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Differences in transport of photosynthates between high-and low-yielding *Ipomoea batatas* L. varieties

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Abstract

Previous studies have focused mainly on the accumulation of photosynthates and less on their distribution in sweet potato (*Ipomoea batatas* L.). In addition, the effect of photosynthate accumulation in root tubers on photosynthate distribution was not considered. Thus, a field experiment was carried out from May to October (2011 and 2012) to clarify the differences in photosynthate transport between high- and low-yielding sweet potato. This study mainly focused on the photosynthetic capacities of leaves, photosynthate distribution, and characteristics of photosynthate accumulation in root tubers. Results showed the high-yielding varieties displayed the higher fresh root tuber yield and the economic coefficient than the low-yielding varieties. They also showed greater net photosynthetic rate with a pronounced increase at the early and middle growth stages (8.9% and 11.4%, respectively). After the growth peak, the leaf area index (LAI) of the high-yielding varieties decreased with time and was maintained at 2~3 until harvest, whereas the LAI of the low-yielding varieties decreased slowly. The high-yielding varieties reached the ^{13}C distribution rate ≥ 50% at the early (2011, 2012) and middle (2011) growth stages, whereas the low-yielding varieties reached it at the late (2011) or middle (2012) growth stages. At harvest, the ^{13}C distribution rates in the branches and root tubers of the high-yielding varieties were 6.0–20.3% and 73.7–91.2%, respectively, whereas those of the low-yielding varieties were 29.6–34.7% and 60.7–63.5%, respectively. The high-yielding varieties showed the remarkable initial potential in root tubers, which was much better than that of the low-yielding varieties. The high-yielding varieties also produced heavier root tubers and the higher number of root tubers per plant at the early bulking stage. The root tubers also attained the greater content of soluble sugar and starch. The high-yielding varieties formed root tubers earlier, showed strong abilities to transport photosynthates into the root tubers, and exhibited a higher mean accumulation rate. These varieties could also reduce the photosynthate consumption in branch leaves and stems. Therefore, the high-yielding varieties established growth advantage for the root tubers earlier. It contributed to a reasonable distribution structure of photosynthates that led to the high root tuber yield. Based on our results, effective agricultural measures can be chosen to improve the root tuber yield of sweet potato.

Additional key words: ^{13}C distribution rate; photosynthate distribution; sweet potato; tuber roots; yield.

Introduction

Sweet potato (*Ipomoea batatas* L.) is a versatile crop, which is grown for its tubers. It produces high yields of root tubers per unit of area and per unit of time even in marginal lands (Nedunchezhiyan *et al.* 2012, Uwah *et al.* 2013). The root tuber yield in the Yangtze River Basin has been divided into three levels, such as the low yield (< 30,000 kg ha^{-1}); middle yield (30,000–37,500 kg ha^{-1}); high yield (≥ 37,500 kg ha^{-1}) (Zhou 2007). No yield standard exists in North China; the categories proposed are as follows: low yield (< 30,000 kg ha^{-1}); middle yield (30,000–45,000 kg ha^{-1}); high yield (45,000–60,000 kg ha^{-1}); and super high yield > 60,000 kg ha^{-1}. Even in the same regions, the root tuber yield differs among varieties. Photosynthesis is the basis for biomass production needed for the root tuber yield formation in sweet potato (Enyi 1977, Bhagsari and Ashley 1990). Studies on

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Abbreviations: C_0 – initial potential of root tubers; D – the accumulation duration (about 90% growth increment accumulated); DAP – days after planting; HY – high-yielding; K – theoretical maximum dry yield of root tubers; LAI – leaf area index; LMA – leaf mass per area; LY – low-yielding; R_{max} – maximum accumulation rate; R_{mean} – mean accumulation rate; T/R value – top/root ratio; T_{max} – time of the maximum accumulation rate.
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photosynthate accumulation show that the varieties with the high root tuber yield exhibit high photosynthetic rate (Bhagsari and Ashley 1990, Huang *et al.* 2012) and high biomass (Hai and Kubota 2001, Xu *et al.* 2008). A significantly positive correlation also exists between the dry matter of root tubers and the photosynthetic rate (El-Sharkawy *et al.* 1990, Peng *et al.* 1991, Xu *et al.* 2008, Huang *et al.* 2012). However, studies on the photosynthate distribution have attracted less attention until now. Available literature indicated that varieties with a high economic coefficient (Bhagsari and Harmon 1982) and a low top (means aboveground part)/root (T/R ratio) value (Zong *et al.* 2001) accumulate more photosynthates in root tubers. Sweet potato usually has a spindly growth of branches, which leads to a low root tuber yield. Thus, an optimal distribution structure is important for the high yield of sweet potato (Bhagsari and Harmon 1982). Traits of the photosynthate distribution among different organs remain unclear. Tsuno and Fujise (1965) pointed out that the rapid development of root tubers improved the photosynthetic rates by accelerating the output of assimilation. The effect of the initiation capacity and developing potential of root tubers on photosynthate distribution is unclear. Previous studies focused on differences between varieties, without dividing the yield into different levels. Therefore, the conclusions from previous studies are sometimes inconsistent. For example, the root tuber yield of Sushu NO.8 (S8) was higher than that of Beijing 553 (B553), but lower than that of Hong Xiangjiao (HXJ). They also ignore the effect of photosynthate accumulation in root tubers on photosynthate distribution. Based on the existing studies, six common varieties in North China were selected in this study and divided into two groups: the high-yielding and low-yielding one. We studied the differences in photosynthate accumulation and distribution between the two groups, particularly, the differences of photosynthate distribution in different organs using isotopic ^{13}C labeling. Furthermore, we analyzed the effect of physiological properties of root tubers on photosynthate distribution that involved the initiation capacity, sink at early bulking stage, and bulking abilities of root tubers by using periodic sampling during storage root development. We aimed to highligh the differences in photosynthate transport that cause differences in the root tuber yield between the high- and low-yielding varieties and to provide a new theoretical basis for high yield cultivation and breeding of sweet potato.

Materials and methods

Experimental site: This experiment was conducted from 2011 to 2012 at the Shandong Agricultural University Agricultural Research Station (Tai'an, Shandong Province, China; 117°09.090'E, 036°09.000'N). The physico-chemical analysis revealed that the experimental soil (40% of sand silt and 60% of clay) was a sandy loam with 13.70 g(organic matter) kg^{-1}, 72.86 mg(alkali-hydrolyzate nitrogen) kg^{-1}, 21.62 mg(available phosphorus) kg^{-1}, and 65.79 mg(available potassium) kg^{-1}. The pH of the soil was 6.75. The climatic conditions during the two trial periods were shown in Table 1. The mean rainfall in 2011 was higher than that in 2012, and the mean radiation was lower than that in 2012. In May and June 2012, the sweet potato plants were irrigated because of the lack of rainfall.

Experimental design: The experiment was laid out according to a completely randomized design using three replications. The net plot size was 20 m^2 (5×4 m). Six varieties with different morphologies and root tuber yields were chosen and divided into two groups, which include high-yielding (HY) and low-yielding (LY) varieties. The HY varieties included Long NO. 9 (L9), Hong Xiangjiao (HXJ), Sushu NO. 8 (S8), and Taizhong No. 6 (T6), whereas the LY varieties included Yizhi 138 (Y138) and Beijing 553 (B553). K_2SO_4 (K_2O, 50%) and urea (N, 46%) were used as the basal fertilizer, with dosages of 24 and 9 g m^{-2}, respectively. All varieties were planted on May 3, 2011 and May 1, 2012 at spacing 80 cm × 25 cm (row × plant) and were harvested on October 22, 2011 and October 19, 2012. The rest of the cultivation managements was the same as in a normal field.

