequate Mg supply can enhance the loading of sucrose into the phloem, alleviating photosynthetic feedback inhibition under P limitation. Notably, Mg promotes the transport of photosynthetic carbon assimilates to roots in P-starved mycorrhizal soybean plants [24].

Previous studies have demonstrated that increased Mg uptake by peanut plants is accompanied by a significant enhancement in P uptake (Zheng et al., 2018). This finding suggests that foliar Mg application, although it does not directly increase soil P availability, may promote the acquisition of limited soil P by enhancing root physiological activity or by regulating the activity of P transport proteins (Supplementary Fig. S3). In addition, this study showed that Mg application reduced the root-to-shoot ratio (Table 1). When considered together with the observed increase in dry matter accumulation, this shift may indicate a reallocation of assimilates toward aboveground growth, thereby providing a larger storage capacity and stronger translocation potential to support enhanced P uptake.

Another important regulatory role of Mg in peanut P nutrition lies in optimizing the intra-plant distribution of P, particularly its transport to reproductive organs. This process is closely associated with the Mg-dependent transport of photosynthetic assimilates. Mg is a key regulator of phloem loading, and sufficient Mg supply ensures the efficient translocation of sucrose from source leaves to sink organs such as pods [38]. This mechanism is critical for the reactivation and reutilization of P within the plant. Zheng et al. (2018) reported that during peanut pod development, Mg uptake markedly promoted P allocation to pods, with a stronger response than that observed in vegetative organs. Consistent with these findings, foliar Mg application in the present study significantly increased hundred-kernel weight and overall yield (Table 3). These yield improvements are attributable not only to enhanced carbon assimilation supply but also, very likely, to more efficient transport and allocation to developing seeds.

As demonstrated by our results, high PPUE genotypes exhibited greater plant height, dry matter accumulation, leaf area, and yield under both P-sufficient and P-deficient conditions (Tables 1 and 3). Furthermore, under P deficiency, these genotypes maintained superior photosynthetic performance, higher electron transport rates, and enhanced thylakoid membrane integrity compared to their low PPUE counterparts (Figs. 2–5). These findings align with a large-scale screening of 235 peanut accessions, which reported substantial genotypic variation in root morphology and P uptake efficiency under low-P stress [43]. Collectively, the evidence indicates significant genetic differences in the physiological responses of peanut varieties to P deficiency.

Our study further reveals that the application of foliar Mg application and the inherent genetic resistance of peanuts operate through both independent and synergistic mechanisms to alleviate P deficiency. Inherent genetic resistance, a stable trait shaped by long-term natural selection and artificial breeding under varying P levels, is primarily governed by a variety's root architecture, P uptake, and internal translocation efficiency [43,44]. Our findings indicate that Mg application under low-P conditions significantly increased P concentration in both shoots and roots (by >15%), concomitant with an approximately 13% enhancement in the net photosynthetic rate (Fig. 2A and Fig. S3). In contrast, under P-sufficient conditions, Mg had a minimal direct effect on Pn, yet still contributed to yield improvement. This suggests that the mechanism of foliar Mg application is dependent on P availability: it indirectly promotes photosynthesis by improving P acquisition and redistribution under P deficiency, while its role shifts towards optimizing assimilate partitioning rather than directly activating photosynthesis when P is ample. This genotype-specific P-Mg interaction is consistent with observations in soybean [25]. Therefore, in practical production, selecting high P-efficient varieties is fundamental for coping with low-P stress, while rational Mg application serves as a complementary agronomic strategy to improve P nutrition and enhance yield. The synergistic use of both approaches presents a promising pathway for achieving cost-effective and efficient peanut production in low-P soils.

The maximum photosynthetic efficiency of PSII (Fv/Fm) is a sensitive indicator of photosynthetic performance [45]. We observed a significant reduction in Fv/Fm under low-P stress, which was mitigated by Mg application (Fig. 3A). Mg enhances photoprotection in PSI and PSII [46] through mechanisms such as (i) enhancing light-energy conversion and utilization to increase the photosynthetic electron transport rate [47], (ii) increasing antioxidant enzyme activity thus mitigating oxidative stress [48], and (iii) promoting chlorophyll synthesis and Rubisco activity to reduce ROS levels and prevent photooxidative damage [49].

