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The Effect of Potassium Deficiency on Growth and Physiology in Sweetpotato [*Ipomoea batatas* (L.) Lam.] during Early Growth

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***Abstract*. Potassium (K^+) is an essential nutrient element for the growth and development of sweetpotato [*Ipomoea batatas* (L.) Lam.]. To investigate growth and physiological responses to K^+ deficiency during early growth stage of sweetpotato, two representative cultivars with different tolerance to K^+ deficiency were chosen. The seedlings of 'Xushu 32' (tolerance to K^+ deficiency) and 'Ningzishu 1' (sensitive to K^+ deficiency) were cultured in three different K^+ concentrations (K0: 0 mmol·L^{-1} K^+; K1: 5 mmol·L^{-1} K^+; and K2: 20 mmol·L^{-1} K^+, the control) of nutrient solution. Results showed that the extreme K^+ deficiency (K0) significantly reduced the total dry weight, leaf number, root length, and chlorophyll content (CCI) compared with K2. However, the growth traits of 'Xushu 32' were less suppressed than those of 'Ningzishu 1'. The net photosynthetic rate (P_n), stomatal conductance (g_S), and transpiration rate (T_r) of 'Ningzishu 1' were significantly decreased in K0 and K1 (low K^+), whereas 'Xushu 32' showed no significant change in K1 treatment. Increasing minimal fluorensence (F_0) of 'Ningzishu 1' comes with decreased maximum quantum efficiency of photosystem II (PSII) photochemistry (F_v/F_m) and photochemical quenching (q_P) at K0 treatment. However, all the chlorophyll fluorescence parameters in 'Xushu 32' were nonsignificantly changed by K^+ deficiency (K0 and K1). These results suggest that 'Xushu 32' could maintain a better growth state to adapt to K^+ deficiency stress, which may be mainly because of a lighter affected photosynthesis and a less damaged PSII reaction center.**

Potassium (K^+) is an essential macronutrient required for crop growth and development, which is known to modify abundant enzyme activations in different metabolic pathways and to regulate cell osmotic pressure and stomatal movements (Coskun et al., 2014; George et al., 2002; Marschner, 2011; Singh et al., 2003). It has been proved that appropriate K^+ additions can increase crop yields and improve crop quality (Bednarz and Oosterhuis, 1999; Constantin et al., 1977; He et al., 2004). Sweetpotato [*Ipomoea batatas* (L.) Lam.] is an important human food, animal feed, and industrial raw material, which is grown in more than 100 countries and mainly produced in China (FAO, 2011; Jin, 2012). Sweetpotato is a typical "K-favoring" crop (Tang et al., 2014); its growth as well as developmental and physiological responses can be affected by conditions of K^+ deficiency (Gajanayake et al., 2014). With an increase in arable soil facing serious K^+ deficiency (Hijmans et al., 2001), it has become a key factor affecting the productivity and quality of sweetpotato (Karam et al., 2009; Yang et al., 2003).

Crops have genotype differences in tolerance to stress. Tolerant cultivars had high absorption efficiency and low effect on growth and production in K^+ deficiency stress (Wang et al., 2012; Zhao et al., 2016). Sweetpotato has been known to exhibit genotypic variation in K^+ uptake and utilization efficiency (George et al., 2002). Exploring its physiological characters of tolerance to K^+ deficiency can provide a basis for increasing the fertilizer utilization and improving the yield in K-deficiency soil. Previous studies have shown that K^+ deprivation can induce changes in the relative growth of roots, nodules, and shoots in higher plants (Høgh-Jensen, 2003; Wang and Wu, 2013). In sweetpotato, its root dry matter yield and biomass productivity significantly affected by K^+ supplied; intraspecific variation among genotypes also existed (Wang et al., 2015a). The negative impact on the T_r, P_n, and g_S in K^+ deficiency condition is well documented in other crops (Kanai et al., 2011; Reddy and Zhao, 2005). Potassium deficiency also affects foliar chlorophyll synthesis and stability, and modifies the chloroplast ultrastructure of leaves (Zhao et al., 2001). Such responses to K^+ deficiency may also exist in sweetpotato.

Chlorophyll fluorescence kinetics is an important way to detect and analyze plant photosynthetic function, and this method has been gradually applied to studies on plant nutrition stress; e.g., for nitrogen (N) (Bürling et al., 2011), magnesium (Mohotti and Lawlor, 2002), and phosphorus (Yang et al., 2004). However, chlorophyll fluorescence kinetics has been rarely reported for sweetpotato in conditions of K^+ deficiency. Prior studies have reported that K^+ deficiency affects plant growth and development processes, particularly when it occurs during the early growth stage of plant establishment (Karam et al., 2009; Ning et al., 2013; Yang et al., 2003; Zhao et al., 2001). As for sweetpotato, the root differentiation process is basically completed in the early growth stage (about 30 d after the cutting being transplanted), and the growth status of root is closely related to the effective sweetpotato number, which has a decisive effect on the final root yield (Wang et al., 2005). It has been proved that, when K^+ deficiency occurs at this stage, the number of branches and leaves, the biomass, and leaf area per plant are significantly decreased, resulting in the reduction of the yield and quality (Ning et al., 2013). Therefore, it is necessary to research the information regarding the growth and physiological responses of sweetpotato to K^+ deficiency in the early growth stage, and the possible mechanisms would provide a basis for further exploration on resistance cultivation and molecular breeding for low K^+ in sweetpotato.

This study presents a comparison between two different low-K-tolerant varieties in terms of their differential physiological responses to K^+ deficiency stress. The aims were to investigate the effects of K^+ deficiency during early growth stage on sweetpotato growth, physiology, photosynthetic, and chlorophyll fluorescence parameters, and to make a preliminary study of the possible mechanism underpinning sweetpotato tolerance to K^+ deficiency.

Materials and Methods

Plant materials. The two cultivars, 'Xushu 32' (tolerant to K^+ deficiency, short vine, dark green leaf, light yellow flesh, and good taste, bred by Xuzhou Sweetpotato Research Center, Jiangsu) and 'Ningzishu 1' (sensitive to K^+ deficiency, purple flesh, and good taste, bred by Jiangsu Academy of Agricultural Sciences) are widely cultivated in China. The two cultivars were screened

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from 31 materials according to their K^+ utilization efficiencies and K^+ sensitivity index (relative root weight) (Tang et al., 2014). In the following field experiment, it has been proved that 'Xushu 32' has a higher total biomass productivity and root yield, as well as higher protective enzyme activities than those of 'Ningzishu 1', in K^+ deficiency condition (Tang et al., 2015).

In this experiment, sweetpotato seedlings with consistent growth were chosen to take the cuttings with a length of 20 ± 0.5 cm, a base stem diameter of 12–13 mm, four leaves, and three internodes. The cuttings were cultured in water and placed in shadow. After 3 d of recovery, they were transplanted to a hydroponic system.

