Screening high potassium efficiency potato genotypes and physiological responses at different potassium levels

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Abstract

Potato (*Solanum tuberosum* L.) growth and production is highly dependent on potassium (K) levels in the soil. Southwest China is the largest potato production region but it has low availability of soil potassium. To assess the genetic variation in K use efficiency, 20 potato genotypes were collected to compare the yield and K content in a pot experiment. Moreover, 'Huayu-5' and 'Zhongshu-19' were cultivated in five K applications to investigate the K distribution and sucrose in different organs. The results indicated that there were highly significant effects of K, genotype and K×G interactions on tuber yield, plant and tuber K content, plant K uptake efficiency and K harvest index. Cluster analysis classified 20 potato genotypes into four types: DH (high efficiency at low and high K application), LKH (high efficiency at low K application), HKH (high efficiency at high K application) and DL (low efficiency at low and high K application). The potassium distribution percentage in the tubers of the potassium-efficient genotype was higher than that of the potassium-inefficient genotype under low potassium application. The sucrose content in the tuber gently declined as the application of K rose in both cultivars, and that in the tuber of 'Huayu-5' was higher than that in 'Zhongshu-19'. 'Huayu-5' reached the highest yield when the potassium application was 159.45 kg ha^{-1}, and 'Zhongshu-19' reached the highest yield when the potassium application was 281.4 kg ha^{-1}. This study indicated that genetic variation for K utilization efficiency existed among 20 genotypes, and yield in low K application and relative yield were suitable criteria for screening K utilization efficiency genotypes.

Keywords: potato; potassium efficiency; potassium distribution; sucrose

Introduction

Potassium (K), which accumulates to 10% of plant dry weight (Adams and Shin, 2014), has many functions in plant growth, such as the smooth progression of cell division and growth (Anschütz *et al.*, 2014), leaf expansion and root elongation (Jordan-Meille and Pellerin, 2004; Song *et al.*, 2017), transportation of carbohydrates, disease resistance and drought tolerance (Saha *et al.*, 2016). The fraction of soil K that can be absorbed directly by plants is generally quite low (0.1- 0.2%) because most soil K forms insoluble complexes

(Huo-Yan *et al.*, 2010; Saha *et al.*, 2016). A study showed that the soil available K in southwest China was lower than that in other regions (He *et al.*, 2016). K is one of the principal nutrient elements required for crop growth and therefore needs to be added as fertilizer to increase the crop yield. K can be more easily leached from the soil than nitrogen (N) or phosphorus (P) (Neirynck *et al.*, 1998), and most of the K applied as fertilizer is lost to the environment, where it poses threats to human and ecosystem health at local to global scales. It is necessary for us to study crop nutrient use efficiency under different environmental conditions and to identify more nutrient-efficient genotypes.

Several studies have proven genetic variations in nutrient efficiency. Variations in nutrient efficiency have been assessed among different crop species, including rice (Mohammed, 2018), wheat (Nguyen *et al.*, 2016), and soybean (Zhou *et al.*, 2016). Recent advances have highlighted genotypic differences in nitrogen and phosphorus use efficiency. Based on the average yield of potato varieties with and without N applications, Dandan *et al.* (2019) classified seven potato varieties into four types. Sandaña (2016) used correlation matrix-based principal component analysis (PCA) based on genotype main effects, phosphorus utilization efficiency and related traits using Statgraphics to assess potato phosphorus efficiency. To date, little focus has been directed towards K efficiency, especially in potato. Nutrient efficiency may be defined as yield per unit of fertilizer available to the crop (Moll *et al.*, 1982). K efficiency is a criterion of genotypic tolerance of K-deficient soil and it can be quantified as the ratio of growth with a deficient and adequate K supply (Damon and Rengel, 2007). However, it is difficult to evaluate crop K efficiency because of different K tolerances and sensitivities in different crop genotypes.

Crops largely transport K from older to younger plant tissues and ensure redistribution of this ion towards growing tissues such as developing leaves and fruits. High K efficiency not only has great uptake and utilization ability but also reasonably redistributes K in all plant organs. A high K-efficiency genotype has a better partitioning of K to the economic sink as well as a higher K concentration associated with the resource-sink relationship at different growth stages (Wang *et al.*, 2017). A previous study reported that K-efficient rice was closely associated with high K translocation to functioning leaves and efficient sodium substitution in older leaves (Jia *et al.*, 2008). Nutrient deficiency also influences biomass partitioning and nutrient allocation among crop tissues (Singh *et al.*, 2014). Increasing nutrient application to a crop drives the production of a greater canopy biomass with the potential for higher photosynthesis. However, the relationship between K and potato tuber development is only partially understood; hence, this experiment determined the effect of K on photosynthetic products and tuber yield. Sugars perform important regulatory functions in plants, including photosynthesis and carbohydrate partitioning (Chiou and Bush, 1998; Rolland *et al.*, 2002). In addition, K is necessary not only for phloem loading but also for sucrose transport in the phloem (Koch *et al.*, 2019). Martineau *et al.* (2017) demonstrated that K deficiency significantly decreased the starch content in leaves. This will lay a foundation for further extensive mechanistic studies directly linking K to carbohydrates in different plant organs.

