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The effects of drought stress and leaf ageing on leaf photosynthesis and electron transport in photosystem 2 in sweet potato (*Ipomoea batatas* Lam.) cultivars

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Abstract

Of the four tested sweet potato cultivars having different features in growth and yield, cv. Koganesengan (KOG) was sustainable in photosynthetic activity through young to aged leaves under drought. One of the causes for this phenomenon may be stomatal conductance (g_s) of this cultivar that was relatively high in both aged and drought-imposed leaves. In these leaves the non-photochemical quenching (NPQ) was low and the quantum yield of photosystem 2 (Φ_e) was high, compared to those of the other cultivars. This helps to prevent excessive accumulation of chemical energy in leaves and a decrease in photoinhibition damage to the photosynthetic function, by which KOG sustains a relatively high photosynthetic activity under the drought and alleviates functional deterioration caused by leaf age.

Additional key words: chlorophyll fluorescence; cultivar differences; dry mass; leaf area; non-photochemical quenching; photorespiration; quantum yield; stomatal conductance.

Introduction

Sweet potato plant is characterised by a simple sink and source relationship in the biomass production system. Since both organs begin to function at the early growth stage and keep the activity throughout the growth season, this crop species has two beneficial features: a quick yield during a short growth period and a stable productivity less affected by climatic factors. The starch accumulating capacity in the tuberous root has so far been regarded as the fundamental determinant for yield. Therefore during streaming to improve the yield of sweet potato focus has been centred on the enhancement of sink organ's function and capacity (Nakatani *et al.* 1988, Kubota *et al.* 1993, Yatomi *et al.* 1996). Nevertheless, for increasing the yield it is also fundamentally important to activate the source function and keep an adequate functional balance between sink and source organs (Kadowaki *et al.* 2001).

In sweet potato leaves cultivar difference in stomatal aperture were observed (Agata and Hakoyama 1991): stomatal movement strongly affected the leaf photosynthetic rate, which created cultivar differences in net photosynthetic rate (P_N). Kubota *et al.* (1993) pointed out that the leaf P_N of sweet potato was more strongly restricted by stomata action than by photosynthetic activity in the mesophyll. In a previous paper, based on the mutual relationship between sink and source function, we also pointed out the importance of leaf photosynthetic activity as one of the main determinants for sweet potato yield (Haimeirong and Kubota 2001).

Studying different sweet potato cultivars grown under various conditions, we observed that the leaf P_N significantly varies with leaf age, and this variation is different among cultivars. The ageing effect on leaf P_N is an important criterion for evaluating the cultivar and strain differences in photosynthetic productivity of sweet potato.

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Abbreviations: a – ratio (0.5) of photons distributed to photosystem 2; b – photon absorption ratio of leaf; BEN – cv. Beniaka; Chl – chlorophyll; ETR – electron transport rate at photosystem 2; $ETR_{2\%}$ – electron transport rate at photosystem 2 determined in 2 % O_2; F_m – the maximum Chl fluorescence; F'_m – Chl fluorescence spike; F_s – steady Chl fluorescence; F_0 – initial Chl fluorescence; g_s – stomatal conductance; I – irradiance; kc – the number of electron equivalents required to reduce 1 molecule of CO_2 in the Calvin cycle; KOG – cv. Koganesengan; LA – leaf area; LWP – leaf water potential; NPQ – non-photochemical quenching; OKI – cv. Okinawa-100; P_G – gross photosynthetic rate; $P_{G2\%}$ – P_G determined in 2 % O_2 air; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS2 – photosystem 2; R_D – dark respiration rate; R_P – photorespiration rate; R_P/T_c – ratio of photorespiration rate to the total CO_2 fixation rate; SWP – soil water potential; T_c – total CO_2 fixation rate; RuBP – ribulose-1,5-bisphosphate; TSU – cv. Tsurunasigengi; ΔM – increase in dry mass; Φ_e – PS2 quantum yield.

In general, of the environmental factors affecting photosynthesis, the water condition in soil and plant strongly affects stomata movement, causing a large change in leaf P_N (Chaves 1991). We also observed that the effect of ageing on leaf photosynthesis varies with soil water content, and the joined effect of ageing and water content is different with cultivars.

In the present study, using four sweet potato cultivars with a large difference in growth and yield, we discussed the joined effect of ageing and soil drought on leaf P_N and the relationship between the photosynthetic response and cultivar difference in productivity. We analysed simultaneously gas exchange and electron transport in photosystem 2 (Haimeirong *et al.* 2002) to elucidate the effects of energy balance on leaf photosynthetic activity.

Materials and methods

Plants: Four Japanese cultivars of sweet potato, *Ipomoea batatas* Lam., cvs. Koganesengan (KOG), Okinawa-100 (OKI), Beniaka (BEN), and Tsurunasigengi (TSU) were used. Both KOG and OKI are characterised by high yield. KOG is a recently released cultivar and OKI is a traditional one. BEN is a high quality cultivar and TSU is a traditional cultivar with low yield. These four cultivars were transplanted in 15 000 cm^3 pots on July 18, 2002. The pots were filled with sandy soil containing a chemical compound fertiliser (N, P, K; each 1.6 g per pot). Until the drought treatment was begun, the plants were grown for 45 d under an adequately irrigated condition in a vinyl house set in the agricultural experimental field of Kyushu University of Japan (33°35'N, 130°23'E). Each of the stems used for measurement in plants was fixed straight on a splint rod in order to provide a uniform light environment to leaves. The cultivations of each cv. were performed in a three-replication design.