Table 1. The main climatic parameters.

Month	Rainfall [mm]		Sunshine duration [h]		Radiation [W m^{-2}]		Mean temperature [°C]	
	2011	2012	2011	2012	2011	2012	2011	2012
5	4.26	0.23	7.35	8.06	570	622	20.10	22.14
6	1.30	0.53	7.14	6.19	593	517	25.81	25.59
7	6.19	6.79	4.71	6.14	411	526	26.97	27.70
8	5.35	1.72	4.71	5.74	346	476	25.48	25.80
9	6.99	2.05	4.87	6.08	349	438	20.06	20.67
10	0.43	0.51	5.67	6.94	315	390	15.08	15.71

Sampling time: Sampling began at the early bulking stage of root tubers (50 days after planting, DAP), in total, 7 times every 20 days until harvest.

Sampling process: Five plants were randomly uprooted to collect storage roots and aboveground organs. The foliage of two randomly selected plants 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 placed in separate polythene bags. Storage roots were then lifted and bagged. The foliage of the plant for the estimation of leaf area was done by separating the leaves, which were weighed with precision to grams and then dried. The storage roots were treated as dry samples to determine carbohydrate content.

Dry sampling method: The storage roots were cut into pieces of approximately 3 mm thick. All dry samples were dried using a *DHG* series heating and drying oven (*Model No. DHG-9203A, Yiheng Technology, Co., Ltd.*, Shanghai, China). The samples were dried at 60°C in the oven, then grounded to powder using Warring blender. The root powder was then packaged in air-tight glass jar and stored at room temperature until analysis.

Carbohydrate content: The contents of starch, soluble sugar, and sucrose of root tubers were determined by sulphuric acid-anthrone colorimetric method according to He (1985). The soluble sugar, and sucrose were extracted in thermostat water bath cauldron (*Model No. HH-4, Changzhou Guohua Electric Application Co., Ltd.,* China) by 80°C with 80% (v/v) alcohol, starch was extracted by boiling water with 9.2 mol L^{-1} $HClO_4$. Then the extract was added to sulphuric acid-anthrone, mixed, and heated in boiling water for 10 min. The mixture was cooled to root temperature, and the absorbance was measured at 620 nm.

Net photosynthetic rate (P_N) was determined according to the method of Liu *et al.* (2013). In this study, the fourth or fifth leaves expanding fully from the shoot apex with the highest P_N were used as functional leaves. P_N of the functional leaves of five plants in each treatment was measured by using a *LI-6400* portable photosynthesis system (*LI-6400, LI-COR Co., Ltd.*, Lincoln, NE, USA). All measurements were carried out from 09:30 to 11:30 h on sunny days with an open circuit gas exchange system with the following conditions/adjustments of the leaf chamber: leaf surface area of 6 cm^2; ambient CO_2 concentration of 340–360 μL L^{-1}, PPFD of 1,200 μmol m^{-2} s^{-1}; air relative humidity of about 60%. The final P_N value was the average of ten replicates.

Leaf area index (LAI) is defined as the one-sided green leaf area per unit of ground area in broad leaf canopies. LAI was determined by following the methods of Jonckheere *et al.* (2004). The gravimetric method correlates the dry mass of leaves and leaf area using predetermined green-leaf-area-to-dry-mass ratios (leaf mass per area, LMA). LMA was determined from a subsample which was extracted from the total field sample. After obtaining the "green" leaf area using scanning planimeter (*Li-3000*, *Licor*, Nebraska), the subsample was dried in an oven at approximately 60°C until a constant mass was reached. The dry mass was subsequently determined using a precision balance and LMA was determined accordingly. Once the LMA was known, the total field sample was oven-dried, and the leaf area was calculated from its dry-mass and the subsample LMA.

Photosynthetic duration: Twenty leaves were labeled in every treatment. They were the first fully expanded leaves of each main stem at 30, 80, and 110 DAP. The plastic label was then checked every four days, and the number of leaves with relatively low photosynthetic rate was recorded until no green leaf was left. Leaves with over 2/3 of yellow leaves area were considered to have the low photosynthetic rate. The photosynthetic duration at each stage was obtained by average of green leaf duration (in days). The average duration of three stages mentioned above stood for the photosynthetic duration of every variety.

^{13}C labeling of sweet potato plants was performed three times (50, 110, and 150 DAP) to cover the complete growth period of sweet potato (Shi *et al*. 2002). At each labeling date, five plants were chosen, and the fourth or fifth fully expanding leaves from the shoot apex of the main stem were covered with an airbag. The volume of the airbag was 400 ml, and the leaves were suspended in the airbag. $^{13}CO_2$ gas (50 ml) was injected into each airbag; the volume of $^{13}CO_2$ was approximately 1% of the total gas. $^{13}CO_2$ inside the airbag was generated through a reaction between $Ba_{13}CO_3$ (99% of atom ^{13}C) and phosphoric acid. The plants were labelled for 30 min under the following growth conditions: radiant and enchanting sunshine, no wind or light wind, temperature of 25 to 30°C, and relative humidity from 80 to 90%. After labeling, the airbags were removed. After 48 h, the plants were randomly uprooted to collect the storage roots and aboveground organs. The main stem was divided into two parts; the upper part was the part above the labeled leaves, whereas the nether part was the one under the labeled leaves. All leaves of the upper stem were designated as the upper leaves, and the unfolded leaves of nether stem were designated as the nether leaves. Stems, except the main stem, were named the branch stems, and leaves of the branch stems were named the branch leaves. The stems were cut into horizontal sections of around 5 cm in length. The storage roots were cut into pieces of approximately 3 mm thick. The samples were dried using a *DHG* Series heating and drying oven (*Model No. DHG-9203A, Yiheng Technology, Co., Ltd.,* Shanghai, China). The leaves and petioles collected, stems, and storage roots were cut and dried at 60°C in the oven, then grounded to powder using

Warring blender. The powder was analyzed by stable isotope ratio mass spectrometer (*Isoprime 100*, *Elementar Analysensysteme GmbH Co. Ltd.*, Germany).

Simulation process of logistic equation: The logistic equation (1) was used to simulate the growth status of root tubers, which included dependent variable of days after planting (*t*) and the independent variables of fresh mass of root tubers (*W*). A and B were the parameters, and K was the theoretical maximum dry yield of root tubers.

$$W = K/(1 + e^{A + Bt}) \quad (1)$$

The accumulation rate equation (υ) was derived from the first derivative of the logistic equation, Eq. 2.

$$\upsilon = W' = -KB^{eA + Bt}/(1+e^{A + Bt})^2 \quad (2)$$

Computing the second derivatives of the logistic equation and stipulating $W'= 0$, the time of the maximum accumulation rate (T_{max}) was obtained, Eq. 3.

$$T_{max} = A/B \quad (3)$$

Other parameters were also acquired, including maximum accumulation rate (R_{max}), Eq. 4; mean accumulation rate (R_{mean}), Eq. 5; initial potential (C_0), Eq. 6; accumulation duration (approximately 90% of growth increment was accumulated during this period, D), Eq. 7.

$$R_{max} = -KB/4 \quad (4)$$
$$R_{mean} = K/D \quad (5)$$
$$C_0 = K/(1 + e^A) \quad (6)$$
$$D = [\ln(1/9)-A]/B \quad (7)$$

Available P and K content: Available P was extracted by sodium bicarbonate and determined using the molybdenum blue method; available K was extracted by ammonium acetate and determined by flame photometry (*Model No. FP64, Shanghai Precision and Scientific Instrument Corporation CO., Ltd.,* China) (Chen 1999, Yang 1999).