Potato is a major world food crop that has higher K requirements than cereals, pulses, oilseeds and other commercial crops. According to Keli *et al.* (2003), producing 1000 kg dry matter yield of potato tubers removes approximately 10 kg K from the soil. Indeed, the K concentrations in the leaves were below the threshold level of 42.3 g kg^{-1}, which is associated with the maximum tuber yield (Reis Jr and Monnerat, 2000). K_2O (270-300 kg ha^{-1}) produced the highest yield in potato production (Zelelew *et al.*, 2016; Zhang *et al.*, 2018). To reduce K fertilizer inputs and environmental pollution, the experiments reported here were designed to identify (1) potato genotypes with high K efficiency for further use in breeding, and (2) the differences in K and sugar distributions between high- and low-K utilization efficiency potato genotypes.

Materials and Methods

Experiment 1: genotype screening

A genotype screening experiment was conducted in 2018 at the Institute of the Tuberous Corps Research, Southwest University, Chongqing, China (29°768 N, 106°380 E, and altitude 241 m). In total, 20 potato genotypes or breeding lines were screened (Table 1). The experimental design was a split zone design with three replications. A pot experiment was conducted from January to May in a plastic box (55×45×23 cm) filled with nutrient-poor vermiculite, in which 5 seed tubers were planted. All plots received an application of 225 kg ha^{-1} urea and 80 kg ha^{-1} calcium superphosphate. Treatments consisted of two K fertilizer rates: (i) 75 kg ha^{-1} K$_2$O (K$_L$) and (ii) 300 kg ha^{-1} K$_2$O (K$_H$). Common cultivation measures were adopted during the growing season. All plant samples were harvested at the maturity stage for each genotype. Aboveground biomass, tuber yield, and K concentration were determined for the calculation of the related K efficiency parameters.

Table 1. The potato varieties in the experiment

No	Variety	No	Variety
1	'378711.7'	11	'S03-0452'
2	'049565'	12	'Lishu-6'
3	'09307-830'	13	'Anlong-5'
4	'2014X3-1'	14	'Qiangyu-6'
5	'B20-7'	15	'08CA0710'
6	'C19'	16	'Enshu78-11'
7	'S21'	17	'Zhongshu-19'
8	'Huayu-5'	18	'Zhengshu-5'
9	'Chuanyu-117'	19	'Zaodabai'
10	'Liangshu-2'	20	'Mira'

Experiment 2: physiological responses

In 2019, two genotypes, 'Huayu-5' (LKH, high efficiency at low K treatment) and 'Zhongshu-19' (HKH, high efficiency at high K treatment), were used in the pot experiments to examine the differences in K concentration, sucrose, yield, and dry weight. The selection of the two genotypes was based on screening of the tuber yield with low K application and relative yield among the 20 potato genotypes in 2018. The pot size was 32 cm diameter by 27 cm tall. The ratio of soil to coconut chaff was 3:1. Soil in the 0-20 cm profile contained 26 mg kg^{-1} bicarbonate-extractable K, 44 mg kg^{-1} bicarbonate-extractable P, 6.5 g kg^{-1} organic matter, and a pH of 6.9. A uniform fertilizer application of 80 kg ha^{-1} calcium superphosphate and 225 kg ha^{-1} urea at seeding was applied. The five K fertilizer rates were (1) 0 kg ha^{-1} K$_2$O (K0), (2) 75 kg ha^{-1} K$_2$O (K1), (3) 150 kg ha^{-1} K$_2$O (K2), (4) 225 kg ha^{-1} K$_2$O (K3), and (5) 300 kg ha^{-1} K$_2$O (K4). One seed tuber per pot was sown. Forty pots were planted for every treatment. Plant samples were collected from three pots at 20, 40, 60, and 80 days after planting (DAP) and were separated into different organs (leaf, stem, root and tuber).

Measurements

In the two experiments, all samples were dried at 105 °C in an oven for 30 min and then air-oven dried at 75 °C until reaching a constant weight. The dried samples were ground with a cyclone mill through a 0.18 mm screen. Subsamples of plant materials were digested in concentrated H$_2$SO$_4$ and H$_2$O$_2$, and the K concentration was measured by a flame photometer (Chen and Gabelman, 1995). The sucrose and reducing sucrose contents were determined (Chi, 2007). The following parameters were calculated in terms of dry matter and the K concentrations in different organs:

(1) K accumulation value (KAV) = dry matter weight × K concentration;
(2) K uptake efficiency (KUpE) = KAV in all organs/K applied;
(3) K utilization efficiency (KIUE) = KAV in all organs/dry matter weight;
(4) K harvest index (KHI) = KAV in tubers/KAV in all organs;
(5) Relative yield =Tuber yield at low K level/Tuber yield at high K level.

