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Genotypic Differences in Potassium Nutrition in Lowland Rice Hybrids

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Abstract: China imports most of its potassium (K) requirements for crop production. The objective of this study was to evaluate *indica* rice hybrids for K-use efficiency. Twenty-eight *indica* rice hybrids were evaluated in nutrient solution. The K influx rate was greatest in genotype Weiyou 64 (684.9 nmol K^+ $plant^{-1}$ h^{-1}) and least in genotype Xie A/909 (457.2 nmol K^+ $plant^{-1}$ h^{-1}). The K-use efficiency was greatest in genotype ShanA/909 [81.8 mg dry matter (DM) produced per mg K taken up] and least in genotype Shanyou 64 (55.9 mg mg^{-1}). The maximum biomass was produced by genotype Shan A/4663-5 (100.8 mg DM per plant), and the least biomass was produced by genotype Xie A/4663-4 (59.1 mg DM per plant). These results suggest that K shortage for rice production can be alleviated by using K-efficient rice genotypes.

Keywords: *Oryza sativa* L., potassium influx rate, potassium-use efficiency, rice hybrids, root and shoot biomass

INTRODUCTION

Rice (*Oryza sativa* L.) is a major food crop, being a staple in the diets of more than 60% of the world population. Hybrid rice has a yield

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advantage of 15–20% over inbred cultivars (Tu et al. 2000; Yuan 2004). It is widely grown in China and elsewhere. Currently hybrid rice is grown on 15 × 10^6 ha, or 50% of China's total rice area. It has played a vital role in enabling China to become self-sufficient in food production (Yuan 2004).

Potassium (K) is a vitally important macronutrient in plant growth and in sustainable rice production (Fageria and Baligar 1997; Wu, Ni, and Luo 1998; Yang et al. 2003). The potassium requirement of rice is greater than nitrogen (N) and phosphorus (P) requirements. De Datta and Mikkelsen (1985) reported that a single lowland rice cultivar producing 9.8 Mg of grain ha^{-1} in about 115 days took up 218 kg N, 31 kg P, and 258 kg K. Hybrid rice in 2001 yielded as much as 18.0 Mg ha^{-1} (Yuan 2004). Because of heterosis in the yield, both biomass and grain, hybrid rice requires more nutrients than conventional rice. Hybrid rice grain contains 18.1% more K than conventional *indica* rice grain (Liu and Liu 1997).

Compared with the conventional rice, hybrid rice requires much more K. However, 70% of China's lowland rice soils are K deficient (Lu 1998). China's recoverable potash reserve is only 1/173 of the world level (Sheldrick 1985), and China produces little K fertilizer, yet China accounts for one third of the world's rice production (FAO 2004; Childs 2005). With increased consumption of both N and P fertilizers and intensified cropping in China, K deficiency has become the primary nutritional limiting factor in further increasing yields of rice (Dobermann and Fairhurst 2000; Yang et al. 2003). Under these situations, the Chinese K requirement for crop production is met by importation, which creates consequently a greater cost of crop production for farmers.

On the other hand, the fertilizer-use efficiency of currently grown rice hybrids and cultivars is quite low (Liu and Liu 1996, 2000) because of their genetic constitution and physiological characteristics. Improvement in nutrient-use efficiency by crops has been largely neglected by most plant breeders, who, like growers, simply supply ample fertilizer to assure high grain yields (Sauerbeck and Helal 1990). Because potash fertilizer is a nonrenewable mineral resource, inefficient use of K fertilizer by rice and other crops must be overcome, so that future generations will not suffer a potash crisis in food production. Because it is neither rational nor practical for China and other developing countries to depend heavily on imported potash fertilizers, a concerted effort must be made to increase the K-use efficiency of rice sufficiently to assure sustainable grain production.

Substantial genetic variability in K-use efficiency has been found in bean (*Phaseolus vulgaris* L.) (Gerloff and Gabelman 1983), tomato (*Lycopersicon esculentum* Mill.) (Gerloff and Gabelman 1983), red clover (*Trifolium pratense* L.), sorghum (*Sorghum bicolor* L. Moench), alfalfa

(*Medicago sativa* L.) (Baligar, Fageria, and He 2001), grape (*Vitis vinifera* L.) (Pinton, Varanini, and Maggioni 1990), rice (Liu and Liu 1996; Wu, Ni, and Luo 1998; Fageria, Slaton, and Baligar 2003; Yang et al. 2003), and maize (*Zea mays* L.) (Baligar, Fageria, and He 2001). Our previous studies revealed that genotypes of *indica* rice that have great biomass production in the seedling stage have high yields in grain. For example, the K-efficient genotype Xiangzaonuo 1 had 99.8 mg plant^{-1} biomass but the K-inefficient genotype P3299F4-78-3-1B-1 had only 69.7 under low-K stress at the five-leaf stage. The former was 43.2% greater than the latter. The grain yield for Xiangzaonuo 1 was 188.7% greater than the grain yield for P3299F4-78-3-1B-1 under a low-K application rate at 60 kg K_2O ha^{-1}; this was because P3299F4-78-3-1B-1 was deficient in K nutrition (Liu and Liu 1996, 2000, 2002). These results show that early evaluation for the K-use efficiency of rice is closely associated with grain yields. Also, the problem of K shortage in China can be alleviated by taking advantage of relevant genetic diversity of rice accessions in the gene banks in the Institute of Crop Sciences, Beijing, and in the China National Rice Research Institute, Hangzhou.

