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Effects of Fertilizer Levels on the Absorption, Translocation, and Distribution of Phosphorus and Potassium in Rice Cultivars with Different Nitrogen-Use Efficiencies

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Abstract

The fertilizer management and the selection of rice cultivars play a vital role in rice production to maximize yield and minimize fertilizer cost. Many researches have elucidated the combined increase of nitrogen (N) accumulation and N use efficiency (NUE) in different rice genotypes, however, the accumulation, translocation, distribution of phosphorus (P) and potassium (K), and the correlation of N, P and K absorption characteristics and their relationships with grain yield in rice cultivars with different NUE is still obscure. For this purpose, two rice cultivars differing in NUE were chosen for this study, one with high-NUE (Dexiang 4103) and the other with low-NUE (Yixiang 3724). Fertilizers were applied at three levels, including low (75 kg N·hm^{-2}, 37.5 kg P_2O_5·hm^{-2}, 75 kg K_2O·hm^{-2}), medium (150 kg N·hm^{-2}, 75 kg P_2O_5·hm^{-2}, 150 kg K_2O·hm^{-2}), high rate (225 kg N·hm^{-2}, 112.5 kg P_2O_5·hm^{-2}, 225 kg K_2O·hm^{-2}). A no-N treatment was included for each level as the control. The results showed that there were obvious interacting effects of cultivars and fertilizer levels on grain yield, as well as the absorption and translocation of P and K. Rice cultivars exhibited markedly stronger effects on total spikelets and the translocation of P and K in leaves, compared to fertilizer levels. The opposite trend was observed for grain yield, P and K accumulation at the main growth stages, and P and K translocation in stem and leaf sheaths. Compared with other treatments, the combined application of NPK fertilizers at medium level promoted nutrient accumulation, increased the nutrient harvest index, facilitated nutrient translocation in vegetative organs, and ultimately improved grain yield in both cultivars. The equilibrium relationship between N, P and K accumulation and grain yield indicated that the grain yield associated with high-NUE cultivar could reach more than 10,000 kg hm^{-2}, with N, P, and K requirements of 180.8-213.3, 47.3-54.7, and 223.5-259.1 kg hm^{-2}, respectively. Additionally, the correlation analysis revealed that accumulation and translocation of P, K during different growth stages was significantly ($P < 0.05$) related to grain yield and nutrient accumulation in different NUE cultivars. This study suggested that varieties with high-NUE also has high P and K use efficiencies, indicating that the conventional screening of varieties with high P or K use efficiencies can be included in the selection of high-NUE varieties. The increase of P and K accumulation and translocation during the period from heading to maturity was helpful to maintain a high-yield and NUE in rice production.

Keywords: fertilizer level, rice, nutrient accumulation, translocation, grain yield

1. Introduction

Nitrogen (N), phosphorus (P) and potassium (K) are three essential nutrient elements for the growth and development of rice cultivars; a deficiency or excess of N, P, and K nutrients directly affects the biochemical metabolism, physiological characteristics, coordinated absorption and utilization of nutrients as well as grain yield in rice (Ao et al., 2008; Sun et al., 2013). Improvement of the grain yield, nutrient absorption and translocation, and fertilizer-use efficiency in rice is presently a hot and challenging topic (Ao et al., 2008; Li et al., 2014; Peng et al., 2002, 2006). To address this issue, extensive research has been conducted. Many researchers have indicated that N-use efficiency (NUE) substantially varies with genotypes of rice; rice cultivars with high NUE can maintain a higher population growth rate in the late growth stages, which is favorable for improving the grain yield and NUE (Broadbent et al.,1987; Li et al., 2013). Additionally, many researches have focused on the effects of different N application on the responses of different rice cultivars (Ohnishi et al., 1999; Mae et al., 2006; Cabangon et al., 2011). It has shown that only the rational application of fertilizers can coordinate source-sink contradiction, improve grain yield and NUE in rice. Published literatures (Broadbent et al., 1987; Cabangon et al., 2011; Li et al., 2013) and our previous studies (Sun et al., 2012, 2013, 2014) further demonstrated that rice cultivars with different NUE and water-N management patterns markedly affect N utilization characteristics and grain yield. Under controlled alternate irrigation, optimal N fertilizer management can simultaneously improve grain yield and NUE in high-NUE rice cultivars. However, uncertainties remain regarding the accumulation, translocation, and distribution of P and K in rice with different NUE. Additionally, previous researches on rice cultivars with different NUE mainly involved N fertilizer management (Ohnishi et al., 1999; Li et al., 2014). Therefore, there is lack of thorough research concerning differences in grain yield and their relationship with nutrient absorption and utilization in rice cultivars with different NUE under different fertilizer application conditions. Moreover, few reports is available regarding whether the combined application of N, P, and K fertilizers can further improve the coordination of high NUE with P and K absorption and translocation in rice. In this study, two rice cultivars with different NUE were selected, and their nutrient absorption characteristics and grain yield were investigated under different fertilizer levels. Accumulation, translocation, distribution of P and K during grain filling stage were systematically compared between the two cultivars. We further elucidated the differences in nutrient absorption of rice cultivars with different NUE and assessed their relationship with nutrient absorption and utilization. This study provides reference data for the cultivation of high-NUE rice cultivars and rice breeding.

2. Materials and Methods

2.1 Experimental Site and Materials

Field experiments were conducted at the farm of Rice Research Institute, Sichuan Agricultural University, Wenjiang, Sichuan Province, China (30°70′N, 103°83′E) from April to early September in 2013 and 2014, separately. The soil was sandy loam (clay 44%, sand 37%, and silt 19%) with 1.32 g kg^{-1} total N, organic matter 20.08 g kg^{-1}, pH 6.40, and available N, P and K at 95.44, 33.32 and 88.46 mg kg^{-1}, respectively. According to research from 2010 to 2012, Dexiang 4103 with growth duration of 150-152 days (d) was selected to represent the rice cultivar of high-NUE and Yixiang 3724 with growth duration of 149-151 d was selected to represent the cultivar of low-NUE. The two cultivars are elite indica three line hybrid rice widely planted in China, which have extensive adaptability, pest-resistance and medium drought resistance compared with other hybrids. Total leaves in the main stem are 17 for the cultivars.