Statistical analysis: The means and standard errors were calculated for three replicates from each treatment. Two-way analysis of variance (*ANOVA*) was conducted using *DPS* (*Data Processing System v7.05*). The statistical significance of the difference between means was determined using the *Duncan*'s new multiple range test. All graphs were drawn using *SigmaPlot 10.0* software.

Results

Capacity of photosynthate production

LAI: LAI is regarded as one of the standards for stem and leaf growth and population size of crops. The LAI of the six varieties increased first, and then decreased (Fig. 1*A*,*B*). At the early growth stage, the LAI of the HY varieties was higher than that of the LY varieties. However, from 90 DAP, the LY varieties exhibited higher LAI than that of the HY varieties. After the growth peak, the LAI of HY varieties dropped faster than that of the LY varieties.

P_N: The two-year data indicated that the P_N of six sweet potato varieties was high at the early growth stage, fell at the middle growth stage, and then increased at the late stage (Fig. 1*C*,*D*). Compared to the LY varieties, the HY varieties showed higher P_N, with a larger increase at the early (2011) or middle (2012) growth stages. The P_N rised again at the late growth stage, and the increase of HY varieties was significantly greater than that of the LY varieties (2011). During the entire growth period, the P_N of L9 was the highest, whereas that of Y138 was the lowest one.

Duration of P_N: T6 exhibited the longest duration of P_N, followed by L9 and Y138. HXJ, S8, and B553 showed the shorter ones (Fig. 2). Compared to B553, the HY varieties maintained effective P_N for a long time.

Regular pattern of photosynthate distribution: The HY varieties gained the higher ^{13}C distribution rate of root tubers than that of the LY varieties during the main growth stages (Table 2). The root tubers of the HY varieties became the photosynthate distribution centre (^{13}C distribution rate ≥ 50%) at the early growth stage. The LY varieties were not a growth centre until the middle and late growth stages. ^{13}C distribution in aboveground parts of the LY varieties was higher than that of the HY varieties and ^{13}C was mainly distributed to the branch leaves and stems. Two-way *ANOVA* indicated that the effect of varieties on all parts was significant. The data of 2011 showed that B553 exhibited the higher ^{13}C distribution rate in aboveground parts than that of Y138, whereas the data of 2012 showed the opposite trend. The effect of year on the other parts was significant except of the upper stem (50, 110, and 150 DAP), labeled leaves (110 DAP), and the upper leaves (150 DAP). HXJ showed lower ^{13}C distribution in the branch leaves and stems, but the higher ^{13}C distribution in the root tubers. T6 and S8 presented high ^{13}C distribution in the branch leaves and stems but lower ^{13}C distribution in the root tubers than the other HY varieties (Table 2). These results meant that the HY varieties exhibited the higher ^{13}C distribution rate in root tubers because of the decreasing ^{13}C allocation in the branch leaves and stems. The two-way *ANOVA* indicated that the effect of varieties and interaction between years and varieties on all plant parts was significant. The interaction between the two years was related to the different climatic conditions. The effect of the different

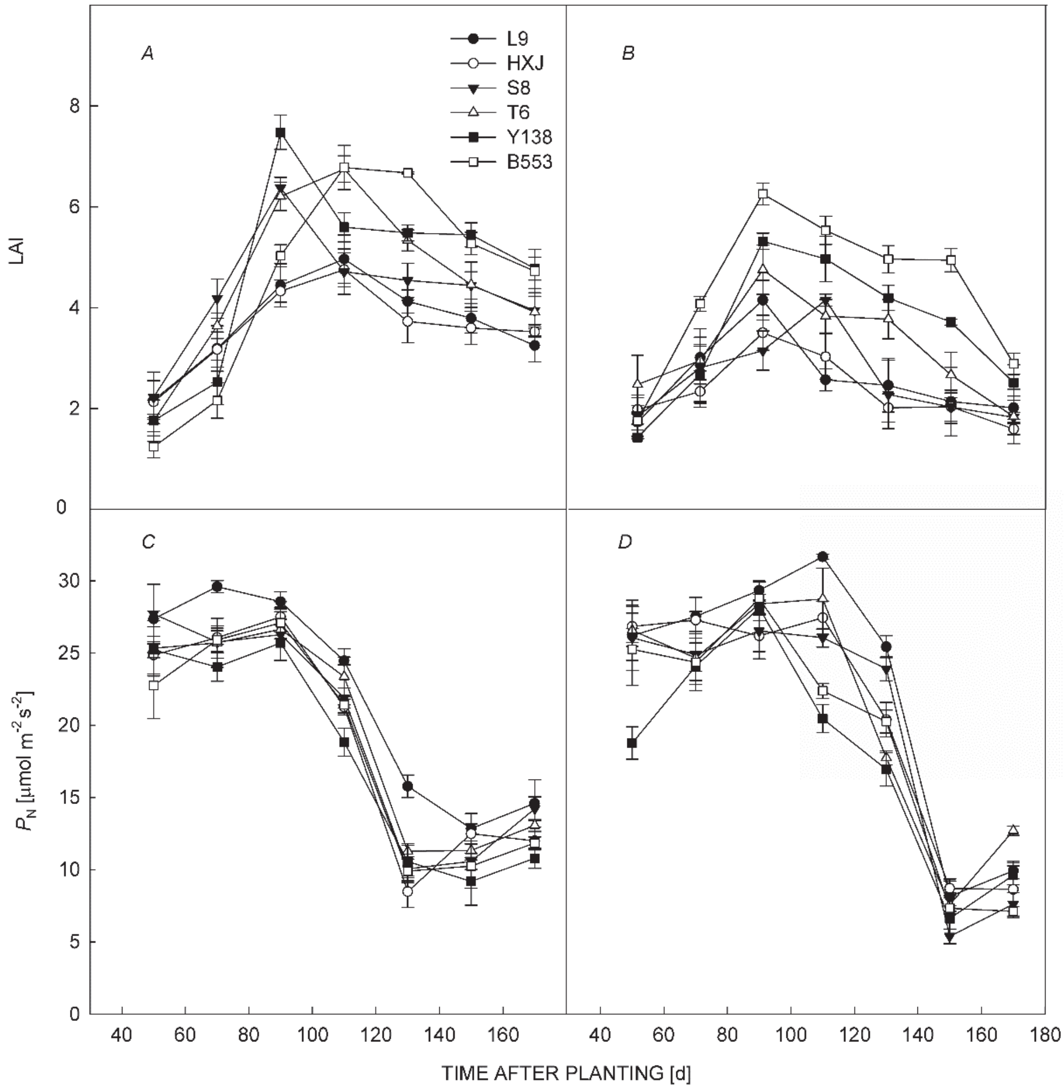

Fig. 1. Changes of leaf area index (LAI) in 2011 (*A*) and 2012 (*B*), and changes of net photosynthetic rate (P_N) in 2011 (*C*) and 2012 (*D*) of functional leaves in six varieties during the whole growth period. L9 – Long NO. 9; HXJ – Hong Xiangjiao; S8 – Sushu NO. 8; T6 – Taizhong No. 6; Y138 – Yizhi 138; B553 – Beijing 553.

stages on all parts of sweet potato was significant, and the effects of the differences in varieties and interaction between stages and varieties were also significant. The possible reason was that different varieties had different growth ability, thus the interaction was significant.