However, little is known about genetic variability in K nutrition in rice hybrids. The development of heterotic rice hybrids involves the use of elite genotypes to create cytoplasmic male sterile lines, maintainer lines, as well as effective fertility restorer lines (Virami, Prasad, and Kumar 1993). The probability of success is enhanced if outstanding parents with the desired gene alleles are selected, which produce hybrids with heterosis in the traits being targeted when they are crossed. The production of superior heterotic hybrid progeny when a parent line is crossed to a series of other parent lines is referred to as the parent line's combining ability (Kempthorne 1957; Singh and Kumar 2004). Thus, the development of rice hybrids adapted for strong performance in K-deficient soils requires detailed knowledge of the traits involved and the identification of outstanding genotypes with both these traits and with favorable combining ability.

It is imperative that elite rice genotypes with superior K metabolism and nutrition be identified and exploited in producing rice hybrids for widespread use. Because of soil heterogeneity (Whitaker, Gerloff, and Gabelman 1976), the identification of genotypes with specific nutrient traits is time-consuming and may be difficult under field conditions; therefore, hydroponic techniques have been used widely for measuring the performance of various genotypes with respect to specific nutrients (Wu, Ni, and Luo 1998). Our previous methodology study showed that the largest coefficient of variance (CV) in K influx rates was gained among different hybrid rice genotypes when the measuring solution had 0.4 mM K. Similarly, the CV of K-use efficiency among the genotypes was much larger at the five-leaf stage than at the three-leaf stage (Liu and Liu 1996).

The objectives of this research were (i) to identify differences in the K influx of hybrid rice genotypes in the seedling stage; (ii) to quantify K-influx rates, K-use efficiencies, biomass production, and K contents of roots and shoots of hybrid rice genotypes; and (iii) to analyze the relationships of K influx rates and use efficiencies of various hybrid genotypes.

MATERIALS AND METHODS

Plant Materials and Growth Condition

Twenty-eight hybrid combinations of *Oryza sativa* L. ssp. *indica* rice hybrids were obtained from the Germplasm Department of China National Rice Research Institute, Hangzhou, and Hunan Academy of Agricultural Sciences, Changsha, China.

The seeds of the hybrid rice were surface-sterilized in 0.5% (v/v) sodium hypochlorite (NaClO) for 15 min and then rinsed four times in deionized (DI) water. The sterilized seeds were soaked in DI water at 32 °C for 24 h and germinated at 37 °C in the dark. Twelve germinated seeds were then placed on each framed nylon net. The frame for each of nylon nets was cut from a Styrofoam plastic sheet, and the net was 4.5 cm in diameter. The nets with germinated seeds were floated on the surface of 10 L of 0.2 mol m^{-3} calcium sulfate ($CaSO_4$) solution in a plastic container in a greenhouse under natural light, where the seedlings were allowed to grow to the three-leaf stage. Before determination, 2 of the 12 seedlings were thinned and the remaining uniform 10 seedlings were kept in each of the nets for determinations. During the growth of the seedlings, 3 mL 3% hydrogen peroxide (H_2O_2) was added to the 10-L solution every 3 days instead of aeration. The nutrient solution was changed into 25% strength Kimura B solution when the plants were at the three-leaf stage. The full-strength nutrient solution contained these macronutrients (mol m^{-3}): 0.36 ammonium sulfate [$(NH_4)_2SO_4$], 0.54 magnesium sulfate ($MgSO_4 \cdot 7H_2O$), 0.18 potassium nitrate (KNO_3), 0.36 calcium nitrate [$Ca(NO_3)_2 \cdot 4H_2O$], and 0.18 potassium dihydrogen phosphate (KH_2PO_4); and these micronutrients (mmol m^{-3}): 40 ethylenediaminetetraacetic acid chelated iron ($NaEDTAFe \cdot 3H_2O$), 13.4 manganese chloride ($MnCl_2 \cdot 4H_2O$), 18.8 boric acid (H_3BO_3), 0.03 ammonium molybdate [$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$], 0.30 zinc sulfate ($ZnSO_4 \cdot 7H_2O$), and 0.32 copper sulfate ($CuSO_4 \cdot 5H_2O$) (Ma et al. 2001). The pH of this solution was 5.0 ± 0.1. The culture solution was changed weekly. The experiments were terminated at the five-leaf stage as reported previously (Liu and Liu 1996, 2002).

