GENOTYPIC VARIATIONS IN POTASSIUM UPTAKE AND UTILIZATION IN COTTON

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Genotypic variations in potassium (K) uptake and utilization were compared for eight cotton cultivars in growth chamber and field experiments. Four of the cultivars (‘SGK3’, ‘SCRC18’, ‘SCRC21’ and ‘SCRC22’) typically produce lower dry mass and the other four (‘Nannong8’, ‘Xiangza2’, ‘Xinluza12’ and ‘Xiangza3’) produce greater dry mass in K-deficient solution (0.02 mM). The mean dry weight of seedlings (five-leaf stage) of cultivars with greater biomass was 155% higher than that of cultivars with lower biomass yield under K deficiency. However, all the genotypes had similar dry matter yields in K-sufficient solution (2.5 mM). Thus, the four cultivars with superior biomass yield under low K medium may be described as K efficient cultivars while the inferior cultivars may be described as K inefficient. Although seeds of the studied cultivars originated from different research institutes or seed companies, there were little differences in seed K content among them, irrespective of their K efficiency. Consequently, there were no significant differences in K accumulation in seedlings (4 d after germination in a K-free sand medium) just before transferring to nutrient solutions. However, the K efficient genotypes, on average, accumulated twice as much K at 21 d after transferring to K-deficient solution (0.02 mM). A much larger root system as well as a slightly higher uptake rate (K uptake per unit of root dry weight) may have contributed to the higher net K uptake by the K efficient cultivars. In addition, the K efficiency ratio (dry mass produced per unit of K accumulated) and K utilization efficiency (dry mass produced per unit of K concentration) of the K efficient cultivars exceeded those of the K inefficient genotypes by 29% and 234%, respectively, under K deficiency. On average, the K efficient cultivars produced 59% more potential economic yield (dry weight of all reproductive organs) under field conditions even with available soil K at obviously deficient level (60 mg kg$^{-1}$). We noted especially that the four K inefficient cultivars studied were all transgenic insect-resistant cotton, suggesting that the introduction of foreign genes (Bt and CpTI) may affect the K use efficiency of cotton.
Keywords: cotton, potassium efficiency, uptake, utilization, genotypic variation

INTRODUCTION

Cotton has a high requirement for potassium (K) and responds more to K fertilizer than does corn or soybeans (Cope, 1981), which may be related to its relatively poor exploitation of the surface soil layer (0–0.10 m) (Brouder and Cassman, 1990) and less dense root system than other crops at soil depths < 0.3 m (Gerik et al., 1987). Biomass production, leaf area expansion, carbon dioxide (CO₂) assimilation capacity, lint yield and fiber quality could be reduced by K deficiency (Pettigrew and Meredith, 1997; Zhao et al., 2001; Pettigrew, 2003; Pervez et al., 2004; Fan et al., 2006; Reddy and Zhao, 2005).

The rapid mining of soil K by increased cotton yield in recent years, coupled with the insufficient application of K fertilizers, has resulted in negative K balances in cotton fields in China. In addition, transgenic insect-resistant cultivars, being popularized in the Yangtze River and Yellow River areas of China, are more sensitive to K deficiency than conventional cotton cultivars (Zhang et al., 2007). Therefore, K deficiency has become one of the major constraints to cotton production.

Because of the low potash deposits in China and the high prices of K fertilizers, an exploitation of the genetic diversity of cotton for enhanced productivity in low K soil is desired for sustainable production. Variation among germplasms in the ability to acquire plant nutrients from the environment has been investigated for decades (Lyness, 1936; Godwin and Blair, 1991). As early as 1976, cultivar differences in cotton response to K were noted by Halevy (1976). Cassman et al. (1989) and Brouder and Cassman (1990) showed that cotton genotypes differ in K uptake and sensitivity to late-season K deficiency. Potassium requirements may also differ in cotton cultivars with contrasting maturity and growth habit (Tupper et al., 1996; Clement-Bailey and Gwathmey, 2007). Jiang et al. (2003, 2005, 2008) investigated genotypic differences in K efficiency among seedlings of 86 cotton cultivars under a hydroponic culture and selected some representative cultivars to study the mechanisms of high K-efficiency. The variation in K uptake was also studied by the analysis of leaf K concentration in cotton varieties grown under conditions of terminal drought (López et al., 2008).

