Australian Journal of Crop Science AJCS
AJCS 7(6):735-743 (2013) ISSN:1835-2707

Effects of potassium on yield, photosynthate distribution, enzymes' activity and ABA content in storage roots of sweet potato (*Ipomoea batatas* Lam.)

Hongjuan LIU, Chunyu SHI *, Haifeng ZHANG, Zhenzhen WANG, Shasha CHAI

Agronomy College, Shandong Agricultural University/State Key Laboratory of Crop Biology, Tai'an 271018, China

***Corresponding author: scyu@sdau.edu.cn**

Abstract

Effects of supplying K_2O at 0, 12, 24 and 36 g m^{-2} soils on distribution of photosynthates (carbohydrates produced by photosynthesis) were studied in plants of *Ipomoea batatas* Lam (Beijing 553). Storage roots yield, photosynthate distribution, sucrose synthase and insoluble acid invertase activities, as well as abscisic acid content in storage roots were determined. The storage root yield first increased and then decreased as the increase in potassium fertilizer supply, with the highest increase of 36.42% under treatment of 24 g K_2O m^{-2} (K24) which was determined to be the optimal amount of fertilization. Under the K24 treatment, the chlorophyll content and P_N of functional leaves were improved in the early growth stage, as was the leaf area index. This treatment also increased the sucrose synthase activity and abscisic acid content of storage roots by 16.47% and 18.27%, respectively, for the whole growth stages, and improved insoluble acid invertase activity by 5.75% in the late growth stage. Larger increases of abscisic acid content appeared in late growth stage. More photosynthates were unloaded to storage roots as a result of the improved sucrose synthase, insoluble acid invertase activities and abscisic acid content which contributed to sink strength. The dry matter distribution rate of storage roots was significantly higher (69.45%) in plants with K24 treatment. In summary, sweet potatos under K24 treatment not only supplied more photosynthates during the early and middle growth stages but also had higher sink strength of storage roots which lead to higher photosynthate distribution in storage roots mainly in the late growth stage. The optimal amount was K_2O 24 g m^{-2}.

Keywords: dry matter distribution rate; photosynthate; K_2O; SS and IAI; storage root yield.
Abbreviations: ABA-Abscisic acid; IAI-insoluble acid invertase; K_2O-Potassium oxide; LAI- Leaf Area Index; P_N-photosynthesis rate; SS-sucrose synthase.

Introduction

Potassium is one of the principal plant nutrients underpinning crop yield production and quality determination (William and Pettigrew, 2008). Investigation has shown that potassium can improve crop yield with different application processes (Akram et al., 2009). Involved in many physiological processes, potassium's impact on photosynthesis and assimilate transport can have direct consequences on crop productivity (Cao and Tibbits, 1991; William and Pettigrew, 2008; Akram et al., 2009). On the other hand, potassium deficiency can lead to an overall reduction in the amount of photosynthetic assimilates available for growth (William and Pettigrew, 2008). Photosynthesis is the main process of biosynthesis, which results in plant yield, and it accounts for more than 90% of the dry matter in plants. Therefore, it is the fundamental way of increasing crop yield to increase net P_N and improve photosynthetic capacity (Hai and Kubota, 2001). Potassium can improve P_N (Sangakkara et al., 2000; Karimi et al., 2009; Römheld and Kirkby, 2010; Ma and Shi, 2011), and insufficient leaf K^+ levels lead to decreased photosynthesis per unit leaf area (William and Pettigrew, 2008). The rapid and excessive growth of sweet potato results in low storage root yield, indicating the photosynthate distribution between aboveground parts and storage roots plays an important role in yield. Potassium can prevent the aboveground parts from growing excessively and thus help to obtain high storage root yield (Tsuno and Fujise, 1964). It has been observed that potassium application tends to increase the proportion of dry matter diverted into the tubers (Tsuno and Fujise, 1964; Enyi, 1972). Similar results among other crops have also been found (Sangakkara et al., 2000; Sawan et al., 2006; Makhdum et al., 2007). In higher plants, sucrose is the principal form in which carbon is translocated between photosynthetic source and non-photosynthetic sink cells (Weber et al., 1995; Ayre, 2011). Studies have suggested that sucrose transported from source leaves to sink organs is controlled by 'sink strength' — the ability of a sink organ to attract sucrose (Sturm and Tang, 1999). The SS and acid invertase activities of sink cells contribute directly to sink strength (Klann et al., 1996; Nguyen-Quoc and Foyer, 2001). In sink organs, invertase can help to maintain sink strength, facilitating unloading by increasing the concentration gradient of sucrose between sink and source oranges (Eschrich, 1980), and the cell wall-bound invertase can maximize the translocation speed of photosynthates toward the sinks (Dali et al., 1992). However, some results have demonstrated that invertase activity was not associated with the sink strength of the tissue (Klann et al., 1996), as previously reported by Yelle et al. (1988). SS appears to be largely responsible for feeding assimilated carbon into sink metabolism (Fu and Park, 1995). Studies on maize, fava bean seeds and carrot tap roots support this theory (Sturm and Tang, 1999). Abscisic acid (ABA) can improve the strength of plants and promote the unloading of photosynthates in phloem as well as their transport, thus promoting the

translocation and accumulation of photosynthates (Dewdney and McWha, 1979; Tietz et al., 1981; Oliver et al., 2007). The similar result was obtained by Clifford et al. (1986) at *Phaseolus vulgaris* L. Many previous studies have confirmed that potassium can enhance the assimilate distribution of sink oranges. However, the effects of potassium on physical mechanism of sucrose distribution remain unclear. Some results show that potassium affects assimilate export from leaves (Sawan et al. 2006), some results indicate that potassium can increase relative growth rate of tubers (Fujise and Tsuno, 1967). This study focused on the effects of potassium on sink strength and determined the key factors that affect sucrose unloading in storage roots. The aim of this paper is to explain the physiological mechanism of potassium on distribution of photosynthates, which is essential for high storage roots yield of sweet potato.