Growth conditions. The experiment was conducted from 13 July to 15 Aug. 2016 in the rainproof greenhouse of the Xuzhou Sweetpotato Research Center, Jiangsu Province, China. As shown in Fig. 1, the hydroponic system was mainly composed of PVC pipes, mini water pump, and nutrient solution container. The PVC pipes were the planting container, with a diameter of 110 mm and a length of 1.6 m; 2 cm in diameter holes were equidistantly distributed (spacing 15 cm, totally 15 holes) at the top. The nutrient solution flowed through the PVC pipes and circulated via water pump. The nutrient solution in the PVC pipes was at shallow depth, to ensure the nutrient solution circulation and adequate oxygen in the root domain. Single cutting fixed with foam collars in a planting basket was put into the hole, and a portion of the stem was immersed in the nutrient solution to promote rooting. Fifteen cuttings of the same variety were planted in one PVC pipe, and the three pipes on same floor were set as one replicate. The experiment was conducted using a randomized design with three replicates per treatment.

The nutrient solution was modified by using Hoagland's nutrient solution to contain 6.0 mmol·L^{-1} $CaCl_2$, 6.0 mmol·L^{-1} $NaNO_3$, 1.0 mmol·L^{-1} $NH_4H_2PO_4$, 4.0 mmol·L^{-1} $MgSO_4$, 0.2 mmol·L^{-1} $FeSO_4$, 0.26 mmol·L^{-1} EDTA, 46 µmol·L^{-1} H_3BO_3, 10 µmol·L^{-1} $MnSO_4$, 0.76 µmol·L^{-1} $ZnSO_4$, 0.32 µmol·L^{-1} $CuSO_4$, and 0.0162 µmol·L^{-1} $(NH_4)_6Mo_7O_{24}$. Three levels of the K^+ treatment were set at 0 mmol·L^{-1} (K0), 5 mmol·L^{-1} (K1), and 20 mmol·L^{-1} (K2) (i.e., control) using K_2SO_4. The nutrient solution was renewed once a week.

Gas exchange and chlorophyll fluorescence measurement. Gas exchange and chlorophyll fluorescence parameters were measured using a portable photosynthesis system (LI-6400 XT, LI-COR, Inc., Lincoln, NE). The P_n, T_r, g_S, and intercellular CO_2 concentration (C_i) were measured on the upper, third fully-expanded leaves of the main stem at 9:30–11:30 AM 10, 17, 24, and 31 d after treatment (DAT). The chamber environment was controlled and set at a constant airflow rate of 500 µmol·s^{-1}, a leaf temperature of 28 ± 0.5 °C, a CO_2 concentration of (400 ± 5) µmol·mol^{-1}, and a photosynthetic photon flux density of 1000 µmol·m^{-2}·s^{-1} provided by a red/blue light source. The chlorophyll fluorescence parameters were measured on the same leaves after keeping in the dark for 30 min on the 24 DAT, including F_0, the maximal fluorescence (F_m), F_v/F_m, q_P, and nonphotochemicalquenching (q_N). Three representative leaves were chosen to evaluate the parameters, and the means were used as the treatment values for each measurement.

Growth characteristics and root activity measurement. Plants were sampled at 10, 17, 24, and 31 DAT. Three seedlings from each replicate were randomly collected to count their number of green leaves, and to measure their shoot and root lengths each time. Total leaf CCI was estimated on the same leaves using a portable chlorophyll meter (CCM-200; Opti-Sciences, Tyngsboro, MA). Roots were cut from the same seedlings and washed with distilled water. Root activity was analyzed by the triphenyl tetrazolium chloride (TTC) method (Wang et al., 2006). In brief, 1.0 g fresh root was immersed in 10 mL of equally mixed solution of 0.4% TTC and phosphate buffer, and kept in the dark at 37 °C for 2 h. Subsequently, 2 mL of 1 mol·L^{-1} H_2SO_4 was added to stop the reaction with the root. The root was dried using filter paper and then extracted with ethyl acetate. The red extractant was transferred into the volumetric flask to reach 10 mL by adding ethyl acetate. The absorbance of the extract at 485 nm was recorded. Root activity was expressed as TTC reduction intensity. Root activity = amount of TTC reduction (µg)/time (h) × fresh root weight (g FW). At 31 DAT, three more plants were sampled and separated into shoot and root parts, which were oven-dried at 105 °C for 30 min and then again at 80 °C for 72 h to a constant weight.

Statistical analysis. All data were analyzed using the software program SPSS (SPSS Statistics v. 17.0), and the results were presented as the sample means ± SD ($n = 3$). Statistical analysis used analysis of variance followed by Turkey's test at a significance level of $P = 0.05$.

Results

Effects of K^+ deficiency on dry weight

The total dry weight of 'Ningzishu 1' (sensitive to K^+ deficiency) significantly decreased in conditions of K^+ deficiency (K0 and K1 levels) (Table 1) at 31.8% and 19.1% compared with the control (K2), respectively. But for 'Xushu 32' (tolerant to K^+ deficiency), the corresponding decrease of K0 and K1 was at 14.1% and 8.0%, respectively, which were lower than those of 'Ningzishu 1'. The total dry weight of 'Ningzishu 1' was significantly lower than the corresponding values of 'Xushu 32' in K0 and K1, respectively, but showed no significant difference in the K2 level. The variations of shoot dry weight of the two varieties were similar to total dry weight, except for that there was no significant difference between the three K^+ level treatments for 'Xushu 32'.

The root dry weight of K2 was significantly higher than that of K0 and K1 for 'Ningzishu 1'. As to 'Xushu 32', there was a slight decrease in root dry weight when the K^+ concentrations were reduced, but no significant difference was shown between the three K^+ levels. In each K^+ level, the root dry weight as well as the root/shoot ratio of 'Ningzishu 1' was significantly lower than that of 'Xushu 32'. The root/shoot ratio of 'Ningzishu 1' was significantly decreased in K0 condition, which was not shown in 'Xushu 32'. The K0 of 'Ningzishu 1' had the lowest values for all the trait responses.

Effects of K^+ deficiency on seedling growth characteristics

Number of expanded leaves. The K^+ deficiency caused a decrease in leaf number in the two cultivars (Fig. 2). In 'Xushu 32', the number of expanded leaves showed statistically significant differences mainly at 31 DAT. By contrast, the 'Ningzishu 1' has shown significant difference in K0 since day 10 by comparing with either K1 or K2. At 31

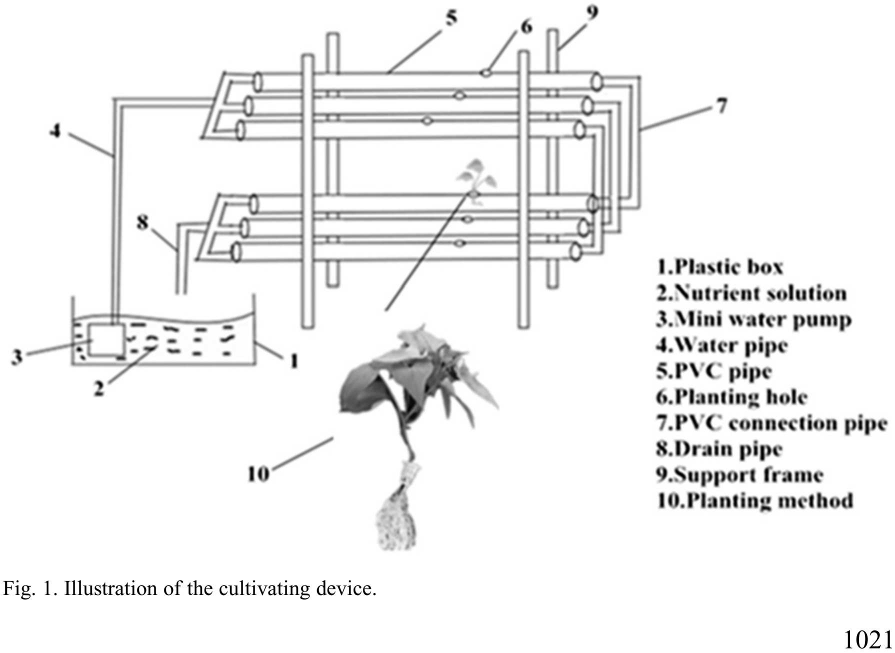

Fig. 1. Illustration of the cultivating device.