Statistical analysis
Experimental data were calculated by office EXCEL 2016 software. Analysis of variance (ANOVA), mean separation and cluster analysis were performed using SPSS 19.0 software (SPSS Inc., Chicago, IL, USA). The data were analysed with one- and two-way ANOVA by Tukey's test. Cluster analysis was performed by the hierarchical cluster method with the Ward method and square Euclidean distance measure.

Results

Variation of potassium uptake and utilization efficiency in potato varieties
There were highly significant effects of K, genotype and K×G interactions on tuber yield, plant and tuber K content, plant K uptake efficiency and K harvest index (Table 2). Potato tuber yield for the 20 genotypes ranged from 65.00 to 515.00 g plant^{-1} at K_L and from 50.00 to 630.00 g plant^{-1} at K_H. Under the K_H treatment, potato yield, tuber K content, KIUE and KHI were improved. There were significant increases in K uptake efficiency in the K_L treatment compared with the K_H treatment. The average yield of the 20 potato genotypes was reduced by 16.4% in the K_L treatment compared with the K_H treatment.

Table 2. Variation of potassium uptake and utilization efficiency in potato varieties and K treatments

Parameter	K treatment	Yield (g plant^{-1})	Plant K content (g plant^{-1})	tuber K content (g plant^{-1})	K uptake efficiency (%)	K utilization efficiency (%)	K harvest index (g^2·g^{-1})
Range	K_L	65.00-515.00	0.14-1.95	0.46-3.46	48.59-268.83	8.48-27.13	30.84-92.22
	K_H	50.00-630.00	0.13-1.86	0.54-5.73	9.49-95.83	6.73-25.02	44.69-96.73
Average	K_L	219.58	0.75	1.52	136.12	17.20	66.98
	K_H	262.42	0.61	1.90	37.57	17.91	75.19
CV（%）	K_L	42.59	60.84	48.73	40.69	20.23	49.70
	K_H	53.01	65.47	55.01	48.02	22.40	46.65
ANOVA	Genotype	**	**	**	**	**	**
	K treatment	**	**	**	**	*	**
	Genotype × K	**	**	**	**	**	**

Two-way ANOVA was used for assessing the variations of different parameters between K availability (K0, K1) and genotype, and *, **, indicate significance at P =0.05, P= 0.01, respectively. Ns; not significant using Tukey's test

Cluster analysis for genotype × potassium level
Clustering of genotypes based on low K yield and relative yield. The clustering result indicated potato genotypes could be divided into four groups (Figure 1). In cluster I, 'S03-0452', 'Mira', 'S21', '049565', 'Enshu78-11', '2014X3-1', 'Anlong-5', 'Zhongshu-19' and 'Zaodabai' had high-tuber yield at K_H treatment and low yield at K_L treatment, which called HKH (high efficiency at high K application). The Clusters II, '08CA0710', '09307-830', 'B20-7' and 'Liangshu-2' had low-tuber yield both at K_H and K_L treatment, which called DL (low efficiency at low and high K application). In cluster III, '318711.7', 'Chuanyu-117' and 'Qiangyu-6' and high-tuber yield at K_H and K_L treatment, which called DH (high efficiency at low and high K application). In cluster IV, 'C19', 'Lishu-6', 'Huayu-5' and 'Zhengshu-5' had high-tuber yield at low K level and low-tuber yield at high K treatment, which called LKH (high efficiency at low K application).
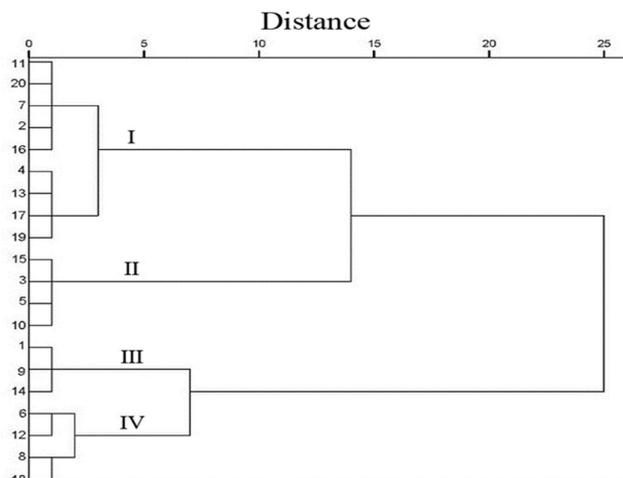
Figure 1. Ward's cluster analysis classifications of 20 potato genotypes based on screening of tuber yield at low potassium application and relative yield

