

## Exploring the impact of potassium fertiliser rate and split ratio on rice yield and quality in China: a meta-analysis

LIJUAN DENG<sup>1,2</sup>, DUOJI WU<sup>1</sup>, WEIQI YUAN<sup>1</sup>, ZONGQIANG WEI<sup>1</sup>,  
YANLAN HUANG<sup>1</sup>, ZHIHUA Hu<sup>1,3</sup>, JIANFU Wu<sup>1\*</sup>

<sup>1</sup>College of Land Resource and Environment, Jiangxi Agricultural University, Nanchang, P.R. China

<sup>2</sup>Jiangxi Environmental Engineering Vocational College, Ganzhou, P.R. China

<sup>3</sup>Jiangxi Institute of Red Soil and Germplasm Resources, Nanchang, P.R. China

\*Corresponding author: wjf6711@126.com

**Citation:** Deng L.J., Wu D.J., Yuan W.Q., Wei Z.Q., Huang Y.L., Hu Z.H., Wu J.F. (2025): Exploring the impact of potassium fertiliser application strategies on rice yield and quality in China: a meta-analysis. Plant Soil Environ., 71: 891–904.

**Abstract:** Potassium (K) is crucial for rice yield and quality, but continuous yield increase reduces protein content, challenging the balance between high yield and quality. This study analysed 3 178 case studies (1994–2024) on K management impacts on rice yield, grain protein, and amylose content, evaluating effects of K fertiliser rates, base-topdressing ratios, planting regions, and soil properties. The results showed that K application significantly increased rice yield, protein content and amylose content by 11.6, 2.0 and 1.0%, respectively. Importantly, we identified targeted K fertilisation strategies tailored to different quality goals: optimising for eating quality, nutritional quality, or synergistic improvement of yield and comprehensive quality. This study provides a scientific basis for precision K management to help growers balance rice yield with specific quality needs.

**Keywords:** productivity; nutrient management; targeted fertilisation strategy; yield-quality trade-off

Rice (*Oryza sativa* L.) is one of the world's three major food crops. China, the world's largest rice producer, has seen its rice output increase by more than 50% since 1980; however, this growth trend has significantly flattened in recent years (Grassini et al. 2013, Rong et al. 2021). For consumers, the nutritional and eating qualities of rice are the most important attributes they value. Rice protein, classified as a low-sensitivity protein, boasts higher digestibility and biological value, and it is a crucial indicator determining the nutritional quality of rice (Helm and Burks 1996). Amylose content, a key factor influencing rice's eating quality, directly determines the hardness and stickiness of cooked rice, which significantly affects consumers' preferences

for different types of rice (Umemoto et al. 2004, Waters et al. 2006, Kong et al. 2015). Previous studies have shown that achieving a balance between the rice production and quality is challenging, and that an increase in rice yield inevitably leads to a decline in rice quality (Chen et al. 2022). The primary approach to meeting the escalating demand for food and ensuring food security within the constraints of limited arable land entails augmenting rice yield while attaining an optimal equilibrium between the rice yield and quality (Deng et al. 2019).

Potassium (K) is generally regarded as the third most important mineral nutrient after nitrogen (N) and phosphorus (P) in plant nutrition, while the demand for K in rice specifically exceeds that for N

Supported by the National Natural Science Foundation of China, Project No. 32260808; by the Key Research and Development Program of Jiangxi Province, Project No 20223BBF61016, and by the Natural Science Foundation of Jiangxi Province, Project No. 20232BAB213092.

© The authors. This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International (CC BY-NC 4.0).

and P (Chen et al. 2023). K mainly exists in plants in the form of cations and is usually used as an enzyme cofactor or regulator (Marschner 2012). It participates in regulating physiological processes in plants, such as photosynthesis, assimilation transportation, and carbohydrate metabolism, while it promotes the absorption of nutrients like nitrogen and phosphorus, and ultimately has an impact on crop yield and product quality (Britto and Kronzucker 2008, Nieves-Cordones et al. 2019, Ma et al. 2022). The primary source of K nutrition for crops is K fertiliser, which is often made by using potassium salts. However, the price of K fertiliser is rising and the worldwide market for it is unstable due to the limited geological deposits of potassium salt and the high economic, social, and environmental costs of its utilisation. As a result, many farmers are forced to reduce the use of K fertiliser and face the threat of crop yield decline caused by soil potassium deficiency (Al Rawashdeh 2020, Brownlie et al. 2023, 2024, Ushakova et al. 2023). Therefore, it is crucial to investigate the effective management method of K fertiliser, improve its utilisation rate, and promote the maximisation of farmers' interests.

Numerous research currently show that K fertiliser application can significantly increase rice yield and encourage the synthesis of starch and protein in grain (Yang et al. 2004, Zörb et al. 2014, Mohamed et al. 2021). However, a variety of factors, including genotype, growth period, climate, soil environment, and human management practices, all have an impact on how well potassium is absorbed and utilised in rice. The quantity of potassium absorbed by the above-ground dry matter of several rice cultivars varied significantly, with the largest absorption rate occurring during the tillering and booting stages (Ye et al. 2020). Beyond genotype, soil conditions also play a critical role: some studies have also indicated that basic soil conditions – such as soil organic matter (SOM), pH, total nitrogen, and the contents of available nitrogen, phosphorus, and potassium – are key factors influencing the productivity of rice-growing areas, as they alter the crop's growth environment, affect its nutrient absorption, and ultimately impact its yield and quality (Zhang et al. 2024, Ye et al. 2024, Wu et al. 2025). In addition, soil potassium supply capacity and K fertiliser rate are the key factors affecting the effectiveness of potassium nutrition crops (Lu et al. 2017). In view of the differences in rice cultivars, fertilisation measures, soil properties and climatic conditions in field experiments, the

previous experimental results were summarised, and the effects of potassium application on rice yield, grain protein and amylose content under different K fertiliser rates and their base-topdressing ratios, planting areas and soil chemical properties were systematically evaluated by meta-analysis. This study aimed to reveal and clarify the comprehensive effects of K fertiliser application on rice yield and quality, and so to provide a basis for rational application of K fertiliser to improve rice yield and quality.

## MATERIAL AND METHODS

**Data collection.** The data for this study were collected from Web of Science and CNKI databases. The keywords "Potassium", "Rice", "Yield", "Protein content", and "Amylose content" were used to search for relevant literature. The articles were screened based on the following criteria: (1) The experimental location is in mainland China, and the experimental material is rice; (2) the study should be based on the data collected from field trials only; (3) included studies were field experiments with an NPK treatment group and an NP control group; and (4) at least one index of yield, effective panicles, grain number per spike, 1 000-grain weight, ripening percentage, grain protein and amylose content should be mentioned in the literature. Various indicators were collected from the literature, including experimental location, experimental time, soil chemical properties, nitrogen, phosphorus and K fertiliser application rates, base-to-topdressing ratio, grain yield, effective panicles, grain number per spike, 1 000-grain weight, ripening percentage, grain protein and amylose content, etc. The data presented in charts in the literature were digitised with Getdata. In total, 100 pieces of literature were included in the study. The experimental year spanned from 1994 to 2024, including 785 sets of grain yield data, 488 sets of effective panicles data, 496 sets of grain number per spike data, 501 sets of 1 000-grain weight data, 454 sets of ripening percentage data, 249 sets of grain protein content data, and 205 sets of grain amylose content data.

**Data analysis.** In our study, we used the logarithm of the response ratio (R) as the effect size (E) to describe the impact of potassium application on rice yield and its components, grain protein content and grain amylose content (Valkama et al. 2013a, 2013b).

$$E = \ln(R) = \ln(X_1/X_0) \quad (1)$$

where: X1 – relevant indices (grain yield, effective panicles, grain number per spike, 1 000-grain weight, ripening per-

Table 1. Classification and grouping of explanatory variables for effects of potassium application on rice yield, its components, grain protein content and amylose content database

Categorical explanatory variable	Groups
Potassium rate (kg K/ha)	≤ 37; 37–75; 75–100; 100–125; > 125
The ratio of base to topdressing	all base; ~2; 1–2; ≤ 1
Planting area	Northeast Plain (NP); Southeast coast (SC); the upstream of the Yangtze River Basin (UY); the midstream of the Yangtze River Basin (MY); the downstream of the Yangtze River Basin (DY);
Grain yield of the control group (t/ha)	≤ 5; 5–6; 6–7; 7–8; 8–9; 9–10; > 10
Grain protein content of the control group (%)	~7; 7–8; > 8
Amylose content of the control group (%)	~16; 16–17; > 17
Soil pH	~5.5; 5.5–6.5; 6.5–7.5; 7.5–8.5
Soil organic matter (SOM, g/kg)	≤ 20; 20–30; > 30
Soil total nitrogen (TN, g/kg)	≤ 1; 1–1.5; 1.5–2; > 2
Soil available nitrogen content (AN, mg/kg)	≤ 90; 90–120; 120–150; > 150
Soil available phosphorus content (AP, mg/kg)	≤ 10; 10–20; 20–40; > 40
Soil available potassium content (AK, mg/kg)	≤ 50; 50–100; 100–150; > 150

The ratio of base to topdressing definitions: All base refers to all K fertiliser applied as base fertiliser before sowing/transplanting, with no topdressing during growth; ~2 means base fertiliser K exceeds 2 times topdressing K; 1–2 means base fertiliser K is 1 to 2 times topdressing K; ≤1 means topdressing K is greater than or equal to base fertiliser K; Data were compiled from multiple studies. Exact analytical methods for soil properties were not uniformly reported, and methodological variability is acknowledged)

centage, grain protein content, grain amylose content) under potassium fertilisation; X0 – same indices without potassium fertilisation.

