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Differential response of root morphology to potassium deficient stress among rice genotypes varying in potassium efficiency*

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Abstract: Disparity in the root morphology of six rice (*Oryza sativa* L.) genotypes varying in potassium (K) efficiency was studied with three K levels: 5 mg/L (low), 10 mg/L (moderate) and 40 mg/L (adequate) in hydroponic culture. Morphological parameters included root length, surface area, volume and count of lateral roots, as well as fine (diameter<0.2 mm) and thick (diameter>0.2 mm) roots. The results indicate that the root growth of all genotypes was reduced under low K, but moderate K deficiency increased the root length of the efficient genotypes. At deficient and moderate K levels, all the efficient rice genotypes developed more fine roots (diameter<0.2 mm) than the inefficient ones. Both fine root count and root surface area were found to be the best parameters to portray K stress in rice. In accordance with the root morphology, higher K concentrations were noted in shoots of the efficient genotypes when grown at moderate and deficient K levels, indicating that root morphology parameters are involved in root uptake for K and in the translocation of K up to shoots. K deficiency affected not only the root morphology, but also the root ultra-structure. The roots of high-efficient genotypes had stronger tolerance to K deficient stress for root membrane damage, and could maintain the developed root architecture to adapt to the low K growth medium.

Key words: Genotypic difference, Potassium (K) efficiency, Root surface area, Fine root development, Root cell ultra-structure
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INTRODUCTION

Potassium (K) is one of the three essential macronutrients required in the largest amount for plant growth and yield. Its deficiency in paddy soils is becoming one of the limiting factors for increasing rice yield in Asia. A majority of the cultivated soils in southern China is deficient in K (Yang *et al*., 2003). It is estimated that production of one ton rice grain needs at least 14.5 kg K (Witt *et al*., 1999). Rice yields at the levels of 4~8 t/ha remove 56~112 kg K from the soil, whereas total K uptake exceeds 200 kg for grain yield greater than 8 t/ha (Dobermann *et al*., 1998).

Potassium efficiency is defined as the plants can obtain higher dry matter yields and/or grain yields under moderate and deficient K levels, with efficient internal and external use efficiencies (Yang *et al*., 2003). Manipulating the genotypic differences in crop cultivars to adapt them to adverse soil conditions such as low nutrients status is one of the key strategies for the sustainable intensification of agricultural systems (Yang *et al*., 2004a). Genotypic differences in K use efficiency have been reported in various crops, e.g., alfalfa (James *et al*., 1995), snapbean (Shea *et al*., 1968), soybean (Sale and Campbell, 1987), tomato (Chen and Gabelman, 1995), ramie (Liu *et al*., 2000),

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corn (Baligar and Barber, 1979), wheat (Zhang *et al*., 1999) and barley (Pettersson and Jensén, 1983). Genetic variation also exists in rice in low K soils (Liu *et al*., 1987; Yang *et al*., 2003; 2004b). Nonetheless, investigations on mechanisms of K efficiency of lowland rice are scanty.

Being a major organ for nutrient uptake, the root plays an important role in soil-plant system (Lynch *et al*., 2007). Its growth is directly related with the growth and biomass yield of shoots. Generally, plants have a characteristic of enhancing their efficiency of nutrient acquisition to overcome the stress from nutrient deficiency or root competition. Flexibility in biomass allocation, root morphology and root distribution pattern has been found to be an important adaptive mechanism to exquisite nutrients (Lynch *et al*., 2007; Xie *et al*., 2006; Yang *et al*., 2005; Rengel and Marschner, 2005).

A high root:shoot ratio and a specific root length are characteristically associated with plants growing in infertile soils (Yang *et al*., 2004a). Root shallowness is a topsoil foraging behavior at minimum metabolic cost, by increasing the total absorptive surface of the root system and lowering inter-root competition (Lynch *et al*., 2007). Høgh-Jensen and Pedersen (2003) found that low and moderate K levels affected the root morphology in pea, red clover, lucerne, barley, rye, perennial ryegrass and oilseed rape. Crops modify their root hair length in response to low K, and thereby maintain the uptake from sparingly soluble K sources. Our previous study shows that rice roots induced marked changes in K fractionation and mobility in rhizosphere (Yang *et al*., 2005), which would ultimately influence K uptake and crop yield. Currently, there is no suitable index of crop response to K deficiency for breeding purpose, which is a major limitation to crop improvement. The objective of this study was to investigate the response of rice root morphology to K supply from physiological perspectives among different genotypes, and to characterize the K efficient genotypes.