2.2 Experimental Design and Crop Cultivation

Field experiment was a complete randomized block design with 2 × 6 (two cultivars and six fertilizer levels) factorials. Each treatment was replicated three times. Plot area was 23.2 m^2 (5.8 × 4.0 m) and plots were separated by a ridge (40 cm in width and 30 cm in height) wrapped with plastic film to ensure no exchange of water and fertilize. In both experiments, urea, single superphosphate, and KCl were applied to reach a final N:P (P_2O_5):K (K_2O) ratio of 1:0.5:1. Three fertilizer levels were designed as the treatments of low ($N_1P_1K_1$), middle ($N_2P_2K_2$), high rate ($N_3P_3K_3$), and added no-N treatment under each level, $N_0P_1K_1$, $N_0P_2K_2$ and $N_0P_3K_3$. For $N_1P_1K_1$, 75 kg $N{\cdot}hm^{-2}$, 37.5 kg $P_2O_5{\cdot}hm^{-2}$, 75 kg $K_2O{\cdot}hm^{-2}$, for $N_2P_2K_2$, 150 kg $N{\cdot}hm^{-2}$, 75 kg $P_2O_5{\cdot}hm^{-2}$, 150 kg $K_2O{\cdot}hm^{-2}$, and for $N_3P_3K_3$, 225 kg $N{\cdot}hm^{-2}$, 112.5 kg $P_2O_5{\cdot}hm^{-2}$, 225 kg $K_2O{\cdot}hm^{-2}$ were applied, respectively. Fertilizer treatments were as follows: 30% N was applied one day before transplanting, 30% N topdressing was applied 7 days after transplanting, and 40% N application was split into two equal applications at 4th and 2nd leaves emergence from the top. Entire dose of P was applied one day before transplanting in all plots. 50% K was applied one day before transplanting, 30% K was applied as 4th leaves emergence from the top, and 20% K was applied as 2nd leaves emergence from the top. Seedlings were raised in the seedbed with sowing date of 7 April, and transplanted on May 9 for both years with the hill spacing of 33.3×16.7 cm and a single plant per hill. Except for the fertilizer application shown above, all other cultivation managements were almost identical for each plot in both years. The main growth stages of mid-tillering, elongation, heading, and maturity dates were determined at 25-26, 50-51, 81-83, and 117-118 d after transplanting, respectively.

2.3 Plant Sampling and Measurements

Five representative hills were sampled from each plot at mid-tillering, elongation, heading and maturity, desiccated at 105 °C, oven dried at 80 °C to a constant weight, weighed and then powdered to pass through a 0.5

mm sieve (Sun, 2012). Dry biomass of the stem and leaf sheaths, leaves, panicles (during grain filling stage) were measured, separately. The N concentration was determined by automatic Kjeldahl Apparatus (FOSS-8400, Sweden) according to micro- Kjeldahl method (Yoshida et al., 1976). The P concentration was determined by the vanadomolybdate yellow method (Jackson, 1958). Change in absorbance value was detected using a UV visible spectrophotometer (Shimadzu-1700, Japan). The K concentration was measured by the method of Zhao (2004) using a flame spectrophotometer (FP640, China). Aboveground biomass and yield components, including number of effective panicles per m^2, number of spikelets per panicle, percentage of filled grains, and 1000-grain weight were determined from 20 plants sampled randomly from each plot. Grain yield was determined from all plants from a 12.0 m^2 site (except border plants) in each plot. Grain moisture content was determined immediately after threshing (Riceter grain moisture meter, Japan) and grain yields are reported at the standard moisture content of 135 g H_2O kg^{-1} fresh weight.

2.4 Calculations and Statistical Analysis

Data was calculated on the basis of dry matter weights and N, P, and K measurements at the main growth stages of mid-tillering, elongation, heading, and maturity, and parameters were defined as follows:

P (K) accumulation (kg hm^{-2}) was calculated as the product of P (K) concentration and yield of above ground parts on a dry matter basis at the afore mentioned stages, and total N accumulation (kg hm^{-2}) was plant N accumulation at maturity.

P (K) harvest index (%) was calculated as P (K) accumulation of grain at maturity divided by P (K) accumulation at maturity.

P (K) translocation (kg hm^{-2}) was calculated as P (K) accumulation in leaves or clum-sheaths at heading minus P (K) remaining in leaves or clum-sheaths at maturity.

P (K) transportation efficiency (%) was calculated as P (K) accumulation in leaves and clum-sheaths from heading to maturity divided by P (K) accumulation at heading multiplied by 100.

P (K) translocation conversion rate of vegetative organ (%) was calculated as P (K) accumulation in leaves and clum-sheaths from heading to maturity divided by P (K) accumulation in panicles from heading to maturity multiplied by 100.

Analysis of variance (ANOVA) was performed using the GLM procedure in SAS (release 8.1, SAS Institute Inc., Cary, NC, USA). Levels of significance in figures are given by ns, *, ** for not significant, significant at $P < 0.05$ and $P < 0.01$, respectively. The graphs were generated with SigmaPlot 10.0 (Systat Software, Inc. CA), and the standard errors of means were calculated and presented in the graphs as error bars. Similar results were obtained for different cultivars and fertilizer levels of each year. Therefore data from all the experiments of two years were averaged.

3. Results

3.1 Grain Yield, Yield Components and N Accumulation

Cultivars and fertilizer levels had extremely significant ($P < 0.01$) effects on grain yield, yield components, and total N accumulation (Table 1). The effects of fertilizer levels on grain yield, seed setting rate, and N accumulation were more significant than those of cultivars. In addition, there were significant ($P < 0.05$) interacting effects of two factors on grain yield, number of grains per spike, total number of spikelets, and N accumulation. The grain yield of different cultivars remained higher with N application compared with the equivalent N_0 treatments. After the combined application of NPK fertilizers, the grain yield of different rice cultivars followed the same order of $N_2P_2K_2 > N_3P_3K_3 > N_1P_1K_1$. The $N_2P_2K_2$ treatment was markedly higher than other treatments and thus was regarded as the optimal NPK combined application. With respect to the response of rice cultivars to N fertilizer, high-NUE Dexiang 4103 produced a substantially higher grain yield and N accumulation than low-NUE Yixiang 3724 did in the equivalent N_0 treatments under the application of P and K fertilizers at same levels. After the combined application of various levels of N fertilizer, Dexiang 4103 displayed a larger yield and N accumulation increase than that of Yixiang 3724. The experimental data of grain yield revealed similar trends, with no significant difference between the two years (paired t-test, t = 0.913, Sig = 0.388).