In a recent study (Zhang et al., 2007), we compared the responses of transgenic insect-resistant and conventional cotton to K deficiency. In the present study, we compared four cotton cultivars with high biomass yield with those yielding relatively lower biomass under low K level (0.02 mM). Parameters compared were K content of seeds, dry matter yields, response to added K, K uptake, and utilization, symptoms of K-deficiency in cotyledons
and dry weight of reproductive organs. The results are expected to assist in cultivar selection, optimal K fertilization of cotton fields and cotton breeding programs.

MATERIALS AND METHODS

Plant Material

A subset of eight cotton genotypes with contrasting dry matter yield in a K deficient solution (0.02 mM) was selected from 50 predominant cotton genotypes in China in 2004, after a preliminary experiment. Four of the inferior cultivars (‘SGK3’, ‘SCRC18’, ‘SCRC21’ and ‘SCRC22’) produced the lowest dry matter at the five-leaf stage, whereas the other four superior cultivars (‘Nannong8’, ‘Xiangza2’, ‘Xinluzao12’ and ‘Xiangza3’) produced the most. All cultivars were obtained from cotton breeding institutes or their associated seed companies.

Growth Chamber Experiment

Seeds were surface-sterilized with 9% hydrogen peroxide (H$_2$O$_2$) for 30 min, and then germinated in a K-free sand medium [soaked in 0.1 M hydrochloric acid (HCl) for 2 h, washed with tap and then de-ionized water several times until the pH of the washed-water equaled that of de-ionized water and the K in it was below the detection limit of the atomic absorption spectroscopy (SpectAA-50/55, Varian, Mulgrave, Australia)]. After emergence (4 d after germination), uniform seedlings were cultured hydroponically by transferring to 16 cm × 13 cm × 16 cm plastic pots filled with 2.2 L of 1/2-strength modified Hoagland’s solution, containing 0.02 mM (K-deficient) or 2.5 mM (K-sufficient) potassium chloride (KCl). Other constituents of the solution were (mM) 2.5 calcium nitrate [Ca(NO$_3$)$_2$], 1 magnesium sulfate (MgSO$_4$), 0.5 ammonium phosphate [(NH$_4$)$_2$PO$_4$], 2×10$^{-4}$ copper sulfate (CuSO$_4$), 1×10$^{-3}$ zinc sulfate (ZnSO$_4$), 0.1 iron sodium ethylenediaminetetraacetic acid (Fe Na EDTA), 2×10$^{-2}$ boric acid (H$_3$BO$_3$), 5×10$^{-6}$ ammonium molybdate [(NH$_4$)$_6$Mo$_7$O$_{24}$] and 1×10$^{-3}$ manganese sulfate (MnSO$_4$). Four uniform seedlings were raised per pot, under 12 h light/12 h dark at 30±2/22±2°C, 70~80% humidity and 600 µmol m$^{-2}$ s$^{-1}$ photosynthetically active radiation. All solutions were changed twice per week; de-ionized water was added daily to replace the water lost by evapotranspiration. Solution pH was maintained at 6.5 by adding concentrated solution of sodium hydroxide (NaOH) and air was bubbled into the solution to provide O$_2$ and achieve nutrient homogeneity.

A completely randomized design was used with three replications (pots). Plants were harvested at the five-leaf stage, about 21 d after transferring, to determine biomass and K concentration.
Field Experiment

A field experiment was conducted in 2006 at Shangzhuang Experiment Station (40°08′N; 116°10′E) of China Agricultural University. The soil was a sandy loam, with a pH of 8.0 (water:soil = 2.5:1.0), organic matter content of 0.92% (digested with potassium dichromate under strong acid condition), available nitrogen of 22.4 mg kg\(^{-1}\) (extracted with 1 M KCl), available phosphorus (P) of 6.9 mg kg\(^{-1}\) [extracted with 0.5 M sodium bicarbonate (NaHCO\(_3\))], and available K of 60 mg kg\(^{-1}\) [extracted with 1 M ammonium acetate (NH\(_4\)OAC)]. Based on the deficiency criteria of available K for cotton (Qin and Zhang, 1983), the soil used in this experiment was K-deficient (<70 mg kg\(^{-1}\)).

Seedlings of the genotypes were raised in a greenhouse to the two-leaved stage and transplanted on 18 May, in rows 6 m long with an inter-row spacing of 1.2 m and an intra-row spacing of 0.4 m for a plant density of 20,800 plant ha\(^{-1}\). A randomized complete block design was adopted with three replications. The field management followed conventional practices. We applied 123 kg nitrogen (N) ha\(^{-1}\) and 60 kg P ha\(^{-1}\), in the form of urea and di-ammonium phosphate before sowing. At the early flowering stage, urea-N was top-dressed at 123 kg N ha\(^{-1}\). Potassium fertilizer was not applied during the growing season. Plots were specially maintained bollworm-free by applying chemical pesticides to prevent damage to cotton. At maturity (13 October), three representative plants from each genotype were harvested for determination of dry weight of reproductive organs, including squares, flowers and bolls.