MATERIALS AND METHODS

Plant culture

Six genotypes of rice (HA-881043, Xinzaozhan, Sanyangai, Jia948, Xiangwanxian3 and Tonglianghuozhong) were grown in hydroponic culture with nutrient solution. The first three genotypes were designated as K-efficient genotypes, while the latter three as K-inefficient genotypes, according to our greenhouse and field screening (Yang *et al*., 2003). The composition of the nutrient solution was the same as described in Yang *et al*.(2003). Each genotype was treated separately with three levels of K, i.e., 5 mg/L (K_1 as low K level), 10 mg/L (K_2 as medium K level) and 40 mg/L (K_3 as high K level or control). It was a two-factor factorial experiment with completely randomized design and three replications. Factor 1 was the K level, and factor 2 was the rice genotype. Rice seeds were surface sterilized, germinated and grown in 1/4 strength of nutrient solution without K in a greenhouse. Five-day old seedlings were carefully transferred into 2.5-L plastic containers. Nutrient solution was replaced twice a week, and deionized water was added daily to recover water lost through evapotranspiration. The pH was maintained daily around 5.0 by adding 1 mol/L HCl and 1 mol/L NaOH. The experiment was conducted in a growth chamber at 30 °C during day and at 25 °C during night, with 10 h light and 14 h dark condition daily. Photo-radiation at the canopy was 450 μmol/(m^2·s).

Measurement of root parameters and potassium

Plants were harvested after having been treated with different K supply levels for 25 d. Dry root weights of rice seedlings of six genotypes were recorded after 10, 15, 20 and 25 d of the treatment. After the 25-day treatment, three representing plants per treatment were selected for measuring root morphological parameters with WinRHIZO (Regent Instruments Company, Canada). Roots were cut every 2 cm and evenly distributed in water before being scanned. At harvest, root and shoot samples per pot were collected, oven dried, weighed, and then grounded for elemental analysis. A given amount of grounded samples were wet-digested with H_2SO_4/H_2O_2, and potassium concentrations in the digested solution were determined using a flame spectrophotometer. Statistical analysis of all the data was performed using the SPSS statistical package (version 11.0).

Root transmission electron microscope (TEM) observation

The K-efficient (HA-881043) and K-inefficient

(Tonglianghuozhong) genotypes were selected for observing root ultrastructure with TEM (JEOL TEM-1200EX, Japan). Rice roots were taken from two treatments viz. 5 mg K/L (K_1) and 40 mg K/L (K_3 or control). After 25-day treatment, small sections of roots tips (1~3 mm in length) were taken as samples. They were fixed in 4% (v/v) glutaraldehyde in 0.2 mol/L PBS (sodium phosphate buffer, pH 7.2) for 6~8 h and post-fixed in 1% (w/w) OsO_4 for 1 h, then again in 0.2 mol/L PBS for 1~2 h. Dehydration was performed in a graded ethanol series (50%, 60%, 70%, 80%, 90%, 95% and 100%) followed by acetone, and then samples were filtrated and embedded in Spurr's resin. Ultra-thin sections (80 nm) were prepared and mounted on copper grids for viewing under TEM at an accelerating voltage of 60.0 or 80.0 kV (Peng *et al.*, 2005).

RESULTS

Dry root weight

The effects of K levels on dry root weights of rice seedlings of six genotypes after 10, 15, 20 and 25 d of the treatment are shown in Fig.1. At Day 10, differences among K treatments in all the genotypes (both inefficient and efficient) were not statistically significant. At Day 15, root biomass of only K-inefficient genotypes at K_1 and K_2 levels was significantly lower than that at K_3 level, but the one of K-efficient genotypes changed little at all K levels. Further, at Day 20 the lower K level treatment decreased root dry weight significantly only for the K-inefficient genotypes (Jia948 and Xiangwanxian3). Finally at Day 25, only Tonglianghuozhong showed significant difference of both K_1 and K_2 with K_3; however, K_1 differed with K_3 for all the genotypes. Genotype HA-881043 was considered to be the most tolerant to K deficiency and Tonglianghuozhong was the most sensitive one. The results reflect that dry root weight had no significant difference in K-efficient genotype HA-881043 at all K levels. But under low K treatment, root biomass was decreased in the K-inefficient genotype Tonglianghuozhong, and the difference became larger with increasing treatment time. These results indicate that K-efficient genotypes have greater tolerance of root growth to low K stress, as compared with the K-inefficient genotypes.