In terms of yield components, the N treatment of different rice cultivars increased the effective panicles, grains per spike, and total spikelets in comparison to the N_0 treatment at each fertilizer level; the opposite trend was observed for the seed setting rate. The effect of fertilizer levels on 1000-grain weight was inconsistent. Both $N_1P_1K_1$ and $N_2P_2K_2$ markedly increased the 1000-grain weight, whereas $N_3P_3K_3$ caused decrease (not significant) in the 1000-grain weight compared with the equivalent N_0 treatments. At the three fertilizer levels, Effects of $N_3P_3K_3$ and $N_2P_2K_2$ treatments were higher than $N_1P_1K_1$ for the effective panicles, grains per spike, and total spikelets; there were no substantial difference between the former two treatments. As for the seed setting rate and 1000-grain weight, $N_1P_1K_1$ and $N_2P_2K_2$ were higher than $N_3P_3K_3$, and a significant difference occurred between the $N_1P_1K_1$ and $N_3P_3K_3$ treatments. Regarding the response of cultivars to fertilizer levels, the yield components (except for 1000-grain weight) of high-NUE Dexiang 4103 were higher than those of low-NUE Yixiang 3724. The superiority of Dexiang 4103 was particularly evident for total spikelets, exhibiting a highly significant correlation ($R^2 = 0.936^{**}$) with grain yield. Moreover, Dexiang 4103 maintained a higher seed setting rate, which was the cause for the superiority of high-NUE to low-NUE cultivars.

Table 1. Effects of fertilizer levels on grain yield and N accumulation in rice cultivars with different NUE

Cultivars	Treatments	Grain yield (kg hm^{-2})		Effective panicles (×10^4 hm^{-2})	Grains (No. per spike)	Total spikelets (×10^6 hm^{-2})	Seed setting rate (%)	1000-grain Weight (g)	Total N accumulation (kg hm^{-2})
		2013y	2014y						
Dexiang 4103	$N_0P_1K_1$	7816.8 ef	7781.1 fg	188.3 e	154.9 ef	291.7 e	85.88 ab	31.27 f	105.04 ef
	$N_1P_1K_1$	8763.6 d	8729.2 d	202.6 b	168.0 c	340.4 b	82.94 d	31.94 e	141.92 d
	$N_0P_2K_2$	8205.8 e	8074.5 ef	191.9 de	160.7 de	308.5 d	86.87 a	30.26 g	109.87 ef
	$N_2P_2K_2$	10539.1 a	10394.3 a	219.5 a	179.4 b	393.8 a	84.25 c	31.74 ef	192.11 b
	$N_0P_3K_3$	8187.2 e	8207.0 e	192.2 de	165.7 cd	318.4 cd	82.51 d	31.51 ef	112.89 e
	$N_3P_3K_3$	9740.3 b	9719.0 b	215.8 a	186.4 a	402.4 a	78.95 f	31.23 f	210.83 a
	Average	**8875.5**	**8817.5**	**201.7**	**169.2**	**342.5**	**83.57**	**31.33**	**145.44**
Yixiang 3724	$N_0P_1K_1$	7177.6 g	7276.8 h	173.7 f	144.9 g	251.6 h	84.10 c	35.02 c	101.99 f
	$N_1P_1K_1$	7943.2 ef	8037.3 ef	190.2 e	151.9 f	289.0 ef	80.94 e	35.73 b	132.81 d
	$N_0P_2K_2$	7620.8 f	7601.1 gh	178.6 f	150.2 fg	268.3 g	85.82 b	34.06 d	104.91 ef
	$N_2P_2K_2$	9312.4 c	9277.2 c	196.4 cd	162.3 cd	318.8 cd	79.97 e	36.49 a	172.01 c
	$N_0P_3K_3$	7690.7 f	7707.6 fg	179.3 f	156.1 ef	279.9 f	82.01 d	35.38 bc	109.82 ef
	$N_3P_3K_3$	8884.1 d	8828.8 d	201.6 bc	163.0 cd	328.5 c	77.50 g	35.10 c	193.16 b
	Average	**8104.8**	**8121.4**	**186.6**	**154.7**	**289.4**	**81.72**	**35.30**	**135.79**
F value	C	44.99^{**}	105.02^{**}	54.86^{**}	77.54^{**}	160.35^{**}	8.75^{**}	125.07^{**}	31.18^{**}
	F	49.78^{**}	126.51^{**}	24.73^{**}	38.19^{**}	77.46^{**}	13.45^{**}	7.41^{**}	191.71^{**}
	C×F	4.21*	3.13^{*}	1.24^{ns}	3.27^{*}	6.54^{**}	0.72^{ns}	0.44^{ns}	3.13^{*}

Note. Values within a column followed by different letters are significantly different at $P < 0.05$; * Significant at $P < 0.05$; ** Significant at $P < 0.01$; ns denote non-significance at $P > 0.05$, respectively. Date are average across 2 years. C: Cultivar; F: Fertilizer treatment; C × F: Cultivar and fertilizer treatment interaction.

3.2 P Accumulation, Translocation, and Distribution

3.2.1 P Accumulation

P accumulation was significantly ($P < 0.05$) or extremely significantly ($P < 0.01$) influenced by fertilizer levels and cultivars at all growth stages except tillering stage. And there were interaction effects between the two factors on P accumulation at different growth stages (Table 2). At each fertilizer level, different cultivars exhibited higher P accumulation but a lower P harvest index in the N treatment compared with the N_0 treatment. In the three NPK combined treatments, P accumulation gradually increased with the progression of plant growth in different cultivars, and the increased P accumulation varied to different degrees with the increase in NPK application rate. However, at the medium fertilizer level, a further increase in NPK fertilizers caused an increase in P accumulation in Yixiang 3724 relative to Dexiang 4103 from heading to maturity, whereas the P harvest index was reduced with an increasing application rate of NPK fertilizers in both cultivars. With regard to the response of cultivars to fertilizer levels, high-NUE Dexiang 4103 obtained a higher P accumulation and P harvest index than did low-NUE Yixiang 3724 during the main growth stages.