Results

Biomass and fresh storage root yield

Biomass first increased and then decreased as the increase in potassium fertilizer supply, and the maximum biomass was detected under K24 treatment to be 24 g K_2O m^{-2} soil (K24). The harvest index increased as the rate of potassium fertilizer increased. However, the difference between treatment with K24 and K36 was not significant (p>0.05). The application of potassium fertilizer increased fresh storage root yield, and K24 treatment gave the highest yield with an increase of 36.42%. The storage root lumps of the plants that received potassium fertilizer were larger than those of the control, and the increase with K36 treatment was significant (p<0.05). Potassium fertilizer application also improved fresh weight per lump in the following order: K24>K36≈K12. Compared with the control, the percentage of dry matter increased significantly as potassium fertilizer increased, but the difference between K24 and K36 treatments was not significant (p>0.05) (see Table 1). In summary, potassium fertilizer application increased biomass and harvest index, which contributed to the increase of fresh storage root yield. This yield was improved mainly by increasing the fresh weight per lump. The percentage of dry matter was increased as well. Under the condition of the test, the optimal amount of potassium fertilizer was K_2O 24 g m^{-2} soils.

Leaf area index (LAI), $P_{N,}$ and chlorophyll content

The data from Table 2 showed potassium (K24) increased the chlorophyll content of functional leaves significantly during the early and middle growth stages but decreased them in the late growth stage, compared with the control. The net P_N of the functional leaves revealed a *down–up–down* pattern, with the maximum appearing at 130 days after planting and dropping quickly afterward. Net P_N was higher by 10.06% for functional leaves under K24 treatment during the early and middle growth stages. Potassium fertilizer (K24) increased LAI significantly by 13.99% in the early and middle growth stages. Nevertheless, it declined LAI by 14.52% in the late growth stage. The reduction in chlorophyll content and LAI caused by potassium fertilizer in the late growth stage was related with the translocation of dry matter from functional leaves to the storage roots.

Distribution of dry matter

As the storage roots expanding, dry matter distribution rate of storage roots increased and the rate of aboveground organs declined little by little. In the first 90 days after planting, over 90% dry matter accumulated in the aboveground organs. Later the distribution center gradually moved to storage roots. The dry matter partitioning rate between aboveground organs and storage roots was about 1:1 at harvest (Table 3). Potassium fertilizer (K24) significantly reduced the rate of dry matter diverted into the aboveground organs within the first 90 days after planting with the average rate of 82.70%. Meanwhile, it promoted the transfer of the dry matter distribution center from the aboveground organs to the storage roots. At 110 days after planting, dry matter distribution ratio between the aboveground organs and storage roots reached 1:1. Thereafter, dry matter accumulated mainly in storage roots, with the rate up to 69.54% at harvest. During the early growth stage, higher dry matter distribution rate under treatment of potassium fertilizer could be useful for earlier storage roots initiation and development; during the late growth stage, the higher rate indicated that potassium was beneficial for transfer of photosynthates to storage roots. These results suggested potassium fertilizer (K24) could make storage roots format earlier and expand faster than that of the control.

Carbohydrate content of different oranges

Carbohydrates are the main components of dry matter. Compared with the control, potassium fertilizer (K24) increased the sucrose content of functional leaves at early growth stage but decreased it during late growth stages by 14.07%. Meanwhile, potassium fertilizer (K24) increased the starch content of functional leaves in the early and middle growth stage but decreased it in the late growth stage. The sucrose content of petioles was increased in the early growth stage and decreased during the middle and late growth stages; the starch content of petioles was decreased within the whole growth stage treated with potassium fertilizer (K24). Compared with the control, sucrose and starch content of stems was decreased during the whole growth stage, and the main decrease appeared at the late growth stage. The sucrose and soluble sugar contents of storage roots reduced firstly, but then rose. Potassium fertilizer (K24) lowered sucrose content in the early stage, but accelerated the accumulation of sucrose in storage roots by18.14% in middle and late growth stages. During the middle and late stages, soluble sugar content of storage root under treatment K24 was increased with an average of 16.98%, which was higher than that in the early growth stage. Meanwhile, starch content of storage root was improved in the early growth stage, but was affected little later (Table 4).

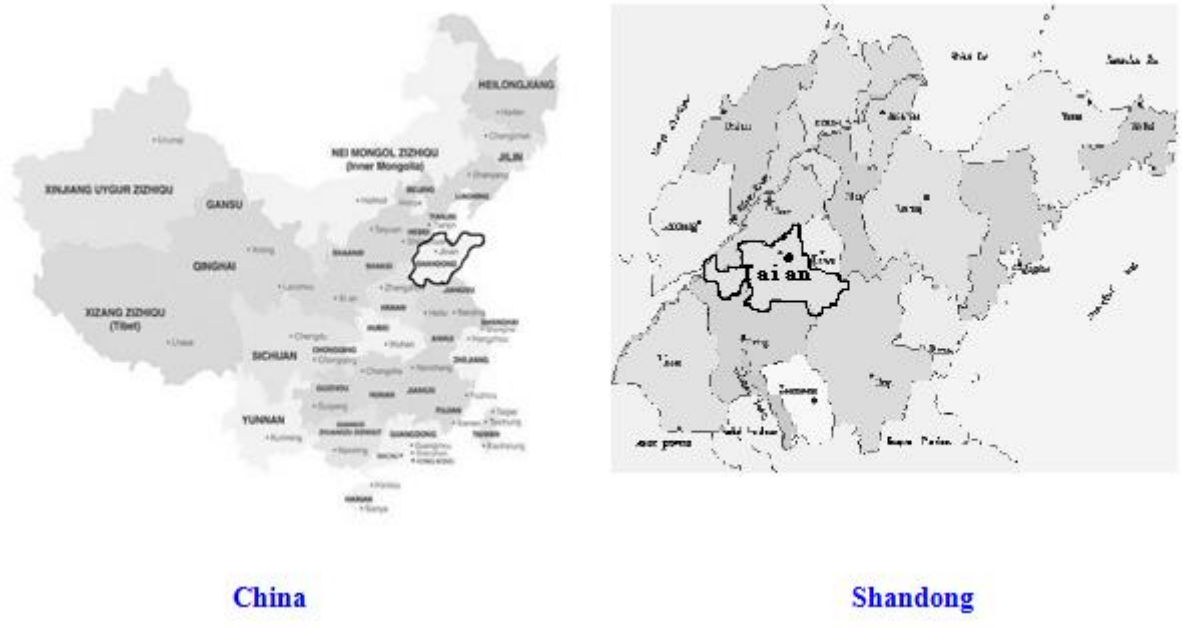
Enzymes activity associated with distribution of dry matter and ABA content