Potassium Influx Rates, Biomass, and K-Use Efficiencies

The K influx rate of each of the 28 hybrid genotypes was determined on the basis of the ion-deletion principle. Thus seedlings at the three-leaf stage were floated on 100 mL of a solution containing 0.4 (mol m^{-3}) K^+ as potassium sulfate (K_2SO_4), 0.2 Ca^{2+} (mol m^{-3}) as calcium sulfate ($CaSO_4$), and 0.3 (mmol m^{-3}) hydrogen peroxide (H_2O_2) in 4 h. These seedlings were maintained at 25 ± 2 °C and exposed to 852.3 ± 43.5 μmol photon m^{-2} s^{-1} of photosynthetically active radiance (PAR).

All of the seedlings were harvested at the five-leaf stage, dried in an oven at 80 °C for 48 h, and then ground into 70-mesh powder. The sample powders were extracted in 1N hydrochloric acid (HCl) for 24 h (Liu and Liu 1996). The K concentrations in both roots and shoots were determined by flame photometry (model FP-640, Shanghai, China). The reciprocal of the K concentration of each root and shoot was calculated as its K-use efficiency. The reciprocal of the K concentration in a whole plant (roots plus shoot) was considered to be the K-use efficiency of the entire plant (Liu and Liu 1996, 2000).

Biomass dry matter (DM) of each tested hybrid genotype was determined at its five-leaf stage. All of the determinations in this study had four repetitions. Data were analyzed using the Statistical Analysis System (SAS) package version 9.1 (SAS Institute 2007).

RESULTS AND DISCUSSION

Potassium Influx Rate among Hybrids

ANOVA analyses of K influx rates of 28 hybrid genotypes showed highly significant ($P < 0.0001$) differences (Table 1). Overall, K influx rate of the hybrid genotypes was 566.2 nmol $plant^{-1}$ h^{-1} with a coefficient of

Table 1. ANOVA p values and critical range values of Duncan's multiple range test for pairwise comparison at $p = 0.05$

Factor	Plant part	$P > F$	Duncan's critical range
K influx rate (nmol $plant^{-1}h^{-1}$)		<0.0001	9.4
K use efficiency (mg mg^{-1})	Root	<0.0001	4.4
	Shoot	<0.0001	1.0
	Root + Shoot	<0.0001	3.2
Biomass (mg $plant^{-1}$)	Root	<0.0001	1.9
	Shoot	<0.0001	2.0
	Root + Shoot	<0.0001	2.5
Root/shoot ratio		<0.0001	0.05
K content (μg $plant^{-1}$)		<0.0001	44.5

variation of 11.8%. Thirteen hybrid genotypes (46% of the total) had greater than average K influx rates. The hybrid Weiyou 64 had the greatest K influx rate of 684.9 ± 4.1 nmol plant^{-1} h^{-1}, and Xie A/909 had the least infux rate of 457.2 ± 13.4 nmol plant^{-1} h^{-1} (Table 2).

Potassium Content among Hybrids

At the five-leaf stage, the K content per single hybrid rice seedling varied from 0.91 to 1.31 mg with an average value of 1.10 mg plant^{-1} (Figure 1). Our previous study showed that a single hybrid rice seed had 0.085 ± 0.006 mg K on average (Liu and Liu 1997). This indicated that 92.3% of the K content in hybrid rice seedlings was taken up from the culture solution. Twelve genotypes contained less K than the average of the 28 hybrids. The K content per seedling was greatest in hybrid Zhenchang A/4663-4 and least in hybrid Xie A/53. The K content of Zhenchang A/4663-4 was 43% more than that of Xie A/53. Genotypic differences in K content of hybrid seedlings were statistically significant (Table 1, Figure 1). Potassium was distributed predominantly in the shoot (Figure 1). Potassium distribution in root varied from 5.9% (hybrid Shanchang A/53) to 11.6% (hybrid Shan A/909), a two-fold variation (Figure 1).

Biomass among Hybrids

Among 28 hybrids, greatest root weight was produced by hybrids Shan A/46635 and Shan A/9010 (29.9 mg plant^{-1}), and least root weight was produced by genotype Xie A/4663-4 (15.81 mg plant^{-1}) (Table 2). Similarly, greatest shoot biomass was produced by hybrid Zhenchang A/4663-4 (71.1 mg plant^{-1}) and Shan A/4663-5 (70.9 mg plant^{-1}). The difference in greatest and least root and shoot biomass production was 89 and 65%, respectively. The greatest root-to-shoot ratio was found in Shan A/909 and Zhaichang A/53 and for both hybrids was 0.44 ± 0.01. Similarly, the least root-to-shoot ratio was produced by hybrid Shan A/3263 with a value of 0.32 ± 0.09. The difference between greatest and least root-to-shoot ratios was 37.5%.

Among the eight indices determined for K-use efficiency in this study, root biomass had the largest (20%) coefficient of variance (Table 1). This suggests that the greatest genetic variability among the eight indices evaluated in this study was for root biomass.