Analysis of K Concentration

Ten uniformly-sized seeds used for the present study as well as seedlings grown in either K-free sand for 4 d (just before transferring to culture solutions) or in K-deficient solution (0.02 mM) for 21 d were sampled per genotype, oven-dried at 80°C for 72 h and weighed. After weighing, the dry samples were ground into a fine powder, screened through a 0.5 mm sieve, soaked in 1.0 M HCl for 5 h, shaken for 30 min and filtered. Filtered solutions were analyzed for K by atomic absorption spectroscopy (SpectAA-50/55, Varian).

Measurement of K-Deficiency Symptoms in Cotyledons

Four days after the full spread of cotyledon, spotted symptoms of K deficiency appeared clearly. Cotyledons of K-deficient seedlings were scanned with an EPSON scanner (G780B, Seiko Epson, Tokyo, Japan), and the spot area as well as total cotyledon area were determined with an image analysis software (Advanced Motic Images 3.1, Xiamen, China). The ratio of spot
area to total cotyledon area (S value) was calculated by dividing the former by the latter.

**Estimation of Parameters Associated with K Nutrition**

The following traits were determined according to dry matter and K concentration: 1) K content of seed: dry mass of seed × K concentration; 2) relative dry weight: relative dry mass of whole plant in K-deficient (0.02 mM) vs. K-sufficient (2.5 mM) medium, being used to evaluate tolerance of K deficiency of genotypes (Gourley et al., 1993); 3) response to K supply: dry matter weight response per unit of added K; 4) K accumulation: dry matter weight of whole plant × K concentration; 5) K uptake efficiency: net K uptake (K accumulation in seedlings grown in nutrient solutions for 21 d minus K accumulation in seedlings just before transferring to nutrient solutions) divided by root dry mass (Elliott and Läuchli, 1985); 6) K efficiency ratio: dry mass produced per unit of K accumulation, i.e., total plant dry mass divided by total K accumulation (Gerloff and Gabelman, 1983); and 7) K utilization efficiency: dry matter produced per unit of K concentration, i.e., dry matter weight × reciprocal of K concentration (Siddiqi and Glass, 1981).

**Definition of K Efficient and K Inefficient Cultivars**

Based on the criteria proposed by Gerloff and Gabelman (1983), K efficient and K inefficient cultivars were defined as producing higher and lower dry mass under K deficiency but having similar yields when an optimal amount of K is available.

**Statistical Analysis of Data**

Analysis of variance and correlation were performed using SAS statistical software (V8, SAS Institute Inc., Cary, NC, USA), and means of genotypes were compared using Duncan’s multiple range test.

**RESULTS**

**Dry Matter Yield of Seedlings in K-Sufficient and Deficient Media**

All the genotypes produced similar dry matter in K-sufficient solution but K deficiency significantly reduced the dry matter yield by between 21% in ‘Xinluza012’ and 76% in ‘SCRC18’ (Table 1). The four cultivars with low biomass yield under K-deficiency, on average, had larger dry mass reductions of 74% while the other four yielding relatively higher biomass had average reductions of only 33% (Table 1). According to Gerloff and Gabelman (1983), the former may be categorized as ‘K inefficient’ while the latter may
**TABLE 1** Effects of potassium (K) availability on the dry matter of K inefficient and K efficient cotton seedlings