SS scatters in the cytoplasm of plant cells freely and can provide energy and carbon sources for cell respiration, cell wall polysaccharides, as well as starch synthesis by cleaving sucrose. As seen in Fig. 3, SS activity was at its highest in the middle growth stage, and it maintained a higher level during the early and late growth stages. Compared with the control, potassium fertilizer (K24) improved SS activity at key growth stages with an average increase of 16.47%. The improvement in SS activity resulted in more decomposition of sucrose, which brought higher sucrose concentration gradient between source and sink organs. The increase in sucrose concentration gradient promoted the photosynthate transport, and the larger increases in the early and late stages contributed to the formation of storage roots and retention of

Table 1. Effects of K application on biomass, fresh yield and economic coefficient

Treatment	Biomass per plant (g DW)	Fresh yield (×1000 kg ha^{-1})	Storage root Lumps per plant (NO.)	Fresh weight per lump (g)	Dry matter percentage of storage roots (%)	Harvest index
K0	280.164 d *	23.60 c	2.63 b	184.57 c	25.32 c	0.487c
K12	338.272 b	29.23 b	2.83 ab	218.86 b	27.85 b	0.613 b
K24	370.089 a	32.20 a	2.77 ab	237.05 a	28.05 ab	0.705 a
K36	302.969 c	29.69 b	2.90 a	218.25 b	28.25 a	0.711 a

*Within a column, values sharing a same letter do not differ significant (p>0.05).



·Experimental site

Fig 1. Map showing the location of the experiment

As shown in the part highlighted in black line in map of China is Shandong province; the part highlighted in black line in map of Shandong province is Tai'an city. Experimental site lies in the northeast of Tai'an city.

sink strength, respectively. Acid invertase can decompose sucrose into glucose and fructose. According to solubility, there are two forms: insoluble and soluble, the former exists in cell wall, and the latter exists in the cytoplasm and vacuole. The decomposition of sucrose causes an increase in the sucrose concentration gradient between the source and sink organs, thereby increases the unloading rate of sucrose (Walker and Ho, 1977; Lowell et al., 1989). Data in Fig 4 indicated that insoluble invertase activity dropped firstly, and then went up, with the minimum value reported at 90 days after planting. Insoluble acid invertase (IAI) activity treated with K24 was higher than that of the control, and larger increases appeared in the late growth stage with an average increase of 5.75% (Fig. 4). Potassium fertilizer (K24) could improve the unloading rate of sucrose, with the major improvement during the late growth stage. ABA can improve phloem unloading and transformation of photosynthates in sink organs by enhancing sink strength, which results in high yield (Dewdney and McWha, 1979). The pattern of changes of ABA content in storage roots appeared to be a *V* shape, and the minimum was reported at 110 days after planting. The content in the late growth stage was higher than that in the early growth stage. Potassium fertilizer (K24) increased ABA content during the whole growth stage, and larger increases appeared in the early and late growth stages with average increases of 13.50% and 27.81%, respectively (Fig. 5). In summary, Potassium fertilizer (K24) enhanced the accumulation of photosynthates in storage roots by increasing ABA content. The major increase happened in both early and late growth stages.

Correlation between carbohydrate contents of different oranges and SS, IAI activity, and ABA content

The correlations between the carbohydrate content of different organs and IAI activity, SS activity, and ABA content were analyzed (Table 5). The result showed that IAI activity had a sharp negative correlation with sucrose content of functional leaves and starch contents of stems. It had a very obvious negative correlation with starch content of storage roots. SS activity displayed a significant negative correlation with the starch content of petioles and a highly significant negative correlation with the sucrose content of stems. There are also significant negative correlations not only between SS activity and sucrose content but between SS activity and soluble sugar content of storage roots. ABA content had a significant positive correlation with the sucrose content of storage roots and a highly significant positive correlation with soluble sugar.

Discussion

Effect of potassium on photosynthate supplement and distribution

The economic yield of crops has relation with the photosynthetic area, photosynthetic time, photosynthetic capacity, and photosynthates consumption and distribution.

Table 2. Effects of K application on LAI, P_N and chlorophyll content of functional leaves.

Items	Treat-ment	Days after planting (d)						
		50	70	90	110	130	150	170
LAI	K0	1.77 b*	3.91 a	5.68 b	4.90 b	5.45 b	5.17 a	4.86 a
	K24	2.13 a	3.90 a	6.86 a	5.83 a	6.01 a	4.67 b	3.93 b
P_N (μmol CO_2 m^{-2} s^{-1})	K0	24.67 b	23.19 b	23.36 a	21.37 b	30.02 b	22.31 a	9.50 b
	K24	26.41 a	26.01a	24.82 a	24.06 a	31.98 a	22.80 a	10.14 a
Chl (a+b)	K0	1.90 b	3.06 b	3.72 a	3.86 b	3.46 a	3.42 a	2.65 a
	K24	2.16 a	3.32 a	3.82 a	4.15 a	2.99 b	2.83 b	2.29 b

*within a column, values (means) sharing a same letter do not differ significant (p>0.05)

I (replication)	II	III
K0	K36	K12
K12	K24	K0
K24	K12	K36
K36	K0	K24

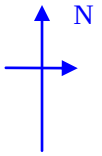


Fig 2. Experimental design showing potassium application treatments.