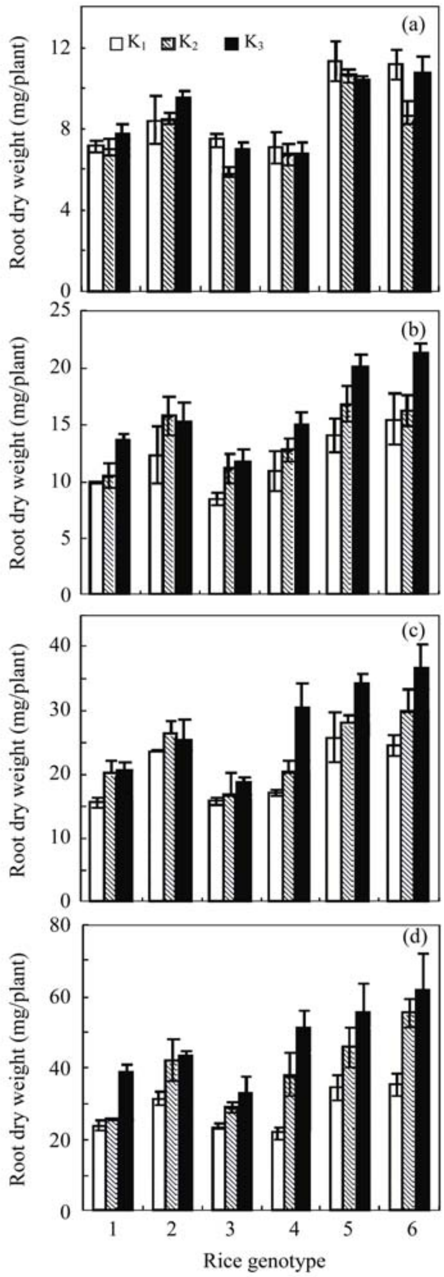

Fig.1 Effect of different K levels on root dry weights of different rice genotypes at different treatment time. (a) 10 d; (b) 15 d; (c) 20 d; (d) 25 d
Rice genotype: 1: HA-881043; 2: Xinzaozhan; 3: Sanyangai; 4: Jia948; 5: Xiangwanxian3; 6: Tonglianghuozhong

Root morphological parameters

The studied parameters of root morphology included root length, volume, surface area and diameter as shown in Table 1. There was more decline in root length of K-inefficient genotypes than in that of K-efficient genotypes under K deficient treatment (5 mg/L), as compared to that in adequate K level. Among K-efficient genotypes, Xinzaozhan was superior to HA-881043 and Sanyangai, but it had fewer lateral roots than Sanyangai. The most decline in root length was in K-inefficient genotype Tonglianghuozhong. Similarly, the root surface area and volume showed a less decrease in the K-efficient genotype Xinzaozhan and a maximum decrease in the inefficient genotype Tonglianghuozhong. However, for number of lateral roots there was a little variation among K-efficient genotypes where Sanyangai (efficient) showed the least reduction with K deficiency treatment, whereas the highest reduction value was recorded again in Tonglianghuozhong (inefficient). At moderate K deficient level (10 mg/L), all these parameters of the K-efficient genotype Xinzaozhan did not show any reduction but higher values than those at 40 mg K/L. Here the maximum reduction in root length and number of lateral roots was for Tonglianghuozhong (inefficient). In view of the overall root morphological response of all the genotypes to K deficiency, it was found that Tonglianghuozhong (inefficient) was the most sensitive genotype and Xinzaozhan (efficient) the most tolerant one.

Reduction in the count of fine (diameter<0.2 mm) and thick (diameter>0.2 mm) roots of K-inefficient and K-efficient rice genotypes at different K levels is shown in Table 2. The most reduction in both types of roots at low and moderate K levels was for K-inefficient genotype Tonglianghuozhong except that thick roots at medium K level have the lowest count for Sanyangai. There was over a 25% increase in the count of fine roots in the K-efficient genotypes of Xinzaozhan and Sanyangai when grown at moderate K deficient levels over that at adequate K levels, and at deficient K level (5 mg/L), a much less decrease in count of fine root was noted in the efficient genotypes of Xinzaozhan and Sanyangai than in the K-inefficient genotypes of Xiangwanxian3 and Tonglianghuozhong (Table 2). These indicate that moderate K deficiency even could stimulate fine root development, which is important to increase root absorption area and absorption efficiency at low K medium. Plants absorb nutrients from the soil mostly by fine roots, so the number of fine roots at low K levels compared to that at adequate K levels showed the tolerance ability of plants to absorb K under low K stress.