<table>
<thead>
<tr>
<th>Genotype</th>
<th>DW(_{0.02}) (g plant(^{-1}))(^z)</th>
<th>DW(_{2.5}) (g plant(^{-1}))(^y)</th>
<th>DW(<em>{0.02}) / DW(</em>{2.5}) (%)(^x)</th>
<th>RKS (mg DW mg(^{-1}) K)(^w)</th>
</tr>
</thead>
<tbody>
<tr>
<td>K inefficient</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SGK3</td>
<td>0.27 c</td>
<td>1.02 a</td>
<td>26.1 c</td>
<td>3.54 ab</td>
</tr>
<tr>
<td>SCRC18</td>
<td>0.28 c</td>
<td>1.18 a</td>
<td>23.5 c</td>
<td>4.23 a</td>
</tr>
<tr>
<td>SCRC21</td>
<td>0.30 c</td>
<td>1.17 a</td>
<td>25.4 c</td>
<td>4.09 a</td>
</tr>
<tr>
<td>SCRC22</td>
<td>0.30 c</td>
<td>1.17 a</td>
<td>25.9 c</td>
<td>4.09 a</td>
</tr>
<tr>
<td>Mean</td>
<td>0.29</td>
<td>1.13</td>
<td>25.2</td>
<td>3.99</td>
</tr>
<tr>
<td>K efficient</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nannong8</td>
<td>0.67 b</td>
<td>1.14 a</td>
<td>58.7 b</td>
<td>2.21 bc</td>
</tr>
<tr>
<td>Xiangza2</td>
<td>0.73 ab</td>
<td>1.17 a</td>
<td>62.6 b</td>
<td>2.07 c</td>
</tr>
<tr>
<td>Xinluzao12</td>
<td>0.76 a</td>
<td>0.96 a</td>
<td>79.0 a</td>
<td>0.95 c</td>
</tr>
<tr>
<td>Xiangza3</td>
<td>0.79 a</td>
<td>1.16 a</td>
<td>68.2 b</td>
<td>1.75 c</td>
</tr>
<tr>
<td>Mean</td>
<td>0.74**</td>
<td>1.10</td>
<td>67.2**</td>
<td>1.69**</td>
</tr>
</tbody>
</table>

\(^{z}\text{Dry weight of seedlings grown in K-deficient solutions (0.02 mM).}\)

\(^{y}\text{Dry weight of seedlings grown in K-sufficient solutions (2.5 mM).}\)

\(^{x}\text{Relative dry weight in K-deficient vs. K-sufficient medium.}\)

\(^{w}\text{Response of dry matter to K supply.}\)

Means within a column followed by the same letter are not significantly different at \(p < 0.01\) (\(n = 12\)) according to Duncan’s multiple range test. ** denotes a significant difference between the means of K inefficient and efficient genotypes at \(P < 0.01\) according to t test.

be classified as ‘K efficient’ genotypes. The genotypic variations in dry weight under K-deficiency among the four K efficient cultivars were significant while those among the K inefficient cultivars were not (Table 1).

As also shown in Table 1, the relative dry weight of K efficient genotypes (ranged from 59% to 79% with a mean of 67%) was greater than that of K inefficient genotypes (ranged from 24% to 26% with a mean of 25%), suggesting that K efficient genotypes also had higher tolerance to inadequate K supply. Alternatively, K inefficient genotypes had better response to K application; averaged for the four cultivars, the increased dry matter yield per unit of added K was 3.99 and 1.69 mg DW mg\(^{-1}\) K for inefficient and efficient cultivars, respectively (Table 1).

**K Content of Seed**

Although the seeds used for this study originated from different research institutes or seed companies, there were negligible differences in seed K content among them (Figure 1). The seed K content ranged from 0.74 to 0.82 mg seed\(^{-1}\) in K inefficient genotypes and 0.76 to 0.89 mg seed\(^{-1}\) in K efficient genotypes, and there were no significant differences in the mean seed K between K efficient and K inefficient genotypes (Figure 1).


Genotypic Variations in Potassium in Cotton

FIGURE 1 Comparison of potassium (K) content in seed (KCS) among K inefficient (SGK3, SCRC18, SCRC 21 and SCRC 22) and K efficient (Nannong8, Xiangza2, Xinluzao12, and Xiangza3) cotton genotypes. Bars with the same letters are not significantly different at $P < 0.01$ according to Duncan’s multiple range test.

**K Accumulation and Uptake Efficiency of Seedlings under K-Deficient Condition**

Potassium accumulation in seedlings (4 d after germination in K-free sand) just before transferring (Table 2) was only slightly lower than the seed K content (Figure 1), suggesting that much of the K accumulated in