Table 1. Effects of potassium deficiency on dry weight and root/shoot ratio of two sweetpotato varieties.

Variety	Treatment	Root dry weight (g/plant)	Shoot dry weight (g/plant)	Total dry weight (g/plant)	Root/shoot
Xushu 32	K0	0.93 ± 0.12 ab^z	3.77 ± 0.25 ab	4.70 ± 0.17 b	0.25 ± 0.04 ab
	K1	1.10 ± 0.17 ab	3.93 ± 0.12 ab	5.03 ± 0.25 ab	0.28 ± 0.04 a
	K2	1.20 ± 0.10 a	4.27 ± 0.23 a	5.47 ± 0.25 a	0.28 ± 0.03 a
Ningzishu 1	K0	0.43 ± 0.12 c	3.00 ± 0.30 c	3.43 ± 0.40 d	0.14 ± 0.03 c
	K1	0.60 ± 0.10 c	3.47 ± 0.21 bc	4.07 ± 0.29 c	0.17 ± 0.02 bc
	K2	0.87 ± 0.06 b	4.17 ± 0.15 a	5.03 ± 0.21 ab	0.21 ± 0.01 ab

K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; K2: 20 mmol·L^{-1} K$^+$ (control).

^{z}Means within same column followed by different letters (a, b, and c) are significantly different between K treatments of the two genotypes ($P < 0.05$). Data are means ± SD ($n = 3$).

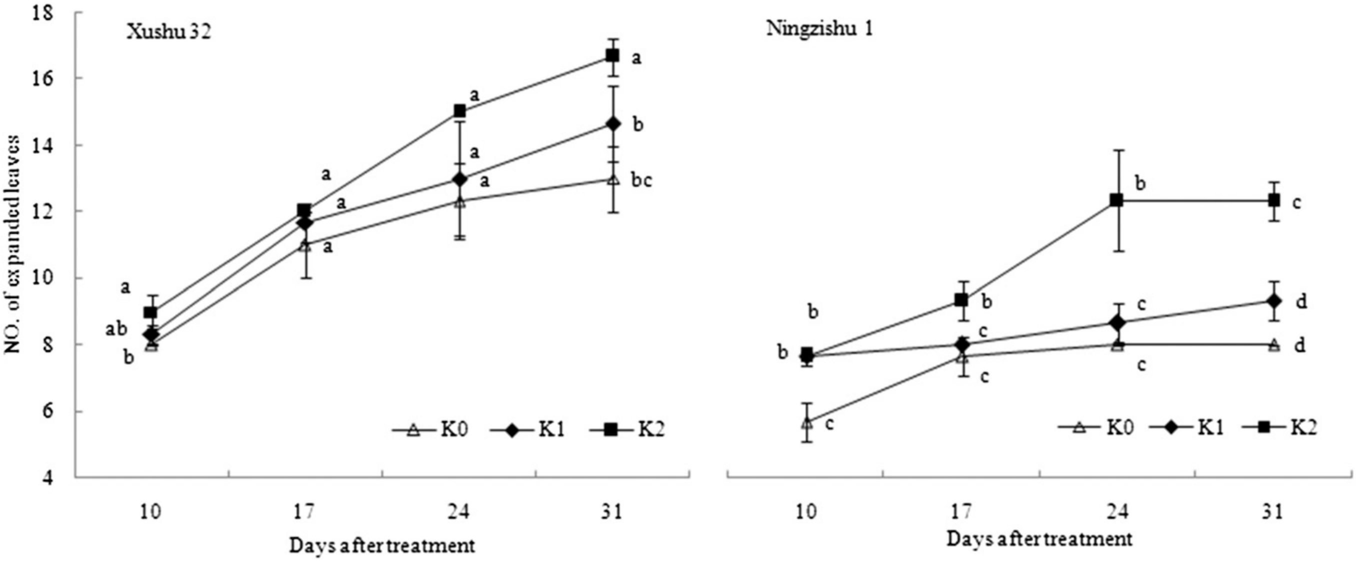

Fig. 2. Effects of potassium deficiency on the number of expanded leaves of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD ($n = 3$). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

DAT, the decrease of K0 and K1 was at 35.1% and 24.3% compared with K2, respectively. For 'Xushu 32', the corresponding decreases were lower, at 22.0% and 12.0%, respectively. On the other hand, the leafing rates of 'Ningzishu 1' were lower than those of 'Xushu 32', in each K$^+$ level condition.

Shoot length and root length. The shoot lengths of 'Xushu 32' were lower than that of 'Ningzishu 1', whereas the response in root lengths showed an opposite pattern (Figs. 3 and 4). Over the experimental period, the shoot lengths for 'Xushu 32' showed few differences among the treatment levels, whereas for 'Ningzishu 1', the shoot lengths were significantly reduced at K$^+$ deficiency conditions (i.e., K0 and K1). At 31 DAT, the shoot lengths of K0 and K1 in 'Xushu 32' had decreased by 8.4% and 5.9% compared with K2, respectively, whereas the corresponding decreases were significant at 20.7% and 13.4% for 'Ningzishu 1'.

The stress of K$^+$ deficiency significantly reduced the root length of both sweetpotato cultivars. At 31 DAT, root length of 'Xushu 32' in K0 and K1 treatment was 15.7% and 13.6% lower than that of K2, respectively. As for 'Ningzishu 1', the corresponding decreases were higher by 22.8% and 18.1%, respectively.

Chlorophyll content. The K$^+$ deficiency caused decreases in CCI in the two cultivars (Fig. 5). Significant differences were evident among the K0, K1, and K2 treatment levels only in 'Ningzishu 1' from 10 to 31 DAT. At 31 DAT, the CCI of K0 and K1 in 'Xushu 32' was 27.5% and 17.1% lower than that of K2, respectively; whereas the corresponding values of 'Ningzishu 1' had significantly decreased by 59.8% and 35.3%. The CCI of the two varieties declined steadily from 10 to 31 DAT. Over this period, the CCI of K0, K1, and K2 in 'Xushu 32' decreased by 47.4%, 44.9%, and 43.3%, respectively. However, in the case of 'Ningzishu 1', the corresponding decreases were more remarkable at 77.7%, 70.3%, and 60.0%, respectively.