Table 1 Genotypic difference in various root morphological parameters of six rice genotypes under different K treatments

K level (mg/L)	Rice genotypes	Root length (m/plant)	Root surface area (cm^2/plant)	Root volume (cm^3/plant)	Number of lateral roots ($\times 10^3$ plant^{-1})
40	HA-881043	5.40±0.13	66.96±4.53	0.76±0.073	2.28±0.77
	Xinzaozhan	4.56±0.24	49.82±4.66	0.60±0.023	3.10±0.43
	Sanyangai	5.23±0.34	73.24±5.44	0.83±0.140	3.02±1.06
	Jia948	4.61±0.10	49.36±3.18	0.49±0.015	2.89±1.29
	Xiangwanxian3	4.61±0.25	53.08±1.03	0.51±0.030	3.21±1.28
	Tonglianghuozhong	6.41±0.06	75.69±4.19	0.71±0.088	4.92±1.23
10	HA-881043	3.76±0.23	51.87±3.93	0.62±0.040	1.91±0.48
	Xinzaozhan	4.97±0.06	60.43±1.12	0.66±0.051	3.58±0.28
	Sanyangai	4.30±0.31	62.43±4.44	0.67±0.028	3.27±0.94
	Jia948	4.26±0.31	50.69±4.10	0.48±0.062	2.98±0.54
	Xiangwanxian3	4.70±0.31	56.03±3.31	0.53±0.043	3.20±0.57
	Tonglianghuozhong	4.75±0.09	61.01±1.85	0.65±0.046	3.76±0.46
5	HA-881043	3.57±0.17	29.32±3.55	0.28±0.019	0.96±0.87
	Xinzaozhan	3.98±0.23	41.79±3.46	0.40±0.013	2.01±0.25
	Sanyangai	3.28±0.16	40.84±2.33	0.40±0.029	2.32±0.22
	Jia948	3.05±0.08	34.78±2.76	0.32±0.010	2.11±0.82
	Xiangwanxian3	3.25±0.17	32.19±0.47	0.29±0.010	1.60±0.68
	Tonglianghuozhong	3.10±0.26	32.01±3.20	0.23±0.010	1.71±0.24

Table 2 Effect of K treatment on the count of fine (diameter<0.2 mm) and thick (diameter>0.2 mm) roots of different rice genotypes at different K levels

Rice genotypes	Number of fine and thick roots ($\times10^2$ plant^{-1})					
	40 mg K/L (Control)		10 mg K/L		5 mg K/L	
	Fine roots	Thick roots	Fine roots	Thick roots	Fine roots	Thick roots
HA-881043	21.75±2.434	0.95±0.068	18.14±1.627	0.84±0.059	9.13±0.833	0.47±0.0115
Xinzaozhan	30.09±3.987	1.14±0.081	34.75±2.892	1.04±0.086	21.15±3.222	0.82±0.0472
Sanyangai	28.94±1.085	1.35±0.050	31.50±3.937	0.87±0.076	22.08±2.254	1.08±0.0116
Jia948	27.96±1.280	0.83±0.023	29.18±2.687	1.08±0.050	20.25±3.659	0.59±0.0416
Xiangwanxian3	31.16±1.260	1.12±0.084	31.17±3.642	0.85±0.038	15.56±1.731	0.43±0.0802
Tonglianghuozhong	47.82±1.203	1.52±0.057	36.54±3.606	1.11±0.076	15.30±1.437	0.45±0.0462

Ultrastructure of roots

The transmission electron microscopic views of K-efficient genotype HA-881043 and K-inefficient genotype Tonglianghuozhong at adequate and low K levels are shown in Fig.2. At 40 mg K/L, the multiple mitochondrions within the root cells for both genotypes were intact; most cristates in the mitochondrion double-deck membranes were evenly distributed. However, at low K level, more severe damage in root ultrastructure was observed in the K-inefficient genotype Tonglianghuozhong than that in the K-efficient genotype HA-881043. At deficient K levels, the structures of nucleus and nucleolus were kept intact, the root cell membrane showed less damaged, and intact vacuoles were kept within the root cell for HA-881043 (efficient). Whereas for Tonglianghuozhong (inefficient), root organelles were heavily damaged, hollowed root cells appeared, big dark particles were precipitated within the root cells and saturated at the root cell walls, and the root cell membrane was totally broken. These results imply that the root membrane of the K-efficient rice had high tolerance to low K stress, which is important to maintain more developed root morphology for K acquisition from low K soil.