Changes in K concentration, proportions and redistribution from various organs

There were some remarkable differences in K concentration among the tissues and growth stages. At 20 and 40 DAP, the root K concentration did not change in response to increased K application. In addition, there was no significant difference in the root K concentration of the same genotype under different K treatments. At 40 DAP, the root K concentrations of 'Huayu-5' and 'Zhongshu-19' peaked at K4 and were 52.80 mg g^{-1} and 52.37 mg g^{-1}, respectively. At 60 DAP, the root K concentration of 'Huayu-5' increased with increasing K application and reached a maximum at K4. The change in root K concentration of 'Zhongshu-19' at 60 DAP showed a trend of first increasing and then decreasing, reaching a maximum in the K3 treatment. At 80 DAP, the root K concentrations of 'Huayu-5' and 'Zhongshu-19' both increased first and then decreased. It can be seen from Table 4 that with the growth and development of the potatoes, most of the root K concentrations showed a trend of increasing and then decreasing under the same K treatment. Compared with roots and leaves, stems had higher K concentrations. A lower K concentration in the stems of both varieties appeared at 20 DAP, and the K concentration gradually increased over time. At 60 and 80 DAP, the stem K concentration of 'Huayu-5' increased with increasing K application. The leaf K concentration was higher than that in roots but lower than that in stems. The leaf K concentration in different potato varieties was significantly higher in the early stages of growth and development, but the leaf K concentration of 'Zhongshu-19' was significantly higher than that in the leaves of 'Huayu-5' in the later stage. At 60 DAP, the leaf K concentration of 'Zhongshu-19' was the highest under the K2 treatment, with a content of 61.72 mg g^{-1}, and 'Huayu-5' was the greatest at the K3 level, which was 52.75 mg g^{-1}.

The accumulation of K in different organs is shown in Table 4. The root K accumulation of 'Zhongshu-19' in the K2, K3 and K4 treatments was 158.34, 161.29 and 160.17 mg plant^{-1}, respectively. The root K accumulation of Zhongshu-19 was significantly higher than that of 'Huayu-5'. The stem K accumulation of Zhongshu-19 showed a trend of first increasing and then decreasing with increasing K application and reached a maximum in the K2 treatment, which was 457.35 mg plant^{-1}. The stem K accumulation of 'Huayu-5' was the lowest without K application and K1 treatment, which was 200.15 and 199.89 g plant^{-1}, respectively. The change trend of tuber K accumulation first increased and then decreased with increasing K application.

Table 3. Difference of potassium concentration in different parts of potato varieties and K treatments

Position	Variety	K treatment	Potassium concentration(mg·g⁻¹)			
			20d	40d	60d	80d
Root	'Huayu-5'	K0	29.41±0.59c	44.83±2.36ab	38.31±1.13d	36.26±2.01d
		K1	29.40±0.16c	40.92±0.83b	44.02±6.27cd	38.96±1.29d
		K2	34.20±1.82b	43.16±2.32b	46.22±4.08bcd	42.09±1.98cd
		K3	28.52±0.93c	44.56±0.12ab	49.38±1.10abc	54.67±2.29a
		K4	33.65±0.50b	52.80±4.87a	50.42±1.53abc	42.35±1.02cd
	'Zhongshu-19'	K0	37.20±0.13a	38.88±0.71b	46.11±1.11bcd	46.95±0.95bc
		K1	34.41±0.41b	46.02±0.94ab	48.56±1.22abc	52.84±2.65ab
		K2	39.75±0.67a	39.60±2.88b	55.12±2.91ab	51.55±1.55ab
		K3	33.93±0.35b	44.71±2.35ab	57.08±2.37a	50.70±0.88ab
		K4	33.49±0.73b	52.37±2.50a	46.12±1.62bcd	46.85±2.82bc
Stem	'Huayu-5'	K0	83.69±4.04abc	102.87±3.51a	89.76±5.85d	84.51±2.95d
		K1	85.27±2.35abc	89.61±2.31bc	88.35±6.04d	95.49±2.64cd
		K2	84.58±3.02abc	102.72±1.38a	104.70±1.40abc	114.64±2.04ab
		K3	92.84±2.21a	99.69±4.37a	91.31±0.85d	97.15±1.01c
		K4	82.12±0.33bc	96.54±2.08ab	88.87±2.74d	83.64±3.63d
	'Zhongshu-19'	K0	89.39±0.42ab	105.02±1.31a	100.86±5.40bcd	119.34±1.81a
		K1	79.38±1.22c	99.43±4.011a	116.07±2.21a	98.26±6.90c
		K2	80.72±5.54bc	96.81±1.10ab	100.82±2.17bcd	117.74±2.75ab
		K3	87.36±0.28abc	98.03±1.02ab	112.15±1.04ab	100.97±3.20c
		K4	84.64±0.19abc	86.17±0.55c	98.84±4.22cd	107.12±3.32bc
Leaf	'Huayu-5'	K0	34.13±2.04cd	50.66±1.93cd	47.26±1.71b	43.51±3.16e
		K1	32.30±0.83d	52.32±1.34bcd	48.98±1.14ab	46.52±1.12de
		K2	32.82±2.33d	50.70±0.90cd	47.4±5.093b	50.62±2.03cd
		K3	39.03±2.25ab	51.08±2.73cd	52.75±1.90ab	53.75±2.36bc
		K4	38.81±0.30ab	49.80±1.39d	47.90±3.00ab	35.89±1.08f
	'Zhongshu-19'	K0	41.22±0.22a	56.49±2.16abc	60.91±2.51ab	61.26±0.19a
		K1	40.45±0.26ab	56.38±0.81abc	54.13±1.02ab	58.18±2.11ab
		K2	38.54±0.14abc	59.39±2.48a	61.72±0.43a	54.08±1.03bc
		K3	35.99±0.22bcd	57.90±1.35ab	52.74±9.54ab	50.20±1.86cd
		K4	37.61±1.08abc	56.72±0.62abc	55.47±3.66ab	58.79±1.73ab