Table 2. Effects of fertilizer levels on P accumulation (kg hm^{-2}) and P harvest index in rice cultivars with different NUE

Cultivars	Treatments	Growth stages				P harvest index (%)
		Tillering	Elongation	Heading	Maturity	
Dexiang 4103	$N_0P_1K_1$	4.74 e	11.06 f	23.74 g	32.24 f	76.50 a
	$N_1P_1K_1$	6.31 c	13.94 de	35.33 d	44.83 d	72.88 cd
	$N_0P_2K_2$	5.54 d	13.03 e	28.95 f	38.96 e	74.91 b
	$N_2P_2K_2$	7.18 b	16.67 b	44.43 a	57.43 a	72.44 cd
	$N_0P_3K_3$	6.46 c	14.42 d	36.16 cd	45.87 d	71.11 ef
	$N_3P_3K_3$	7.68 a	18.03 a	46.22 a	59.45 a	67.43 g
	Average	**6.32**	**14.52**	**35.80**	**46.46**	**72.55**
Yixiang 3724	$N_0P_1K_1$	4.53 e	9.88 g	20.62 h	28.57 g	73.42 c
	$N_1P_1K_1$	6.27 c	13.04 e	32.00 e	41.20 e	71.81 de
	$N_0P_2K_2$	5.51 d	11.25 f	25.95 f	34.44 f	73.01 c
	$N_2P_2K_2$	7.27 b	15.40 c	37.47 c	49.57 c	70.29 f
	$N_0P_3K_3$	6.33 c	13.45 e	32.10 e	41.32 e	68.49 g
	$N_3P_3K_3$	7.57 ab	17.00 b	40.88 b	53.78 b	64.90 h
	Average	**6.25**	**13.34**	**31.50**	**41.48**	**70.32**
F value	C	2.25^{ns}	39.58^{**}	87.27^{**}	69.13^{**}	5.43^{*}
	F	94.31^{**}	122.05^{**}	202.19^{**}	181.36^{**}	7.34^{**}
	C×F	0.43^{ns}	3.84^{*}	9.60^{**}	5.90^{**}	4.14^{*}

Note. Values within a column followed by different letters are significantly different at $P < 0.05$; * Significant at $P < 0.05$; ** Significant at $P < 0.01$; ns denote non-significance at $P > 0.05$, respectively. Date are average across 2 years. C: Cultivar; F: Fertilizer treatment; C × F: Cultivar and fertilizer treatment interaction.

3.2.2 P Translocation and Distribution

P translocation in leaves, stem and leaf sheaths was extremely significantly (P < 0.01) influenced by fertilizer levels and cultivars from heading to maturity, the interaction effects between the two factors were significantly (P < 0.05) or extremely significantly (P < 0.01) (Table 3). At each fertilizer level, different cultivars showed a higher PT in leaves, stem and leaf sheaths and a greater P increase in the panicles during grain filling under the N treatment compared with the N_0 treatment. However, at the high fertilizer level, PTCRV was reduced after the application of a high level of N fertilizer compared with the equivalent N_0 treatment. In the three NPK combined treatments, both cultivars first increased before decreasing for PT in leaves, stem and leaf sheaths and P increase in the panicles during grain filling stage, whereas PTE and PTCRV decreased with an increase in the application rate of NPK fertilizers. For each cultivar, P accumulation in leaves, stem and leaf sheaths at maturity increased with the application rate of the P fertilizer (Figure 1). However, because of the reduced PTCRV from heading to maturity (Table 3), the distribution proportion of P in the grains decreased markedly. The combined application of NPK fertilizers at the $N_3P_3K_3$ level reduced the P accumulation in grains. At each fertilizer level, the combined application of N fertilizer substantially increased the P accumulation in vegetative organs relative to the N_0 treatment. Regarding the response of cultivars to fertilizer levels, high-NUE Dexiang 4103 was higher than low-NUE Yixiang 3724 to varying degrees at each fertilizer level in terms of PT and PTE in vegetative organs, P increase in panicles, and PTCRV during grain filling stage (Table 3), as well as P distribution in vegetative organs at maturity (Figure 1).

Table 3. Effects of fertilizer levels on P translocation in leaves, stem and leaf sheaths from heading to maturity in rice cultivars with different NUE

Cultivars	Treatments	Leaf		Stem and leaf sheaths		P increase in panicle (kg hm^{-2})	PTCRV (%)
		PT (kg hm^{-2})	PTE (%)	PT (kg hm^{-2})	PTE (%)		
Dexiang 4103	$N_0P_1K_1$	2.30 f	71.26 a	12.15 f	64.63 a	22.95 f	62.96 cd
	$N_1P_1K_1$	2.85 c	66.47 c	16.45 c	60.54 c	28.80 c	67.01 a
	$N_0P_2K_2$	2.71 d	68.78 b	14.45 de	62.85 ab	27.17 d	63.16 bcd
	$N_2P_2K_2$	3.35 a	66.25 c	19.90 a	58.49 d	36.25 a	64.14 b
	$N_0P_3K_3$	2.97 bc	67.04 bc	16.91 bc	58.92 cd	29.59 c	67.18 a
	$N_3P_3K_3$	3.05 b	61.46 e	19.05 a	52.20 f	35.33 a	62.56 d
	Average	**2.87**	**66.88**	**16.49**	**59.61**	**30.02**	**64.50**
Yixiang 3724	$N_0P_1K_1$	2.10 g	67.38 bc	10.35 g	62.63 b	20.00 g	62.25 d
	$N_1P_1K_1$	2.75 d	63.75 d	15.30 d	60.35 c	27.25 d	66.24 a
	$N_0P_2K_2$	2.51 e	63.71 d	11.75 f	58.71 cd	22.75 f	62.69 d
	$N_2P_2K_2$	2.80 cd	62.72 de	17.70 b	57.91 d	32.40 b	63.27 bcd
	$N_0P_3K_3$	2.48 ef	62.00 de	13.76 e	53.62 f	25.46 e	63.79 bc
	$N_3P_3K_3$	2.65 de	58.90 f	16.85 bc	49.74 g	32.39 b	60.19 e
	Average	**2.55**	**63.08**	**14.29**	**57.16**	**26.71**	**63.07**
F value	C	141.67^{**}	19.18^{**}	111.01^{**}	9.81^{**}	74.12^{**}	5.01^{*}
	F	77.92^{**}	7.78^{**}	124.78^{**}	21.21^{**}	113.69^{**}	6.19^{*}
	C×F	7.47^{**}	2.93^{*}	5.69^{**}	4.74^{*}	5.25^{*}	2.97^{*}

Note. Values within a column followed by different letters are significantly different at $P < 0.05$; * Significant at $P < 0.05$; ** Significant at $P < 0.01$; ns denote non-significance at $P > 0.05$, respectively. PT: P translocation; PTE: P transportation efficiency; PTCRV: P translocation conversion rate of vegetative organ. Date are average across 2 years. C: Cultivar; F: Fertilizer treatment; C×F: Cultivar and fertilizer treatment interaction.