High-production varieties had high P_N, large photosynthetic area and long photosynthetic time generally (Hai and Kubota, 2001). The appropriate amount of potassium increased chlorophyll content and improved P_N (Sangakkara et al., 2000; Akram et al., 2009; Karimi et al., 2009; Ma and Shi, 2011). It has also been reported that the LAI (Farley and Draycott, 1974; Pettigrew and Meredith, 1997) and harvest index are enhanced by potassium, too (William and Pettigrew, 2008). However, some results showed that LAI was not affected by potassium (Gunasena and Harris, 1971; Melton and Dufault, 1991). Our study demonstrated the optimum amount of potassium (K24 treatment) increased not only the LAI but the net P_N and chlorophyll content of functional leaves during early and middle growth stages. But it decreased the LAI and chlorophyll content at late growth stage. P_N in the experiment was similar to that in control in the late growth stage. Moreover, this research found the optimum amount of potassium increased the sucrose and starch contents of functional leaves in the early growth stage but caused their reduction in the late growth stage. This may be attributed to the larger amount of photosynthates exported by functional leaves in the late growth stage. The optimum amount of potassium reduced the sucrose and starch contents of stems, especially during late growth stage. These reductions probably associated with the smooth transport of dry matter from stems to storage roots in the late growth stage. Dry matter distribution of storage roots was increased during the whole growth stages, so it was earlier for storage roots to become dry matter distribution center than that with the control. In summary, the optimum amount of potassium ensured an abundant supply of photosynthates from source during early and middle growth stages and promoted the translocation of photosynthates to storage roots mainly at late growth stage. Both contributed to increasing production of storage roots.

Physiological mechanism of potassium on improving distribution of photosynthates in storage roots

Sink strength of an organ is referred to its capacity of absorbing photosynthates, which is affected mainly by sink activity (Sturm and Tang, 1999). Sucrose hydrolysis is the first step toward either metabolism or synthesis of storage product (Weber et al., 1995). SS activity is regarded as one of the decisive factors for sink strength (Dali et al., 1992; N'tchobo et al., 1999). Invertase exited through cell wall regulates sucrose unloading out of phloem and plays an important role in regulating the rate of its translocation towards sink orange (Walker et al., 1978; Dali et al., 1992). The effects of SS and invertase on sink strength vary among different crops (Yelle et al., 1988; Klann et al., 1996). The results of this study showed that SS activity had a significant negative correlation with the sucrose content of storage roots but a positive correlation with their starch content. IAI activity had a positive correlation with sucrose and soluble sugar content of storage roots but a highly significant negative correlation with their starch content. These results indicate that SS and IAI are both directly correlated with sucrose unloading capacity, contributing directly to sink strength in sweet potato, which is in good agreement with previous studies (Klann et al., 1996; Nguyen-Quoc and Foyer, 2001). However, sucrose unloaded by two enzymes played different roles in growth. Sucrose unloaded by SS mainly contributed to starch synthesis, whereas sucrose unloaded by IAI was mainly used for growth. This study also found a significantly negative correlation between SS and the sucrose content of stems, significantly negative correlations between IAI and the sucrose content of functional leaves as well as between IAI and the starch content of stems. These findings suggest that high SS and IAI activities probably represent high sucrose exportation of the aboveground parts. Compared with the control, the optimum amount of potassium increased SS and IAI activities mainly during the early and late growth stages. Higher SS activity in the early stage could result in earlier storage roots initiation. The previous report showed that potassium application caused earlier tuber initiation (Enyi, 1972). The optimum amount of potassium increased dry matter distribution in two ways: one is by enhancing strength of storage roots, and the other is by improving sucrose export from leaves and stems. ABA is a key phytohormone that regulates apoplastic unloading, and it plays an important role in assimilate transport (Tietz et al., 1981; Hubbard et al., 1991; Yang et al., 2006). ABA can enhance sink strength of plants, which contributes to loading in phloem and transformation of photosynthates in sink (Tietz et al., 1981; Clifford et al., 1986). In this study, ABA content had a significantly positive correlation with sucrose content, and a highly significant positive correlation with soluble sugar content of storage roots, both confirming the above conclusions. Compared with the control, the optimum amount of potassium increased the ABA content, with larger increases in the late growth stage. These findings indicated the optimum amount of potassium promoted a higher ABA content with a higher photosynthate distribution of storage

Table 3. Effects of K application on the distribution ratios of dry matter in different organs.

Distribution rates of dry matter (%)	Treatment	Days after planting (d)						
		50	70	90	110	130	150	170
Overground parts	K0	94.87 a*	90.58 a	74.46 a	64.87 a	57.44 a	58.90 a	52.35 a
	K24	84.80 b	80.60 b	60.88 b	51.58 b	49.71 b	36.56 b	30.55 b
Storage root	K0	5.13 b	9.42 b	25.54 b	35.13 b	42.56 b	41.10 b	47.65 b
	K24	15.20 a	19.40 a	39.12 a	48.42 a	50.29 a	63.44 a	69.45 a
Ratio (Top/Root)	K0	18.51	9.62	2.92	1.85	1.35	1.43	1.10
	K24	13.50	8.99	1.24	1.32	1.06	0.68	0.66

*within a column, values (means) sharing a same letter do not differ significant (p>0.05).

roots. Tang et al. (2009) reported that ABA increased SS activity. In this study, ABA content had non-significant positive correlations with SS activity (r^2 = 0.21) and IAI activity (r^2 = 0.860). These results suggested that ABA might heighten translocation of photosynthates to storage roots by other ways.