To reflect the effect of potassium application on rice yield and its components, grain protein content and grain amylose content more intuitively, the combined effect value in this study was converted to Change (%), which represents the magnitude of the increase in yield and its components, grain protein content and grain amylose content.

$$\text{Change (\%)} = [\text{Exp}(E) - 1] \times 100\% \quad (2)$$

If the 95% confidence interval of the value overlaps with zero, the effect of potassium application is considered insignificant; conversely, it is significant. In subgroup analysis, if the 95% confidence intervals of values in different groups overlap, the difference between groups is considered insignificant; otherwise, is significant (Hedges et al. 1999).

To assess the heterogeneity of the data, the Fail-safe N (Nfs) was used for the heterogeneity test. When Nfs was greater than  $5 \times n + 10$ , the data was considered unbiased (Egger et al. 1997). As indicated in Table 2, there was no bias in the data from this study.

In addition, the agronomic efficiency of K fertiliser (AEK) and the partial productivity of K fertiliser (PFPK) were calculated to explore the utilisation efficiency of K fertiliser (Bi et al. 2014).

$$\text{AEK} = (Y1 - Y0)/K \quad (3)$$

$$\text{PFPK} = Y1/K \quad (4)$$

where: AEK – agronomic efficiency of potassium; Y1 – yield under potassium fertilisation; Y0 – yield without potassium fertilisation; K – mineral K fertiliser rate (kg K/ha).

Table 2. Fail-safe N results of publication bias analysis for rice growth and grain quality traits

Item	n	Fail-safe N (Nfs)
Grain yield	785	862 039 563
Effective panicles	488	45 480 014
Grain number per spike	496	43 712 001
Thousand-grain weight	501	3 026 656
Ripening percentage	454	4 705 206
Grain protein content	249	1 173 107
Grain amylose content	205	4 846 942

n – number of studies included in the meta-analysis for each trait; Fail-safe N (FsN) – a statistic used to assess publication bias

In this study, SPSS 27 (Armonk, USA); SigmaPlot 15.0 (San Jose, USA); RStudio (Boston, USA) were used for meta-analysis. The heterogeneity test was conducted with RStudio, and the effect value analysis was primarily carried out with 5 000 bootstraps in IBM SPSS Statistics 27.0. Additionally, regression analysis was performed with IBM SPSS Statistics 27.0. The charts in this paper were created with SigmaPlot 15.0.

## RESULTS

**Effects of potassium application rate on rice yield, its components, grain protein and amylose content.** Compared with the no-potassium treatment, K application significantly increased rice yield by 11.6% (average 185 kg N/ha, 35 kg P/ha, 106 kg K/ha). The highest yield gain (13.6%) was observed at a rate of 100–120 kg K/ha (average 187 kg N/ha, 34 kg P/ha, 117 kg K/ha), though no significant differences in yield increase magnitude were found across different K application ranges (Figure 1A). Additionally, K application notably improved key yield components: effective panicles (5.6%), grains per spike (5.8%), 1 000-grain weight (1.8%), and ripening rate (1.7%) (Figure 2). K application significantly increased rice grain protein content by 2.0% (average 162 kg N/ha, 32 kg P/ha, 91 kg K/ha). The magnitude of this increase varied significantly with K application rates, peaking at 7.7% when the rate was 100–125 kg K/ha (average 186 kg N/ha, 29 kg P/ha, 111 kg K/ha) (Figure 1B). K application significantly increased rice grain amylose content by 1.1% (average 154 kg N/ha, 29 kg P/ha, 93 kg K/ha), with the magnitude of this increase varying sig-

nificantly across different K application rates. The highest amylose gain (6.8%) was observed at a rate of 75–100 kg K/ha (average 164 kg N/ha, 35 kg P/ha, 95 kg K/ha) (Figure 1C).

**Effects of different base-topdressing ratios of K fertiliser on rice yield, grain protein and amylose content.** There were significant differences in the effects of potassium application on rice yield, grain protein and amylose content under different potassium base-topdressing ratios. When the base-topdressing ratio of K fertiliser was > 2, the magnitude of the increase in yield and amylose content reached the maximum, which was 24.7% (average 184 kg N/ha, 33 kg P/ha, 91 kg K/ha) and 6.0% (average 187 kg N/ha, 41 kg P/ha, 129 kg K/ha), respectively, significantly higher than those of other base-topdressing ratios (Figure 3A, C). However, as for the grain protein content, when the K fertiliser was all basal, the increase in protein content magnitude was the highest, reaching 9.9% (average 198 kg N/ha, 37 kg P/ha, 118 kg K/ha). When the base-topdressing ratio was > 2, the increase in protein content magnitude was not significant (Figure 3B).

**Effects of potassium application on rice yield and quality under different control groups of yield/grain protein content/grain amylose content.** The effects of potassium application on rice yield, grain protein content, and amylose content differed significantly across baseline levels of the control group (Figure 4). A marked negative correlation was observed: as the baseline yield, protein content, or amylose content in the control group increased, the magnitude of potassium-induced increments declined significantly. When the control yield was below 5 t/ha, potassium application resulted in a 46.6% yield increase (average 175 kg N/ha, 30 kg P/ha, 93 kg K/ha);

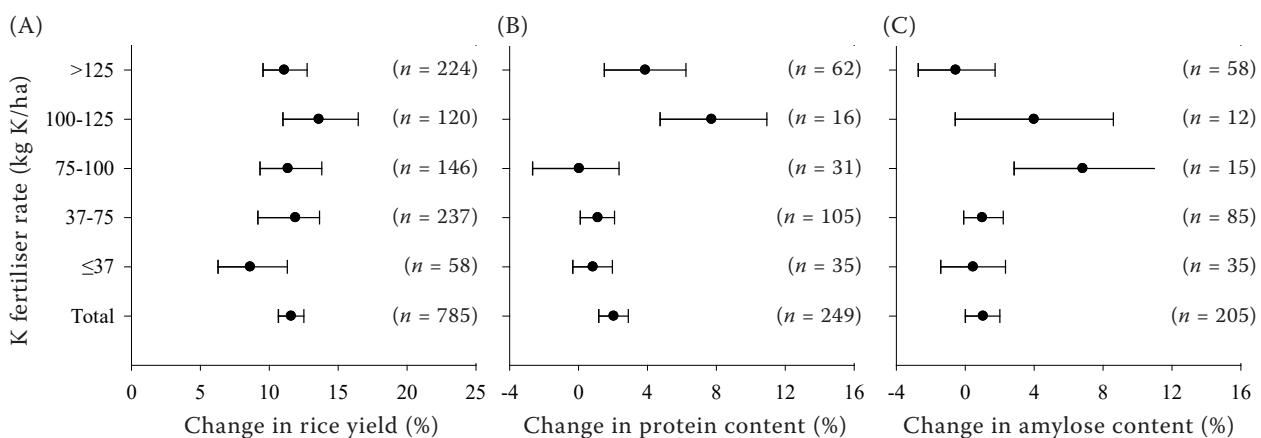


Figure 1. The effects of different potassium application rates on (A) rice yield; (B) grain protein content, and (C) amylose content