Genotypes with different letters are significantly different (Tukey's test, $p < 0.05$)

The tuber K accumulation of 'Huayu-5' maintained the largest accumulation in the K2 treatment (1124.10 mg plant⁻¹) and the lowest accumulation in the K0 treatment (453.69 mg plant⁻¹). The tuber K accumulation of 'Zhongshu-19' was significantly different among the treatments. The highest tuber K accumulation appeared in the K3 treatment, which was 1847.78 mg·plant⁻¹, and the lowest tuber K accumulation appeared in K0, which was 761.75 mg·plant⁻¹. With increasing K application, the K accumulation of the whole plant showed a trend of increasing first and then decreasing. The K accumulation of 'Huayu-5' at the K1 and K2 levels was respectively 64.63% and 98.78% higher than that with no K application. The K of the whole 'Zhongshu-19' plant in the K2 treatment was 29.57% higher than that in the K1 treatment. At 80 DAP, the tuber K proportion of the total plants was 55.18–72.32% and 54.52–67.39% for 'Huayu-5' and 'Zhonshu-19' with different K applications, respectively.

The accumulation and distribution rate of K in various organs of the potato plants were tuber>stem>leaf>root (Figure 2). K had no significant effect on the root K distribution rate of 'Zhongshu-19', and its range was 5.04-7.39%. However, there was a relatively large effect on the root K distribution of 'Huayu-5', and its range was 1.66-4.89%. Under different K applications, the K distribution rate of 'Huayu-5' tubers initially increased and then decreased. The highest K distribution rate appeared in the K1 treatment (72.32%), and the lowest K distribution rate was in the non-K treatment (55.18%). The K distribution rate in the tubers of 'Zhongshu-19' increased with increasing K application. The K distribution rate of the stems was opposite to that of the tubers, indicating that K can promote the transfer of nutrition from potato stems to tubers.

**Table 4.** Potassium accumulation and distribution of different potato varieties

Variety	K treatment	Root (mg)	Stem (mg)	Leaf (mg)	Tuber (mg)	Total (mg)
'Huayu-5'	K0	32.93±4.18cd	200.15±18.47d	132.68±17.37c	453.69±72.05f	819.44±107.72e
	K1	22.17±1.63d	199.89±10.34d	150.39±14.37bc	973.05±45.57cd	1345.5±60.09cd
	K2	39.44±3.05cd	306.64±19.22abcd	156.67±6.55abc	1124.1±49.99c	1626.85±34.41bc
	K3	59.63±3.7cd	245.92±31.47cd	148.02±23.88bc	767.24±66.8de	1220.8±101.41d
	K4	39.13±2.56cd	269.16±32.95bcd	119.77±12.38c	597.74±46.72ef	1025.8±15.56de
'Zhonshu-19'	K0	70.69±5.61bc	336.52±65.79abcd	231.12±18.79abc	761.15±30.69de	1399.48±100.23cd
	K1	136.37±2.12a	373.62±24.09abcd	283.84±5.22ab	1063.65±38.58c	1857.47±59.81b
	K2	158.34±17.53a	457.35±120.5a	215.94±17.96abc	1576.36±33.16b	2407.99±66.01a
	K3	161.29±8.19a	436.37±19.22ab	296.79±117.33a	1847.78±162.85a	2742.22±203.78a
	K4	160.17±13a	407.22±47.78abc	224.03±2.13abc	1581.96±108.07ab	2373.38±168.28a