Feature parameter for accumulation of root tuber dry matter: The result of the two-way *ANOVA* showed that the effects of different varieties on K, T_{max}, R_{max}, R_{mean}, and D were significantly different. Compared to the LY varieties, the HY varieties showed the higher fresh yield of root tubers (K) and the higher initial potential (C_0) for root tuber initiation. The C_0 value ranged in the HY varieties from 0.31 to 1.48 (2011) and 0.26 to 0.65 (2012), whereas those of the LY were from 0.01 to 0.03 (2011) and from 0.02 to 0.06 (2012). The difference in K between the two years was significant, whereas the difference in C_0 was insignificant (Table 4). Meanwhile, HXJ showed higher C_0 than other varieties. L9 exhibited the maximum accumulation rate among the varieties in both 2011 and 2012. The smallest mean accumulation rate of the HY varieties was 2.06 and 2.34 in 2011 and 2012, whereas the biggest mean accumulation rate of the LY varieties was 1.61 and 1.83 (Table 4). The effect of years on R_{mean} was insignificant. In general, the HY varieties obtained the higher dry root tuber yield than that of the LY ones because of the earlier formation of root tubers and the higher mean accumulation rate (R_{mean}) during the root tubers bulking period. Beijing 553 and Y138 showed the higher fresh root tuber yield because of the relatively high mean accumulation rate for 2012 and 2011, respectively. Two-way *ANOVA* indicated that the interaction between the varieties and years significantly affected C_0, T_{max}, R_{max}, R_{mean}, and D. The difference in climate conditions (mainly

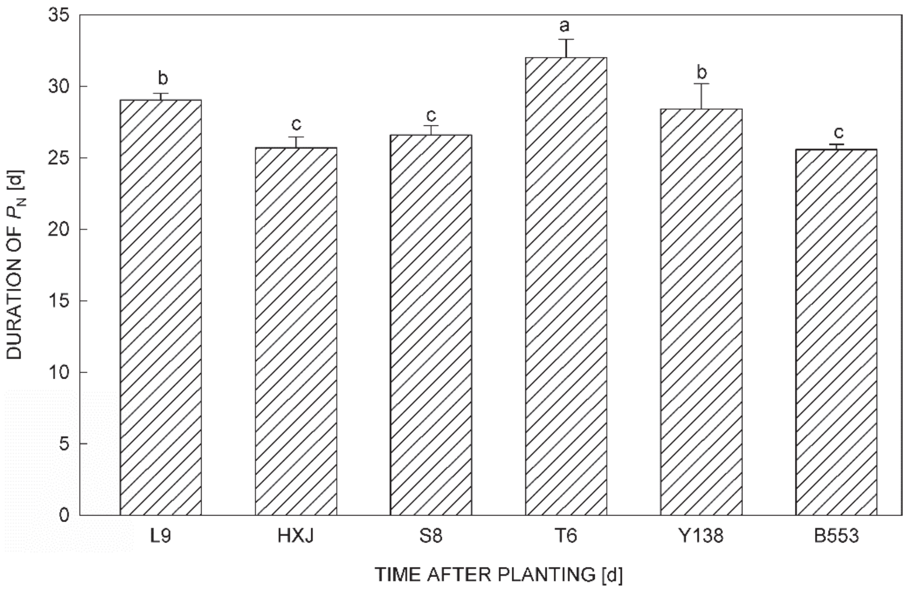

Fig. 2. The duration of net photosynthetic rate (P_N) of six varieties during the whole growth stages (2012). Values sharing *the same letter* are not significantly different at the 5% level by *Duncan*'s multiple range test. L9 – Long NO. 9; HXJ – Hong Xiangjiao; S8 – Sushu NO. 8; T6 – Taizhong No. 6; Y138 – Yizhi 138; B553 – Beijing 553.

rainfall and radiation) between two years caused changes in C_0, T_{max}, R_{max}, and D of each variety, thus the interaction among the varieties and years occurred. The significant differences in the interaction were mainly caused by the significant differences of varieties on C_0, T_{max}, R_{max}, R_{mean}, and D.

Sink of root tubers at early bulking stage (50 DAP): Compared to the LY varieties, the HY varieties exhibited the higher root tuber mass per plant and more root tubers per plant at the early bulking stage of root tubers (Table 5). Similar results were obtained in both years. HXJ showed the heaviest root tubers per plant, followed by L9 for two years, and T6 reached the highest number of root tubers per plant. The effect of varieties on the root tubers mass per plant and the root tuber number per plant was significant, but the effect of year was insignificant. Sucrose was the main form of photosynthates transported from source to sink organs. Starch was the main storage compound, which came from the photosynthates. The results of the sucrose content were controversial for 2011 and 2012. The starch contents of the HY varieties were significantly higher than that of the LY varieties. The effect of the varieties on the sucrose and starch content was significant, and the effect of year on them was significant as well. Our results meant that the HY varieties had higher number of root tubers per plant and superior capability for photosynthate conversion and both were beneficial to photosynthate allocation into root tubers.

Fresh root tuber yield of six sweet potato varieties: Two-way *ANOVA* showed that the effect of varieties on biomass, fresh yield of root tubers, economic coefficient, and dry matter content was significant. The effect of year on biomass, fresh yield of root tubers, and economic coefficient was also significant. The fresh root tuber yield of the HY varieties appeared significantly higher than that of the LY varieties. The fresh root tuber yields of L9 and HXJ were higher than that of S8 and T6, and the difference was remarkable for 2011 and insignificant for 2012. The biomass was insignificantly different among the varieties, except B553 in 2011 and T6 in 2012, which was the lowest yield that year (Table 6). However, a significant difference in the economic coefficient was found between the HY and LY varieties. The HY varieties had the higher economic coefficient, and S8 was lower than that of the other HY varieties. Two-way *ANOVA* indicated that the interaction between varieties and years had significant effect on biomass, fresh yield of root tubers, economic coefficient, and dry matter content. The interaction between the two years was related to climate change, mainly to the rainfall and radiation.

Discussion

Photosynthate accumulation and distribution: The crop yield exhibits close relationship to the efficiency of photosynthesis and distribution of photosynthates. Higher accumulation of photosynthates is the premise and foundation of the high yield (Sasaki and Ishii 1992, Hai and Kubota 2001). Whether or not photosynthetic rate (especially net photosynthetic rate) plays the decisive role in yield formation remains uncertain (Evans 1984, Jiang

Table 2. ^{13}C distribution rate in different organs of six sweet potato varieties during the key growth periods (%, the distribution rate was calculated on dry matter base) L9 – Long NO. 9; HXJ – Hong Xiangjiao; S8 – Sushu NO. 8; T6 – Taizhong No. 6, Y138 – Yizhi 138; B553 – Beijing 553. Values within the same column of the same stage followed by *the same letter* are not significantly different at the 5% level by *Duncan*'s multiple range test.