Materials and methods

Experimental site

This experiment on potassium fertilizer management using sweet potato planted in spring was conducted from 2009 to 2010 at the Shandong Agricultural University Agricultural Research Station (Tai'an, Shandong Province, China; 117°09.090′ E, 036°09.000′ N) (see Fig. 1). Physico-chemical analysis revealed the experimental soil was a sandy loam with 13.70 g kg^{-1} organic matter, 72.86 mg kg^{-1} alkaline nitrogen, 21.62 mg kg^{-1} available phosphorus, and 65.79 mg kg^{-1} available potassium. The pH of the soil was 6.75.

Layout and the experimental design

The experiment was laid out according to completely random design using three replications (see Fig. 2). The net plot size was 20 m^2 (5×4m). Sweet potato (*Ipomoea batatas* Lam.; Beijing 553) and K_2SO_4 (K_2O, 50%) were used as the cultivar and basal fertilizer, respectively. Four K_2O treatments were used: K0, 0 g m^{-2} soil; K12, 12 g m^{-2} soil; K24, 24 g m^{-2} soil; and K36, 36 g m^{-2} soil. Beijing 553 was planted on May 6th at spacing (row × plant) 80×25 cm, and harvested on October 22nd. The rest cultivation management was the same as that of normal field.

Sampling of sweet potato plant (leaves, petioles, stems and storage roots)

Sampling time

Sampling began at the formation of storage roots (50 days after planting) and ended at harvest, once every 20 days, and 7 times in total.

Sampling process

Five plants were randomly uprooted for storage roots and the aboveground organs. The foliage of one plant, selected randomly, was cut at ground level and transferred to a polythene bag for the subsequent determination of leaf area. The remaining plants were treated similarly and the foliage was put in separate polythene bags. Storage roots were then lifted and bagged. All samples were taken to the laboratory, where separation into leaves, petioles, stems and storage

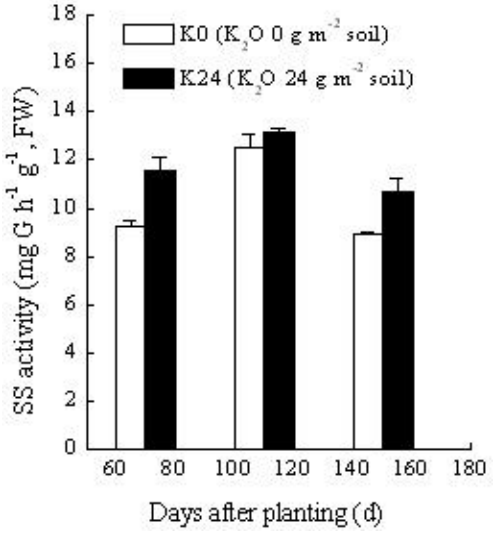


Fig 3. Effect of K application on activity of SS (Bars are the ±SE of means).

roots was carried out immediately. The foliage of the plant for the estimation of leaf area was dealt with firstly with separated leaves weighed to the nearest gram, put in bags again and refrigerated until use. The storage roots were separated into two parts: one part consisted of fresh samples for the determination of enzymatic activities and ABA content, whereas the other part was treated as dry samples to determine the contents of starch, total soluble sugar, and sugar components. The aboveground organs (leaves, petioles, and stems) were treated as dry samples to determine the contents of starch, total soluble sugar, and sugar components as well.

Fresh sampling method

Fresh samples were taken at the center of fresh storage roots. The samples were sliced into sections of 3~5 mm thickness. They were quick-frozen in liquid nitrogen and then stored at -40 °C until the analysis.

Dry sampling method

The stems were cut into a number of horizontal sections of around 5 cm in length. The storage roots were cut into pieces of about 3 mm thickness. The samples were dried using a DHG Series Heating and Drying Oven (*Model No. DHG-9203A, Yiheng Technology*, Co., Ltd., Shanghai). The leaves and petioles collected, stems and storage roots samples were cut and dried at 60 °C in the oven, then grounded to powder using Warring blender, packaged in air-tight glass jar, and stored at room temperature until analysis.

Table 4. Effect of K application on carbohydrates content (%) in different organs of sweet potato plants.

Organ	Content	Treatment	Days after planting (d) 50-90	90-130	130-170
Leaves	Sucrose	K0	2.16 b	3.07 a	4.34 a
		K24	2.57 a	3.04 a	3.73 b
	Starch	K0	10.20 b	11.68 b	15.13 a
		K24	11.04 a	13.00 a	14.41 b
Petiols	Sucrose	K0	3.74 b	2.96 a	7.37 a
		K24	5.64 a	2.64 b	5.96 b
	Starch	K0	10.68 a	10.65 a	11.43 a
		K24	8.90 b	9.76 b	10.24 b
Stems	Sucrose	K0	4.76 a	3.16 a	4.69 a
		K24	3.80 b	2.72 b	3.22 b
	Starch	K0	16.26 a	18.83 a	18.10 a
		K24	16.13 a	17.96 b	16.29 b
Storage root	Sucrose	K0	8.72 a	6.45 b	7.98 b
		K24	7.97 b	7.19 a	9.96 a
	Soluble sugar	K0	17.98 b	13.46 b	18.09 b
		K24	19.71 a	15.81 a	21.07 a
	Starch	K0	44.79 b	66.75 a	61.46 a
		K24	49.09 a	66.55 a	62.44 a

*within a column of each content (Data in different treatments of the same content in the same organs were compared with analysis of variance. Take sucrose content of leaves for example, it was equal to ratio of sucrose matter of leaves to dry matters of leaves.), values (means) sharing a same letter do not differ significant ($p>0.05$).

Table 5. Correlation coefficients (r^2) between carbohydrate content of organs and IAI, SS, ABA.