<table>
<thead>
<tr>
<th>Genotype</th>
<th>$\text{K}_{\text{A0d}(\text{mg plant}^{-1})}$</th>
<th>$\text{K}_{\text{A21d}(\text{mg plant}^{-1})}$</th>
<th>$\text{NKU (mg plant}^{-1})$</th>
<th>RDW (g plant$^{-1}$)</th>
<th>KUE (mg K g$^{-1}$ RDW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SGK3</td>
<td>0.61 a</td>
<td>0.94 c</td>
<td>0.33 cd</td>
<td>0.032 b</td>
<td>10.31 bc</td>
</tr>
<tr>
<td>SCRC18</td>
<td>0.61 a</td>
<td>1.08 c</td>
<td>0.47 c</td>
<td>0.038 b</td>
<td>12.37 ab</td>
</tr>
<tr>
<td>SCRC21</td>
<td>0.71 a</td>
<td>0.99 c</td>
<td>0.28 d</td>
<td>0.038 b</td>
<td>7.37 c</td>
</tr>
<tr>
<td>SCRC22</td>
<td>0.73 a</td>
<td>1.13 c</td>
<td>0.40 cd</td>
<td>0.042 b</td>
<td>9.52 bc</td>
</tr>
<tr>
<td>Mean</td>
<td>0.67</td>
<td>1.03</td>
<td>0.37</td>
<td>0.038</td>
<td>9.87</td>
</tr>
<tr>
<td>Nannong8</td>
<td>0.70 a</td>
<td>1.82 b</td>
<td>1.12 b</td>
<td>0.091 a</td>
<td>12.51 ab</td>
</tr>
<tr>
<td>Xiangza2</td>
<td>0.69 a</td>
<td>2.04 ab</td>
<td>1.35 a</td>
<td>0.097 a</td>
<td>13.92 ab</td>
</tr>
<tr>
<td>Xinluzao12</td>
<td>0.80 a</td>
<td>2.25 a</td>
<td>1.45 a</td>
<td>0.097 a</td>
<td>14.95 a</td>
</tr>
<tr>
<td>Xiangza3</td>
<td>0.69 a</td>
<td>2.11 a</td>
<td>1.42 a</td>
<td>0.106 a</td>
<td>13.40 ab</td>
</tr>
<tr>
<td>Mean</td>
<td>0.72</td>
<td>2.06**</td>
<td>1.34**</td>
<td>0.098**</td>
<td>13.67**</td>
</tr>
</tbody>
</table>

$^a$K accumulation in seedlings just before transferring to solutions.

$^b$K accumulation in seedlings grown in solutions for 21 d.

$^c$Net K uptake in seedlings during hydroponic culture period.

$^d$Root dry weight.

$^e$K uptake efficiency.

Means within a column followed by the same letter are not significantly different at $p < 0.01$ ($n = 12$) according to Duncan’s multiple range test. ** denotes a significant difference between the means of K inefficient and efficient genotypes at $P < 0.01$ according to $t$ test.
seeds can be utilized. In addition, there were no significant differences in K accumulation among genotypes. However, after 21 d period of hydroponic culture, seedlings of K efficient genotypes accumulated twice as much K under K-deficiency. For example, the mean total K accumulation for K inefficient cultivars was 1.03 mg plant\(^{-1}\) (range: 0.94 to 1.13 mg plant\(^{-1}\)), whereas it was 2.06 mg plant\(^{-1}\) (range: 1.82 to 2.25 mg plant\(^{-1}\)) for the K efficient cultivars (Table 2). These results illustrated that K efficient cultivars uptake 262\% more K during hydroponic culture (Table 2).

The size of the root system and physiology of uptake are considered to be mechanisms of uptake efficiency (Steingrobe and Claassen, 2000). The higher net K uptake of K efficient cultivars mainly resulted from their larger root system, which exceeded that of K inefficient cultivars by 158\% (Table 2). Furthermore, K efficient cultivars had an advantage in uptake activity to some extent. The mean K uptake efficiency (calculated as total net K uptake divided by root dry weight) of K efficient cultivars was 38\% \((P < 0.01)\) higher than that of K inefficient cultivars, despite the marginal differences among genotypes (Table 2).

**K Utilization Efficiency of Seedlings under K-Deficient Condition**

In contrast to the K accumulation, the K concentration in the whole plant of K efficient cultivars was generally lower than that of K inefficient cultivars under K-deficient condition. The former ranged from 2.68 to 2.97 mg K g\(^{-1}\) DW, with a mean of 2.80 mg K g\(^{-1}\) DW; and the latter ranged from 3.34 to 3.89 mg K g\(^{-1}\) DW, with a mean of 3.62 mg K g\(^{-1}\) DW (Table 3). Because K efficiency ratio (g DW mg\(^{-1}\) K) is equivalent to the reciprocal of K con-