Year	Time after planting [d]	Varieties	Labeled leaves	Upper leaf	Upper stem	Nether leaf	Nether stem	Branch leaf	Branch stem	Root tuber
2011	50	L9	2.49^{cd}	3.19^{b}	0.84^{c}	13.95^{c}	1.07^{d}	33.04^{ab}	14.12^{c}	31.30^{b}
		HXJ	1.02^{e}	2.13^{b}	0.99b^{c}	8.10^{d}	3.45^{bc}	20.81^{c}	10.14^{d}	53.36^{a}
		S8	2.78b^{c}	7.50^{a}	2.24^{a}	21.17^{b}	5.01^{b}	34.00^{a}	15.18^{c}	12.12^{d}
		T6	1.64^{de}	3.21^{b}	1.11^{bc}	9.09^{d}	3.37^{bc}	37.35^{a}	19.03^{b}	25.20^{c}
		Y138	4.66^{a}	7.82^{a}	1.27^{b}	21.07^{b}	10.58^{a}	33.68^{ab}	8.10^{d}	12.82^{d}
		B553	3.75^{ab}	7.18^{a}	1.86^{a}	27.31^{a}	2.10^{cd}	28.73^{b}	22.43^{a}	6.64^{e}
	110	L9	0.44^{b}	0.84^{b}	0.18^{b}	3.09^{b}	2.41^{abc}	17.2^{cd}	12.67^{c}	63.16^{b}
		HXJ	0.28^{c}	0.54^{c}	0.19^{b}	2.63^{b}	1.93^{bc}	14.7^{d}	10.33^{c}	69.40^{a}
		S8	0.46^{b}	0.79^{b}	0.24^{b}	2.67^{b}	1.72^{c}	17.65^{c}	12.16^{c}	64.30^{b}
		T6	0.51^{b}	0.76^{bc}	0.21^{b}	2.16^{b}	1.47^{c}	15.81^{cd}	12.73^{c}	66.35^{ab}
		Y138	0.56^{b}	0.76^{bc}	0.25^{b}	5.58^{a}	3.49^{a}	24.19^{b}	18.93^{b}	46.24^{c}
		B553	0.81^{a}	1.5^{a}	0.51^{a}	3.71^{b}	3.32^{ab}	32.8^{a}	24.51^{a}	32.85^{d}
	150	L9	0.25^{c}	0.33^{ab}	0.06^{bc}	2.14^{a}	1.76^{bc}	10.21^{c}	9.59^{d}	75.65^{c}
		HXJ	0.22^{c}	0.10^{c}	0.02^{d}	1.25^{bc}	1.21^{c}	2.53^{e}	3.48^{f}	91.20^{a}
		S8	0.32^{abc}	0.36^{a}	0.07^{b}	2.27^{a}	2.93^{a}	9.12^{c}	11.19^{c}	73.74^{c}
		T6	0.27^{bc}	0.22^{b}	0.03^{cd}	0.86^{c}	1.29^{bc}	5.74^{d}	8.09^{e}	83.50^{b}
		Y138	0.39^{ab}	0.36^{a}	0.08^{b}	1.95^{ab}	1.81^{c}	15.56^{a}	19.12^{a}	60.73^{d}
		B553	0.41^{a}	0.42^{a}	0.12^{a}	2.48^{a}	3.41^{a}	13.11^{b}	16.51^{b}	63.54^{d}
2012	50	L9	1.06^{c}	1.53^{b}	0.23^{c}	7.67^{c}	2.29^{c}	23.44^{b}	7.82^{c}	55.97^{b}
		HXJ	1.23^{c}	1.54^{b}	0.65^{c}	4.94^{e}	2.44^{c}	20.14^{c}	10.69^{b}	58.37^{ab}
		S8	1.09^{c}	1.39^{b}	0.22^{c}	5.91^{d}	0.91^{d}	24.44^{b}	5.89^{d}	60.15^{a}
		T6	0.90^{c}	1.19^{b}	0.17^{c}	10.63^{b}	2.82^{bc}	23.12^{b}	8.47^{c}	52.70^{c}
		Y138	4.97^{a}	6.97^{a}	1.76^{b}	8.02^{c}	3.35^{b}	36.44^{a}	14.43^{a}	24.05^{d}
		B553	3.84^{b}	6.45^{a}	5.83^{a}	13.91^{a}	5.72^{a}	35.65^{a}	15.51^{a}	13.10^{e}
	110	L9	0.27^{d}	0.68^{b}	0.09^{c}	2.51^{d}	1.41^{c}	11.88^{d}	11.33^{d}	71.82^{a}
		HXJ	0.29^{d}	0.35^{c}	0.12^{c}	6.29^{a}	4.57^{a}	4.30^{e}	8.29^{e}	75.80^{a}
		S8	0.48^{c}	0.66^{b}	0.21^{bc}	4.31^{bc}	2.94^{b}	13.42^{c}	13.30^{c}	64.68^{b}
		T6	0.33^{d}	0.50^{bc}	0.22^{bc}	2.52^{d}	2.95^{b}	20.04^{b}	15.98^{b}	57.47^{c}
		Y138	0.94^{a}	1.65^{a}	0.45^{a}	3.48^{cd}	2.92^{b}	30.86^{a}	24.33^{a}	35.37^{d}
		B553	0.63^{b}	0.66^{b}	0.36^{ab}	4.64^{b}	2.74^{bc}	19.06^{b}	12.63^{cd}	59.27^{bc}
	150	L9	0.22^{b}	0.24^{bc}	0.04^{b}	5.51^{a}	4.41^{a}	5.39^{b}	6.45^{d}	77.73^{b}
		HXJ	0.19^{b}	0.14^{c}	0.04^{b}	1.25^{de}	1.28^{d}	3.74^{c}	4.21^{e}	89.14^{a}
		S8	0.19^{b}	0.18^{bc}	0.05^{b}	0.97^{e}	1.72^{cd}	13.28^{a}	11.25^{b}	72.37^{c}
		T6	0.20^{b}	0.24^{bc}	0.05^{b}	2.27^{cd}	2.75^{bc}	5.77^{b}	11.99^{b}	76.75^{bc}
		Y138	0.48^{a}	0.47^{a}	0.14^{a}	2.55^{c}	3.96^{ab}	6.23^{b}	14.00^{a}	72.17^{c}
		B553	0.25^{b}	0.29^{b}	0.12^{a}	3.75^{b}	5.28^{a}	5.06^{bc}	9.05^{c}	76.21^{bc}

1988), and the correlation between photosynthetic rate and yield is still controversial. Previous studies also indicate that a strong correlation exists between the leaf area/leaf growth and a tuber yield (Kakaty *et al.* 1992, Mannan *et al.* 1992). If the varieties obtain the highest LAI early and the highest LAI is maintained for a long time, then they can produce a high yield (Zhou 2007). Our results also showed that in addition to being affected by the photosynthate accumulation, the photosynthate distribution has an important effect on the yield as well. However, the present research on photosynthate distribution mainly focused on T/R and dry matter distribution of organs; the results showed that the varieties with the low T/R and high dry matter distribution rate of root tubers reached the high root tuber yield (Bhagsari and Harmon 1982, Huang *et al.* 2012, Uwah *et al.* 2013). The timely and efficient distribution of assimilate to root tubers is the base for the high yield in sweet potato (Chen 1961), and the root tubers are formed and developed faster if assimilates are transported to root tubers earlier (Chen 1982).