Genotypes with different letters are significantly different (Tukey's test, p < 0.05)
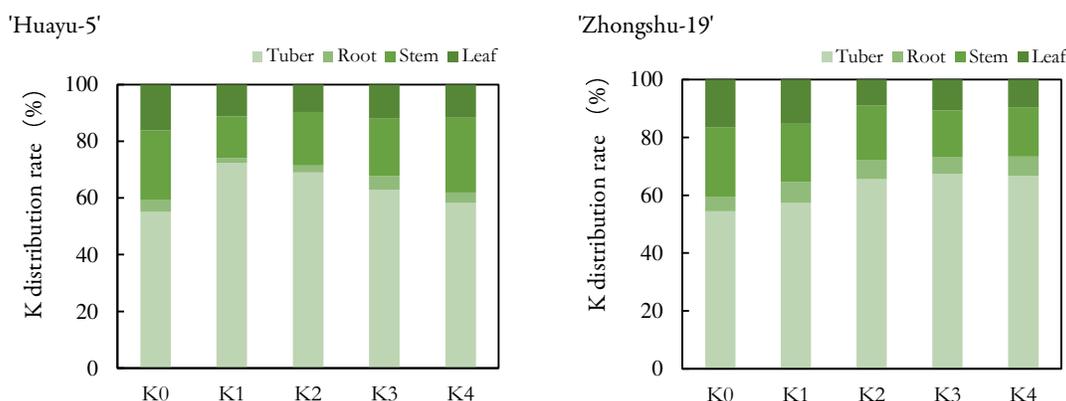
Figure 2. Potassium application on the K distribution rate in potato plant

Differences in sucrose and reducing sucrose content between different K-efficiency varieties

Figure 3 shows that the average sucrose content in the leaves of 'Zhongshu-19' was not statistically different among the K applications. The maximum sucrose content of 'Zhongshu-19' was 5.79 mg g⁻¹ in the K0 treatment, and the smallest was 1.27 mg g⁻¹ in the K3 treatment. The sucrose content in the leaves of Huayu-5 increased with increasing K application and reached the highest level of 13.97 mg g⁻¹ in the K4 treatment. With increasing K application rate, the sucrose content in the tubers decreased from 15.61 to 6.43 mg g⁻¹ in Huayu-5 and from 9.42 to 4.41 mg g⁻¹ in 'Zhongshu-19'. The sucrose content of 'Huayu-5' tubers was higher than that of the 'Zhongshu-19' tubers at the same K treatment. This shows that the content of tuber sucrose has an inevitable relationship with potato K.
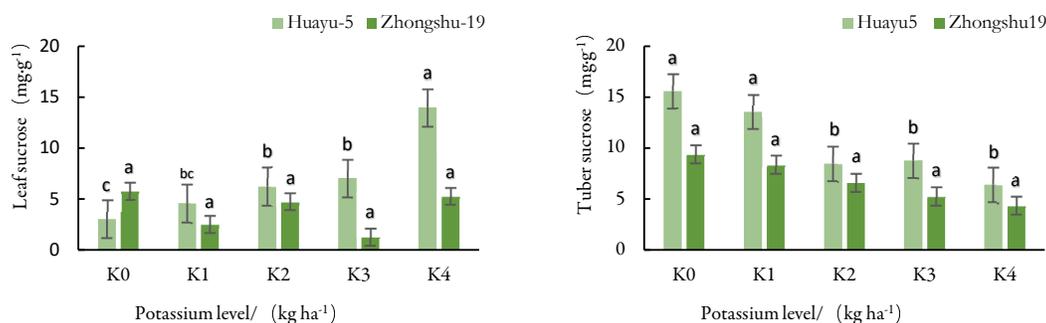
Figure 3. Differences of sucrose in different genotypes of potato
Different letters on each column are significantly difference at the 5 % level by Tukey's test among potato varieties