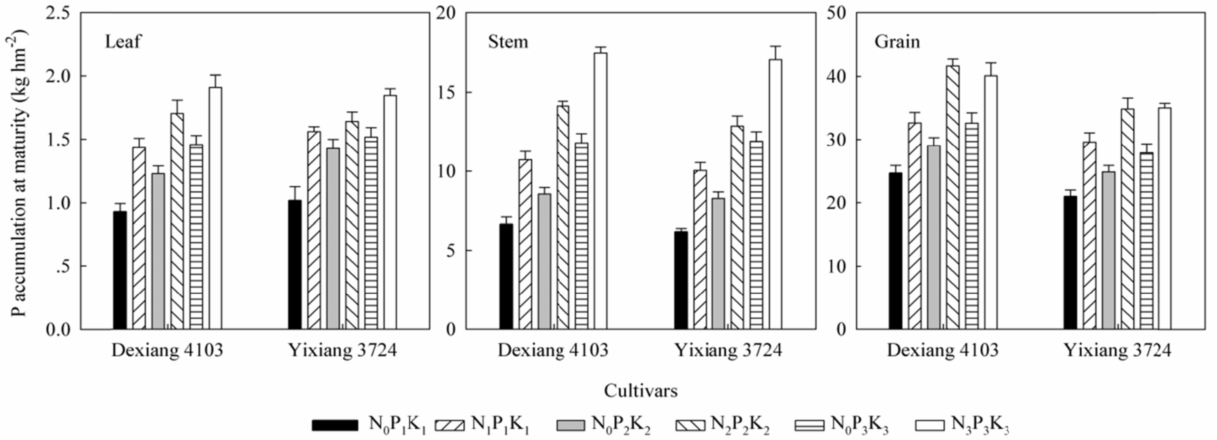

Figure 1. Proportion of P accumulation in leaves, stem and leaf sheaths, and grains at maturity stage

Note. Date are average across 2 years. Vertical bars represent ± S.E. of the mean. The S.E. was calculated across 3 replicates for each year and average for the 2 years. The experiment was conducted at Sichuan Agricultural University farm, Wenjiang, Sichuan Province, southwest China (2013-2014).

3.3 K Accumulation, Translocation, and Distribution

3.3.1 K Accumulation

The effects of fertilizer levels and cultivars on K accumulation were consistent with their effects on P accumulation at the main growth stages. However, these two factors showed extremely significantly (P < 0.01) interaction effects on K accumulation from elongation to heading, which occurred earlier than the effects on P accumulation (Table 4). At each fertilizer level, the K accumulation increased during the main growth stages to varying degrees with an increase in the application rate of the K fertilizer but was less affected by the combined application of N and P. At the same fertilizer level, the N treatment of different cultivars increased the K accumulation during the main growth stages to varying degrees compared with the equivalent N_0 treatment; the opposite trend was observed for the K harvest index. As for the response of cultivars to fertilizer levels, the K accumulation and K harvest index were higher for high-NUE Dexiang 4103 relative to low-NUE Yixiang 3724; these differences were highly significant at each fertilizer level, except that no difference was found at tillering.

Table 4. Effects of fertilizer levels on K accumulation (kg hm^{-2}) and K harvest index in rice cultivars with different NUE

Cultivars	Treatments	Growth stages				K harvest index (%)
		Tillering	Elongation	Heading	Maturity	
Dexiang 4103	$N_0P_1K_1$	16.94 f	67.20 h	127.03 i	138.03 h	23.23 a
	$N_1P_1K_1$	18.97 ef	82.60 fg	156.91 g	171.45 fg	21.24 bc
	$N_0P_2K_2$	23.10 d	88.38 ef	167.27 f	182.03 f	21.06 c
	$N_2P_2K_2$	25.21 bc	103.98 bc	199.51 d	218.43 cd	20.33 cd
	$N_0P_3K_3$	26.80 b	105.64 bc	211.81 c	229.40 c	19.73 d
	$N_3P_3K_3$	31.40 a	122.10 a	251.88 a	273.15 a	17.56 f
	Average	**23.74**	**94.98**	**185.73**	**202.08**	**20.53**
Yixiang 3724	$N_0P_1K_1$	17.28 f	61.99 h	119.64 i	131.59 h	22.10 b
	$N_1P_1K_1$	19.38 e	76.31 g	146.62 h	163.36 g	21.01 c
	$N_0P_2K_2$	23.53 cd	77.19 g	153.30 gh	166.18 g	20.95 c
	$N_2P_2K_2$	25.78 b	93.67 de	185.54 e	201.45 e	18.72 e
	$N_0P_3K_3$	26.73 b	98.37 cd	193.44 de	207.45 de	18.54 ef
	$N_3P_3K_3$	30.88 a	109.01 b	232.41 b	246.82 b	15.65 g
	Average	**23.93**	**86.09**	**171.82**	**186.14**	**19.49**
F value	C	0.63^{ns}	20.79^{**}	52.33^{**}	23.22^{**}	26.33^{**}
	F	97.79^{**}	127.77^{**}	148.11^{**}	119.56^{**}	72.33^{**}
	C×F	0.48^{ns}	9.05^{**}	12.00^{**}	3.81^{*}	10.17^{**}

Note. Values within a column followed by different letters are significantly different at $P < 0.05$; * Significant at $P < 0.05$; ** Significant at $P < 0.01$; ns denote non-significance at $P > 0.05$, respectively. Date are average across 2 years. C: Cultivar; F: Fertilizer treatment; C × F: Cultivar and fertilizer treatment interaction.

3.3.2 K Translocation and Distribution

K translocation in leaves, stem and leaf sheaths was extremely significantly (P < 0.01) influenced by fertilizer levels and cultivars from heading to maturity except K transportation efficiency in stem and leaf sheaths. There were interaction effects between the cultivars and fertilizer levels for the KT in the stem and leaf sheaths, K increase in the panicles, and the KTCRV from heading to maturity except for the KT in the leaves (Table 5). At each fertilizer level, the N treatment of different cultivars was higher than the equivalent N_0 treatment in terms of KT in the leaves, stem and leaf sheaths and K increase in the panicles. However, the combined application of N caused a great reduction in KTCRV compared with the equivalent N_0 treatment. In the three NPK combined treatments, different cultivars showed increases in both the KT in leaves, stem and leaf sheaths and the K increase in panicles, whereas KET and KTCRV decreased to varying degrees, with an increase in the application rate of NPK fertilizers. With respect to the treatments with fertilizer levels and cultivars, the distribution of K in different organs followed the order of stem and leaf sheaths > panicles > leaves (Figure 2), which was different from that of N and K at maturity. For the same cultivar, the K accumulation in vegetative organs increased, whereas the distribution proportion of K in the grains markedly decreased, with an increase in the application rate of the K fertilizer. Regarding the response of cultivars to fertilizer levels, high-NUE Dexiang 4103 surpassed low-NUE Yixiang 3724 to varying degrees in terms of KT and KTE in the vegetative organs, K increase in the panicles, and KTCRV at grain filling stage (Table 5), as well as the distribution of K in vegetative organs at maturity (Figure 2). However, Dexiang 4103 showed a higher KT in leaves than in stem and leaf sheaths, whereas the opposite result was obtained from Yixiang 3724.