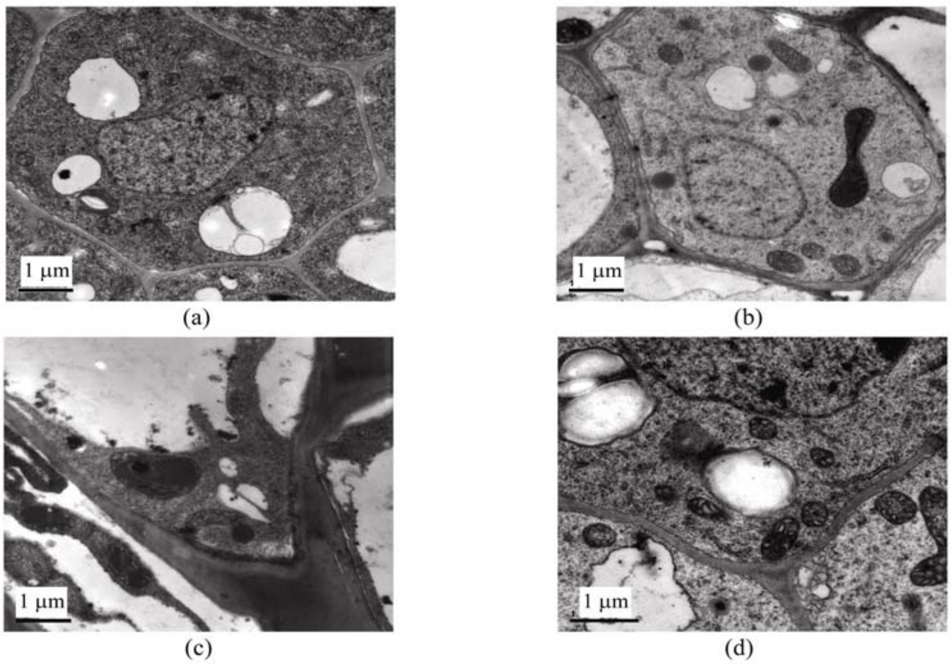

Fig.2 The ultrastructures of the roots in K-efficient (HA-881043) and K-inefficient (Tonglianghuozhong) rice genotypes at adequate and deficient K levels. (a) and (b): Root ultrastructures at adequate K level for Tonglianghuozhong (inefficient) and HA-881043 (efficient), respectively; (c) and (d): Root ultrastructures at deficient K level for Tonglianghuozhong (inefficient) and HA-881043 (efficient), respectively

Potassium (K) concentration

The K concentrations in the roots and shoots of different genotypes of rice at variable K levels are shown in Fig.3. With the decrease of K level in the growth medium, K concentrations were significantly lowered in all the genotypes. The highest K concentrations in both roots and shoots were with K_3, which were statistically higher than those with K_1 and K_2; still there was a significant difference between K_1 and K_2 as well. The decrease rates of K concentrations in the roots of HA-881043 (efficient) and Jia948 (inefficient) were the highest ones, and K concentrations with K_1 were about 7 times lower than that with K_3. These genotypes also showed the highest K concentrations in shoots with K_3, which were close to 6 times higher than those with K_1. Under K deficiency, the absorption, transport and accumulation of K in K-efficient as well as K-inefficient genotypes were restrained. It indicates that under extreme K deficiency, K-efficient genotypes could take up and transport K to the shoot from the medium. With K_2 treatment (10 mg K/L), the K concentrations in roots and shoots differed significantly among various genotypes, but with extremely low K level (K_1) there was no significant difference observed. It illuminates that 5 mg K/L could not entirely distinguish the difference in the tolerance ability to low K stress among different genotypes.