<https://doi.org/10.17221/315/2025-PSE>

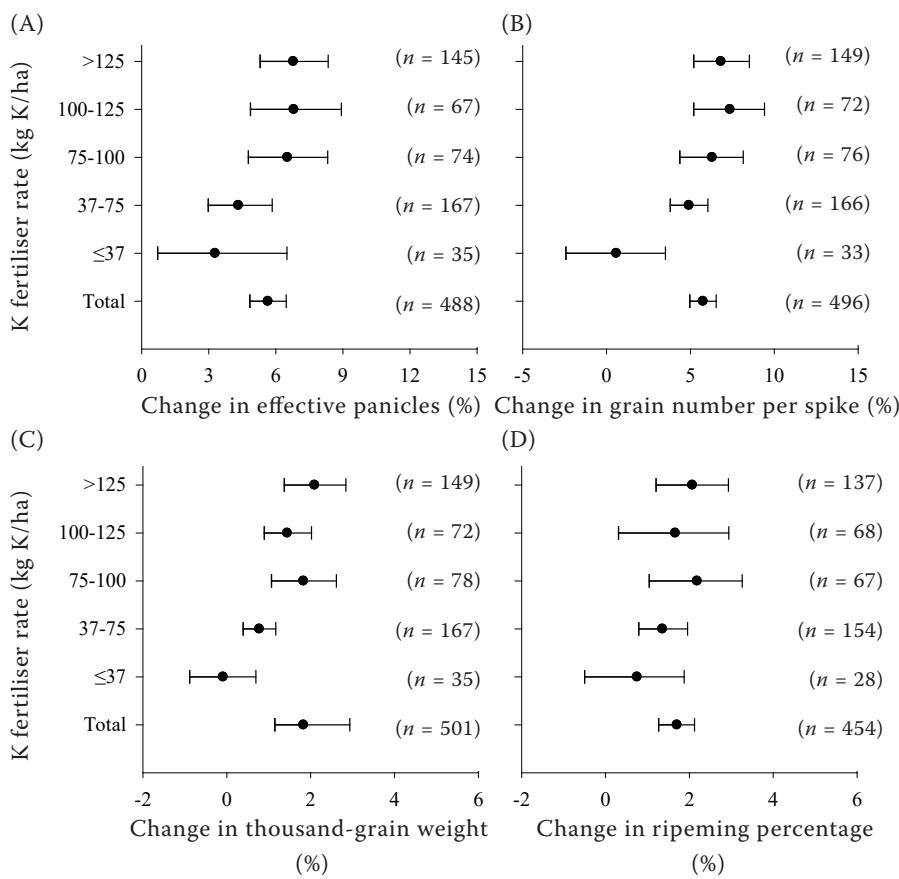


Figure 2. The effects of different potassium application rates on yield components of rice. (A) effective panicles; (B) grain number per spike; (C) thousand-grain weight, and (D) ripening percentage

in contrast, when the control yield exceeded 10 t/ha, the yield increment dropped to 4.5% (average 203 kg N/ha, 44 kg P/ha, 125 kg K/ha), representing a 90.4% reduction. A 4.6% increment was achieved when the control protein content was < 7.0% (average 169 kg N/ha, 37 kg P/ha, 70 kg K/ha), with no significant difference compared to the 7.0–8.0% control group (average 167 kg N/ha, 33 kg P/ha, 102 kg K/ha). No statistically significant increments were detected

when the control protein content exceeded 8.0% (average 151 kg N/ha, 28 kg P/ha, 83 kg K/ha). Potassium application increased amylose by 4.4% in the control group with amylose < 16% (average 158 kg N/ha, 26 kg P/ha, 92 kg K/ha), which was significantly higher than the non-significant effect observed in the control group with amylose > 16%.

#### Effects of potassium application on grain yield and protein content under different planting re-

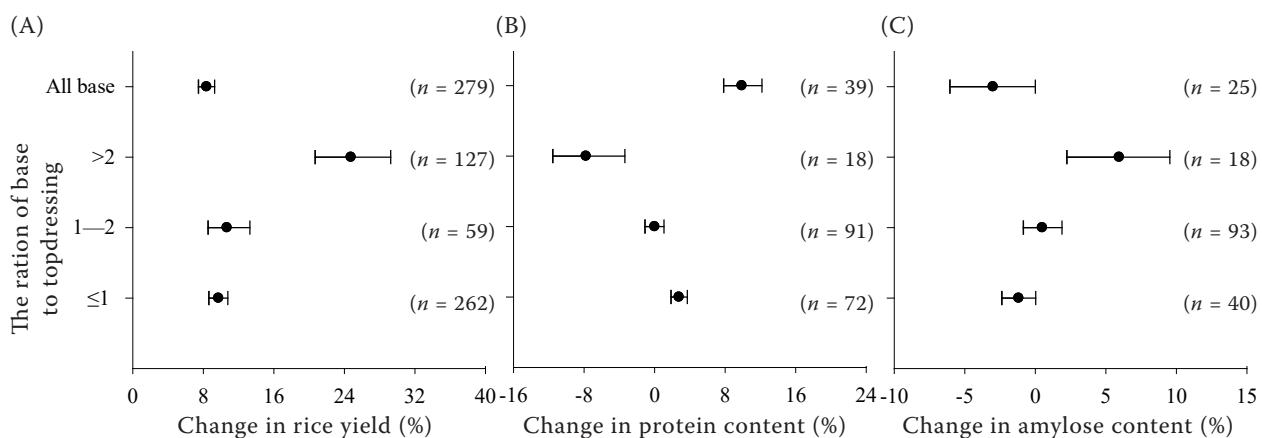
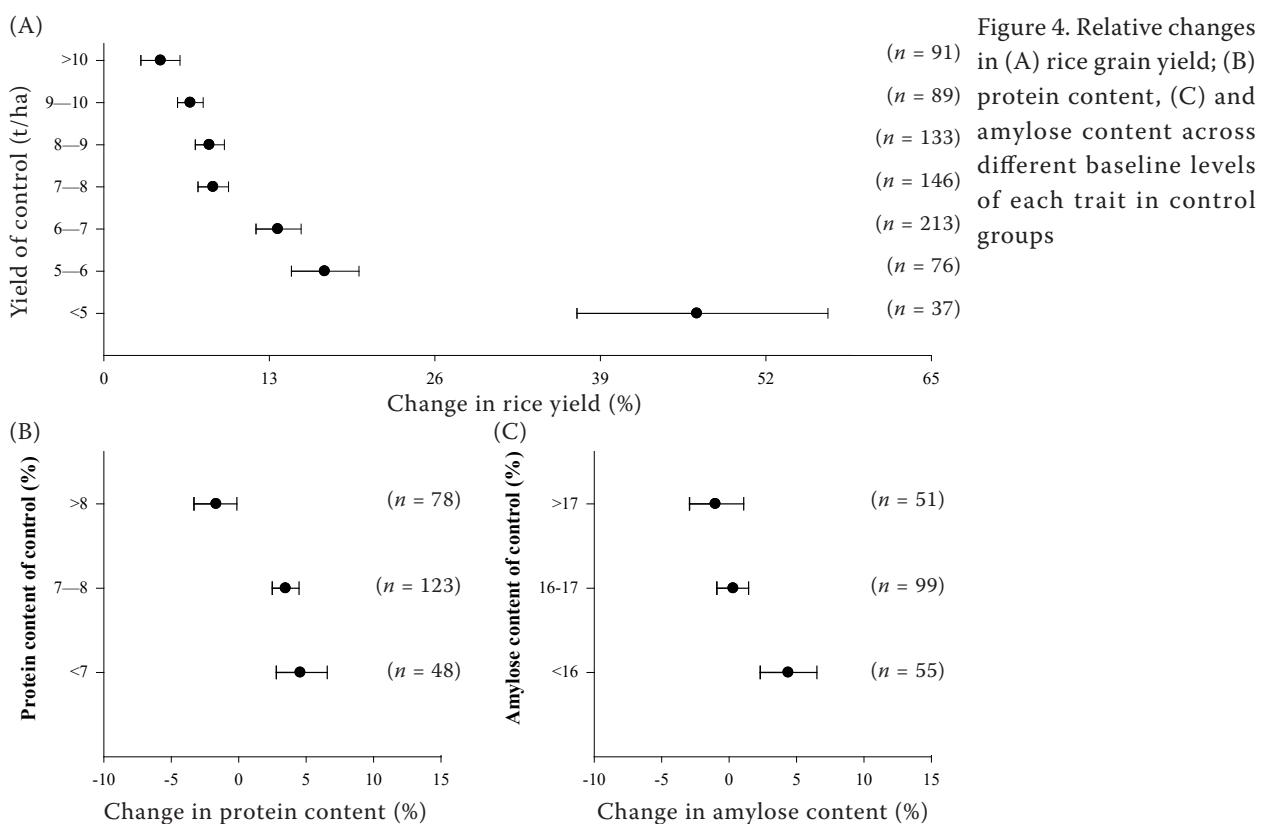


Figure 3. The effects of different potassium levels at different base ratios on (A) rice yield; (B) grain protein content, and (C) grain amylose content



**gions of rice.** In the Northeast Plain (Mainland China), the application of potassium significantly increased rice yield by 16.5% (average 159 kg N/ha, 30 kg P/ha, 81 kg K/ha), significantly higher than that in the upstream of the Yangtze River Basin (4.6%, average 163 kg N/ha, 36 kg P/ha, 105 kg K/ha) and the Southeast China coastal areas (10.8%, average 195 kg

N/ha, 31 kg P/ha, 113 kg K/ha) (Figure 5A). In the upstream of the Yangtze River Basin, the magnitude of the increase in protein content was the highest (12.4%, average 180 kg N/ha, 40 kg P/ha, 112 kg K/ha), significantly higher than that in the Southeast China coastal areas (2.6%, average 172 kg N/ha, 28 kg P/ha, 95 kg K/ha), the Northeast Plain (1.4%, average 142 kg