Effects of K$^+$ deficiency on root activity. Root activity variations are shown in Fig. 6. The K$^+$ deficiency decreased root activity in the two cultivars, but only 'Ningzishu 1' showed significant differences between K0 and K2 level from 24 to 31 DAT of the experiment. For 'Ningzishu 1', their root activity in the K0 and K1 conditions was reduced by 43.9% and 20.7% compared with that of K2, respectively. Moreover, the reduction of K0 and K1 in 'Ningzishu 1' was 54.7% and 40.8%, respectively, from 10 to 31 DAT, whereas the corresponding reduction was 39.6% and 36.8%, for 'Xushu 32'.

Effects of K$^+$ deficiency on leaf photosynthesis

Net photosynthesis. The extreme K$^+$ deficiency (K0) caused significant decreases in P_n of the two cultivars from 10 to 31 DAT (Fig. 7). At 31 DAT, the P_n of K0 and K1 in 'Xushu 32' decreased by 44.6% and 29.9% compared with K2, respectively; the corresponding decreases of 'Ningzishu 1' were 59.7% and 30.8%. At 10 DAT, the P_n of each K$^+$ level in 'Ningzishu 1' was higher than that of 'Xushu 32', but was lower than that of 'Xushu 32' at 31 DAT. The P_n of the two sweetpotato varieties decreased gradually from 10 to 31 DAT. By 31 DAT, relative to 10 DAT, the decline in their P_n was 54.0%, 51.5%, and 45.0% for K0, K1, and K2 in 'Xushu 32', respectively, which was obviously lower than the corresponding decline of 80.0%, 68.6%, and 61.1% in 'Ningzishu 1', respectively.

Stomatal conductance. The changes in g_S in the two cultivars are shown in Fig. 8. A lower K$^+$ concentration applied revealed a lower g_S response, as significantly shown from 24 to 31 DAT for 'Ningzishu 1'. For 'Xushu 32', the corresponding decreases were also shown but much lower, and there was no significant difference between K0 and K1. The g_S of 'Xushu 32' decreased from 10 to 31 DAT, amounting to 43.0%, 50.3%, and 49.7% for K0, K1, and K2, respectively. However, in the case of 'Ningzishu 1', the corresponding g_S values were reduced by 90.2%, 84.3%, and 77.5%, respectively. Furthermore, the g_S of three treatment levels in seedlings of 'Ningzishu 1' was greater than

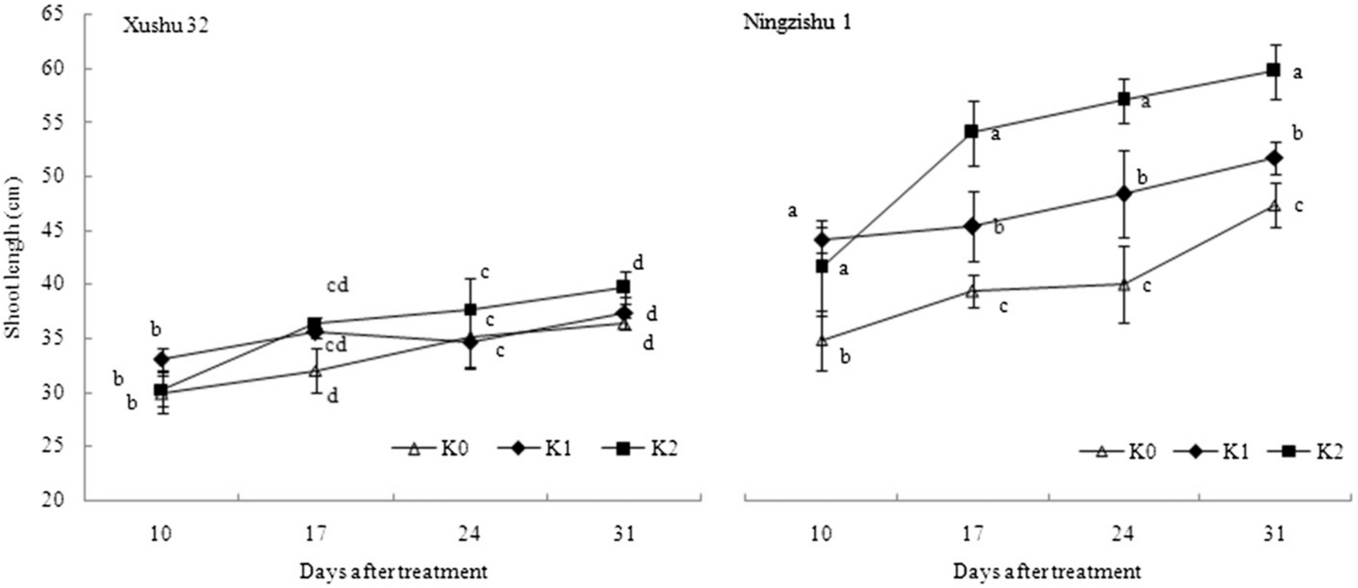

Fig. 3. Effects of potassium deficiency on the shoot length of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD (n = 3). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

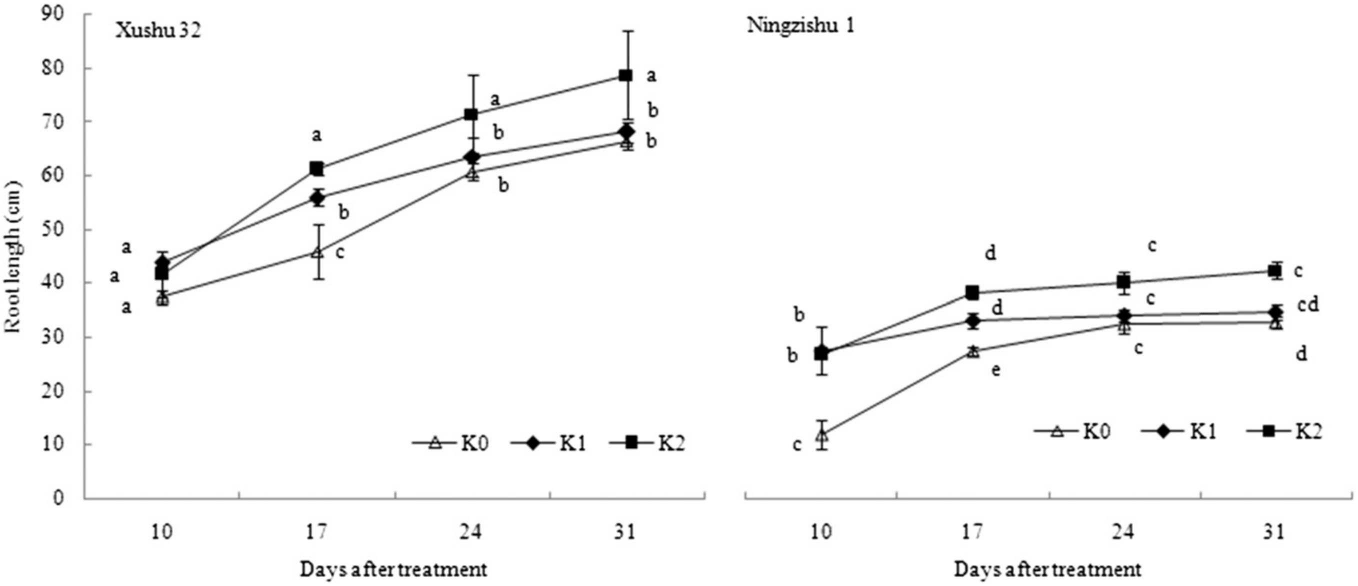

Fig. 4. Effects of potassium deficiency on the root length of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD (n = 3). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

those in ‘Xushu 32’ at 10 DAT, respectively, whereas this was reversed at 31 DAT.