Relationship between K Influx Rate and Biomass Production

A genotype that has both a large K influx rate and well-developed root system may have a poor K-use efficiency if µmol g^{-1} fresh weight root is

Table 2. Potassium influx rate, K-use efficiency, root and shoot biomass, and root/shoot ratio of 28 *indica* rice hybrids

Genotype	K influx rate (nmol plant^{-1} h^{-1})	K utilization efficiency (mg mg^{-1})		Biomass (mg plant^{-1})		Root/shoot
		Root	Shoot	Root	Shoot	
Shan A/4663-5[a]	541.9 h[b]	222.2 i	62.9 b	29.9 a	70.9 a	0.42 a
Zhenchang A/4663-4	615.4 c	238.1 g	59.9 d	28.8 a	71.1 a	0.41 a
Shan A/909	477.1 lm	217.4 ij	64.5 a	29.9 a	68.0 b	0.44 a
Xie A/9010	615.4 c	227.3 h	65.4 a	26.0 b	67.2 bc	0.39 a
Zhenchang A/9010	505.9 k	204.1 l	62.5 cb	25.8 b	64.3 d	0.40 a
Zhenchang A/4663-5	599.4 e	238.1 g	60.6 d	23.9 bc	65.3 cd	0.37 ab
Xie A/4663-5	580.2 f	238.1 g	65.4 a	22.9 c	64.4 d	0.36 abc
Shan A/3263	684.1 a	217.4 ij	55.3 g	20.7 def	64.1 d	0.32 d
Zhaichang A/53	612.2 cd	222.2 i	61.7 c	25.6 b	58.6 fg	0.44 a
Zhenchang A/909	526.7 ij	303.0 a	58.1 e	22.5 cd	61.7 e	0.36 abc
Weiyou 64	684.9 a	208.3 kl	56.8 f	22.0 cde	59.1 f	0.37 ab
Zhenchang A/3263	605.8 cde	256.4 e	53.2 h	19.0 fghij	56.9 gh	0.33 cd
Hualian 2	561.9 g	243.9 f	53.8 h	19.3 fghi	56.5 gh	0.34 bcd
Shanchang A/53	585.8 f	277.8 c	51.8 i	18.7 fghijk	55.5 hi	0.34 bcd
Shan A/9010	604.2 de	285.7 b	51.0 ij	20.1 efg	54.0 i	0.37 ab
Zhaichang A/3263	664.2 b	208.3 kl	53.5 h	19.6 fgh	54.0 i	0.36 abc
Zhaichang A/909	520.3 j	212.8 jk	51.5 i	19.9 efgh	53.5 i	0.37 ab
Xie A/3263	563.5 g	212.8 jk	55.0 g	18.7 fghijk	51.4 j	0.36 abc
Zhaichang A/4663-5	525.1 j	263.2 d	50.8 ij	17.8 hijkl	50.1 jk	0.36 abc
Weiyou 48	528.3 ij	263.2 d	49.5 k	17.2 ijkl	49.9 jk	0.34 bcd
Xie A/909	457.2 n	243.9 f	55.3 g	17.9 ghijk	49.2 kl	0.36 abc
Shanyou 64	666.6 b	222.2 i	44.3 m	18.9 fghij	46.3 m	0.40 a
Zhaichang A/9010	535.5 hi	243.9 f	53.2 h	16.5 kl	49.0 kl	0.34 bcd

Table 2. Continued

Genotype	K influx rate (nmol plant^{-1} h^{-1})	K utilization efficiency (mg mg^{-1})		Biomass (mg plant^{-1})		Root/shoot
		Root	Shoot	Root	Shoot	
Zhaichang A/4663-4	615.4 c	181.8 m	46.7 l	17.3 ijkl	47.2l m	0.37 ab
Shan A/53	469.9 m	208.3 kl	47.4 l	17.1 ijkl	44.0 n	0.39 a
Shan A/4663-4	482.7 l	212.8 jk	44.8 m	17.1 ijkl	43.4 n	0.39 a
Xie A/53	467.5 m	212.8 jk	51.5 i	16.8 kjl	43.0 n	0.39 a
Xie A/4663-4	557.1 g	243.9 f	50.3 jk	15.8 l	43.3 n	0.36 abc
Avergae	566.2	233.2	54.9	20.9	55.8	0.37
Coefficient of variance (%)	11.8	11.8	11.2	20.0	15.7	8.2

[a] The part of the hybrid's name to the left of the forward slash is the maternal parent, which is a product of a cytoplasmic male sterile line and a maintainer line, and the part to the right of the slash is the paternal parent from a fertility restorer line bearing this name.

[b] Means followed by different letters within columns are significantly different at $p = 0.05$ by each genotype.