Non-photochemical quenching (NPQ) within the LHCII antennae is another protective mechanism under excess light conditions, dissipating surplus excitation energy as heat [50]. Under abiotic stress, NPQ can dissipate up to 75% of absorbed light energy [51]. Low-P availability generally down-regulates PSI activity, as evidenced by a significant reduction in Y(I) (Fig. 3B). PSI can also undergo photoinhibition due to ROS generation when the reducing activity of PSI exceeds the capacity to use reducing equivalents for downstream reactions [22,52]. In this study, Mg increased Y(I) and Y(II) by reducing Y(ND) and Y(NPQ), thereby alleviating PSI and PSII damage induced by low-P stress.

During photosynthetic electron transfer, protons are transported from the substrate into the thylakoid cavity, resulting in cavity acidification and an increased membrane potential. This process generates a PMF on the thylakoid membrane, comprising ΔpH and Δψ, which collectively drive ATP synthase activity to produce ATP [53]. While both components contribute equally to ATP synthesis, ΔpH specifically regulates the photosynthetic electron transport rate by acidifying the thylakoid cavity [54]. The regulation of photosynthesis by ΔpH must meet three physiological requirements: (1) ATP production for CO_2 fixation, (2) NPQ induction in both photosystems, and (3) photosynthetic control at the cytochrome b_6f level [55,56]. The concentration of protons within the lumen is dictated by two factors: the rate of photosynthetic electron transport and the level of activity of ATP synthase [57]. Under P deficiency, the regeneration of ATP synthase substrates—phosphate (Pi) and adenosine diphosphate (ADP)—is impaired, causing disruptions in the Calvin–Benson–Bassham cycle and leading to negative feedback regulation of ATP synthase activity.

Excessive acidification of thylakoids can disrupt membrane integrity, impair cytochrome b_6f complex activity, and decrease linear electron transport [58]. It can also destabilize plastocyanin and deactivate PSII [59]. Based on these results, we surmise that Mg reduces photosystem damage under low-P stress by increasing ATP synthase activity and decreasing ΔpH. Mg is a key catalyst and substrate for ATP synthesis and various metabolic processes [49]. Variation in its concentration can significantly affect the activity of Mg-dependent enzymes, including ATP synthase [60]. ATP synthase regulates light reactions by adjusting thylakoid ΔpH, sensing the metabolic state of chloroplasts, which regulates excitation energy transfer from LHCII to PSII and PSI and electron transfer from PSII to PSI via the cytochrome b_6f complex. Using the P515–535 module of the Dual-PAM system to monitor ATP synthase activity and PMF, we found that foliar Mg application under low-P stress stimulated proton expulsion via ATP synthase, promoting ΔpH conversion to Δψ and enhancing PMF (Fig. 5). Su et al. [46] also observed similar Mg-mediated photoprotection under aluminum stress [46]. In conclusion, Mg enhances plant tolerance to low-P availability by maintaining efficient photosynthesis and preventing excessive thylakoid lumen acidification.

In this study, the application of foliar Mg application significantly enhanced source strength (e.g., Pn); however, this enhancement was not fully translated into yield formation (e.g., sink filling). This source-sink discrepancy could be attributed to the following potential causes: (i) Sink limitation under enhanced source activity. When photosynthetic output exceeds the sink capacity (e.g., pod number, grain filling potential), photosynthesis may be subject to feedback inhibition, leading to carbohydrate accumulation in vegetative parts rather than economic yield [61,62]. (ii) Assimilate partitioning imbalance. The interaction and coordination between source and sink are critical determinants of high yield [63,64]. Although Mg facilitates phloem loading, a weak "sink pull" may still restrict the efficient allocation of assimilates to developing pods [49]. Ultimately, yield is an integrated outcome of the coordinated functioning of source, sink, and transport (flow). (iii) Other co-limiting factors. Yield formation, particularly during grain filling, is also influenced by multiple environmental and physiological factors, including water availability, temperature, and hormonal regulation [65,66]. Thus, despite the improvement in leaf-level photosynthesis induced by Mg, the realization of these gains in final yield may still be constrained by other developmental and physiological processes.