Table 5. Effects of fertilizer levels on K translocation in leaves and stem and leaf sheaths from heading to maturity in rice cultivars with different NUE

Cultivars	Treatments	Leaf		Stem and leaf sheath		K increase in panicle (kg hm^{-2})	KTCRV (%)
		KT (kg hm^{-2})	KTE (%)	KT (kg hm^{-2})	KTE (%)		
Dexiang 4103	$N_0P_1K_1$	8.90 e	40.32 a	7.87 h	7.82 bc	27.77 e	60.39 bc
	$N_1P_1K_1$	9.58 d	36.40 cd	9.23 f	7.24 de	33.36 d	56.40 ef
	$N_0P_2K_2$	11.98 b	40.21 a	11.56 d	8.41 a	38.30 c	61.47 a
	$N_2P_2K_2$	12.79 a	37.25 bc	12.65 bc	7.66 c	44.36 b	57.36 d
	$N_0P_3K_3$	13.67 a	37.50 b	13.54 a	7.74 c	44.80 b	60.73 b
	$N_3P_3K_3$	13.29 a	32.36 f	13.03 b	6.19 f	47.59 a	55.30 g
	Average	**11.70**	**37.34**	**11.31**	**7.51**	**39.36**	**58.61**
Yixiang 3724	$N_0P_1K_1$	7.14 f	36.02 d	8.10 h	8.27 a	27.19 e	56.03 f
	$N_1P_1K_1$	7.60 f	32.47 f	8.81 g	7.22 de	33.15 d	49.50 h
	$N_0P_2K_2$	9.48 d	37.09 bc	10.32 e	8.22 ab	32.68 d	60.60 bc
	$N_2P_2K_2$	9.77 d	32.80 f	10.71 e	6.93 e	36.39 c	56.28 ef
	$N_0P_3K_3$	10.90 c	34.53 e	12.17 c	7.58 cd	37.08 c	60.25 c
	$N_3P_3K_3$	11.26 c	30.70 g	12.64 bc	6.47 f	38.31 c	56.49 e
	Average	**9.36**	**33.94**	**10.46**	**7.45**	**34.13**	**56.52**
F value	C	267.79^{**}	51.03^{**}	33.67^{**}	0.38	110.95^{**}	2.99^{*}
	F	109.18^{**}	21.14^{**}	124.09^{**}	32.65^{**}	91.33^{**}	10.70^{**}
	C×F	2.01^{ns}	0.81^{ns}	4.87^{**}	2.82^{*}	10.42^{**}	6.47^{**}

Note. Values within a column followed by different letters are significantly different at $P < 0.05$; * Significant at $P < 0.05$; ** Significant at $P < 0.01$; ns denote non-significance at $P > 0.05$, respectively. KT: K translocation; KTE: K transportation efficiency; KTCRV: K translocation conversion rate of vegetative organ. Date are average across 2 years. C: Cultivar; F: Fertilizer treatment; C × F: Cultivar and fertilizer treatment interaction.

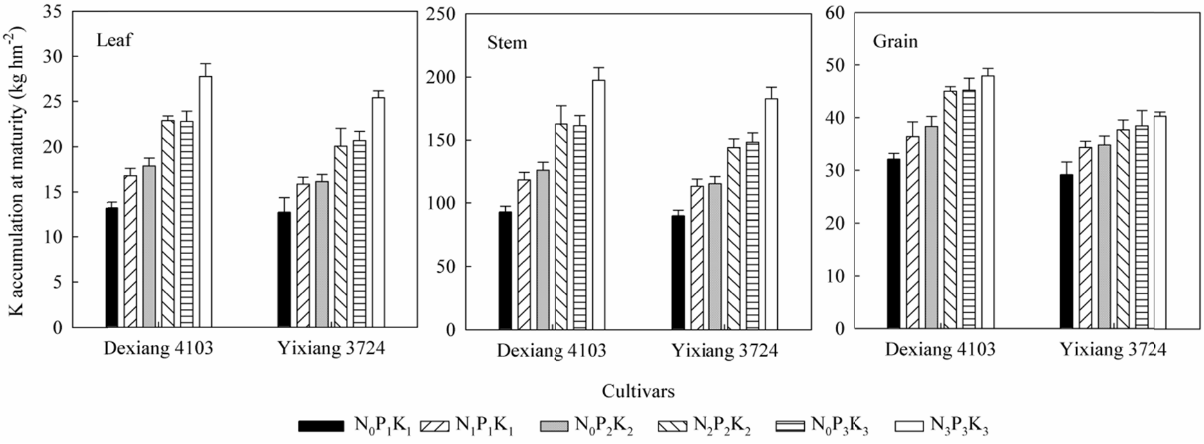

Figure 2. Proportion of K accumulation in leaves, stem and leaf sheaths, and grains at maturity stage

Note. Date are average across 2 years. Vertical bars represent ± S.E. of the mean. The S.E. was calculated across 3 replicates for each year and average for the 2 years. The experiment was conducted at Sichuan Agricultural University farm, Wenjiang, Sichuan Province, southwest China (2013-2014).

3.4 Relationship between Yield Formation and Nutrient Requirements in Rice Cultivars with Different NUE

There were significant ($P < 0.05$) positive correlations between nutrient accumulation in every growth period and grain yield, and N, P, and K accumulate in different NUE cultivars (Table 6). However, high-NUE Dexiang 4103 was higher than low-NUE Yixiang 3724 in terms of correlation coefficient between every index. As for the relationship between grain yield in cultivars and nutrient requirements at various fertilizer levels was fitted using an open downward quadratic function (Figure 3). This illustrates that the combined application level of NPK fertilizers must be reasonable and that there is an appropriate value between grain yield and N, P, and K requirements of shoots in rice. The equilibrium relationship between nutrients and grain yield was obtained according to the fitting functions presented in Figure 3. The results showed that the grain yield of Dexiang 4103 could reach more than 10,000 kg hm^{-2} under the experimental conditions, and the N, P, and K requirements of the plants were 180.8-213.3, 47.3-54.7, and 223.5-259.1 kg hm^{-2}, respectively. The grain yield of Yixiang 3724 could reach more than 8,800 kg hm^{-2} under the experimental conditions, and the N, P, and K requirements of the palnts were 170.0-211.6, 44.3-49.5, and 197.8-292.0 kg hm^{-2}, respectively.