<table>
<thead>
<tr>
<th>Genotype</th>
<th>K concentration (mg K g(^{-1}) DW)</th>
<th>K efficiency ratio (g DW mg(^{-1}) K)</th>
<th>K utilization efficiency (g(^2) DW mg(^{-1}) K)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SGK3</td>
<td>3.53 c</td>
<td>0.28 de</td>
<td>0.075 c</td>
</tr>
<tr>
<td>SCRC18</td>
<td>3.89 a</td>
<td>0.26 f</td>
<td>0.071 c</td>
</tr>
<tr>
<td>SCRC21</td>
<td>3.34 d</td>
<td>0.30 d</td>
<td>0.089 c</td>
</tr>
<tr>
<td>SCRC22</td>
<td>3.72 b</td>
<td>0.27 ef</td>
<td>0.082 c</td>
</tr>
<tr>
<td>Mean</td>
<td>3.62</td>
<td>0.28</td>
<td>0.079</td>
</tr>
<tr>
<td>Nannong8</td>
<td>2.72 f</td>
<td>0.37 ab</td>
<td>0.246 b</td>
</tr>
<tr>
<td>Xiangza2</td>
<td>2.82 ef</td>
<td>0.36 b</td>
<td>0.259 b</td>
</tr>
<tr>
<td>Xinluzao12</td>
<td>2.97 c</td>
<td>0.34 c</td>
<td>0.255 b</td>
</tr>
<tr>
<td>Xiangza3</td>
<td>2.68 f</td>
<td>0.37 a</td>
<td>0.295 a</td>
</tr>
<tr>
<td>Mean</td>
<td>2.80**</td>
<td>0.36**</td>
<td>0.264**</td>
</tr>
</tbody>
</table>

Means within a column followed by the same letter are not significantly different at \(p < 0.01\) \((n = 12)\) according to Duncan’s multiple range test. ** denotes a significant difference between the means of K inefficient and efficient genotypes at \(P < 0.01\) according to \(t\) test.
centation, this parameter was generally higher for K efficient cultivars than K inefficient cultivars. The mean K efficiency ratio for K efficient cultivars (0.72 g DW mg\(^{-1}\) K) was 29% higher \((P < 0.01)\) than that for K inefficient cultivars (0.56 g DW mg\(^{-1}\) K) (Table 3). Similarly, the K utilization efficiency (i.e., total dry mass per unit of K concentration) averaged across the four K efficient cultivars was 233% higher \((P < 0.01)\) than that of the four K inefficient cultivars (Table 3).

**K-Deficiency Symptoms in Cotton Cotyledons**

Under K-deficiency, once the cotyledon spread fully, symptoms (in form of spots) of K deficiency appeared clearly several days later. Significant differences among genotypes were found in the ratio of spotted area to the total area of cotyledons \((S\text{ value})\) (Figure 2). For the K inefficient genotypes, the \(S\) values ranged from 50% in ‘SCRC18’ to 65% in ‘SCRC22’ with a mean of 55%. For the K efficient genotypes, they ranged from 3% in ‘Xinluza12’ to 25% in ‘Xiangza3’ with a mean of only 16%, being 71% lower \((P < 0.01)\) than the former (Figure 2).

**Dry Weight of Reproductive Organs Determined from the Field Experiment**

Although there were obvious differences in growth medium and environmental factors, the plant parameters at the seedling stage in growth chamber and in field experiments showed similar genotypic variations in K inefficient and K efficient cultivars. For each K inefficient cultivar, the dry weight of reproductive organs was significantly \((P < 0.01)\) lower than that of

![FIGURE 2](https://example.com/fig2.png)

**FIGURE 2** Comparison of the ratio of spotted area caused by potassium (K) deficiency to total cotyledon area \((S\text{ value})\) among K inefficient (SGK3, SCRC18, SCRC21 and SCRC22) and K efficient (Nannong8, Xiangza2, Xinluza12 and Xiangza3) genotypes. Bars with the same letters are not significantly different at \(P < 0.01\) according to Duncan’s multiple range test.
FIGURE 3 Comparison of dry weight of reproductive organs (RODW, including squares, flowers and bolls) among K inefficient (SGK3, SCRC18, SCRC21 and SCRC22) and K efficient (Nannong8, Xiangza2, Xinluzao12 and Xiangza3) cotton genotypes at field maturity with available soil potassium (K) at an obviously deficient level (60 mg kg$^{-1}$). Bars with the same letters are not significantly different at $P < 0.01$ according to Duncan’s multiple range test.

‘Xiangza3’, which had the lowest value among the four K efficient cultivars (Figure 3). Also, the mean dry weight of reproductive organs averaged across the four K efficient cultivars was 212.0 g plant$^{-1}$ or 59% higher than the 133.2 g plant$^{-1}$ for the four K inefficient cultivars.