Although the absolute yield increase induced by Mg application in this study (approximately 4–5%) may appear modest, its agronomic and economic significance should be evaluated in the context of P-limited conditions. Based on previous work [16], a soil Olsen-P concentration below 12.7 mg kg^{-1} was defined as the critical threshold for low-P stress in peanuts. This threshold delineates the applicable boundary of the present findings: the yield benefits of Mg fertilization described here are primarily relevant to production systems where soil available P is below this critical level. Importantly, the observed yield increase was statistically stable, indicating that the effect is both real and reproducible. Similar responses have been reported in rice-growing regions with insufficient soil Mg (<80 mg kg^{-1}), where Mg fertilization resulted in yield increases of 4.9–7.2% and profit gains of 4.3–5.5% [67]. From a cost-effective perspective, foliar application of 30 mM Mg sulfate represents a low-input and easily implementable agronomic practice. The technical threshold is low, and the combined costs of materials and labor are substantially lower than those associated with phosphate fertilization. Under conditions where soil Olsen-P falls below the crop P threshold, as in this study (<12.7 mg kg^{-1}), Mg application may therefore constitute a cost-effective strategy to overcome P limitation and unlock yield potential. In this context, a 4–5% yield increase represents a meaningful gain achieved through precise micronutrient regulation under severe nutrient constraints. This study only investigated the effect of a single concentration of foliar Mg sulfate under low-P conditions. Future research can further explore the effects of different Mg concentrations, application frequencies, and especially the effects of new nano-Mg fertilizers and other forms. Nanotechnology provides a new paradigm for precise and efficient nutrient delivery, and its application prospects in the development of high-efficiency fertilizers are broad [68]. Future research should integrate multi-omics approaches—including transcriptomics, proteomics, and metabolomics—to systematically analyze the spatiotemporal dynamics of key genes and proteins involved in the "source–sink–flow" continuum under Mg regulation. Such insights will provide a theoretical foundation for optimizing Mg fertilization strategies and synergistically improving P and Mg use efficiency.

5. Conclusions

Low-P stress negatively affected the peanut photosynthetic apparatus, leading to reduced foliar photosynthetic capacity, dry matter accumulation (26%), and yield (10%). Interestingly, foliar Mg application restored peanut foliar photosynthetic performance (13%) by enhancing stomatal conductance (18%). Specifically, foliar Mg application alleviated photoinhibition caused by low-P stress by maintaining thylakoid membrane integrity and enhancing ATP synthase activity, thus preventing excessive acidification of the thylakoid lumen. The relationship between photosynthetic efficiency and P availability, as evidenced in two peanut varieties with different PPUE, warrants further research. Our study underscores the potential of foliar Mg applications as an effective strategy for restoring peanut photosynthesis and improving yield under P-limited conditions, offering an effective solution for restoring peanut production.

CRediT authorship contribution statement

Mingzhu Ma: Writing – review & editing, Writing – original draft, Conceptualization. **Chunming Bai:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Zhiyu Sun:** Data curation. **Siwei Zhang:** Data curation. **Huan Liu:** Data curation. **Shaikh Amjad Salam:** Data curation. **Jiayin Pang:** Writing – review & editing, Conceptualization. **Jean Wan Hong Yong:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Conceptualization. **Yifei Liu:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Hans Lambers:** Writing – review & editing, Supervision, Conceptualization. **Kadambot HM. Siddique:** Writing – review & editing, Supervision, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jafr.2026.102764.

Data availability

Data will be made available on request.

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