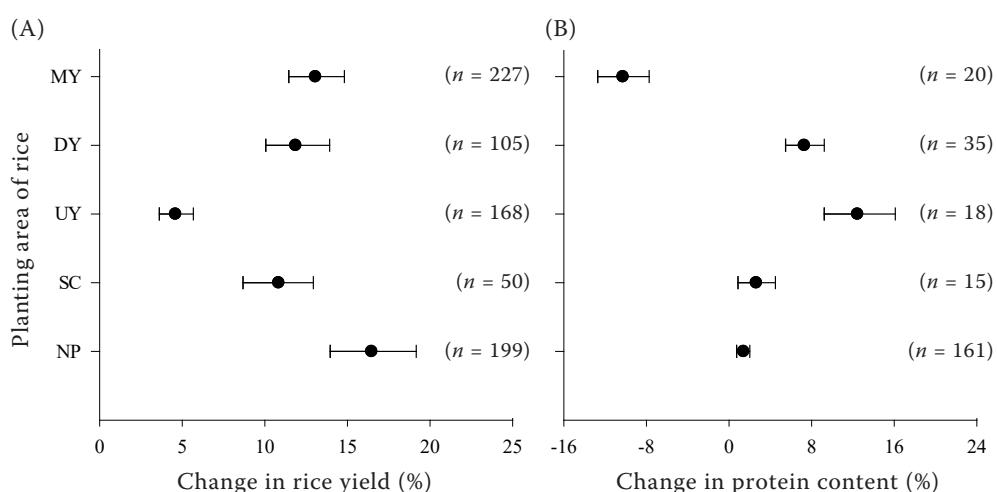


Figure 5. The effects of individual growing areas on potassium application-induced changes in (A) grain yield and (B) protein content of rice. NP – Northeast Plain; SC – Southeast Coast; UY – the upstream of the Yangtze River Basin; MY – the midstream of the Yangtze River Basin; DY – the downstream of the Yangtze River Basin

<https://doi.org/10.17221/315/2025-PSE>

N/ha, 28 kg P/ha, 75 kg K/ha) and the midstream of the Yangtze River Basin (−10.3%, average 180 kg N/ha, 39 kg P/ha, 120 kg K/ha) (Figure 5B).

**Effects of potassium application on grain yield, grain protein and amylose content under different rice types.** Potassium application significantly increased the yield of conventional rice and hybrid rice, and the magnitude of the increase in conventional rice was as high as 13.0% (average 179 kg N/ha, 32 kg P/ha, 100 kg K/ha), 1.3 times that of hybrid rice (average 187 kg N/ha, 37 kg P/ha, 113 kg K/ha) (Figure 6A). On the contrary, the magnitude of the increase in protein content in conventional rice was lower than that in hybrid rice (Figure 6B). The magnitude of the increase in amylose content of hybrid rice was negative, with no significant effect (Figure 6C). The magnitude of the increase in the yield of midseason rice was significantly higher than that of early-mature rice and late rice (Figure 6A). The magnitude of the increase in protein content of early-mature rice was significantly higher than that of midseason rice, and there was no significant

difference from late rice (Figure 6B). There was no significant difference in the magnitude of the increase in amylose content among late rice, early-mature rice and midseason rice (Figure 6C).

**Effects of potassium application on grain yield, grain protein and amylose content under different soil conditions.** Soil properties significantly modulated the yield, protein content and amylose content response of rice to potassium fertilisation (Figure 7). Under extreme potassium deficiency (exchangeable K  $\leq$  50 mg/kg), mild deficiency (50–100 mg/kg), moderate levels (100–150 mg/kg), and relative sufficiency ( $>$  150 mg/kg), potassium fertilisation increased rice yields by 14.6, 12.1, 8.7, and 7.1% respectively; protein content changed by −10.3, 3.1, 1.6, and −1.1% respectively with potassium application; amylose content increased by 7.3, −0.4, −1.9 and 1.0%, respectively. Similarly, under acidic soils (pH  $<$  5.5), slightly acidic (pH 5.5–6.5), neutral (pH 6.5–7.5) and alkaline (pH 7.5–8.5) conditions, potassium fertilisation increased rice yields by 9.5, 10.7, 17.0 and 14.9%, respectively; protein content

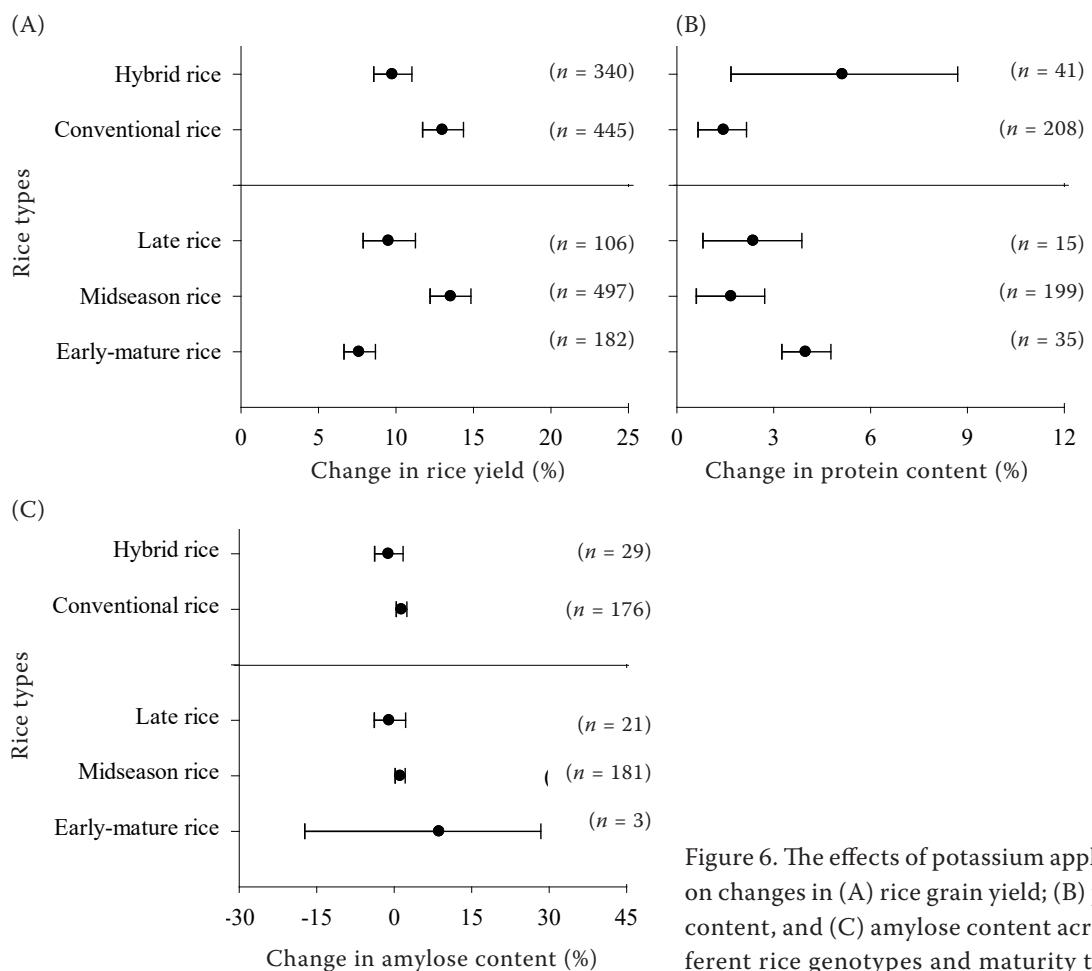


Figure 6. The effects of potassium application on changes in (A) rice grain yield; (B) protein content, and (C) amylose content across different rice genotypes and maturity types