**DISCUSSION**

The term ‘nutrient efficiency’ has been used widely as a measure of the capacity of a plant to acquire and utilize nutrients for economic production (Gourley et al., 1994). Gerloff and Gabelman (1983) proposed that germplasms differing in yields under nutrient stress could only be designated efficient and inefficient if they have similar yields when an optimal amount of the nutrient is available. If the same maximum yield is not achieved, factors other than the nutrient are likely to be influencing plant growth. Following the definition proposed by Gerloff and Gabelman (1983), the four cultivars producing higher dry mass under K deficiency in the present study may be categorized as ‘K efficient’, while the other four with lower dry mass may be classified as ‘K inefficient’ genotypes.

It has been well documented that genotypic differences in nutrient efficiency within a plant species result from differences in uptake efficiency and/or utilization efficiencies (Gerloff, 1977; Gerloff and Gabelman, 1983). Use efficient plants could produce high yields with a low K concentration in their dry matter; uptake efficient plants could realize a higher K uptake in spite of low K availability to guarantee better growth.

Generally, use efficiency is defined as total plant biomass produced per unit nutrient absorbed (i.e. nutrient efficiency ratio), which is equivalent
to the reciprocal of nutrient concentration in the entire plant (McLachlan, 1976; Gerloff and Gabelman, 1983; Elliott and Läuchli, 1985). However, Siddiqi and Glass (1981) argued that the reciprocal of nutrient concentration does not consider the yield of the crop. Instead they suggested that the product of yield and the reciprocal of nutrient concentration (i.e., K utilization efficiency) was a more appropriate measure of utilization efficiency.

Nevertheless, when the mechanisms for enhanced nutrient utilization are considered, K efficiency ratio may be better than K utilization efficiency because a truly efficient germplasm could require fewer nutrients than an inefficient germplasm for normal metabolic processes. The calculation of utilization efficiency, however, includes both yield and plant nutrient concentration, and is likely to complicate the identification of potential mechanisms associated with enhanced nutrient efficiency (Gourley et al., 1994). Therefore, using just one efficiency indicator may usually not be sufficient to adequately describe the K efficiency of a crop (Gourley et al., 1994; Gerendás et al., 2008). In the present study, the K efficient cultivars had either higher K efficiency ratio or higher K utilization efficiency than the K inefficient cultivars, but the differences in the former between two groups of cultivars were less pronounced (Table 3).

For ions such as K$^+$ that moves to the root surface primarily by diffusion, plant uptake from soil is most associated with root surface area (Silberbush and Barber, 1983). In agreement with this, Brouder and Cassman (1990) found that differences in root surface area at 0.10–0.30 m depth were positively correlated with cotton cultivar differences in K uptake, and K-efficient cultivar Acala GC510 had a 58% more total root surface area and a 37% more K than the K-inefficient cultivar Acala SJ-2 after peak bloom. Under hydroponic culture, however, root size theoretically does not limit K uptake unless the uptake capacity of root is saturated (i.e., uptake at $V_{\text{max}}$), because K$^+$ reaches roots quickly enough in a nutrient solution, and supply is not any more a constraint to K uptake. Well then, does the uptake capacity of cotton root under conditions of this study reach the maximum or not? According to our unpublished data about other cotton cultivars grown under similar conditions, $K_m$ (the concentration where influx is one-half of $V_{\text{max}}$) for K uptake was only about 0.003 mM, which was much less than the K concentration (0.02 mM) in nutrient solution. Hence, we speculate that the rate of K absorption of cotton seedling roots has reached the maximum, and thus there is a high correlation between root size and K uptake in the present study. Considering the 158% more root dry weight in K efficient genotypes compared with K inefficient genotypes, it was concluded that the root size actually contributed more to K uptake by the former (Table 2). Moreover, the uptake rate (net K uptake per unit root dry weight) was also 38% higher for K efficient genotypes.

Based on the response of the cultivars to K supply and their dry weight potential at low K supply (Gerloff, 1977), the K efficient genotypes can be
classified as efficient non-responders, able to maintain a relatively high yield under K deficiency, thus having good adaptation to K-limited conditions; in contrast, the K inefficient genotypes are inefficient responders, adaptable to high K input.