There were significant differences between the two potato genotypes in terms of reducing sugars in leaves and tubers (Figure 4). In the K0 treatment, 'Zhongshu-19' had the highest reducing sugars in the leaves and tubers, and its contents were 25.44 mg g^{-1} and 29.42 mg g^{-1}, respectively. With increasing K application, the reducing sugar content in the leaves and tubers of 'Zhongshu-19' gradually decreased. K can promote the conversion of reducing sugars and reduce their accumulation in leaf cells. However, the reducing sugar content in the leaves and tubers of 'Huayu-5' increased first and then decreased with increasing K application. The reducing sugar content of the leaves reached the highest level of 29.32 mg g^{-1} in the K1 treatment. The changing trend of reducing sugar content in the tubers increased slowly with increasing K application and decreased after the K3 treatment.
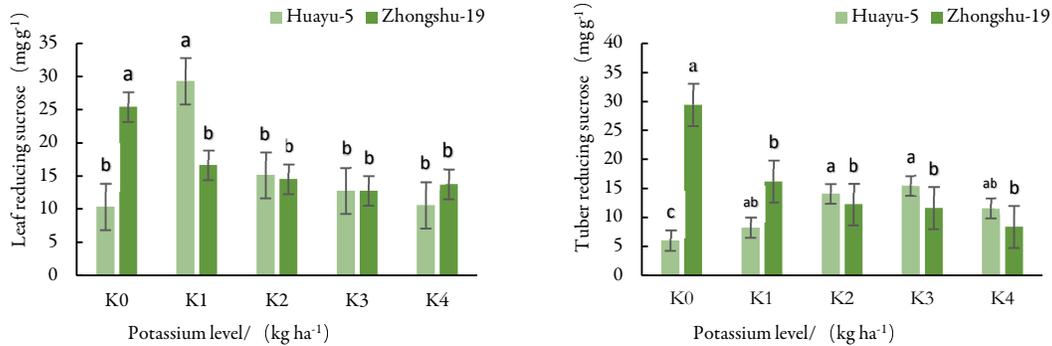
Figure 4. Differences of reducing sucrose in different genotypes of potato
Different letters on each column are significantly difference at the 5 % level Tukey's test among potato varieties

Regression relationship between potassium supply level and potato yield

To determine the optimum K application of 'Huayu-5' and 'Zhongshu-19', tuber yield data were evaluated by the binary equation (Figure 5). The highest yield of 'Huayu-5' was 181.37 g plant^{-1}, which was obtained from the application of 150 kg ha^{-1}. However, a further increase in the K rate caused the yield of 'Huayu-5' to decrease. With K fertilizer application between 0 and 225 kg ha^{-1}, the yield of 'Zhongshu-19' increased substantially. At the highest K application rate (300 kg ha^{-1}), no further yield increase occurred. 'Huayu-5' reached the highest yield when K application was 159.45 kg ha^{-1}, and 'Zhongshu-19' reached the highest yield when K application was 281.4 kg ha^{-1}.
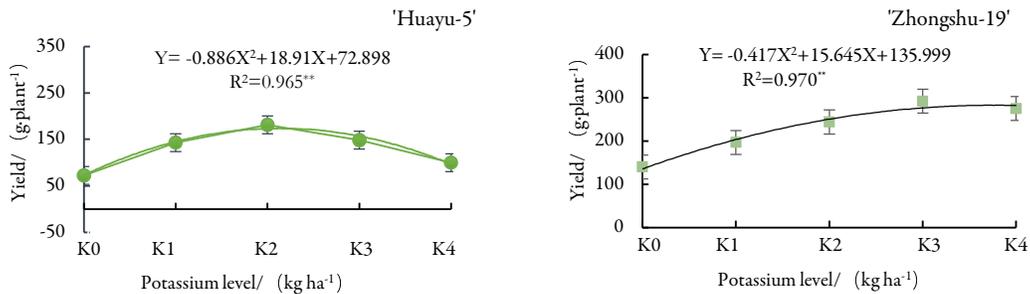
Figure 5. Effect of K fertilization on total tuber yield

Discussion

Genetic variations in potassium utilization efficiency and K selection criteria

The pot experiments showed that genetic variation in K nutrient uptake and use efficiency existed among different potato genotypes. Several studies have identified genetic variations of nutrient efficiency in different crops (wheat: Woodend and Glass, 1993; maize: Duvick, 2005; sweet potato: Wang *et al.*, 2017). Genetic engineering and conventional breeding are crucial strategies to increase crop yields and nutrient use efficiency. In addition, the criteria are very important for the selection of genotypes with high nutrition efficiency. Previous studies of access KUE always emphasize K deficiency tolerance, which is K uptake and yield per unit of k taken up. To date, little focus has been directed towards crop nutrition sensitivity, which represents the change ratio of yield with increasing nutrition application. The Michaelis–Menten equation is a suitable method because it obviously shows the highest yield, the optimum nutrition application and the change in yield (Greenwood *et al.*, 2005). However, obtaining suitable measures of the parameters requires experiments with at least six different K levels, which greatly reduces the number of genotypes that can be tested (Greenwood *et al.*, 2006). To maximize the screening of genotypes for K response, trials usually include only a few K treatments and typically no more than two. According to previous studies, most potato cultivars have the highest yield at 270-300 kg ha^{-1} K$_2$O application (Zelelew *et al.*, 2016; Zhang *et al.*, 2018). This study chose 300 kg ha^{-1} K$_2$O as the high potassium treatment. Identifying tolerant and sensitive genotypes using different parameters, such as relative growth rate reduction (RGRRED) and use efficiency (UE), is expected to give different outputs (Mohammed, 2018). Therefore, the selection criteria in this study based on screening of tuber yield at low K application and relative yield can: (1) compare the tuber yield per plant in the 20 varieties (lines) studied under low K stress and (2) compare the change in tuber weight per plant under low K stress and high K application.