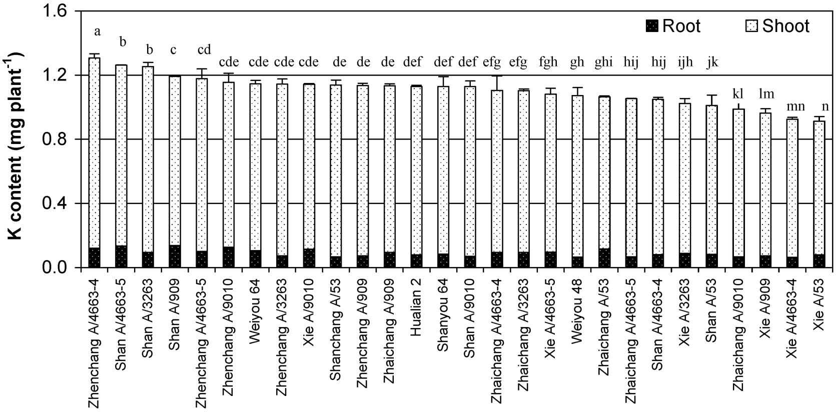

Figure 1. Potassium contents of roots and shoots in seedlings of 28 rice hybrids. The values differ significantly at p = 0.5 when the columns do not share the same letter. The critical range of Duncan's multiple range test is 44.5 μg plant^{-1} for pairwise comparison at p = 0.05.

used and vice versa. Therefore, in this study the K influx rate was measured as nmol plant^{-1} h^{-1} because the corresponding methodology is noninvasive and the measured seedlings may be used subsequently for culture. Figure 2 shows that there was neither a linear nor a nonlinear relationship between K influx rate and the amount of biomass produced. Figure 2 was divided into quadrants in the same manner as explained for Figure 3. The genotypes in quadrant A, such as Shan A/3263 and Zhenchang A/4663-4, may be considered the agronomically best genotypes because they exhibited both a great K influx rate and high biomass production, which were not achieved by genotypes in quadrants B, C, and D. The genotypes in quadrant A may have great potential to be used under poor K fertility conditions. In contrast, the 13 genotypes in quadrant D lack both in high biomass production and great K influx

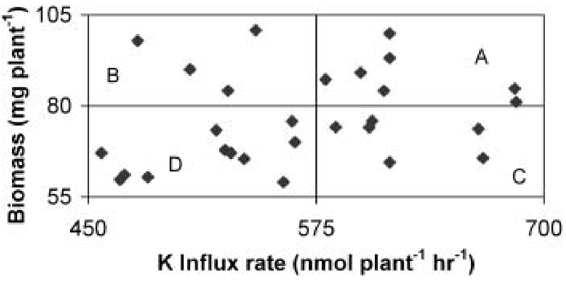

Figure 2. Relationship between biomass production and the K influx rate in five-leaf-stage seedlings of 28 *indica* rice hybrids.

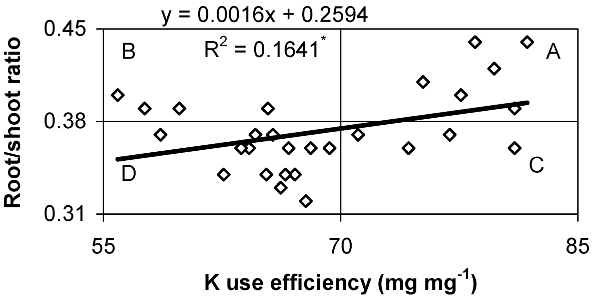

Figure 3. Relationship between K-use efficiency and the root/shoot ratio in five-leaf-stage seedlings of 28 *indica* rice hybrids. $R^2_{0.005,26} = 0.1398$.

rates and may be discarded. Unlike the K influx rate, the K content of whole plants had a close linear relationship with the amount of biomass produced by the 28 hybrids (Figure 4). This indicates that the greater the K content, the greater the amount of biomass produced. Zhenchang A/4663-4 ranked first in the combination of K content (Figure 1) and second in biomass produced (Table 2), whereas Xie A/4663-4 ranked lowest in both these parameters.

These two hybrids had the same male parent but different mothers. This suggests the importance of careful selection and matching of parents in developing K-use-efficient hybrids for rice.

Potassium-Use Efficiency among Hybrids

The hybrids varied significantly in K-use efficiency (Table 1). Genotype Zhenchang A/909 (303.0 ± 18.8 mg mg^{-1}) was most efficient in K-use efficiency, and the genotype Zhaichang A/4663-4 was least efficient in K-use efficiency (181.8 ± 12.8 mg mg^{-1}) (Table 2). The variation in K-use efficiency between most efficient and least efficient genotypes was 66.6%.

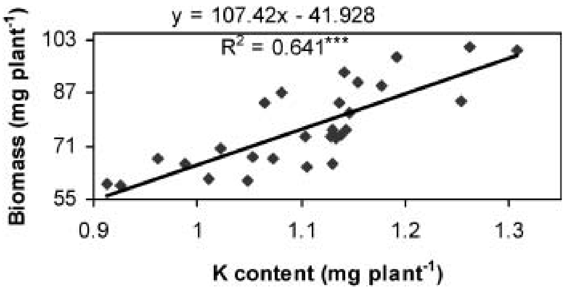

Figure 4. Relationship between biomass production and K content in five-leaf-stage seedlings of 28 *indica* rice hybrids. $R^2_{0.001,26} = 0.3458$.

The K-use efficiency in shoot was best for genotypes XieA/9010 and XieA/4663-5 (64.5 mg mg^{-1}) and worst for genotype Shanyou 64 (44.3 mg mg^{-1}). Hence, the variation in K-use efficiency in shoot between both most and least efficient genotypes was 52%.