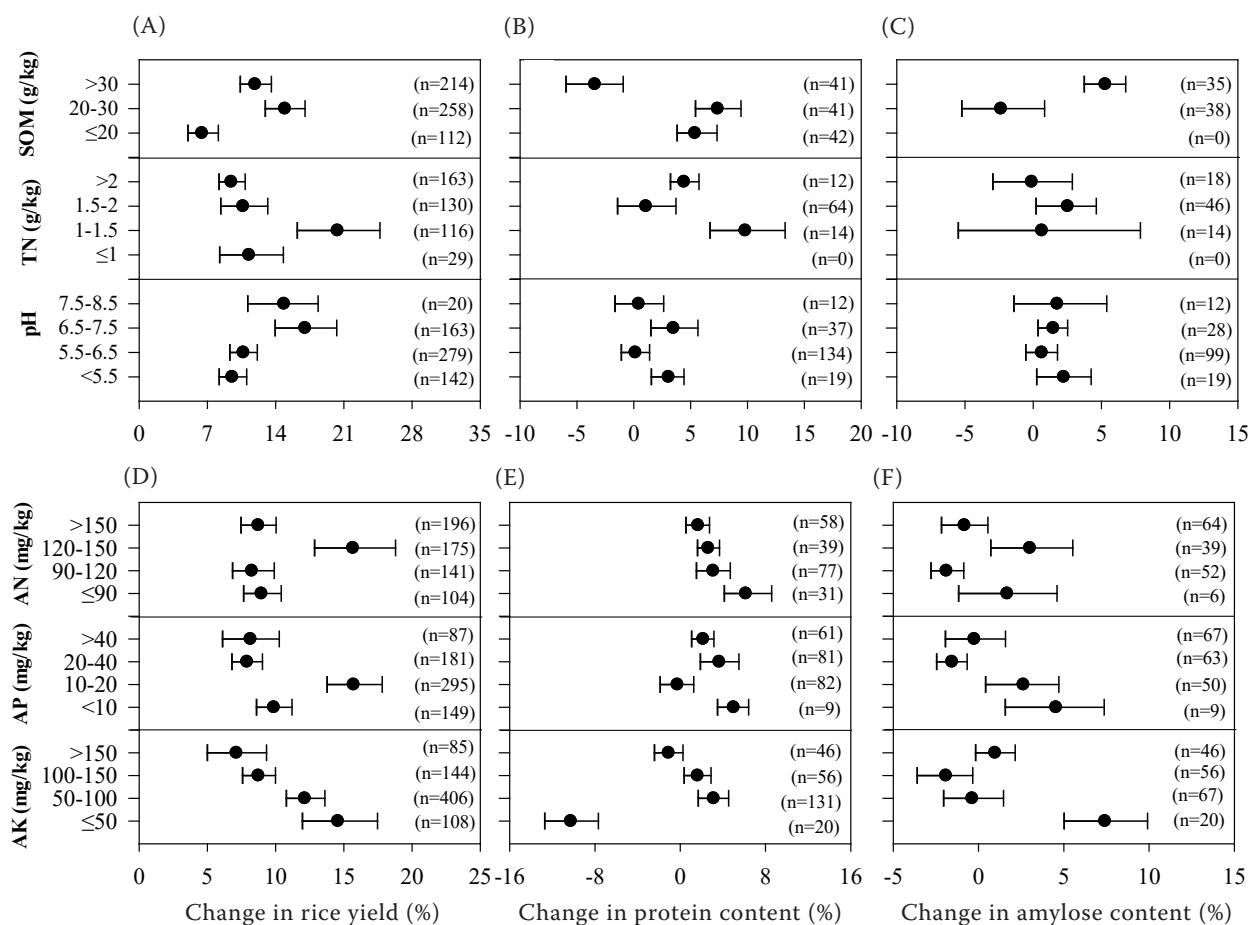


Figure 7. The effects of individual soil parameter levels on potassium application-induced changes in rice grain yield, protein content, and amylose content. SOM – soil organic matter; TN – total nitrogen; AN – available nitrogen; AP – available phosphorus; AK – available potassium

increased by 3.1, 0.1, 2.7, and 0.4% respectively; no significant difference in the magnitude of the increase in amylose content. Soil organic matter, total nitrogen, available nitrogen, and available phosphorus also shaped yield responses, with peak increases observed at 20–30 g/kg (15.0%), 1–1.5 g/kg (20.4%), 120–150 mg/kg (15.7%), and 10–20 mg/kg (15.7%), respectively. The largest protein gains occurred at soil organic matter of 20–30 g/kg (7.4%), total nitrogen of 1–1.5 g/kg (9.8%), available nitrogen  $\leq$  90 mg/kg (6.2%), and available phosphorus of 20–40 mg/kg (3.7%). The higher magnitude of the increase in amylose content was observed when the soil organic matter was  $>$  30 g/kg (5.3%), the soil-available nitrogen content was 120–150 mg/kg (3.0%) and the soil-available phosphorus content was  $<$  10 mg/kg (4.5%), respectively. There are significant difference in the magnitude of the increase in amylose content under different total nitrogen contents, but no clear trend can be identified.

**The impact of optimising K fertiliser management on rice yield and quality.** At a potassium rate of 100–125 kg K/ha (OPT1), yield increased by 14.7%. When the potassium fertiliser base-to-topdressing ratio  $>$  2 (OPT2, for yield), the yield gain reached 27.3%, representing an 86.2% increase in yield-increasing effect compared to OPT1. Simultaneous optimisation of both the potassium rate and base-to-topdressing ratio  $>$  2 (OPT4) further increased yield by 31.9% – a 117.4% rise *versus* OPT1 and a 16.7% increase *versus* OPT2, though the latter difference was not significant (Figure 8A). At a rate of 100–125 kg K/ha (OPT1), protein content increased by 7.8%. When potassium was applied entirely as base fertiliser (OPT2, for protein content), the protein gain reached 10.2%. Comprehensive optimisation of potassium rate with total potassium applied as base fertiliser (OPT3) also enhanced protein content, though not significantly compared to single-factor optimisation (Figure 8B).

<https://doi.org/10.17221/315/2025-PSE>

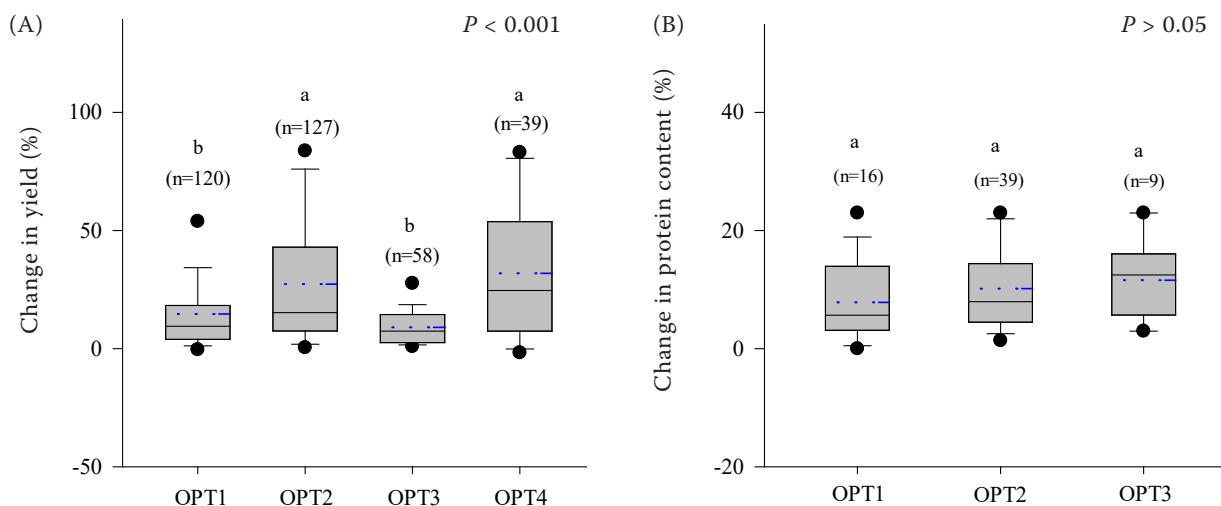


Figure 8. Comprehensive analysis of the effect of potassium fertiliser management on rice yield. OPT1 – optimise the amount of potassium fertiliser, 100–125 kg K/ha; OPT2 – optimise the base-topdressing ratio of potassium fertiliser, for yield, it optimises the K base-topdressing ratio  $> 2$ ; for protein content, it applies K entirely as base fertiliser; OPT3 – optimise the application amount of potassium fertiliser and total base fertiliser was applied; OPT4 – optimise the application amount of potassium fertiliser and the base-topdressing ratio of potassium fertiliser was controlled at  $> 2$

## DISCUSSION

The results of meta-analysis showed that compared with no potassium application, potassium application could significantly increase rice yield by 11.6% (Figure 1A), which was mainly attributed to the increase of effective panicles, grain number per spike, 1 000-grain weight, and ripening percentage of rice by potassium application (Figure 2), indicating that potassium application could significantly increase rice yield, which was basically consistent with the results of Wang et al. (2022) on the effect of fertilisation on yield increase of midseason rice in the Yangtze River Basin. The formation of rice yield mainly depends on the grain filling process (Xu et al. 2023), for 28% of the photosynthetic assimilates required for grain filling are stored in the stem sheath in the form of non-structural carbohydrates (NSC) before flowering, and more than 70% are derived from photosynthesis after flowering (Pan et al. 2011, Wang et al. 2016). Adequate potassium supply can promote root development and shoot growth, increase the activity of nitrogen metabolism-related enzymes, and enhance the accumulation of NSC in stems, thereby increasing the absorption of nitrogen nutrients by rice, enhancing the filling ability, and ultimately promoting the increase of yield (Hou et al. 2019, Zhang et al. 2019).