Transpiration rate. The changes in T_r in the two cultivars are shown in Fig. 9. The K$^+$ deficiency caused T_r to significantly decrease in the two cultivars. At 31 DAT, the T_r of K0 and K1 had decreased by 42.7% and 22.9% when compared with K2 in ‘Xushu 32’, respectively; this change was lower than that in ‘Ningzishu 1’ (66.0% and 39.4% decrease, respectively). At 31 DAT, relative to 10 DAT, the reductions in T_r were 54.6%, 42.7%, and 40.7% for K0, K1, and K2 in ‘Xushu 32’, respectively, which were lower than the corresponding reductions of 88.7%, 80.3%, and 63.1% in ‘Ningzishu 1’.

Intercellular CO_2 concentration. The variations of C_i of the two cultivars were inconsistent (Fig. 10). The K$^+$ deficiency caused the C_i of ‘Xushu 32’ to decrease at 17 DAT after treatment, after which it exceeded the control (K2). Nevertheless, no significant differences were found among three treatment levels during the experimental period. Although the C_i of K1 in ‘Ningzishu 1’ remained below that of K2, the C_i in K0 decreased linearly. At 31 DAT, the C_i in K1 decreased by 11.0% compared with that of K2, whereas the decrease in K0 was 36.2% and significant.

Effects of K$^+$ deficiency on chlorophyll fluorescence parameters

The chlorophyll fluorescence parameters of the two cultivars in different K$^+$ levels at 24 DAT are shown in Table 2. For ‘Ningzishu 1’, the F_0 was significantly increased, whereas the F_v/F_m and q_P of the K0 treatment were significantly decreased comparing with those of K2, respectively. These decreases were also showed in K1, but no significant difference in K0 and K2. The variations of F_0, F_v/F_m, and q_P in K0 and K1 of ‘Xushu 32’ were similar to those of ‘Ningzishu 1’, but no significant difference was revealed among the K$^+$ treatment levels. The q_N of ‘Ningzishu 1’ showed an increasing response trend with K$^+$ level reduction, but no significant difference were detected among the three K$^+$ levels, which was similar to ‘Xushu 32’.

Discussion

Plant growth and physiological response to K$^+$ deficiency. Plants require K$^+$ in a larger

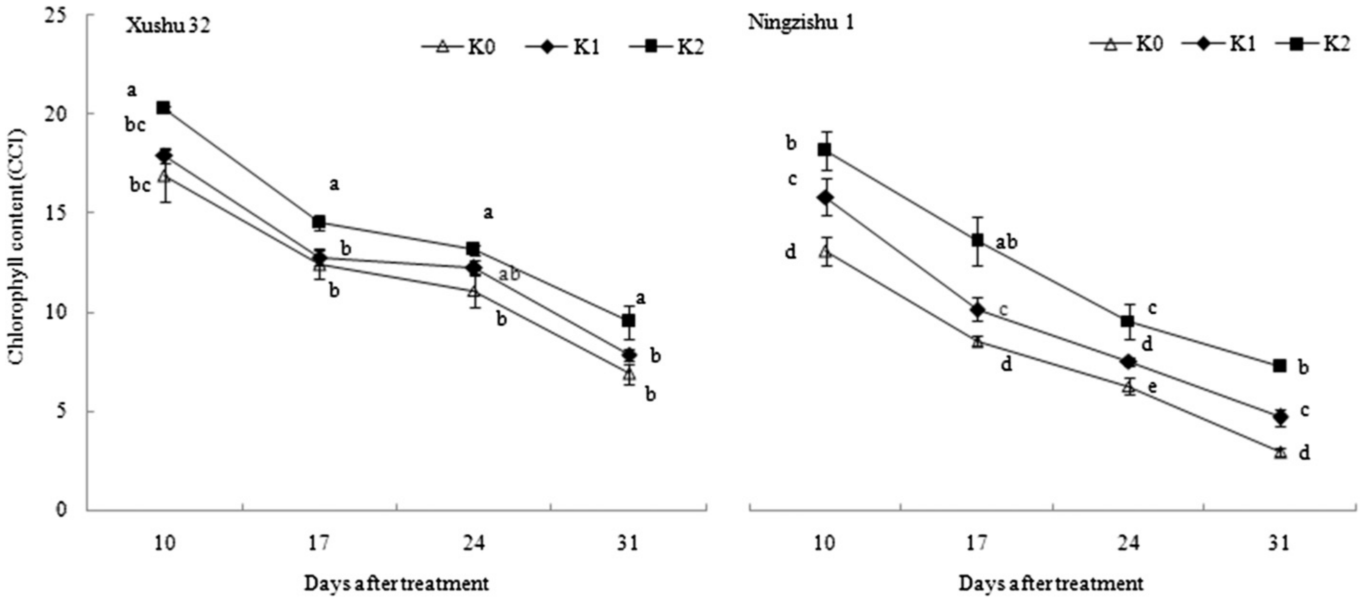

Fig. 5. Effects of potassium deficiency on the chlorophyll content (CCI) of two sweetpotato varieties. K0: 0 mmol·L^{-1} K^+; K1: 5 mmol·L^{-1} K^+; and K2: 20 mmol·L^{-1} K^+ (control). Data are means ± SD ($n = 3$). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