Relationship between K-Use Efficiency and Biomass Production

Potassium-use efficiency has been defined in several ways (Gerloff and Gabeman 1983; Liu and Liu 2000; Baligar, Fageria, and He 2001; Yang et al. 2003). However, all of these definitions include the amount of biomass or of economic yield produced per unit of K taken up by the plant. In this study, K-use efficiency is defined as mg of biomass produced per mg of K absorbed by rice seedlings.

The relationship between K-use efficiency and plant biomass production (root plus shoot) at the five-leaf stage was linear in the 28 hybrids (Figure 5); hence, the greater the K-use efficiency, the greater the amount of biomass produced, and vice versa. The hybrid Shan A/909 was best both in biomass production and K-use efficiency even though its biomass ranked the third largest among the 28 genotypes (Table 2). On the other hand, Shan A/4663-4 was most inferior in K-use efficiency and biomass production, although both of these genotypes shared the same maternal parent but had different paternal parents. These widely divergent results show that parentage plays an important role in assuring that high biomass production is commensurate with great K-use efficiency. This conclusion is supported by the finding of Liu and Liu (2002) that at the five-leaf stage, *indica* rice hybrid genotypes on average had a 30% greater K influx rate and 8% more biomass than conventional *indica* rice genotypes. Nevertheless, the K-use efficiency in conventional genotypes may be as much as 88.9 mg mg^{-1} (Liu and Liu 2000), which is 8.6% more than that of the most K-use-efficient hybrid genotype (Shan

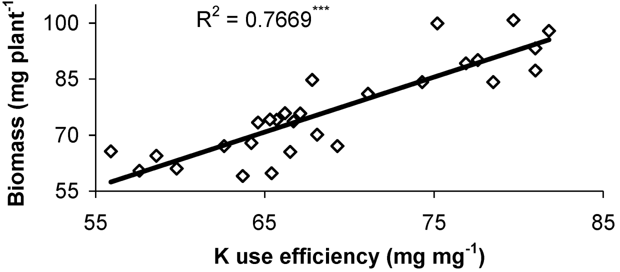

Figure 5. Relationship of plant biomass production (root plus shoot) to K-use efficiency in five-leaf-stage seedlings of 28 *indica* rice hybrids. $R^2_{0.001,26} = 0.3458$.

A/909) in this study. The relatively poorer K-use efficiency of hybrid genotypes may be one of the reasons why they have a greater K requirement than conventional genotypes.

The relationship between the root/shoot ratio and K-use efficiency differed from that of biomass of the whole seedling and K-use efficiency. When the root/shoot ratio was plotted against K-use efficiency, a significantly ($p = 0.05$) positive linear regression was obtained (Figure 3). Figure 3 was divided into quadrants based on the median values of K-use efficiency and root/shoot ratio. Six genotypes fall in quadrant A of Figure 3, having a relatively large root system and better K-use efficiency. These genotypes were elite combinations of K-use-efficient hybrids with large root systems. In contrast, quadrant D had 14 genotypes (50% of the tested genotypes) that were inferior both in root development and K-use efficiency. These genotypes are the least desirable in developing K-use-efficient rice genotypes. Hybrids that fall in quadrant B can contribute to a large root system and those that fall in quadrant C could contribute great K-use efficiency to a hybrid, but neither set of hybrids can express both essential traits and use them harmoniously to efficiently produce much biomass.

Because K-use efficiency is actually the reciprocal of K content in plants (Liu and Liu 1996; Baligar, Fageria, and He 2001) (i.e., amount of biomass produced per unit of K taken up by the plant) the K-use efficiency of a genotype with a high K influx rate would be poor if the genotype produces little biomass. For K-use efficiency of a genotype to be great, it must produce high biomass. For example, Shanyou 64 ranked third in K influx rate but 28th in K-use efficiency because its biomass ranked only 22nd (Table 2, Figure 1). In other words, a high K influx rate may militate against great K-use efficiency in some genotypes.

The K-use efficiency, like other traits, in rice hybrids is closely related to the combining ability of the three parental genotypes (Tan et al. 1999). For example, Xie A/53 and Zhaichang A/53 (Table 2) both share the same restorer line, "53," as a paternal parent, but the K influx rate of Xie A/53 ranked only 27th, whereas that of Zhaichang A/53 ranked eighth. The K-use efficiency of Xie A/9010 was 81.0 mg mg^{-1} but that of Shan A/9010 was only 65.7 mg mg^{-1} even though both hybrids shared the same restorer line. When the sterile line, Xie A, was crossed with the restorer line, 9010, the resulting hybrid, Xie A/9010, produced 93.2 mg of biomass plant^{-1}, but when Xie A was crossed with the restorer line, 4663-4, the resulting hybrid, Xie A/4663-4, produced only 59.1 mg of biomass plant^{-1} (Table 2). The variance was 57.7% between Xie A/9010 and Xie A/4663-4.

In creating a highly productive rice hybrid, special attention must be given to the choice of elite parents and, in particular, to assuring that they have favorable combining ability. In this way, elite hybrids can be developed with the genetic potential to efficiently use nutrients both from the soil and applied fertilizers.