The application rate of potassium fertiliser is a key factor affecting rice yield. Previous studies have shown

that inadequate potassium application will limit the increase of crop yield (Das et al. 2019, Hu et al. 2021). The results of meta-analysis showed that the minimum magnitude of the increase in effective panicles was 3.3% when the K fertiliser rate was  $\leq 37$  kg K/ha, and the magnitude of the increase in grain number per panicle, 1 000-grain weight and ripening percentage was not significant, and the magnitude of the increase in rice yield was only 8.6% (Figure 1A, Figure 2). This may be related to potassium deficiency interfering with the transport of photosynthates to grains (Zhang et al. 2010). When the application rate increases to 100–125 kg K/ha (average pH: 6.1, SOM: 27.5 g/kg, TN: 2.8 g/kg, AN: 138.4 mg/kg, AP: 21.7 mg/kg, AK: 96.9 mg/kg), the increases in effective panicles, grain number per spike and yield reach the maximum; beyond this range, there is no significant difference in the increase (Figures 1A, 2A, B). Excessive application will lead to a continuous increase in potassium absorption by straw, soil potassium leaching and resource waste (Islam and Muttaleeb 2016, Nest et al. 2017, Ye et al. 2020). Notably, this optimal K range is significantly higher than that reported for rice cultivation in Bangladesh (Akter et al. 2023), primarily due to differences in soil properties between regions. Such variations are not limited to international comparisons – even within China, rice yield responses to K application differ markedly across major rice-growing areas, driven by the synergy of regional soil properties and local management practices.

The magnitude of the increase in rice yield in the Northeast Plain is significantly higher than that in the Southeast Coast and the upstream/downstream of the Yangtze River Basin (Figure 5A), with soil conditions and rice cultivars being the two most critical driving factors. Data comparison revealed that soil pH, AK, and rice cultivar were the primary drivers of these regional differences. As shown in the results of Figure 7D, when soil AK content was below 100 mg/kg, the yield-increasing effect of K application was significantly higher than the average level. However, the average soil AK content in the Northeast Plain was 122 mg/kg, which was higher than that in other regions (all below 100 mg/kg), while the yield-increasing effect of K application was still significantly higher than in other regions. This phenomenon can be explained from two aspects. On the one hand, although the average soil AK content in the Northeast Plain (122 mg/kg) was relatively higher, it might still fail to fully meet the K demand of rice under local growth conditions, or the K utilisation efficiency of local rice cultivars was relatively higher, so exogenous K application still exerted a significant yield-increasing effect – unlike the general rule that K fertiliser efficiency is higher in K-deficient soils (Liu et al. 2023). On the other hand, soil pH played a crucial regulatory role. The average soil pH in the Northeast Plain was 6.5 (near-neutral), in contrast to only 5.7 (acidic) in the southeastern coastal areas. Acidic soils inhibit root growth, reduce nutrient uptake, and enhance potassium fixation – ultimately weakening the yield-increasing effect of potassium application (Feyisa et al. 2024). These adverse effects of acidic soils on K availability and uptake in the Southeast Coast and Yangtze River Basin regions ultimately weakened the yield-increasing effect of K application, even though the initial soil AK content in these regions was lower. In contrast, the near-neutral soil environment in the Northeast Plain promoted root development and K absorption, thereby maximising the yield-increasing potential of exogenous K application.

Rice cultivar also plays a crucial role. In the Northeast Plain, 94% of the rice cultivated was conventional rice, while in the upper reaches of the Yangtze River Basin, 71% was hybrid rice. Studies have shown that potassium application has a better yield-increasing effect on conventional rice than on hybrid rice, and conventional rice is more dependent on potassium fertilisation than hybrid rice (Yang et al. 2016), this is consistent with the results of our

study. Additionally, more fields in the Northeast Plain used a K base-topdressing ratio  $> 2$  (aligning with the optimal regime), the meta-analysis showed that, compared with all basal application of K fertiliser, the yield increase magnitude was significantly increased by 196.2% when the base-topdressing ratio of K fertiliser was  $> 2$  (Figure 4A). This not only conforms to the demand law of rice for rapid potassium accumulation during the tillering-booting stage (Ye et al. 2020), but also promotes the accumulation of non-structural carbohydrates (NSC) in stems and the transfer of nutrients to grains (Fu et al. 2011, You et al. 2021). Potassium application at the booting stage can further increase effective panicles, ripening percentage and 1 000-grain weight (Chen et al. 2022). Accurate control of the application rate and basal-topdressing ratio of K fertiliser could improve the effective utilisation rate of K fertiliser without increasing input, and achieve rice yield increase.

The protein and amylose contents of rice are influenced by tillage management (Armengaud et al. 2009, Jiang et al. 2016, Liu et al. 2019). This study revealed that potassium application can significantly increase the protein content and amylose content of rice grains by 2.0% and 1.1%, respectively (Figures 1B–C). As an important nutrient element, potassium activates aminoacyl-tRNA synthetase and polypeptide synthetase, promoting protein synthesis in crops, and potassium also enhances the cycles of carbon and nitrogen metabolism, leading to greater starch accumulation in grains (Hou et al. 2018, 2019, Cui and Tcherkez 2021). However, the effects of potassium application on protein content and amylose content can vary within the same application rate. When the potassium application rate is between 75 and 100 kg K/ha, the amylose content increases by 6.8%, while the magnitude of the increase in protein content is not significant. Conversely, at the potassium application rate of 100–125 kg K/ha, the maximum magnitude of the increase in protein content is 7.7%, and the magnitude of the increase in amylose content is not significant (Figure 1B–C). Similar results were observed with different base – topdressing ratios. Previous studies also indicated that applying K fertiliser during the late growth stage could increase the protein content of rice while decreasing the amylose content (Mirtaleb et al. 2021). This may occur because increased starch accumulation could dilute protein content to a certain extent (Barneix 2007).

Soil condition is a vital factor affecting how potassium application increases grain protein and amylose

content. Grain amylose formation relies on phosphorus and potassium absorption during vegetative growth and their transfer to the grain (Zhang et al. 2022). In extremely potassium-deficient soils ( $AK \leq 50 \text{ mg/kg}$ ), potassium application leads to a 7.4% increase in amylose content, while protein content decreases by 10.3%. As soil available potassium content increases, the magnitude of the increase in protein content initially rises and then falls, while the effect on amylose content does the opposite (Figures 7E–F). This indicates that in potassium-deficient soils, potassium primarily promotes starch formation, boosting yield, which explains the lower protein content increase observed in the midstream of the Yangtze River Basin when being compared to that in other areas. Furthermore, in soils with low organic matter or nitrogen and phosphorus, the magnitude of the increase in protein content is more significant (Figures 7B, E), as potassium application enhances nitrogen absorption and protein synthesis in rice.

Optimisation of K fertiliser management is crucial for elevating rice yield and improving resource efficiency. When the K fertiliser rate was optimised in the range of 100–125 kg K/ha (OPT1), the rice yield increased by 14.67% and the protein content increased by 7.7% (Figure 8A,B), which was close to the results of Zhang et al. (2021). Apparently, optimising the application amount of K fertiliser can achieve the synergistic improvement of rice yield and rice nutritional quality. Management involves not only the quantity but also the base-to-topdressing ratio of potassium. On the basis of optimising the K fertiliser rate, if all K fertiliser were applied as base fertiliser (OPT3), the yield increase magnitude decreased by 38.8%, and the protein content increased by 48.7%, but the difference was not significant. If the base-topdressing ratio of K fertiliser was optimised to  $> 2$  (OPT4), the magnitude of the increase in yield was significantly increased by 117.0%, and there was insufficient data to support the increase magnitude of protein content (Figure 8). These results indicate that the combination of base fertiliser and topdressing (OPT4) is advantageous for maximising rice yield and efficiently utilising K fertiliser resources, while single basal application (OPT3) or optimal rate alone (OPT1) may be more favourable for nutritional quality improvement. This is largely because starch constitutes over 80% of the dry weight of rice grains (Syahariza et al. 2013, Liu et al. 2020). Yield gain driven by enhanced starch accumulation tends to dilute protein content to a certain extent

(Barneix 2007), making it challenging to simultaneously maximise yield and nutritional quality. Thus, specific K fertiliser management strategies should be tailored to the target rice quality requirements.

Within the optimal range of potassium application, the effect of potassium application on the increase of amylose content was not significant, which may enhance rice eating quality. The relationship between protein content and rice quality is controversial. Some studies indicated that higher protein content inhibited water absorption, swelling, and gelatinisation of starch granules, reducing quality (Lim et al. 1999, Lyon et al. 2000, Ma et al. 2024), while others asserted that taste depended more on the variety rather than protein levels (Xiang et al. 1990). Additionally, cereal grain proteins include easily absorbable albumin, globulin, and glutenin, as well as prolamin which negatively impacts eating quality (Amaglian et al. 2017, Balindong et al. 2018); gel consistency and gelatinisation temperature also influenced eating quality (Zhang et al. 2018). These complexities mean that rice eating quality cannot be judged solely by changes in protein and amylose content.