K portioning and translocation

Generally, research on K efficiency has mostly focused on K uptake or utilization efficiency, which are essential for the selection of K high-efficiency crops (Woodend and Glass, 1993; Guoping *et al.*, 1999; Bilal *et al.*, 2019). However, the redistribution and accumulation abilities of K are both important parameters in assessing the K efficiency of crops (Wang *et al.*, 2017). In this study, the K ion concentration was different among the four stages in roots, stems and leaves. Koch *et al.* (2019) found that the leaves, tubers and roots of K-deficient plants had significantly lower K concentrations than those of K-sufficient plants. Even in fertilized fields, rapid K uptake by plants can lead to K shortages in the root environment, particularly in the early stage (Kellermeier *et al.*, 2013). The data reported here were consistent with the observation that the K concentration at 20 DAP was lower than that at 40 DAP. This phenomenon was particularly obvious in the leaves, which may be caused by them being at the distal end of potassium transportation and the fast expansion of the leaves in the early stage. Better translocation of K into different organs and a greater capacity to maintain the cytosolic K concentration within optimal ranges are the main mechanisms underlying K utilization efficiency (Rengel and Damon, 2008). The main assimilation product from photosynthesis in potato, sucrose, is transported from the aboveground biomass to the tubers through the phloem and then decomposed into hexoses in the tubers to provide the energy and carbon skeletons required for cell division and storage tuber bulking. K, as the most abundant inorganic cation in phloem vessels, has an additional function in counterbalancing mobile anions in the phloem (Zörb *et al.*, 2014). In this study, the K concentration in the phloem was higher than that in the leaves and roots. Partitioning of dry matter to the tubers was markedly reduced by K deficiency (Jenkins and Mahmood, 2003). This study showed that low K leads to a decrease in the ratio of K accumulation and distribution in potato tubers, and too high K application will also decrease the ratio of K accumulation. The K distribution ratio in seeds of the K-efficient genotype were higher than that of the K-inefficient genotype (Liu *et al.*, 2019). In this study, the greatest K distribution ratio of 'Huayu-5' appeared in the K1 treatment (72.32%), and the greatest K distribution ratio of 'Zhongshu-19' appeared in the

K3 treatment (67.39%). The K distribution ratio may be of crucial importance for high K use efficiency. To improve K use efficiency and reduce fertilizer input, study should focus on how to reduce K distribution ratio in fruit.

Sucrose and reducing sucrose accumulation in tuber and leaf

Carbohydrates formed by photosynthesis play an important role in fruit production since they are not only raw materials for fruit growth but also major determinants of fruit quality (Georgelis *et al.*, 2004; Keller *et al.*, 2008). Soluble sugar content is positively correlated with soil K, so increasing the supply of K increases sugar accumulation (Zushi and Matsuzoe, 1998); additionally, K is beneficial for increasing the dry matter content and improving fruit quality under drought stress (Mohammed, 2018). Therefore, increased K could lead to increased sucrose in the leaves, loading it in the phloem and transporting it to the roots for storage as starch, enhancing the yield of root crops (Omondi *et al.*, 2020). In this study, the sucrose content of 'Huayu-5' in the leaves significantly declined as the concentration of K in the soil increased. These findings are congruent with those reported earlier by Omondi *et al.* (2020). However, the sucrose content of 'Zhongshu-19' in the leaves was not significantly different under the different K treatments. Sucrose in the tuber significantly declined with increasing K application in both genotypes. One possible explanation may be that K promotes the conversion of sucrose into starch. At the same K treatment, the tuber sucrose of 'Huayu-5' was higher than in 'Zhongshu-19', which was a difference in KUE. A suitable amount of K applied during the growing season is an efficient cultivation measure for increasing yield, as it promotes the transport of photo-assimilates from the leaves down to the storage roots (Du *et al.*, 2020).

Conclusions

In conclusion, the present results demonstrated genetic variation difference in tuber yield, plant and tuber K content, plant K uptake efficiency and K harvest index. Based on the tuber yield with low K application and relative yield, twenty potato genotypes could be classified into four types: DH (high efficiency at low and high K application), LKH (high efficiency at low K application), HKH (high efficiency at high K application) and DL (low efficiency at low and high K application). Low K and high efficiency ('Huayu-5') and high K and high efficiency ('Zhongshu-19') had significant differences in K distribution in different positions. Increasing K application decreased the tuber sucrose content in both cultivars.

Authors' Contributions

Conceptualization: CL; Funding acquisition: CL and XL; Investigation: ZD, JY and HH; Data curation: ZD and JY; Visualization: ZD and YC; Writing-original draft: ZD; Writing-review and editing: CL, JW, XL and XY. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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