Items	The carbohydrate content of different organs (%, dry matter)								
	Leaves		Petioles		Stems		Storage roots		
	Sucrose	Starch	Sucrose	Starch	Sucrose	Starch	Sucrose	Soluble sugar	Starch
IAI	-0.74*	-0.7	-0.35	-0.44	-0.2	-0.72*	0.67	0.45	-0.86**
SS	-0.02	-0.53	-0.78	-0.98*	-1.00**	-0.43	-0.98*	-0.97*	0.59
ABA	0.18	0.27	0.64	0.05	0.41	-0.64	0.78*	0.93**	-0.5

* Significant at 0.05 probability level, ** significant at 0.01 probability level.

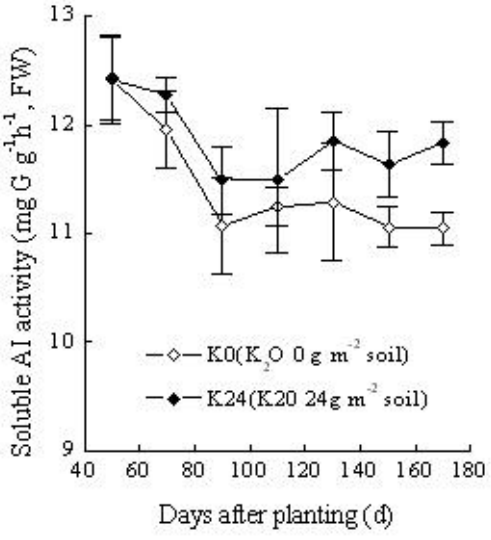


Fig 4. Effect of K application on activity of insoluble acid invertase (Bars are the ±SE of means).

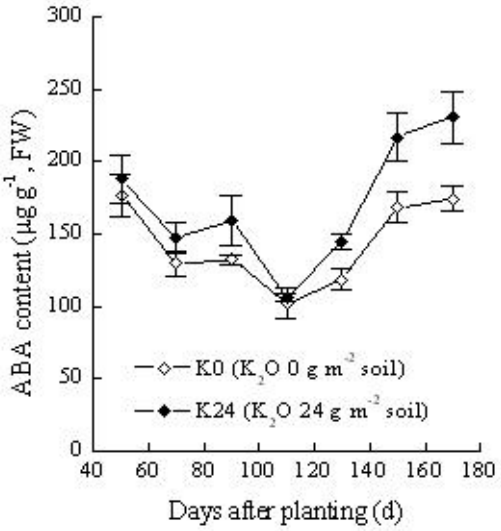


Fig 5. Effect of K application on ABA content (Bars are the ±SE of means).

Net P_N determination

Functional leaves are leaves capable of photosynthesis, accumulating organic matter, and transporting organic matter to the growth center. In this study, leaves with the highest P_N, which were the fourth or fifth leaves expanded fully from the shoot apex, were used as functional leaves. The net P_N of the functional leaves of five plants in each treatment were measured by using a LI-6400 Portable Photosynthesis System (*LI-6400, LI-COR Inc.*, Lincoln, NE, USA). All measurements were conducted from 9:30 to 11:30 a.m. on sunny days with an open circuit gas exchange system with the following conditions/adjustments of the leaf chamber: leaf surface area 6 cm^2; ambient CO_2 concentration 340~360μL L^{-1}; PFD 1200 μmol/(m^2 s^1) or so; air relative humidity about 60%. The final P_N value was the average of 10 replicates.

Chlorophyll content determination

10~20 functional leaves were chosen from normally growing plants in each treatment, then punched avoiding the main veins, at last put about 0.1g discs taken from punching into 20 mL 95% (v/v) ethanol. Seal up and stand in darkness till the pieces fade away completely (48 h or so), shake test tubes 2-3 times during extraction. The chlorophyll content was calculated according to the equations of Arnon (1949).

Leaf area index determination

Leaf area index determination was carried out by the methods of Jonckheere et al. (2004). The gravimetric method correlates dry weight of leaves and leaf area using predetermined green-leaf-area-to-dry-weight ratios (leaf mass per area, LMA). LMA is determined from a sub sample extracted from the global field sample. After "green" leaf area using scanning planimeter (*Li-3000*, Licor, Nebraska), the sub-sample is dried in an oven at about 60 °C until a constant weight is reached. The dry weight is subsequently determined using a precision balance and LMA is determined accordingly. Once the LMA is known, the entire field sample is oven-dried and leaf area is calculated from its dry-weight and the sub sample LMA.

Carbon-metabolizing enzymes activities determination

SS activity determination

SS activity was determined according to the methods of Douglas et al. (1988) and Ou-lee (1985), but with some modifications. Samples of fresh storage roots (1.5 g or so) were cut into small pieces and homogenized in 8 mL volumes of Hepes-NaOH buffer solution (containing 50 Mm Hepes, 5 Mm EDTA, 1 mM DTT, 2 mM KCL, 1% PVP) in a cooled mortar. After centrifugation at 10,000 g, 4 ^oC for 10 min, the supernatants were used as the crude soluble enzyme extract. SS activity was assayed by mixing 50 μL volumes of reaction liquid (100 mM L^{-1} UDP and 100 mM L^{-1} sucrose) with 50 μL volumes of enzyme extraction at 4 ^oC and then incubating the mixture. The reaction liquid was placed in an ice bath for 5 min before the enzyme extract was added. Incubation lasted for 30 min at 30 °C. The reaction was stopped by boiling for 1 min and reducing sugars were measured using dinitrosalicylic acid. Enzymes were killed by boiling before added for the blank control.