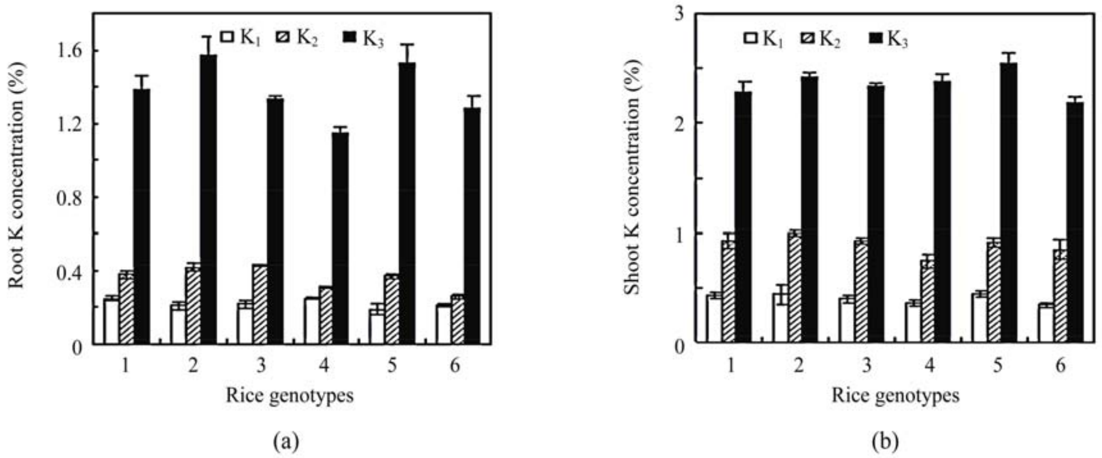

Fig.3 Effect of different K levels on K concentrations in roots (a) and shoots (b) of different rice genotypes
Rice genotype: 1: HA-881043; 2: Xinzaozhan; 3: Sanyangai; 4: Jia948; 5: Xiangwanxian3; 6: Tonglianghuozhong

DISCUSSION

Root morphological characteristics of both K-inefficient and K-efficient genotypes were not significantly affected by decreasing K level to moderate deficiency (10 mg K/L) in the growth medium. However, at the deficient level (5 mg K/L) all the recorded root morphology attributes were decreased significantly, and there was more decline in K-inefficient genotypes. With low and high K level treatments, the gradient counts of rice roots elucidate the differential ability of these genotypes for adapting to low K stress. The K deficient stress reduced the root count per plant in both K-inefficient (Tonglianghuozhong, Jia948 and Xiangwanxian3) and K-efficient (HA-881043, Sanyangai and Xinzaozhan) genotypes, but both categories had significant difference. Previous findings also indicate that K stress influences the physiology mechanism of different rice genotypes variably (Yang *et al*., 2003; 2004a). We found that the phenomenon of root count decline appeared earlier in the K-inefficient genotypes, and the decrease rate was higher in the K-inefficient genotypes than in the K-efficient genotypes (unpublished data).

Root growth consumes photosynthates and energy. In terms of root structure, Tonglianghuozhong (inefficient) was inferior to HA-881043 (efficient) that has a stronger K-absorbing capacity. The uptakes of water, minerals and heavy metals are directly affected by root morphological characteristics (Marschner, 1995). Results in the present study show that the roots of high efficient genotype had a greater ability to tolerate low K stress and absorb K from deficient medium. At low K level, the length, surface area, volume and count of the roots of K-efficient genotypes were higher (Table 1), and had significant relations with K concentrations in roots and shoots (Fig.2), while reverse was true for K-inefficient genotypes. It indicates that the genotypic difference for K efficiency in rice had a close relationship with root morphology, fine root development and physiology characters. This is first report in rice, and the results are in good agreement with those in soybean (Wang *et al*., 2005), wheat (Zou *et al*., 2001), and ryegrass (Mengel and Steffens, 1985). Zou *et al*.(2001) advocated that morphological and physiological characters of roots could be the reference only to screen for efficient K uptake, and kinetics parameters should be an index for high K efficiency and tolerance to low K stress. Therefore, it is better to combine the morphological characters of roots with kinetics parameters as major indexes. The mechanisms behind tolerance of fine root development and root cell membrane function to K deficient stress in the K-efficient genotypes need to be further clarified.

CONCLUSION

K deficiency not only affects the root ultrastructure, but also results in small root morphology and growth. In the present studies, we observed rice genotypes differed in their response to low, moderate and adequate levels of K in growth medium, and the K-efficient genotypes had a superior root architecture to adapt to a low K medium.

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