Table 6. Coefficients of correlation between P, K accumulation and translocation during different growth stages and grain yield and nutrient accumulation of different NUE cultivars (number of samples is 36)

Indexes		Growth stages	Dexaing 4103				Yixiang 3724			
			Grain yield	TNA	TPA	TKA	Grain yield	TNA	TPA	TKA
P accumulation		TS-ES	0.885^{**}	0.925^{**}	0.974^{**}	0.907^{**}	0.711^{**}	0.840^{**}	0.941^{**}	0.844^{**}
		ES-HS	0.926^{**}	0.932^{**}	0.991^{**}	0.852^{**}	0.738^{**}	0.832^{**}	0.892^{**}	0.792^{**}
		HS-MS	0.893^{**}	0.901^{**}	0.936^{**}	0.809^{**}	0.650^{**}	0.792^{**}	0.903^{**}	0.800^{**}
K accumulation		TS-ES	0.715^{**}	0.753^{**}	0.912^{**}	0.988^{**}	0.448^{ns}	0.666^{**}	0.790^{**}	0.936^{**}
		ES-HS	0.596^{*}	0.702^{**}	0.843^{**}	0.995^{**}	0.416^{ns}	0.469^{ns}	0.552^{*}	0.272^{ns}
		HS-MS	0.781^{**}	0.959^{**}	0.950^{**}	0.975^{**}	0.729^{**}	0.815^{**}	0.846^{**}	0.695^{**}
P translocation	leaves	HS-MS	0.880^{**}	0.726^{**}	0.895^{**}	0.745^{**}	0.825^{**}	0.649^{**}	0.767^{**}	0.568^{*}
	stem and leaf sheaths	HS-MS	0.910^{**}	0.848^{**}	0.972^{**}	0.825^{**}	0.927^{**}	0.887^{**}	0.950^{**}	0.755^{**}
K translocation	leaves	HS-MS	0.514^{*}	0.449^{*}	0.698^{**}	0.879^{**}	0.525^{*}	0.405^{ns}	0.605^{*}	0.812^{**}
	stem and leaf sheaths	HS-MS	0.533^{*}	0.469^{*}	0.727^{**}	0.886^{**}	0.527^{*}	0.428^{*}	0.631^{*}	0.834^{**}

Note. TS-ES: the duration from tillering to elongation stage; ES-HS: the duration from elongation to heading stage; HS-MS: the duration from heading to maturity stage. TNA: Total N accumulation; TPA: Total P accumulation; TKA: Total K accumulation; * Significant at $P < 0.05$; ** Significant at $P < 0.01$; ns denote non-significance at $P > 0.05$, respectively.

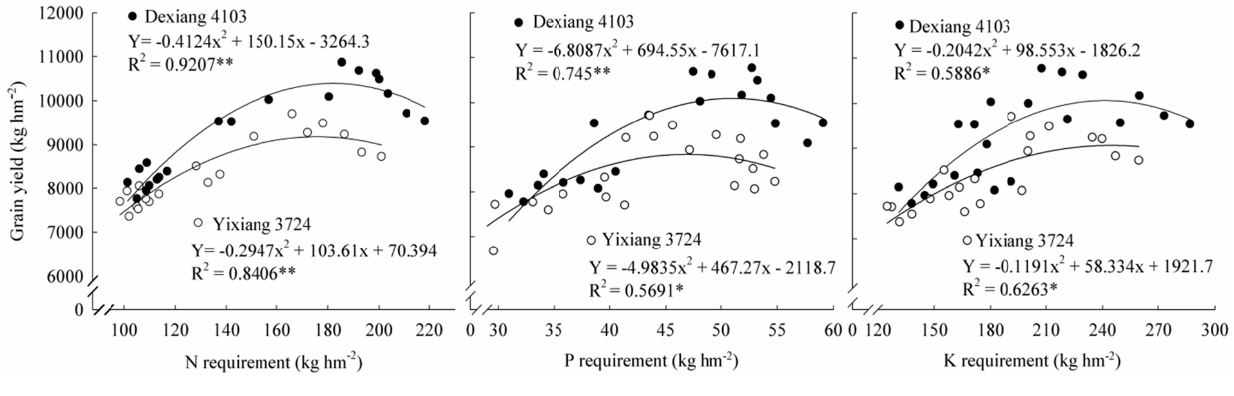

Figure 3. Relationship between grain yield and N, P, K accumulation requirement of different NUE cultivars

4. Discussion

Numerous studies have reported on the theory and technology regarding how to reduce the application of fertilizers, improve the efficient absorption and utilization of N, P, and K nutrients, and thereby achieve a high and stable yield in rice (Sun et al., 2011; Jiang et al., 2004; Pan et al., 2010; Pampolino et al., 2007; Wang et al., 2011). Meanwhile, extensive research has shown that appropriate measures can facilitate great increases in the accumulation of N, P, and K at the maturity and grain yield of rice while substantially reducing the application rate of fertilizers. Examples include N fertilizer application (Pan et al., 2010; Sun et al., 2011), site-specific nitrogen management (Peng et al., 1996; Pampolino et al., 2007), combined application of NPK fertilizers (Wang et al., 2011), combined application of chemical and organic fertilizers (Xu et al., 2008), water-N interaction (Sun et al., 2011, 2012, 2014), and straw retention (Xu et al., 2008). However, the degree of N, P, and K absorption and utilization by rice varies with different management measures. Ao et al. (2008) reported that excess absorption exists in rice, leading to relatively low nutrient-use efficiency; the N, P, and K requirements of rice plants per unit area do not grow with increasing grain yield. Wang et al. (2011) reported that the greatest interaction effects of rice for N, P, and K absorption are the N-K, N-P, and P-K interactions. They proposed that fertilizers have multifaceted effects on rice plant growth; the application rate and ratio of fertilizers should therefore be determined based on a full consideration of grain yield, quality, and fertilizer-use efficiency. Moreover, Li et al. (2014) indicated that the coordination of efficient absorption of N, P, and K nutrients remains to be improved under high yield conditions. The results in this study indicate that the combined application of N, P, and K fertilizers at 150 kg N·hm^{-2}, 75 kg P_2O_5·hm^{-2}, 150 kg K_2O·hm^{-2} can benefit nutrient accumulation at the main growth stages and facilitate nutrient translocation during grain filling stage. When the lower limits of N, P, and K requirements for plant of high-NUE cultivars are satisfied (180.8-213.3, 47.3-54.7, and 223.5-259.1 kg hm^{-2}, respectively), high grain yield and simultaneous improvements in the nutrient harvest index and use efficiency can be achieved (Tables 1, 2, and 4). Moreover, this strategy can give play to the superiority of high-NUE cultivar (Tables 1-5) and the interaction effects of fertilizer management. The present results further confirm and supplement previous findings, including our prior research (Ao et al., 2008; Sun et al., 2011; Jiang et al., 2004; Pan et al., 2010; Pampolino et al., 2007; Wang et al., 2011).