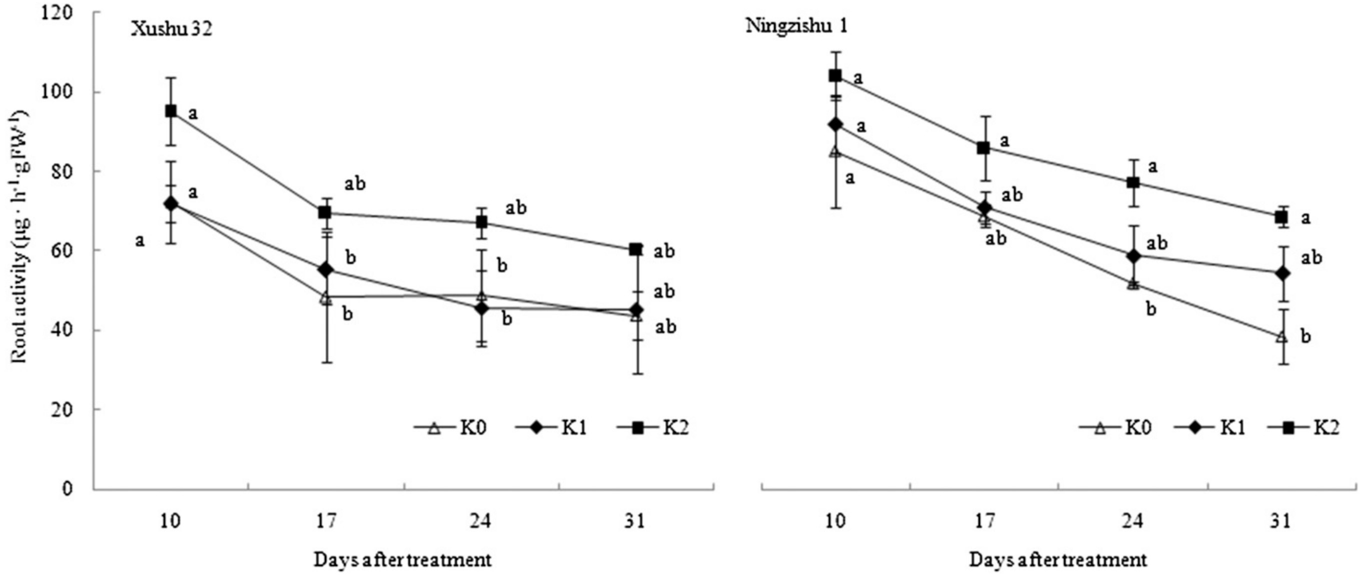

Fig. 6. Effects of potassium deficiency on the root activity of two sweetpotato varieties. K0: 0 mmol·L^{-1} K^+; K1: 5 mmol·L^{-1} K^+; and K2: 20 mmol·L^{-1} K^+ (control). Data are means ± SD ($n = 3$). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

amount than any other mineral element except for N, and K^+ is a nutrient that often affects crop growth, yields, and quality (Jin et al., 2011). Preferable root morphology and high root activity are the prerequisites to uptake and utilization efficient of K^+ in plants and these are also the typical characteristics of K-efficient crop varieties (Den Herder et al., 2010). The results of this study showed that the low-K-tolerant variety, 'Xushu 32', maintained greater root lengths in the three treatment levels than 'Ningzishu 1' (Fig. 4), which led to its greater root dry weight and higher root/shoot ratio (Table 1). Hence, the 'Xushu 32' could maintain high root activities in K^+ deficiency conditions (Fig. 6). By contrast, the shorter root and weaker root activities in 'Ningzishu 1' seedlings probably led to less underground assimilation, and thus finally to a lowered root/shoot ratio in K^+ deficiency stress. These results suggest that K^+ deficiency strongly inhibit plant dry weight production, and decreases the root/shoot ratio in a sweetpotato variety sensitive to K^+ deficiency. These findings are similar to the results from the field experiment and sand culture experiment (Tang et al., 2015), suggesting that K^+ deficiency depresses considerable translocation of the assimilation product from leaves to root in the sweetpotato.

Chlorophyll is an important index reflecting crop senescence and photosynthetic capacity. Potassium deficiency restrains the synthesization of chlorophyll (Lu et al., 2016). In this study, the CCI of the two sweetpotato cultivars were reduced, especially in 'Ningzishu 1' in the K^+ deficiency condition (Fig. 5) which may be associated with the decreased P_n (Fig. 7). The photoassimilate accumulation reduction caused by P_n decrease probably resulted in less green leaves and a lower shoot dry weight (Table 1). As a whole, the decreases in dry weight, shoot length, CCI, and root activity of the each K^+ deficiency level in 'Xushu 32' were all lower than those of 'Ningzishu 1', and the growth of the 'Ningzishu 1' were more restricted, showing 'Xushu 32' had more tolerance to K^+ deficiency.

However, the root activity, CCI, and photosynthesis of the two cultivars also

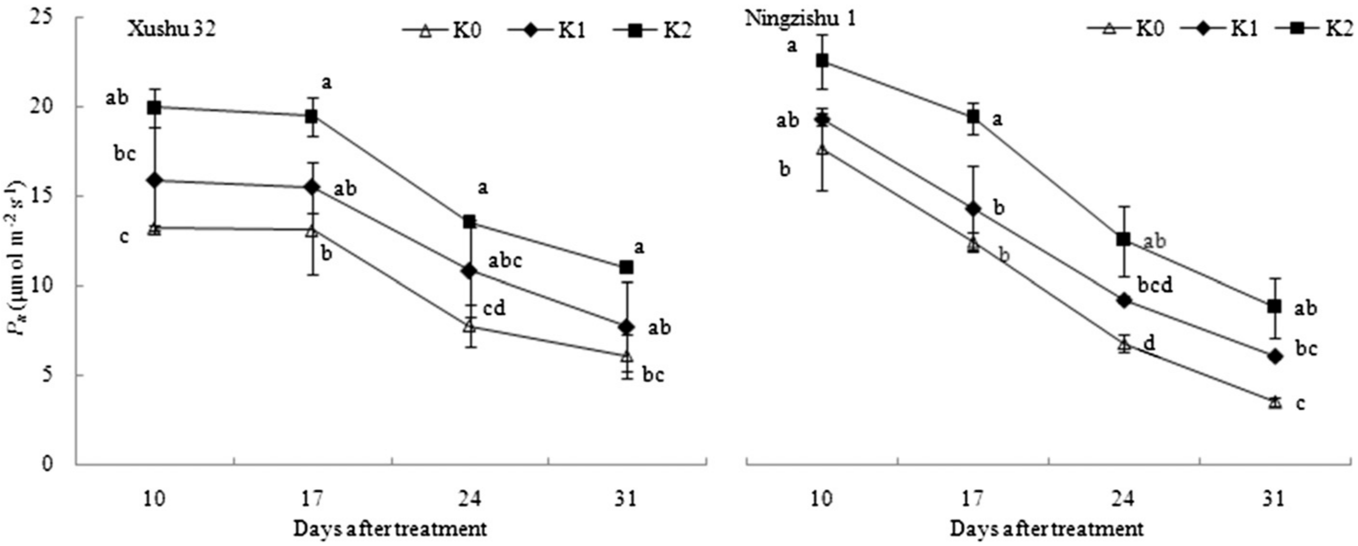

Fig. 7. Effects of potassium deficiency on the net photosynthetic rate (P_n) of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD ($n = 3$). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