Insoluble acid invertase determination

We determined the activity of IAI using a modified version of the method described by Lowell et al. (1989). The enzyme was extracted and desalted at 0 to 5 °C. The fresh storage roots samples were homogenized with mortar by a ratio of 1 g storage root/5 mL volumes of 200 mM potassium phosphate buffer (pH 7.8). The relatively high molarity of buffer (200 mM) was used to inhibit binding of soluble enzymes to the insoluble fraction during homogenization. Homogenate was filtered through four layers of cheesecloth, rinsed with 5 mL extraction buffer minus PVPP, and centrifuged at 20,000 g, 4 °C for 10 min. Cell wall materials for assays of insoluble invertase were washed in 150 to 200 mL dilute (1:40 v/v) extraction buffer minus PVPP. The precipitate was homogenized with 10 mL 200 mM potassium phosphate buffer (pH 7.8) twice, and centrifuged at 20,000 g, 4 °C for 10 min. The precipitate was suspended in 3 mL 50 mM Hepes-NaOH buffer (pH 7.5) with 0.25 mM Na-EDTA. Insoluble invertases were assayed in a total volume of 1 mL containing extract, 80 mM acetate-K_3PO_4 (pH 4.5) and 100 mM sucrose. 0.2 to 0.5 g cell wall materials were added, and the reactions were incubated for 15 to 30 min at 45 °C. Addition of Nelson's reagent A (Nelson, 1944) terminated insoluble invertase assay, and production of glucose and fructose was quantified by completing the Nelson assay.

ABA content determination

ABA was determined following the method of Broquedis (1987)**.** One gram fresh storage roots sample was homogenized and extracted in 100% cooled acetonitrile containing 30 μg mL^{-1} sodium diethyldithiocarbamatre as an antioxidant. Samples were then centrifuged (5000 g; 4 °C; 10 min) and filtered. After filtration, the extracts were purified with PVPP, and then acidified with formic acid to pH 3.0, after that partitioned twice with peroxide-free diethyl ether (ratio of organic to aqueous phases was 1:3). Finally, ABA extracts were diluted with 1 mL volume of mobile phase. ABA determination was carried out by HPLC. Analyses were carried out using a Waters (Milford, MA, USA) Alliance 2414 HPLC system, consisting of an autosampler and a quaternary pump, and a Waters Symmetry C_{18} column (4.6×150 nm i.d., 5.0μm). ABA was isocratically eluted with formic acid/0.075% acetic acid (45:55, v/v). The solvent flow rate was 0.7 mL min^{-1}. The injector volume selected was 15 μL. Columns were kept at 30 °C. The peak wavelength was 254 λm.

The yield of fresh storage root was determined at harvest, and yield components were investigated as well.

Statistical analysis

Means and standard errors were calculated for three replicates from each treatment. One-way ANOVA was conducted using DPS. The statistical significance of the difference between means was determined by LSD test. All graphical constructions were completed using the Microsoft Excel 2003 software package.

Conclusion

The reasonable distribution of photosynthates is related to the yield of sweet potato. The yield level of storage root is closely related to sink strength. Under the conditions of this study, the optimum amount of potassium was K_2O 24 g m^{-1} soil.

It improved P_N and LAI during the early and middle growth stages, contributing to photosynthates accumulation. Meanwhile, it strengthened sink strength by improving SS and IAI activities and ABA content, thus contributing to photosynthate distribution in storage roots and resulting in high storage root yield. The effect of potassium on sink strength of sweet potato found in this study contributes to filling gaps in our knowledge and to the understanding of relationships between this nutrients affecting photosynthate distribution in different organs, and storage roots yield of sweet potato. It also provides technical directions for high yield cultivation of sweet potato.

Acknowledgements

This research was financially supported by National Natural Science Foundation of China (NSFC no. 31000689).

References

Akram MS, Ashraf M, Akram NA (2009) Effectiveness of potassium sulfate in mitigating salt-induced adverse effects on different physio-biochemical attributes in sunflower (*Helianthus annuus* L.). Flora. 204:471-483.

Arnon DI (1949) Copper enzymes in isolated chloroplasts, polyphenoxidase in beta vulgaris. Plant Physiol. 24: 1-15.

Ayre BG (2011) Membrane-transport systems for sucrose in relation to whole-plant carbon partitioning. Mol Plant. 4(3):377-394.

Broquedis M (1987) Utilisation de la dialyse et de la chromato-graphie ultra-rapide pour le dosage de l'acide abscissique: Application à la vigne. Vitis. 26:19-26.

Cao W, Tibbits TW (1991) Potassium concentration effect on growth, gas exchange and mineral accumulation in potatoes. J Plant Nutr. 14:525-537.

Clifford PE, Offler CE, Patrick JW (1986) Growth regulators have rapid effects on photosynthate unloading from seed coats of *Phaseolus vulgaris* L. Plant Physiol. 80:635-637.

Dali N, Michaud D, Yelle S (1992) Evidence for the involvement of sucrose phosphate synthase in the pathway of sugar accumulation in sucrose-accumulating tomato fruits'. Plant Physiol. 99(2):434-438.

Dewdney SJ, McWha JA (1979) Abscisic acid and the movement of photosynthetic assimilates towards developing wheat (*Triticum aestivum* L.) grains. Z Pflanzenphysiol. 92(2):183-186.

Douglas CD, Tsung MK, Frederick CF (1988) Enzymes of sucrose and hexose metabolism in development kernels of two inbreds of maize. Plant Physiol. 86:1013-1019.

Enyi BAC (1972) Effect of staking, nitrogen and potassium on growth and development in lesser yams: Dioscorea esculenta. Ann Appl Biol. 72(2):211-219.

Eschrich W (1980) Free space invertase: its possible role in phloem unloading. Ber Deut Bot Ges. 93(1):363-378

Farley RF, Draycott AP (1974) Growth and yield of sugar beet in relation to potassium and sodium supply. J Sci Food Agr. 26(4):385-392.

Fu H, Park WD (1995) Sink and vascular-associated sucrose synthase functions are encoded by different gene classes in potato. Plant Cell. 7(9):1369-1385.

Fujise, K, Tsuno, Y. (1967) Effect of potassium on the dry matter production of sweet potato. Paper presented at Proceedings of the International Symposium on Tropical Root Crops, Trinidad, 20-33, 1967.