In summary, potassium fertiliser management should be flexibly adjusted based on the desired rice quality traits: for scenarios prioritising high yield and resource use efficiency, the combination of optimal K rate (100–125 kg K/ha) and base-topdressing ratio  $> 2$  is recommended as it maximises yield while ensuring efficient K utilisation; for scenarios emphasising nutritional quality, the optimal K rate (100–125 kg K/ha) with full basal application can be adopted to promote protein accumulation without significant yield loss; and for scenarios focusing on eating quality, the optimal strategy was a rate (75–100 kg K/ha) with a base – topdressing ratio  $> 2$ , maximising amylose content to improve cooking and eating quality, with further adjustments possible based on variety-specific traits and local soil conditions. This targeted management strategy not only addresses the trade-off between rice yield and quality but also provides practical guidance for sustainable rice production with diverse quality requirements.

**Acknowledgment.** We thank all the authors of this manuscript.

## REFERENCES

Akter S., Kamruzzaman M., Khan M.Z., Amin M.S. (2023): Enhanced potassium fertilisation improved rice (*Oryza sativa*) yield and nutrient uptake in coastal saline soil of Bangladesh. *Journal of Soil Science and Plant Nutrition*, 23: 1884–1895.

Al Rawashdeh R. (2020): World peak potash: an analytical study. *Resour Policy*, 69: 101834.

Amaglian L., O'Regan J., Kelly A.L., O'Mahony J.A. (2017): The composition, extraction, functionality and applications of rice proteins: a review. *Trends in Food Science and Technology*, 64: 1–12.

Armengaud P., Sulpice R., Miller A.J., Stitt M., Amtmann A., Gibon Y. (2009): Multilevel analysis of primary metabolism provides new insights into the role of potassium nutrition for glycolysis and nitrogen assimilation in *Arabidopsis* roots. *Plant Physiology*, 150: 772–785.

Balindong J.L., Ward R.M., Liu L., Rose T.J., Pallas L.A., Ovenden B.W., Snell P.J., Waters D.L.E. (2018): Rice grain protein composition influences instrumental measures of rice cooking and eating quality. *Journal of Cereal Science*, 79: 35–42.

Barneix A.J. (2007): Physiology and biochemistry of source-regulated protein accumulation in the wheat grain. *Journal of Plant Physiology*, 164: 581–590.

Bi L., Xia J., Liu K., Li D., Yu X. (2014): Effects of long-term chemical fertilization on trends of rice yield and nutrient use efficiency under double rice cultivation in subtropical China. *Plant, Soil and Environment*, 60: 537–543.

Britto D.T., Kronzucker H.J. (2008): Cellular mechanisms of potassium transport in plants. *Physiologia Plantarum*, 133: 637–650.

Brownlie W.J., Alexander P., Maslin M., Cañedo-Argüelles M., Sutton M.A., Spears B.M. (2024): Global food security threatened by potassium neglect. *Nature Food*, 5: 111–115.

Brownlie W.J., Sutton M.A., Cordell D., Reay D.S., Heal K.V., Withers P.J.A., Vanderbeck I., Spears B.M. (2023): Phosphorus price spikes: a wake-up call for phosphorus resilience. *Frontiers in Sustainable Food Systems*, 7: 1088776.

Chen G.Y., Peng L.G., Li C.M., Tu Y.B., Lan Y., Wu C.Y., Duan Q., Zhang Q.Q., Yang H., Li T. (2023): Effects of the potassium application rate on lipid synthesis and eating quality of two rice cultivars. *Journal of Integrative Agriculture*, 22: 2025–2040.

Chen L.Q., Zhang W.Z., Gao J.P., Liu Y.Z., Wang X., Liu Y.Q., Feng Y.Y., Zhao Y.Z., Xin W. (2022): Effects of precise K fertilizer application on the yield and quality of rice under the mode of light, simple, and high-efficiency N fertilizer application during the panicle stage. *Agronomy-Basel*, 12: 1681.

Cui J., Tcherkez G. (2021): Potassium dependency of enzymes in plant primary metabolism. *Plant Physiology and Biochemistry*, 166: 522–530.

Das D., Dwivedi B.S., Datta S.P., Meena M.C., Agarwal B.K., Shahi D.K., Singh M., Chakraborty D., Jaggi S. (2019): Potassium supplying capacity of a red soil from eastern India after forty-two years of continuous cropping and fertilization. *Geoderma*, 341: 76–92.

Deng N.Y., Grassini P., Yang H., Huang J.L., Cassman K.G., Peng S.B. (2019): Closing yield gaps for rice self-sufficiency in China. *Nature Communications*, 10: 1725.

Egger M., Smith G.D., Schneider M., Minder C. (1997): Bias in meta-analysis detected by a simple, graphical test. *BMJ-British Medical Journal*, 315: 629–634.

Feyisa D.S., Jiao X.Q., Mojo D. (2024): Wheat yield response to chemical nitrogen fertilizer application in Africa and China: a meta-analysis. *Journal of Soil Science and Plant Nutrition*, 24: 102–114.

Fu J., Huang Z.H., Wang Z.Q., Yang J.C., Zhang J.H. (2011): Pre-anthesis non-structural carbohydrate reserve in the stem enhances the sink strength of inferior spikelets during grain filling of rice. *Field Crops Research*, 123: 170–182.

Grassini P., Eskridge K.M., Cassman K.G. (2013): Distinguishing between yield advances and yield plateaus in historical crop production trends. *Nature Communications*, 4: 2918.

Hedges L.V., Gurevitch J., Curtis P.S. (1999): The meta-analysis of response ratios in experimental ecology. *Ecology*, 80: 1150–1156.

Helm R.M., Burks A.W. (1996): Hypoallergenicity of rice protein. *Cereal Foods World*, 41: 839–843.

Hou W.F., Xue X.X., Li X.K., Khan M.R., Yan J.Y., Ren T., Cong R.H., Lu J.W. (2019): Interactive effects of nitrogen and potassium on: grain yield, nitrogen uptake and nitrogen use efficiency of rice in low potassium fertility soil in China. *Field Crop Research*, 236: 14–23.

Hou W.F., Yan J.Y., Jakli B., Lu J.W., Ren T., Cong R.H., Li X.K. (2018): Synergistic effects of nitrogen and potassium on quantitative limitations to photosynthesis in rice (*Oryza sativa* L.). *Journal of Agricultural and Food Chemistry*, 66: 5125–5132.

Hu W.S., Lu Z.F., Meng F.J., Li X.K., Cong R.H., Ren T., Lu J.W. (2021): Potassium fertilization reduces silique canopy temperature variation in *Brassica napus* to enhance seed yield. *Industrial Crops and Products*, 168: 113604.

Islam A., Muttaleeb A. (2016): Effect of potassium fertilization on yield and potassium nutrition of Boro rice in a wetland ecosystem of Bangladesh. *Archives of Agronomy and Soil Science*, 62: 1530–1540.

Jiang Q., Du Y.L., Tian X.Y., Wang Q.S., Xiong R.H., Xu G.C., Yan C., Ding Y.F. (2016): Effect of panicle nitrogen on grain filling characteristics of high-yielding rice cultivars. *European Journal of Agronomy*, 74: 185–192.

Kong X.L., Zhu P., Sui Z.Q., Bao J.S. (2015): Physicochemical properties of starches from diverse rice cultivars varying in apparent amylose content and gelatinisation temperature combinations. *Food Chemistry*, 172: 433–440.

Lim S.T., Lee J.H., Shin D.H., Lim H.S. (1999): Comparison of protein extraction solutions for rice starch isolation and effects of residual protein content on starch pasting properties. *Starch-Starke*, 51: 120–125.

Liu X., Li M., Guo P., Zhang Z.X. (2019): Optimization of water and fertilizer coupling system based on rice grain quality. *Agricultural Water Management*, 221: 34–46.

Liu J.G., Pei X.F., Ding W.L., Guo Z., Zhang Y.F., Sheng J., Zhou W., Huang S.D. (2023): Effect of soil physical and chemical proper-

<https://doi.org/10.17221/315/2025-PSE>

ties on rice quality in high quality rice producing areas of Jiangsu province. *Jiangsu Journal of Agricultural Sciences*, 39: 956–965.

Liu Q.Y., Tao Y., Cheng S., Zhou L., Tian Z.P., Liu G.D., Wei H.Y., Zhang H.C. (2020): Relating amylose and protein contents to eating quality in 105 varieties of Japonica rice. *Cereal Chemistry*, 97: 1303–1312.

Lu D.J., Li C.Z., Sokolowski E., Magen H., Chen X.Q., Wang H.Y., Zhou J.M. (2017): Crop yield and soil available potassium changes as affected by potassium rate in rice-wheat systems. *Field Crops Research*, 214: 38–44.