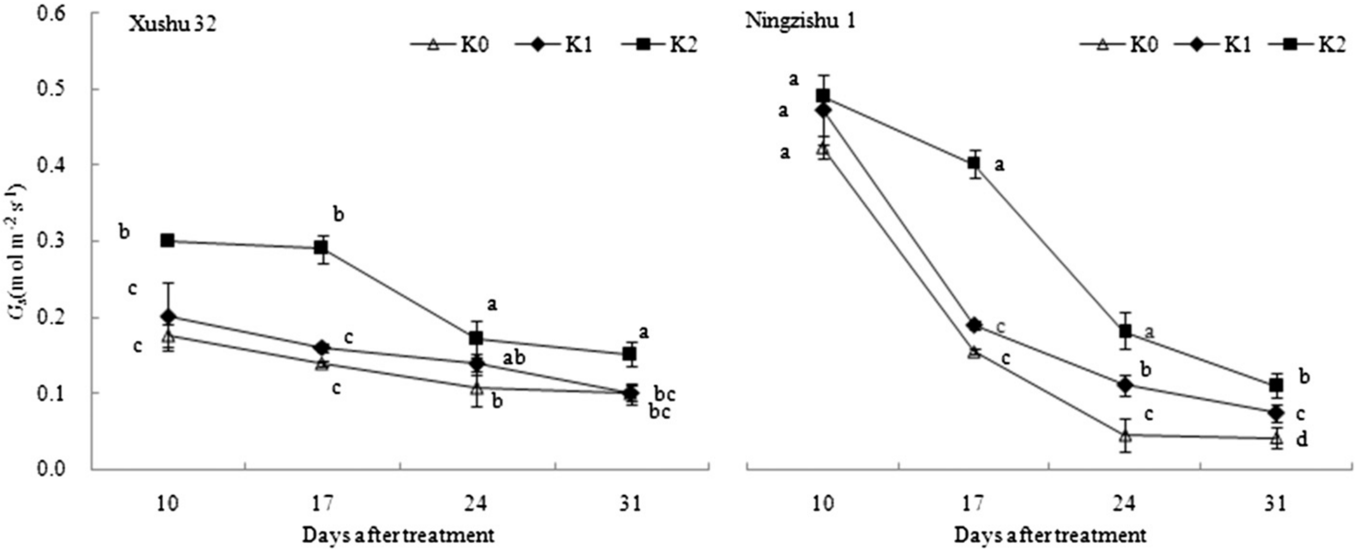

Fig. 8. Effects of potassium deficiency on the stomatal conductance (g_S) of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD ($n = 3$). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

showed decreases in the control condition in this study. These plants also showed premature aging in the later stage of the experiment. We presumed the reason was that the hydroponic culture condition has nutrition limitation, which is difficult to provide enough nutrition for the fast growing plants. The phenomenon was also showed in other hydroponic experiments (Peng et al., 2006; Wang et al., 2015b). It indicates that nutrient solution concentration or quantity should be adjusted with the growth of plants to ensure sufficient nutrients in hydroponic experiments. But on the other side, the hydroponic condition with controllable nutrient elements is beneficial to obtain typical symptoms of sweetpotato in K$^+$ deficiency stress instead of a soil substrate.

Photosynthesis response to K$^+$ deficiency. Potassium is an important element for photosynthetic metabolism that requires high concentrations (Marschner, 2011). In this study, as the K$^+$ supply was reduced, the P_n (Fig. 7), g_S (Fig. 8), and T_r (Fig. 9) of the two varieties were also reduced, in a pattern similar to previous studies done on other crops (Jin et al., 2011; Wang et al., 2015b). Previous studies have found that a decrease of P_n attribute to stomatal limitation when C_i and g_S declined, whereas it is attributable to nonstomatal limitation (a larger mesophyll resistance, a lower capacity of the CO$_2$-fixation cycle, or both) when C_i increased and g_S decreased (Bednarz et al., 1998; Gerardeaux et al., 2009; Xu, 1995). In view of the reductions of g_S and C_i, the main reason for the decrease of P_n in 'Ningzishu 1' should be the stomatal limitation factor in the study. However, in 'Xushu 32', the C_i showed decline first and then increase in K$^+$ deficiency, with a gradually decrease in g_S. This performance was inconsistent with other published reports (Bednarz et al., 1998; Wang et al., 2015b). We suppose that the decreases of P_n in K$^+$ deficiency in 'Xushu 32' were probably caused by the common effects of stomatal and nonstomatal factors. However, the changes of C_i in 'Xushu 32' were nonsignificant and were generally steady during the experimental period. In addition, other photosynthesis traits in 'Xushu 32' were also changed less than those of 'Ningzishu 1', in conditions of K$^+$ deficiency. These findings indicate that 'Xushu 32' could maintain relatively higher photosynthetic capacity than 'Ningzishu 1', which might be a direct physiological basis of the low-K-tolerant cultivar to maintain a better growth status.

Chlorophyll fluorescence parameters response to K$^+$ deficiency. The changes of

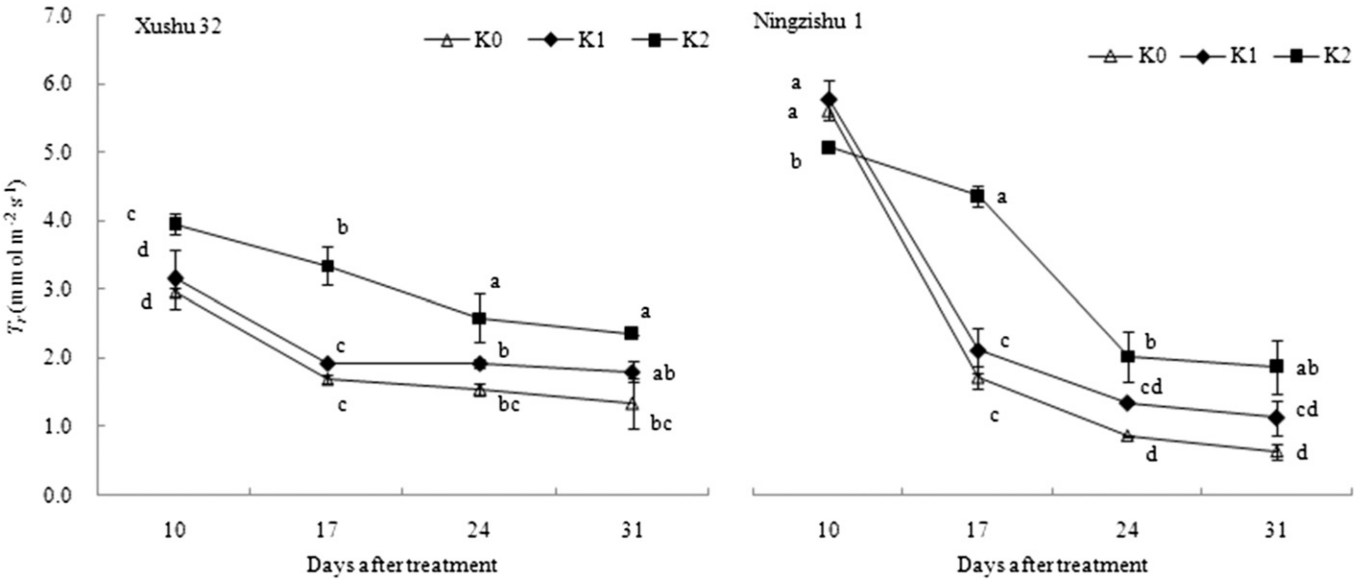

Fig. 9. Effects of potassium deficiency on the transpiration rate (T_r) of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD (n = 3). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