The inherent superiority of rice cultivars provides another pathway for high yield and high nutrient-use efficiency. Researchers have performed comparative studies on different genotypes of rice (Broadbent et al., 1987), super rice (Ao et al., 2008), high-NUE rice (Li et al., 2012, 2013, 2014), and have analyzed the differences between cultivars. In particular, scientists have investigated material accumulation and translocation (Li et al., 2013), root growth (Li et al., 2012), stem characteristics (Li et al., 2012), and nutrient absorption and utilization (Cabangon et al., 2011) concerning the superiority of cultivars with high NUE. However, the design of existing studies on rice cultivars has mainly involved the management of N levels in fertilizers (Peng et al., 1996; Pampolino et al., 2007; Li et al., 2012, 2013, 2014). Few reports are available on the difference in the response of rice cultivars to varying levels of NPK combined application or the mechanisms of nutrient translocation. The present study showed that the medium-fertilizer treatment primarily improved nutrient accumulation in rice plants during the main growth stages and facilitated nutrient translocation in vegetative organs at grain filling stage, thereby significantly increasing grain yield and NUE in the high-NUE cultivar. Additionally, rice cultivars showed markedly higher regulation effects than did fertilizer levels in terms of total spikelets, and nutrient translocation of P and K in leaves at grain filling stage (Tables 1, 3, and 5). Moreover, to obtain the equivalent 1000 kg of grain productivity under the experimental conditions, Yixiang 3724 would increase the requirements of N, P, and K nutrients by 1.2-2.7 kg, 0.16-0.30 kg, and 0.10-7.30 kg, respectively, compared with Dexiang 4103. Therefore, we should further strengthen the screening of high-NUE cultivars, develop indicators for identifying these cultivars, and integrate high-yielding, fertilizer-saving, and efficient cultivation technology systems. Furthermore, the current results showed that high-NUE Dexiang 4103 produced higher values of average total spikelets, seed setting rate, nutrient accumulation, and harvest index during the main growth stages than did low-NUE Yixiang 3724 under different fertilizer levels. Dexiang 4103 was especially favorable for P and K translocation and redistribution from leaves, stem and leaf sheaths into grains at grain filling stage and thus improved the grain production efficiency and fertilizer-use efficiency. This is the main reason that the high-NUE cultivar achieved high nutrient-use efficiency relative to the low-NUE cultivar.

With respect to the coordination of high yield with P and K nutrient absorption, Chen et al. (2004) have suggested that an N fertilizer can facilitate P and K absorption by rice plants. Hu et al. (2003) have shown that increasing the application rate of a K fertilizer can coordinately improve the N and P fertilizer-use efficiency in hybrid rice. Additionally, Ao et al. (2008) have shown that at various fertilizer levels, there are no significant differences in the N, P, and K contents of rice plants at either heading or maturity; the difference in nutrient absorption mainly originates from different levels of dry matter production per unit area. Li et al. (2014) have reported that the P and K grain production efficiency is reduced with an increasing NUE of high-yield rice cultivars; thus, the coordinated absorption and utilization of P and K remain to be improved. In the present study, we further clarified, at various fertilizer levels, that after an appropriate combined application of NPK fertilizers, rice cultivars show significant coordination in P and K accumulation at the main growth stages (Tables 2 and 4) and nutrient translocation in vegetative organs during grain filling (Tables 3 and 5), which is favorable for high yield. The $N_3P_3K_3$ treatment caused a higher retention of nutrients in leaves, stem and leaf sheaths during grain filling, with markedly lower nutrient translocation conversion rates; the coordinated N, P, and K absorption, translocation, and utilization capacities were reduced, leading to substantially reduced grain yield and fertilizer-use efficiency. The present study elucidated the characteristics of nutrient absorption by a high NUE rice cultivar under high-yielding conditions. On this basis, the application rate and ratio of NPK fertilizers in practice should be determined upon a full consideration of the rice cultivar, nutrient absorption and utilization, and yield potential. It is important to pay attention to the supply of nutrients (particularly N and K) during the late growth stages and improve the translocation of nutrients to grains at grain filling, to realize the coordination of high yield and NUE with P and K absorption in rice.

5. Conclusions

This study demonstrated that rice cultivars with different NUE when grown with different fertilizer levels significantly ($P < 0.05$) affected grain yield, absorption, translocation and distribution of P and K during the main growth stages. Under the experimental conditions, the combined application of NPK fertilizers at 150 kg $N\cdot hm^{-2}$, 75 kg $P_2O_5\cdot hm^{-2}$, 150 kg $K_2O\cdot hm^{-2}$, respectively, was favorable for nutrient accumulation at the main growth stages and translocation of P, K during grain filling in cultivars with different NUE. When the N, P and K requirements of plant are satisfied at 180.8-213.3, 47.3-54.7, and 223.5-259.1 $kg\cdot hm^{-2}$, respectively, the grain production efficiency and NUE of the high-NUE cultivar could be markedly improved, achieving simultaneous increases in grain yield and fertilizer-use efficiency. The high-NUE cultivar obtained significantly higher values of total spikelets, P and K accumulation than did the low-NUE cultivar. The rice varieties with high-NUE also has high P and K use efficiencies, indicating that the conventional screening of varieties with high P or K use efficiencies can be included in the selection of high-NUE varieties. The increase of P and K accumulation and translocation during the period from heading to maturity can be helpful to the high-yield and NUE in rice.

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