Relationship between K-Use Efficiency and K Influx Rate

The K influx rate of rice hybrids seems rather important in the efficient use of K resources in both soils and fertilizers. The K concentration in soil solutions is quite low (Xi 1998), but a soil solution is a nutrient buffer system, which allows the soil to gradually release K ions into solution. Genotypes with great K influx rates may have a competitive advantage because they can take up more of the scarce K than those with poor K influx rates. Thus the greater the influx rate, the more K the genotype is able to absorb and the greater its competitiveness. This study (Table 2, Figures 2 and 6) suggests that there is a great potential to breed elite rice hybrids with great K influx rates by choosing great K influx elite genotypes as the parents of hybrids. In practice, it should be sustainable and economical to breed and popularize elite hybrid combinations with great K influx rates because they would spare the use of potash fertilizers in rice production.

Potassium-use efficiency is calculated as the amount of biomass produced per unit of K uptake. The more biomass produced per unit of K uptake, the greater the K-use efficiency. Liu and Liu (1996) suggested that the threshold K requirement of protein synthesis is rather low, and Fageria, Slaton, and Baligar (2003) found that K can be reused repeatedly. This is significant for the economical and efficient use of K and in breeding for tolerance to low-K stress.

Some genotypes possessed great K influx rates but poor K-use efficiency and vice versa. Shan A/909 ranked the best in K-use efficiency but 25th in K influx rate among 28 genotypes. In contrast, Shanyou 64 had the worst K-use efficiency but ranked third in K influx rate.

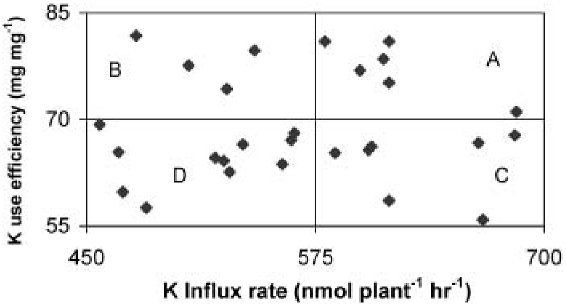

Figure 6. Relationship between K-use efficiency and the K influx rate in five-leaf-stage seedlings of 28 *indica* rice hybrids.

Nevertheless, some of the genotypes possessed both a great K-use efficiency and a great K influx rate. For example, Xie A/9010's ranked sixth in K influx, and its K-use efficiency was second highest. Similarly, Zhenchang A/4663-4's K-use efficiency and K influx rate both ranked seventh. In contrast, hybrids Shan A/53's K influx rate and K-use efficiency were 26th and 25th among 28 genotypes, respectively.

Biomass production is the most important characteristics of K-use efficiency. Genotypes with a poor influx rate and with a large amount of biomass must have a good K-use efficiency. The hybrid Xie A/9010 is an example of this sort of genotype. In contrast, K-use efficiency was very poor when the genotype's K influx rate and biomass production were both very poor, as in the case of Shan A/4663-4. On the other hand, when the genotype has a poor K influx rate and high biomass production, it must have great K-use efficiency, as in the case of Shanyou 64 (Table 2).

The genotypes with great K influx rates showed that their root systems had very strong affinities to K (Santa-Maria et al. 1999), and hence, they are highly competitive with other organisms sharing the same low-K environment. The genotypes with great K-use efficiencies had very low K requirement threshold values for protein synthesis (Leigh and Wyn Jones 1984). Therefore, K is re-useable in the plants. These two traits, great K-use efficiency and low K requirement, are equally important and essential in rice hybrids. Only a small fraction of the genotypes possess both traits, but these traits provide the basis in plant physiology for the selection of the elite genotypes to be used in breeding K-efficient and productive rice hybrids.

Data obtained in this study show that there is neither a linear nor a nonlinear relationship between K influx rate and K-use efficiency (Figure 6) in the 28 hybrids. For the purposes of developing rice hybrids with great K influx rates and K-use efficiencies, the genotypes in quadrant A of Figure 6 may be most desirable and those in quadrant D are most undesirable. Those genotypes in quadrant B can contribute to great K-use efficiency but not to grand K influx rates, whereas those in quadrant C can contribute to great K influx rates but not to excellent K-use efficiencies. Based on this research, 21% of the genotypes had both great K influx rates and great K-use efficiencies, and these genotypes should be potentially useful in developing K-efficient rice hybrids.

Relationship between K-Use Efficiency of Hybrid Progeny and Their Parents

Results of this research show that the genetics (including combining ability) of the parents of hybrids are highly important in determining K-use efficiency of the F_1 hybrids. For example, the biomass of a Shan A/

4663-5 seedling was 100.8 g plant^{-1}, but that of Shan A/53 was only 61.1 mg plant^{-1} (Table 2). Both of these two genotypes had the same mother but different fathers and a 65% difference in biomass. This may be attributed to the greater genetic potential of the former genotype's father than that of the latter's father, or the former genotype might have better combining ability than the latter. Similarly, Shan A/909 and Zhaichang A/909 shared the same father but had different mothers, their K-use efficiencies were 81.8 and 64.4 mg mg^{-1}, respectively. The former had a 27% advantage over the latter. These may result from the genetic superiority of the mother of Shan A/909 over the mother of Zhaichang A/909. However, more research on the parents is needed to better understand the relationship of genetic potential and the combining ability of the parents and their hybrid offspring.