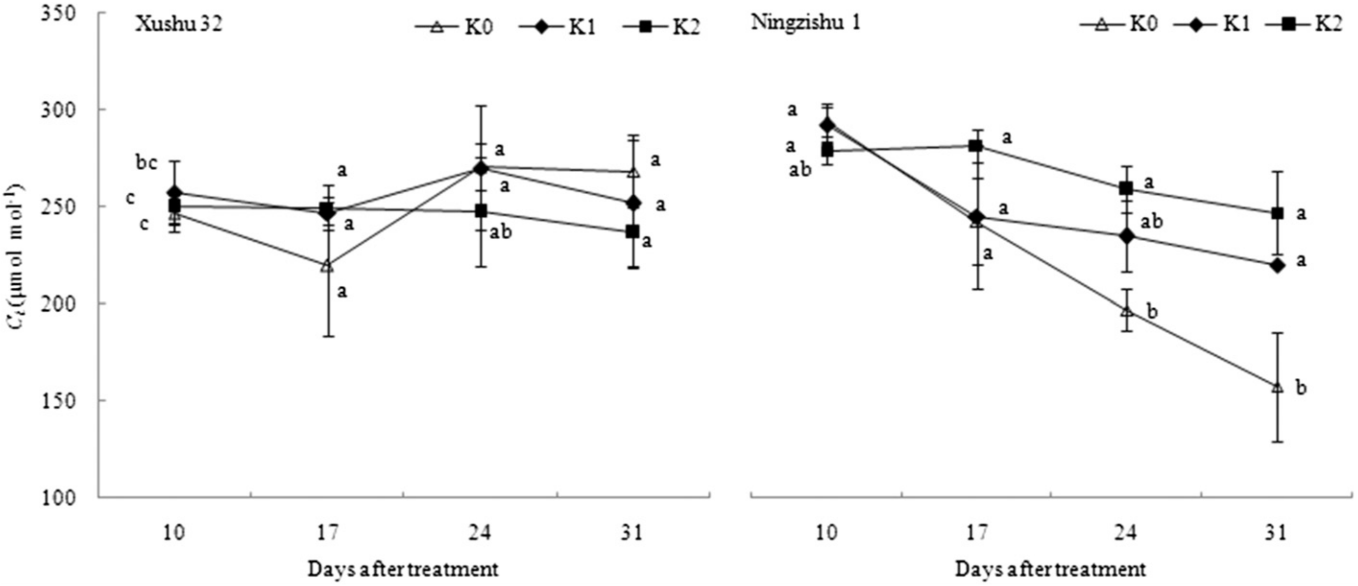

Fig. 10. Effects of potassium deficiency on the intercellular CO$_2$ concentration (C_i) of two sweetpotato varieties. K0: 0 mmol·L^{-1} K$^+$; K1: 5 mmol·L^{-1} K$^+$; and K2: 20 mmol·L^{-1} K$^+$ (control). Data are means ± SD (n = 3). Treatments with different letters (a, b, and c) are significantly different at $P < 0.05$ level.

Table 2. Effects of potassium deficiency on the chlorophyll fluorescence parameters of two sweetpotato varieties.

Chlorophyll fluorescence parameters	Xushu 32			Ningzishu 1		
	K0	K1	K2	K0	K1	K2
F_0	599.1 ± 29.6 abc^z	572.2 ± 14.2 bc	511.6 ± 5.2 c	671.8 ± 66.2 a	650.6 ± 13.3 ab	566.0 ± 38.6 bc
F_m	1,535.5 ± 354.9 a	1,646.5 ± 13.3 a	1,885.2 ± 84.0 a	1,596.4 ± 277.3 a	1,640.3 ± 306.8 a	2,098.7 ± 158.8 a
F_v/F_m	0.597 ± 0.112 ab	0.641 ± 0.02 0 ab	0.729 ± 0.019 a	0.570 ± 0.033 b	0.632 ± 0.105 ab	0.730 ± 0.013 a
q_P	0.225 ± 0.023 ab	0.231 ± 0.037 ab	0.265 ± 0.039 a	0.173 ± 0.016 b	0.200 ± 0.007 ab	0.239 ± 0.007 a
q_N	0.929 ± 0.031 a	0.935 ± 0.015 a	0.914 ± 0.041 a	0.947 ± 0.024 a	0.943 ± 0.012 a	0.919 ± 0.010 a

K0 = 0 mmol·L^{-1} K$^+$; K1 = 5 mmol·L^{-1} K$^+$; K2 = 20 mmol·L^{-1} K$^+$ (control); F_0 = the minimal fluorescence; F_m = the maximal fluorescence; F_v/F_m = the maximum quantum efficiency of PSII photochemistry; q_P = photochemical quenching; q_N = nonphotochemical quenching.

[z] Means within same column followed by different letters (a, b, and c) are significantly different between K treatments of the two genotypes ($P < 0.05$). Data are means ± SD (n = 3).

chlorophyll fluorescence parameters are helpful to understand the photosynthetic light absorption, distribution, and dissipation in the photosynthesis process, which can reflect the stress of plants (Maxwell and Johnson, 2000; Morant-Manceau et al., 2004). The increase of F_0 indicates a reversible inactivation or irreversible damage of the reaction centers of PSII, and the decrease of F_v/F_m indicates the primary conversion of light energy of PSII was reduced (Lichtenthaler and Babani, 2004). The significant changes of F_0 and F_v/F_m in 'Ningzishu 1' in the extreme K^+ deficiency condition (K0) (Table 2) suggests that the structure and function of the reaction center were damaged and destroyed in a certain degree. These findings of sweetpotato are similar to those of other plants (Li et al., 2011; Wang et al., 2015b). Also, these variations were related to the decline of P_n (Fig. 7). The main reason of F_v/F_m decrease of 'Ningzishu 1' should be the significant increase of F_0.

The q_P of the two cultivars showed an decreasing trend in response to K^+ level reduction, significant difference was showed in K0 condition compared with K2 in 'Ningzishu 1'. The decrease of q_P indicates that the opening proportion of PSII reaction centers and the electrons involved in CO_2 fixation were decreased, and these decreases will weaken the photosynthetic electron transport capacity, block the dark reaction of leaf, and decrease the P_n (Dannehl et al., 1996). In this study, it can be found that the decreased q_P is consistent with the decrease of P_n (Fig. 7). The q_N is an important nonphotochemical quenching parameter, reflecting the changes in the plant heat dissipation capacity (Müller et al., 2001). The q_N of the two cultivars revealed particular increases in the tested conditions of K^+ deficiency. This result suggests that the leaves improve heat dissipation to consume exceed excitation energy through nonphotochemical quenching pathway, it may be a way to adapt to K^+ deficiency stress.

Generally, all the chlorophyll fluorescence parameters in 'Xushu 32' were less affected comparing with 'Ningzishu 1', indicating that the PSII reaction centers were less damaged. A higher actual photochemical efficiency was maintained in low-K-tolerant sweetpotato variety in K^+ deficiency stress.

Conclusion

Compared with 'Ningzishu 1' (sensitive to K^+ deficiency), the dry weight, number of leaves, root length, and CCI of 'Xushu 32' (tolerance to K^+ deficiency) were less varied with the K^+ deficiency time extending, which indicated tolerance to K^+ deficiency cultivar could maintain higher growth. In addition, only in K0 condition were the P_n, g_S, and T_r of 'Xushu 32' reduced significantly, and the decreases were all less pronounced than those of 'Ningzishu 1' in both K0 and K1 treatments. On the 24 DAT, all the chlorophyll fluorescence parameters in 'Xushu 32' were slight and not significantly changed, whereas for 'Ningzishu 1', the F_0 was significantly increased, and the F_v/F_m and q_P were significantly decreased. These results indicated that the tolerance to K^+ deficiency cultivar could maintain a better growth state in K^+ deficiency stress, which may be mainly because of a lighter affected physiological role and photosynthesis, and a less damaged structure and function of PSII reaction center.

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