Table 3. Two-way *ANOVA* of ^{13}C distribution rate in different organs at different stages during different years. Y – year; V – variety; Y×V – year×variety; S – stage; S×V – stage×variety. *, ** and *** – statistically significant values at 5%, 1%, and 0.1% level of significance, respectively.

Year	Time after planting [d]	Source	Labeled leaves *p* value	Upper leaf	Upper stem	Nether leaf	Nether stem	Branch leaf	Branch stem	Root tuber
2011-2012	50	Y	0.0014**	<.0001***	0.3512	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
		V	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
		Y×V	0.0014**	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
	110	Y	0.4332	0.0111*	0.3687	0.0112*	0.0078**	<.0001***	0.0004***	0.0284*
		V	<.0001***	<.0001***	<.0001***	<.0001***	0.0006***	<.0001***	<.0001***	<.0001***
		Y×V	<.0001***	<.0001***	0.0056**	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
	150	Y	0.0114*	0.0599	0.2383	<.0001***	<.0001***	<.0001***	0.0107*	<.0001***
		V	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
		Y×V	0.0224*	0.0016	0.0125*	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
2011	50-110	S	0.0499	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	0.4454	<.0001***
		V	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001**	<.0001***	<.0001***
		S×V	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***
	110-150	S	<.0001***	<.0001***	<.0001***	<.0001***	0.1047	<.0001***	0.0317*	<.0001***
		V	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	0.0102	<.0001***
		S×V	0.0228*	<.0001***	0.0002***	0.0048**	0.0065**	<.0001***	<.0001***	<.0001***
2012	50-110	S	<.0001***	<.0001***	<.0001***	<.0001***	0.9945	<.0001***	<.0001***	<.0001***
		V	<.0001***	<.0001***	<.0001***	<.0001***	0.0001***	<.0001***	<.0001***	<.0001***
		S×V	<.0001***	<.0001***	<.0001***	<.0001***	0.0001***	<.0001***	<.0001***	<.0001***
	110-150	S	<.0001***	<.0001***	<.0001***	<.0001***	0.1072	<.0001***	<.0001***	<.0001***
		V	<.0001***	<.0001***	<.0001***	<.0001**	0.0007***	<.0001***	<.0001***	<.0001***
		S×V	<.0001***	<.0001***	<.0001***	<.0001***	0.0001***	<.0001***	<.0001***	<.0001***

Table 4. Feature parameter for photosynthate accumulation of root tubers dry mass. K – theoretical maximum fresh yield of root tubers; r^2 – coefficient of determination; a, b – parameters, C_0 – initial potential; R_{max} – maximum accumulation rate; R_{mean} – mean accumulation rate; $T_{max.R}$ – date of the maximum accumulation rate; D – the accumulation duration (about 90% of growth increment accumulated). L9 – Long NO. 9; HXJ – Hong Xiangjiao; S8 – Sushu NO. 8; T6 – Taizhong No. 6, Y138 – Yizhi 138; B553 – Beijing 553. Y – year; V – variety; Y×V – year×variety. Values within the same column of the same year followed by *the same letter* are not significantly different at the 5% level by *Duncan*'s multiple range test. *, ** and *** – statistically significant values at 5, 1, and 0.1% level of significance, respectively.

Year	Varieties	K	C_0	r^2	A	B	T_{max} [d]	R_{max} [g d^{-1} per plant]	R_{mean} [g d^{-1} per plant]	D [d]
2011	L9	496.00^{a}	0.87^{ab}	0.95^{a}	6.36^{bc}	–0.06^{a}	115.44^{b}	6.81^{a}	3.19^{a}	155.35^{a}
	HXJ	395.50^{b}	1.48^{a}	0.92^{a}	5.80^{c}	–0.06^{a}	102.92^{c}	5.55^{b}	2.78^{b}	142.51^{bc}
	S8	312.81^{c}	0.31^{bc}	0.94^{a}	6.93^{b}	–0.06^{a}	115.47^{b}	4.70^{c}	2.06^{d}	152.10^{ab}
	T6	322.02^{c}	0.66^{bc}	0.95^{a}	6.40^{bc}	–0.06^{ab}	103.08^{c}	5.00^{bc}	2.32^{c}	138.95^{c}
	Y138	250.14^{d}	0.03^{c}	0.98^{a}	9.04^{a}	–0.07^{b}	124.92^{a}	4.53^{cd}	1.61^{e}	155.29^{a}
	B553	186.48^{e}	0.01^{c}	0.98^{a}	9.67^{a}	–0.08^{c}	114.94^{b}	3.92^{d}	1.32^{f}	141.08^{bc}
2012	L9	354.81^{a}	0.26^{b}	0.98^{a}	7.20^{c}	–0.07^{b}	100.23^{c}	6.37^{a}	2.71^{a}	130.81^{b}
	HXJ	368.17^{a}	0.59^{a}	0.99^{a}	6.44^{d}	–0.06^{a}	106.25^{b}	5.54^{ab}	2.58^{ab}	142.50^{a}
	S8	341.27^{a}	0.65^{a}	0.98^{a}	6.29^{d}	–0.06^{a}	107.04^{b}	4.84^{b}	2.36^{b}	144.51^{a}
	T6	344.59^{a}	0.61^{a}	0.94^{b}	6.35^{d}	–0.06^{a}	109.30^{b}	4.96^{b}	2.34^{b}	147.17^{a}
	Y138	185.81^{b}	0.06^{c}	0.96^{ab}	8.07^{b}	–0.07^{b}	115.76^{a}	3.36^{c}	1.26^{d}	147.29^{a}
	B553	225.20^{b}	0.02^{c}	0.96^{ab}	9.38^{a}	–0.09^{c}	100.08^{c}	4.27^{b}	1.83^{c}	123.64^{b}
		p value								
Y		0.0056**	0.0768	0.1413	0.0056**	0.0645	<.0001***	<.0001***	0.5142	0.0003***
V		<.0001***	<.0001***	0.7281	<.0001***	<.0001***	<.0001***	<.0001***	<.0001***	0.0002***
Y×V		<.0001***	0.0248*	0.0427*	0.0071**	0.0322*	<.0001***	<.0001***	<.0001***	0.0008***

Table 5. Sink capacity and carbohydrate content of root tubers at 50 day after planting L9 – Long NO. 9; HXJ – Hong Xiangjiao; S8 – Sushu NO. 8; T6 – Taizhong No. 6, Y138 – Yizhi 138; B553 – Beijing 553. Y – year; V – variety; Y×V – year×variety. Values within the same column of the same year followed by *the same letter* are not significantly different at the 5% level by *Duncan*'s multiple range test. *, ** and *** – statistically significant values at 5%, 1%, and 0.1% level of significance, respectively.