Lyon B.G., Champagne E.T., Vinyard B.T., Windham W.R. (2000): Sensory and instrumental relationships of texture of cooked rice from selected cultivars and postharvest handling practices. *Cereal Chemistry*, 77: 64–69.

Ma J.Y., Chen T.T., Lin J., Fu W.M., Feng B.H., Li G.H., Li H.B., Li J.C., Wu Z.H., Tao L.X., Fu G.F. (2022): Functions of nitrogen, phosphorus and potassium in energy status and their influences on rice growth and development. *Rice Science*, 29: 166–178.

Ma Z.H., Zhu Z.Y., Song W.W., Luo D., Cheng H.T., Wang X.J., Lyu W.Y. (2024): Effects of nitrogen fertilizer on the endosperm composition and eating quality of rice varieties with different protein components. *Agronomy-Basel*, 14: 469.

Marschner P. (2012): *Marschner's Mineral Nutrition of Higher Plants*. 3<sup>rd</sup> Edition. San Diego, Elsevier Academic Press Inc.

Mirtaleb S.H., Niknejad Y., Fallah H. (2021): Foliar spray of amino acids and potassic fertilizer improves the nutritional quality of rice. *Journal of Plant Nutrition*, 44: 2029–2041.

Mohamed A.A., Zayed B., Hafaz E., Eltobgy R., Hafez Y.M., Abdelaal K.A. (2021): Effect of potassium fertilizer treatments and harvest date on rice grain yield and quality of rice plants (giza 179 variety). *Fresenius Environmental Bulletin*, 30: 1010–1020.

Nest T.V., Vandecasteele B., Ruysschaert G., Merckx R. (2017): Prediction of P concentrations in soil leachates: results from 6 long term field trials on soils with a high P load. *Agriculture, Ecosystems and Environment*, 237: 55–65.

Nieves-Cordones M., Rodenas R., Lara A., Martinez V., Rubio F. (2019): The combination of K<sup>+</sup> deficiency with other environmental stresses: what is the outcome? *Physiologia Plantarum*, 165: 264–276.

Pan J.F., Cui K.H., Wei D., Huang J.L., Xiang J., Nie L.X. (2011): Relationships of non-structural carbohydrates accumulation and translocation with yield formation in rice recombinant inbred lines under two nitrogen levels. *Physiologia Plantarum*, 141: 321–331.

Rong L.B., Gong K.Y., Duan F.Y., Li S.K., Zhao M., He J.Q., Zhou W.B., Yu Q. (2021): Yield gap and resource utilization efficiency of three major food crops in the world – a review. *Journal of Integrative Agriculture*, 20: 349–362.

Syahariza Z.A., Sar S., Hasjim J., Tizzotti M.J., Gilbert R.G. (2013): The importance of amylose and amylopectin fine structures for starch digestibility in cooked rice grains. *Food Chemistry*, 136: 742–749.

Umemoto T., Aoki N., Lin H.X., Inouchi N., Sato Y., Yano M., Hirabayashi H., Maruyama S. (2004): Natural variation in rice starch synthase. IIA affects enzyme and starch properties. *Functional Plant Biology*, 31: 671–684.

Ushakova E., Perevoshchikova A., Menshikova E., Khayrulina E., Perevoshchikov R., Belkin P. (2023): Environmental aspects of potash mining: a case study of the verkhnekamskoe potash deposit. *Mining*, 3: 176–204.

Valkama E., Salo T., Esala M., Turtola E. (2013a): Grain quality and N uptake of spring cereals as affected by nitrogen fertilization under Nordic conditions: a meta-analysis. *Agricultural and Food Science*, 22: 208–222.

Valkama E., Salo T., Esala M., Turtola E. (2013b): Nitrogen balances and yields of spring cereals as affected by nitrogen fertilization in northern conditions: a meta-analysis. *Agriculture, Ecosystems and Environment*, 164: 1–13.

Wang J.L., Huang X.M., Wang B.B., Xu X.P., Ding W.C., Yang L.F., Qiu S.J., Zhao S.J., He P. (2022): Effects of fertilization on the yield of mid-season rice in the Yangtze River Basin and its influencing factors. *Journal of Huazhong Agricultural University*, 41: 105–114.

Wang D.R., Wolfrum E.J., Virk P., Ismail A., Greenberg A.J., McCouch S.R. (2016): Robust phenotyping strategies for evaluation of stem non-structural carbohydrates (NSC) in rice. *Journal of Experimental Botany*, 67: 6125–6138.

Waters D.L.E., Henry R.J., Reinke R.E., Fitzgerald M.A. (2006): Gelatinization temperature of rice explained by polymorphisms in starch synthase. *Plant Biotechnology Journal*, 4: 115–122.

Wu J.J., Fu W.T., Sun Y.N., Xie X.B., Huang S. (2025): Effect of soil fertility on grain quality of good-taste double-season rice cultivars. *Acta Agriculturae Universitatis Jiangxiensis*, 47: 21–31.

Xiang Y.H., Tang Q.Y., Huang Y.X. (1990): The relativity of rice grain quality characteristics – relations between eating quality and other grain quality characteristics of indica non-waxy rice. *Journal of Hunan Agricultural College*, 4: 325–330.

Xu W.T., Li J.M., Feng J.C., Shao Z.Z., Huang W.F., Hou W.F., Gao Q. (2023): Nitrogen and potassium interactions optimized asynchronous spikelet filling and increased grain yield of japonica rice. *PeerJ*, 11: e14710.

Yang X.E., Liu J.X., Wang W.M., Ye Z.Q., Luo A.C. (2004): Potassium internal use efficiency relative to growth vigor, potassium distribution, and carbohydrate allocation in rice genotypes. *Journal of Plant Nutrition*, 27: 837–852.

Yang Z.P., Nie J., Liao Y.L., Xie J., Lu Y.H., Zhou X., Huang K.Y. (2016): Effect of potassium on yield, K uptake and utilization of different early rice varieties. *Chinese Agricultural Science Bulletin*, 32: 1–10.

Ye T.H., Xue X.X., Lu J.W., Hou W.F., Ren T., Cong R.H., Li X.K. (2020): Yield and potassium uptake of rice as affected by potassium rate in the middle reaches of the Yangtze River, China. *Agronomy Journal*, 112: 1318–1329.

Ye C., Zheng G.J., Tao Y., Xu C.M., Chen S., Liu Y.H., Zhang X.F., Wang D.Y. (2024): Effect of soil texture on soil nutrient status and rice nutrient absorption in paddy soils. *Agronomy-Basel*, 14: 1339.

You C.C., Wang H., Huang Y.R., Xu P., Wu L.Q., Yu F.H., Zhong X.Y., Gao J., Zhang L.L., He H.B., Ke J. (2021): Relationship between the vascular bundle structure of panicle branches and the filling of inferior spikelets in large-panicle japonica rice. *Frontiers in Plant Science*, 12: 774565.

Zhang T.T., He X.P., Chen B.L., He L.X., Tang X.R. (2021): Effects of different potassium (K) fertilizer rates on yield formation and lodging of rice. *Phyton-International Journal of Experimental Botany*, 90: 815–826.

Zhang L., He Y.L., Lin D.S., Yao Y.P., Song N.N., Wang F.L. (2022): Co-application of biochar and nitrogen fertilizer promotes rice performance, decreases cadmium availability, and shapes rhizosphere bacterial community in paddy soil. *Environmental Pollution*, 308: 119624.

Zhang C., Huang J., Shen Z., Li J.W., Han T.F., Ai D., Yan J., Chen J., Liu K.L., Zhang H.M. (2024): Analysis of the key soil fertility factors of rice yield variation in different counties. *Transactions of the Chinese Society of Agricultural Engineering*, 40: 90–99.

Zhang J.F., Lu Z.F., Pan Y.H., Ren T., Cong R.H., Lu J.W., Li X.K. (2019): Potassium deficiency aggravates yield loss in rice by restricting the translocation of non-structural carbohydrates under *Sarocladium oryzae* infection condition. *Physiologia Plantarum*, 20: 207.

Zhang H.M., Xu M.G., Shi X.J., Li Z.Z., Huang Q.H., Wang X.J. (2010): Rice yield, potassium uptake and apparent balance under long-term fertilization in rice-based cropping systems in southern China. *Nutrient Cycling in Agroecosystems*, 88: 341–349.

Zhang H., Yu C., Hou D.P., Liu H.L., Zhang H.T., Tao R.R., Cai H., Gu J.F., Liu L.J., Zhang Z.J., Wang Z.Q., Yang J.C. (2018): Changes in mineral elements and starch quality of grains during the improvement of japonica rice cultivars. *Journal of the Science of Food and Agriculture*, 98: 122–133.

Zörb C., Senbayram M., Peiter E. (2014): Potassium in agriculture – status and perspectives. *Journal of Plant Physiology*, 171: 656–669.

Received: July 17, 2025

Accepted: December 1, 2025

Published online: December 17, 2025