Gunasena HPM, Harris PM (1971) The effect of CCC, nitrogen and potassium on the growth and yield of two varieties of potatoes. J Agr Sci. 76:33-52.

Hai MR, Kubota F (2001) Changes in photosynthetic rate, photorespiration rate and quantum yield of photosystem in sweet potato (*Ipomoea batatas* Lam.), Leaves with ageing and their cultivaral difference. Sci B Fac Agr Kyushu. 56(1):73-81.

Hubbard NL, Pharr DM, Huber SC (1991) Sucrose-phosphate synthase and other sucrose metabolizing enzymes in fruits of various species. Plant Physiol. 82(2):191-196

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F (2004) Methods for leaf area index determination. Part I: Theories, techniques and instruments. Agric Forest Meteorol. 121, 19-35.

Karimi E, Abdolzadeh A, Sadeghipour HR (2009) Increasing salt tolerance in Olive, *Olea europaea* L. plants by supplemental potassium nutrition involves changes in ion accumulation and anatomical attributes. Int J Plant Prod. 3(4):49-60.

Klann EM, Hall B, Bennett AB (1996) Antisense acid invertase (*TIV1*) gene alters soluble sugar composition and size in transgenic tomato fruit. Plant Physiol. 112(3):1321-1330.

Lowell CA, Tomlinson PT, Koch KE (1989) Sucrose-metabolizing enzymes in transport tissue and adjacent sink structures in developing citrus fruit. Plant Physiol. 90(4):1394-1402.

Ma L, Shi Y (2011) Effects of potassium fertilizer on physiological and biochemical index of *Stevia rebaudiana* Bertoni. Energy Procedia. 5:581-586.

Makhdum MI, Pervez H, Ashraf M (2007) Dry matter accumulation and partitioning in cotton (*Gossypiumhirsutum* L.) as influenced by potassium fertilization. Biol Fert Soils. 43:295–301.

Melton RR, Dufault RJ (1991) Nitrogen, phosphorus, and potassium fertility regimes affect tomato transplant growth. Hort Science. 26(2):141-142.

Nelson N (1944) A photometric adaptation of the Somogyi method for the determination of glucose. J Biol Chem.153: 357-380.

Nguyen-Quoc B, Foyer CH (2001) A role for 'futile cycles' involving invertase and sucrose synthase in sucrose metabolism of tomato fruit. J Exp Bot. 52(358):881-889.

N'tchobo H, Dali N, Nguyen-Quoc B, Foyer CH, Yelle S (1999) Starch synthesis in tomato remains constant through-out fruit development and is dependent on sucrose supply and sucrose synthase activity. J Exp Bot. 50(338):1457-1463.

Oliver SN, Dennis ES, Dolferus R (2007) ABA regulates apoplastic sugar transport and is a potential signal for cold-Induced pollen sterility in rice. Plant Cell Physiol. 48(9):1319-1330

Ou-Lee TM, Setter TL (1985) Effect of increased temperature in apical regions of maize ears on starch-synthesis enzymes and accumulation of sugars and starch. Plant Physiol. 79(3):852-855.

Pettigrew WT, Meredith WR Jr (1997) Dry matter production, nutrient uptake, and growth of cotton as affected by potassium fertilization. J Plant Nutr. 20(4&5):531-548.

Römheld V, Kirkby EA (2010) Research on potassium in agriculture: needs and prospects. Plant Soil. 335:155-180.

Sangakkara UR, Frehner M, Nösberger J (2000) Effect of soil moisture and potassium fertilizer on shoot water potential, photosynthesis and partitioning of carbon in mungbean and cowpea. J Agron Crop Sci. 185(3):201-206.

Sawan ZM, Hafez SA, Basyony AE, Alkassas AR (2006) Cottonseed, protein, oil yields and oil properties as affected by nitrogen fertilization and foliar application of potassium and a plant growth retardant. World J Agr Sci. 2(1): 56-65, 2006.

Sturm A, Tang G-Q (1999) The sucrose-cleaving enzymes of plants are crucial for development, growth and carbon partitioning. Trends Plant Sci. 4(10):401-407.

Tang T, Xie H, Wang YX, Lü B, Liang JH (2009) The effect of sucrose and abscisic acid interaction on sucrose synthase and its relationship to grain filling of rice (*Oryza sativa* L.). J Exp Bot. Vol. 60(9):2641-2652.

Tietz A, Ludewig M, Dingkuhn M, Dörffling K (1981) Effect of abscisic acid on the transport of assimilates in barley. Planta. 152(6):557-561.

Tsuno Y, Fujise K (1964) Studies on the dry matter production of sweet potato. The effect of potassium on dry matter production of sweet potato. Bull Nat Inst Agric Sci. Japan. 33:236-241.

Walker AJ, Ho LC (1977) Carbon translocation in the tomato: carbon import and fruit growth. Ann Bot-London. 41(4):813-823.

Walker AJ, Ho LC, Baker DA (1978) Carbon translocation in the tomato: pathway to carbon metabolism and the rate of translocation. Ann Bot-London. 42(4):901-909.

Weber H, Borisjuk L, Heim U, Buchner P, Wobus U (1995) Seed coat-associated invertases of Fava Bean control both unloading and storage functions: cloning of cDNAs and cell type-specific expression. Plant Cell. 7(11):1835-1846.

William T, Pettigrew (2008) Potassium influences on yield and quality production for maize, wheat, soybean and cotton. Physiol Plant. 133(4): 670-681.

Yang J, Zhang J, Wang Z, Liu K, Wang P (2006). Post-anthesis development of inferior and superior spikelets in rice in relation to abscisic acid and ethylene. J Exp Biol 57, 149–160.

Yelle S, Hewitt JD, Robinson NL, Damon S, Bennet AB (1988) Sink metabolism in tomato fruit III. Analysis of carbohydrate assimilation in a wild species. Plant Physiol. 87(3):737-740.