Year	Varieties	Root tubers		Sucrose [%]	Starch [%]
		Mass per plant [g]	Number per plant		
2011	L9	42.43^{bc}	5.00^{a}	12.60^{a}	55.25^{b}
	HXJ	102.02^{a}	4.30^{ab}	6.82^{b}	69.23^{a}
	S8	18.84^{c}	2.70^{ab}	7.72^{b}	56.96^{b}
	TZ6	54.86^{b}	4.50^{bc}	7.53^{b}	61.87^{b}
	YZ138	7.15^{d}	1.50^{c}	12.94^{a}	46.00^{c}
	BJ553	4.22^{d}	0.50^{c}	7.93^{b}	24.44^{d}
2012	L9	50.02^{ab}	3.00^{bc}	11.03^{bc}	70.73^{b}
	HXJ	62.39^{a}	2.67^{bc}	11.71^{a}	80.89^{a}
	S8	61.32^{a}	4.00^{ab}	12.19^{a}	77.84^{a}
	TZ6	34.34^{b}	5.00^{a}	10.71^{c}	74.57^{ab}
	YZ138	4.00^{c}	1.67^{cd}	11.56^{ab}	46.44^{c}
	BJ553	3.43^{c}	0.50^{d}	11.94^{a}	38.24^{d}
		p value			
Y		0.3952	0.3876	<.0001***	<.0001***
V		<.0001***	<.0001***	0.0016**	<.0001***
Y×V		<.0001***	0.1395	0.0004***	0.0029*

Table 6. Yield, yield components, and economic coefficient of six sweet potato varieties. L9 – Long NO. 9; HXJ – Hong Xiangjiao; S8 – Sushu NO. 8; T6 – Taizhong No. 6, Y138 – Yizhi 138; B553 – Beijing 553. Y – year; V – variety; Y×V – year×variety. Values within the same column of the same year followed by *the same letter* are not significantly different at the 5% level by *Duncan*'s multiple range test. *, ** and *** – statistically significant values at 5%, 1%, and 0.1% level of significance, respectively.

Year	Varieties	Biomass [g]	Fresh yield of root tubers [×10^3 kg ha^{-1}]	Economic coefficient	Dry matter [%]
2011	L9	2,348.80^{ab}	68.16^{a}	0.81^{a}	23.61^{ab}
	HXJ	2,509.66^{ab}	62.47^{b}	0.80^{a}	24.62^{ab}
	S8	2,644.59^{a}	51.36^{d}	0.71^{b}	24.22^{ab}
	T6	2,278.53^{ab}	57.10^{c}	0.86^{a}	27.55^{a}
	Y138	2,211.69^{b}	47.36^{d}	0.65^{b}	20.93^{b}
	B553	1,739.07^{c}	21.28^{e}	0.56^{c}	27.55^{a}
2012	L9	2,055.09^{a}	55.49^{a}	0.87^{ab}	20.53^{d}
	HXJ	1,677.41^{abc}	53.46^{a}	0.91^{a}	23.94^{c}
	S8	1,751.38^{abc}	48.99^{a}	0.82^{b}	23.98^{c}
	T6	1,523.08^{bc}	46.49^{ab}	0.86^{ab}	28.76^{b}
	Y138	1,377.86^{c}	29.08^{c}	0.64^{d}	20.60^{d}
	B553	1,862.90^{ab}	36.69^{bc}	0.75^{c}	31.16^{a}
		p value			
Y		<.0001***	0.0003***	<.0001***	0.6392
V		0.0055**	<.0001***	<.0001***	<.0001***
Y×V		0.0025**	<.0001***	<.0001***	0.0093*

In this study, the HY varieties had the higher photosynthetic rates and LAI at the early bulking stage (50 DAP). After the growth peak, LAI of the HY varieties decreased in time, whereas that of the LY varieties was maintained at a higher value (Fig. 1*A,B*). Similar results were obtained during both years. The photosynthetic duration of the HY varieties was from 25.7 d (HXJ) to 32.0 d (T6) and that of the LY varieties was 25.6 d (B553) to 28.4 d (Y138). At the early bulking stage, the root tubers of the HY varieties turned into the ^{13}C distribution centre, whereas in the LY varieties, the aboveground parts, especially the branch leaves and stems, became the ^{13}C distribution centres (Table 2). The ^{13}C distribution rates of root tubers of the HY varieties were higher than those of the LY varieties at the main growth stages, and the increase at harvest was 16.1–50.2% (2011). Moreover, the rate of branching of the LY varieties was 1.46–5.76 times higher than those of the HY varieties (2011). Similar results were obtained in 2012, but the changes were smaller. The results of the two-way *ANOVA* showed that in both parameters, the type of variety was the main determining factor (Tables 2, 3). In conclusion, photosynthate distribution had a greater influence on the root tuber yield than photosynthate accumulation. The HY varieties exhibited a desirable distribution structure of photosynthates and distributed more photosynthates into the root tubers. By contrast, the LY varieties consumed more photosynthates for the growth of the aboveground parts, which delayed the transformation time of the growth centre from the aboveground parts to root tubers, caused spindling growth, and the time delay of leaf senescence.

Accumulation characteristics of root tubers: The cultivars display different tuber yielding potentials, which can be attributed to the variation in days to tuber initiation, rate of photosynthesis, and efficiency of assimilate partitioning to the tubers (bulking rate) and maturity period (Tekalign and Hammes 2005, Ravi *et al.* 2009). The assimilation of dry matter to the tubers should be increased or/and the utilization by other organs should be reduced to favour tuber growth (Tekalign and Hammes 2005). The onset of storage root initiation determines the majority of storage root yield at harvest (Villordon 2010). The root yield per plant is a function of the number of roots per plant, root length, and root diameter (Nedunchezhiyan and Byju 2005). So far, the starch accumulating capacity in the tuberous root is regarded as the fundamental determinant of the yield (Hai and Kubota 2003). In late bulking cultivars, high bulking rate for short duration may also result in increase of the storage root yield (Ravi *et al.* 2009).

The distribution of assimilates is the controlling factor for crop yield and it is regulated by their transport into the sink organs (Patrick 1988). Both P_N of leaves and the transport of assimilates are regulated by sink organ feedback; thus, a total sink capacity must be magnified to achieve a high crop yield. The physiological activities of sink organs have a positive role in promoting the photosynthate export from leaves, and the economic organs are initiative to obtain photosynthetic products from source organs, but they do not accept assimilation passively (Ling 2000). In this study, the results indicated that the HY varieties had the greater initial potential (C_0) and the yield potential (K) than the LY varieties, with a relatively high increase in 2011 (Table 4). At the critical period of root tuber formation (50 DAP), the single tuber mass and root tuber number per plant of the HY varieties were 9.6 and 4.1 (2011), respectively, which were 14.0 and 3.4 (2012) times higher, respectively, than those of the LY varieties. The higher C_0 was obtained as well. Both methods proved that the root tuber formation of the HY varieties was earlier than that of the LY varieties, which could improve the photosynthate distribution to root tubers. At the early bulking stage, the HY varieties acquired higher starch contents, which increased from 20.1% to 183.3% (2011) and from 52.3 to 111.5% (2012). These results illustrate smooth photosynthate conversion in root tubers, which facilitates photosynthate accumulation in root tubers. At the early bulking stage, the HY varieties established growth advantage for root tubers earlier. During the middle and late stages, the HY varieties maintained the higher accumulation rate. Root tubers were bulking early and accelerated the output of photosynthates of leaves, which contributed to the establishment of reasonable distribution structure, and promoted the photosynthate distribution in root tubers.

Conclusion: Compared with the LY varieties, the HY varieties produced the significantly higher fresh root tuber yield because of the formation of a favourable photosynthate distribution structure, which was affected by the characteristics of photosynthate accumulation in root tubers. The HY varieties established growth advantage of the root tubers earlier at the critical period for root tuber formation because of their remarkable initial potential of root tuber formation and their superior ability to transform photosynthates into storage sugars in root tubers.