Holistic Evaluation of Hybrid Rice Genotypes

Because biomass production, K influx rate, and K-use efficiency are the main factors that combine to impart tolerance to low-K stress in rice, it is appropriate to use quantitative measurements of these traits to quantify the tolerance to low-K stress of hybrid genotypes.

In this study, the quantification of the level of expression of each component of low-K tolerance was readily accomplished, but the quantification of the combined expression of the various component traits poses difficulties because some of the relationships between these traits considered two at one time were neither linear nor nonlinear (Table 2, and Figures 1–6). Nevertheless, an equation for calculating a quantitative holistic score (HS) for the combined contribution of the three major components to low-K tolerance of a given genotype was formulated as follows:

$$\mathrm{HS} = \left(\frac{I_i}{I_m} + \frac{E_i}{E_m} + \frac{B_i}{B_m}\right)\left(\frac{1}{3}\right) \times 100 \qquad (1)$$

where HS is the holistic score of a particular genotype, and I_i, E_i, and B_i are the K influx rate, the K-use efficiency, and the amount of biomass produced by genotype i, respectively. I_m, E_m, and B_m are the mean values of the corresponding K influx rate, K-use efficiency, and biomass of genotype i, respectively, and 3 is the number of the component traits included in the evaluation. The holistic scores obtained by these calculations are shown in Figure 7. The holistic scores may be divided into three categories as follows: (1) HS $>$ 115, elite genotypes with high tolerance to low K, (2) 100 $<$ HS $<$ 115, genotypes with intermediate tolerance to low K, and (3) HS $<$ 100, genotypes with poor tolerance to low-K stress. According to this categorization, only 2 of the 26 genotypes

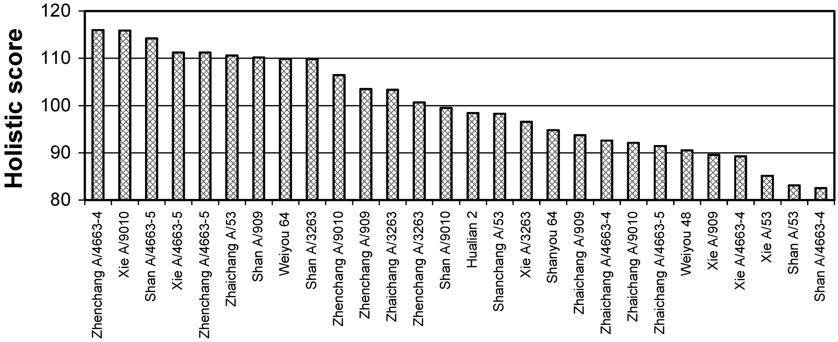

Figure 7. Holistic scores of the low K tolerance of 28 *indica* rice hybrids based on measurements of K influx rate, K-use efficiency, and the amount of biomass produced by the genotype in five-leaf-stage seedlings.

are elite low-K tolerant (i.e., Zhenchang A/4663-4 and Xie A/9010), 11 are intermediate low-K tolerant genotypes, and 15 are poor low-K tolerant genotypes. The elite genotypes may be used for rice production, but the 15 poor ones should not be grown commercially in low-K soils. Additionally, because the integrated performance of a rice hybrid is dependent on the appropriate genes for K nutrition and metabolism and for combining ability in each of the three-line parents, more research is needed to evaluate the various components of low-K tolerance and relevant combining ability in parent genotypes to be used to construct rice hybrids.

CONCLUSIONS

Potassium shortage is the main limiting factor in rice production in China. This study was carried out with 28 important *indica* hybrid genotypes grown in hydroponics. The main findings in this study were as follows: (1) Among 28 tested hybrid rice genotypes obtained from China's leading rice germplasm repositories, there were 50.0% genotypic differences in K influx rates at three-leaf stage. This shows that it is possible to develop K-efficient rice hybrid genotypes. (2) The 28 hybrid genotypes differed by 70.6% in biomass production, 43.2% in K accumulation in plant tissues, and 46.3% in K-use efficiency at five-leaf stage. This indicates that there is a great potential to develop crop gene resources and use the elite genotypes to alleviate K deficiency in paddy soils. (3) There was significant linear correlation between biomass and K-use efficiency but there was not linear correlation between K influx rate and K-use efficiency. (4) Hybrid rice differs from conventional rice in that each hybrid's pedigree includes parents from three lines, and this study showed that the genotypes from these three lines combine or interact to profoundly affect the efficiency of the hybrid's performance in K nutrition. However, measurements of the K nutrient features of the three parental lines in each hybrid's pedigree were not made in this study. Such measurement should be made to further improve the matching of the three parental lines and to construct more K-efficient hybrids, which are needed urgently for sustainable rice production.

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