Caradus (1994) observed that genotypic variation in P efficiency among white clover cultivars under greenhouse conditions was not identical and was poorly correlated with the variation under field conditions. However, we obtained a high correlation \((r = 0.7339, P < 0.05, n = 8)\) between total dry weight of seedlings grown in low K solution (0.02 mM) and dry weight of reproductive organs in field experiment with available soil K at an obviously deficient level (60 mg kg\(^{-1}\)). This indicated that K efficient genotypes, identified in low K solution at the seedling stage, also had higher economic yield under low field K. However, we also noticed that the genotypic variation among K efficient and inefficient cultivars in field experiment was less than that under solution culture condition. This might have been due to differences in growth medium (nutrient solution vs. soil), environment (growth chamber vs. field), and growth stage (seedling stage vs. maturity stage). In addition, Gerendás et al. (2008) pointed out that efficiency indicators based on total dry matter fail to provide an adequate picture when considering agronomic yield, unless the harvest index is maintained. Thus the less genotypic variation in field experiment in the present study might also be owed to the differences in harvest index among genotypes.

Although Yan et al. (1995) attributed differences in P efficiency among common bean genotypes to differences in seed P content, we found no relationship between the K content in seed and genotypic variation in K efficiency of cotton. The mean K content in the seed of K efficient genotypes was similar to that of K inefficient genotypes, whereas its mean S value was 71\% lower than that of the latter (Figure 2), and dry weights of seedlings and reproductive organs at maturity were 157\% and 59\% higher (Table 1 and Figure 3).

It is interesting that the four K inefficient cultivars ('SGK3', 'SCRC18', 'SCRC21', and 'SCRC22') in the present study were all transgenic insect-resistant cultivars. In a previous study (Zhang et al., 2007), we also found that the transgenic insect-resistant cultivars, CCRI41 and DP99B were more sensitive to K deficiency than the non-transgenic insect-resistant cultivars, CCRI36 and CCRI35. In yet another study (Tian et al., 2008), in which we classified forty-eight cotton genotypes into thirty-three transgenic insect-resistant and fifteen non-transgenic insect-resistant genotypes, we noted that the tolerance of the former to low-K was inferior, and their total dry weight, K accumulation and K utilization efficiency at the seedling stage and dry weight of reproductive organs in the field decreased by 20\% \((P < 0.01)\), 15\% \((P < 0.05)\), 24\% \((P < 0.01)\) and 21\% \((P < 0.05)\), respectively, as compared to those of the latter. It therefore seems that the lower K efficiency is a general phenomenon of transgenic insect-resistant cotton.
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rather than a phenomenon particular to cultivars selected for the present investigations.

Furthermore, Huang (2007) indicated that the cotton germplasm used for foreign genes (Bt and CpTI) transformation included the descendant of interspecific (G. barbadense × G. hirsutum) or trispecific (G. barbadense × G. thurberi × G. hirsutum) hybrid (such as ‘SGK3’, ‘SCRC22’), Uganda cotton (such as ‘SCRC21’), and Empire cotton (such as CCRI41). In addition, the recurrent parent of DP99B was Delta and Pineland cotton. Consequently, the lower K efficiency of transgenic insect-resistant cotton is possibly due to the introduction of foreign genes (Bt and CpTI) encoding insecticidal protein into plants and may be independent of the cotton germplasm used for transformation.

It is known that the mechanism for controlling Lepidoptera by Bacillus thuringiensis endotoxin is that hydrolysis of the toxin yields an inhibitor of K transport, presumably a polypeptide, in midgut (Harvey and Woltersberger, 1979; Crawford and Harvey, 1988). Therefore, it is need to design further studies to investigate the effect of Bacillus thuringiensis endotoxin produced endogenously in plants of transgenic insect-resistant cotton on K uptake. Recently, Yan et al. (2007) observed that deficiencies of P and K in nutrient solution caused a large increase in the total amino acid and soluble sugar secretions from root of both transgenic cotton containing Bt (Bt-cotton) and wild-type (WT) control, but with larger increases in the former. This implied that consumption of substances and energy in Bt-cotton was more than WT under K deficiency, which was probably in relation to the decreased K use efficiency of transgenic insect-resistant cotton grown in K deficient solution (Table 3).

In summary, the transgenic insect-resistant cotton usually needed more potassium fertilizer than non-transgenic insect-resistant cotton to achieve a comparable yield and fiber quality (Guo and Huang, 2004; Bai et al., 2005; Li and Liu, 2005). Of the four K efficient cultivars studied, three (‘Nannong8’, ‘Xiangza2’, and ‘Xiangza3’) were hybrid cotton, indicating that heterosis might be involved in the K efficiency of cotton.

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