References

Bhagsari A.S., Ashley D.A.: Relationship of photosynthesis and harvest index to sweet potato yield. – J. Am. Soc. Hortic. Sci. **115**: 288-293, 1990.

Bhagsari A.S., Harmon S.A.: Photosynthesis and photosynthate partitioning in sweet potato genotypes. – J. Am. Soc. Hortic. Sci. **107**: 506-510, 1982.

Chen C.Z. [Determination of potassium.] – In: Lu R.K., Zhu H.Z., He P.A. (ed.): [Methods of Soil Agricultural Chemistry Analysis.] Pp. 56. Chin. Agr. Sci. Technol. Press, Beijing 1999. [In Chinese]

Chen Y.C.: [Preliminary study of assimilate accumulation and development of sweet potato root tubers.] – Sci. Agric. Sin. **2**: 25-29, 1961. [In Chinese]

Chen X.K.: [The discussion of the relationship between source and sink of sweet potato.] – J. Shandong Agric. Univ. **13**: 79-87, 1982. [In Chinese]

El-Sharkawy M.A., Cock J.H., Lynam J.K. *et al*.: Relationships between biomass, root-yield and single-leaf photosynthesis in field-grown cassava. – Field Crop. Res. **25**: 183-201, 1990.

Enyi B.A.C.: Analysis of growth and tuber yield in sweet potato (*Ipomoea batatas*) cultivars. – J. Agr. Sci. **88**: 421-430, 1977.

Evans L.T., Visperas R.M., Vergara B.S.: Morphological and physiological changes among rice varieties used in the Philippines over the seventy years. – Field Crop. Res. **8**: 105-124, 1984.

Hai M.R., Kubota F.: The effects of drought stress and leaf ageing on leaf photosynthesis and electron transport in photosystem 2 in sweet potato (*Ipomoea batatas* Lam.) cultivars. – Photosynthetica **41**: 253-258, 2003.

Hai M.R., Kubota F.: Changes in photosynthetic rate, photorespiration rate and quantum yield of photosystem II in sweet potato, *Ipomoea batatas* Lam., leaves with aging and their cultivaral difference. – Sci. Bull. Fac. Agr. Kyushu. Univ. **56**: 73-81, 2001.

He Z.F.: [The fast determination method for content of glucose, frutose, sucrose and starch by anthrone colorimetry.] – In: He Z.F. (ed.): [Grain Quality and it's Analysis Technology.] Pp. 144-150. Agricultural Press, Beijing 1985. [In Chinese]

Huang Y.M., Li Y.Q., Wu C.R. *et al*.: [Dry matter accumulation and photosynthetic characteristics of sweet potato at different growth stages.] – J. South. Agric. **43**: 1287-1290, 2012. [In Chinese]

Jiang C.Z., Hirasawa T., Ishihara K.: Physiological and ecological characteristics of high yielding varieties in rice plants: I. Yield and dry matter production. – Jpn. J. Crop Sci. **57**: 132-138, 1988.

Jonckheere I., Fleck S., Nackaerts K. *et al*.: Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. – Agr. Forest. Meteorol. **121**: 19-35, 2004.

Kakaty B.M., Thamburaj S., Stalin P.: Study on the growth and yield of sweet potato at different stages of harvest. – J. Root Crops **18**: 73-76, 1992.

Ling Q.H.: Indices and regulation of wheat population quality. – In: Ling Q.H. (ed.): Crop Population Quality. Pp. 217-249. Shanghai Sci. and Techn. Publ., Shanghai 2000.

Liu H.J., Shi C.Y., Zhang H.F. *et al*.: Effects of potassium on yield, photosynthate distribution, enzymes' activity and ABA content in storage roots of sweet potato (*Ipomoea batatas* Lam.). – Aust. J. Crop. Sci. **7**: 735-743, 2013.

Mannan M.A., Bhuiyan M.K.R., Quasem A. *et al*.: Study on the growth and partitioning of dry matter in sweet potato. – J. Root Crops **18**: 1-5, 1992.

Nedunchezhiyan M., Byju G., Jata S.K.: Sweet potato agronomy. – In: Nedunchezhiyan M., Byju G., Jata S.K. (ed.): Fruit, Vegetable and Cereal Science and Biotechnology. Pp. 1-10. Global Science Books, Isleworth 2012.

Nedunchezhiyan M., Byju G.: Effect of planting season on growth and yield of sweet potato (*Ipomoea batatas* L.) varieties. – J. Root Crops **31**: 111-114, 2005.

Patrick J.W.: Assimilate partitioning in relation to crop productivity. – Hort Sci. **23**: 33-40, 1988.

Peng S.B., Krieg D.R., Girma F.S.: Leaf photosynthetic rate is correlated with biomass and grain production in grain sorghum lines. – Photosynth. Res. **28**: 1-7, 1991.

Ravi V., Naskar S.K., Makeshkumar T., Binoy Babu P.K.B.S.: Molecular physiology of storage root formation and development in sweet Potato (*Ipomoea batatas* Lam.). – J. Root Crops **35**: 1-27, 2009.

Sasaki H., Ishii R. Cultivar differences in leaf photosynthesis of rice bred in Japan. – Photosynth. Res. **32**: 139-146, 1992.

Shi C.Y., Wang Z.L., Zhao B.Q. *et al*.: [Effects of potassium on the parenchyma cell structure of storage root, the distribution of ^{14}C photosynthates and yield in sweet potato.] – J. Plant Nutr. Fert. Sci. **8**: 335-339, 2002. [In Chinese]

Tekalign T., Hammes P.S.: Growth and productivity of potato as influenced by cultivar and reproductive growth: II. Growth analysis, tuber yield and quality. – Sci. Hortic.-Amsterdam **105**: 29-44, 2005.

Tsuno Y., Fujise K.: Studies on the dry matter production of sweet potato. – Bull. Natl. Inst. Agr. Sci. Japan, Ser. D. **13**: 1-131, 1965.

Uwah D.F., Undie U.L., John N.M., Ukoha G.O.: Growth and yield response of improved sweet potato (*Ipomoea batatas* (L.) Lam) varieties to different rates of potassium fertilizer in Calabar, Nigeria. – J. Agr. Sci. **5**: 61-69, 2013.

Villordon A.: Development of a prototype bayesian network model representing the relationship between fresh market yield and some agroclimatic variables known to influence storage root Initiation in sweetpotato. – HortScience **45**: 1167-1177, 2010.

Xu K., Zhou S., He B.W., Zhang Z.Y.: [Comparison of the photosynthesis characters and bioyield among three sweet potato breeds. Chin.] – Agric. Sci. Bull. **24**: 172-175, 2008. [In Chinese]

Yang D.P.: Determination of phosphorus. – In: Lu R.K., Zhu H.Z., He P.A. (ed.): Methods of Soil Agricultural Chemistry Analysis. Pp. 96. Chin. Agr. Sci. Technol. Press, Beijing 1999.

Zong X.F., Zhang J.K., Zhou Q.Y. *et al.*: [A preliminary study on the relationship between photosynthesis indexes and dry matter yield of tuber in sweet potato.] – J. Southwest Agric. Univ. **23**: 216-218, 2001. [In Chinese]

Zhou Q.L.: [Research of dry matter accumulating characters on autumn sweet potato varieties of different types.] – PhD. Thesis. Pp. 6-7. Southwest University, Chongqing 2007. [In Chinese]