The drought treatment period was 16 d, which was divided into three stages: the mild drought (A-stage for 7 d), the drought (B-stage for 2 d), and the re-watering (C-stage for 7 d). At first the drought stress application was gradually increased with time at A-stage during which water supply to plants was decreased day-by-day. Following this stage the watering was completely halted during 2 d (B-stage), the gas exchange rate, chlorophyll (Chl) fluorescence of leaves, and other parameters related to photosynthesis were measured using the methods described below. At the same time, leaf and soil water potentials were measured using a psychrometer (*L-51*, *Wescor*, USA) and a dew-point meter (*WP4*, *Decagon Devices*, USA), respectively.

After the measurements, the plants were re-watered and grown for 7 d (C-stage), and sampled together with the control plants at the final day of C-stage. The sampled plants were divided into leaf, stem, roots, and dead part, and weighed after 5-d desiccation at 80 °C in an oven. Leaf area was measured with an automatic area meter (*AAM-8*, *Hayasi-denko*, Japan).

Measurements of photosynthesis and Chl fluorescence: Leaves were numbered according to the age: the full opened youngest leaf on a stem was termed 1st leaf, and then counted in the order of 2nd, 3rd, 4th *etc.* on the stem. The most active leaf in function was the 5th or 6th leaf. In this experiment, the 6th, 12th, 18th, and 24th leaves were used to investigate the effects of ageing and drought stress on photosynthetic activity. With these leaves, P_N, g_s, and Chl fluorescence were simultaneously measured according to Haimeirong *et al.* (2002).

For the measurements of P_N and g_s a sandwich-type assimilation chamber (*PLD-B*, *ADC*, Hoddesdon, UK) was used. The relative humidity and CO_2 concentration of air sent into the chamber were adjusted to 50 % and 360 cm^3 m^{-3}, respectively. The O_2 concentration of air was 21 or 2 %. Leaf temperature was 30 °C and photosynthetic photon flux density (PPFD) was 500 µmol m^{-2} s^{-1}. The leaf area set in the assimilation chamber was 6.25 cm^2 and the flow rate of air through the chamber was controlled at 16.67 cm^3 s^{-1}. The gross photosynthetic rate (P_G) was calculated as P_N plus the dark respiration rate (R_D). P_G determined in 2 % O_2 air was termed $P_{G2\%}$, and this parameter means the rate of photosynthesis without photorespiration. The CO_2 concentration and vapour pressure in the reference and sample air were monitored with an infrared CO_2 analyser (*Li-6262*, *LI-COR*, USA). The concentration of O_2 was adjusted using a gas concentration controller (*GM-3A*, *KOFLOC*, Japan).

The Chl fluorescence of PS2 was monitored with a fluorescence probe (*PAM-2000*, *Walz*, Germany) equipped on the assimilation chamber. Using a leaf dark-adapted under a measuring beam (3.2 µmol m^{-2} s^{-1} PPFD, 4.8 kHz), the initial fluorescence (F_0) in the non-photosynthetic situation was measured. Then the maximum fluorescence (F_m) was determined by giving a 1.2 s pulse irradiation of "white saturation light" (1 800 µmol m^{-2} s^{-1} PPFD) to the leaf. After this, the time course of quenching in the fluorescence (F_s) was monitored at an irradiance of 500 µmol m^{-2} s^{-1} PPFD while a fluorescence spike (F'_m) was periodically measured by giving a pulse of "white saturation light".

Calculation: The quantum yield and photorespiration rate (R_P) were determined according to Haimeirong *et al.* (2002). Based on the measurements of fluorescence intensity, PS2 quantum yield (Φ_e) and electron transport rate (ETR) were calculated from the equations (1) and (2), respectively.

$$\Phi_e = (F'_m - F_s)/F'_m \qquad (1)$$

$$\mathrm{ETR} = \Phi_e\, I\, a\, b \qquad (2)$$

where I is irradiance (500 µmol m^{-2} s^{-1} PPFD) on the leaf, and b is the ratio (b = 0.93) of leaf-absorbed photons to the incident photons. Assuming the absorbed photons are distributed even to the two photosystems, 0.5 is used here (a = 0.5). ETR measured at 2 % O_2 air was termed $ETR_{2\%}$.

The parameter kc is the number of electron equivalents required to reduce 1 mol of CO_2 in the Calvin cycle, and calculated from the Eq. (3):

$$\mathrm{kc} = P_{G2\%}/\mathrm{ETR}_{2\%} \tag{3}$$

R_P was obtained by subtracting P_G from the total CO_2 assimilation rate (T_c) as shown in Eq. (4):

$$R_P = T_c - P_G \tag{4}$$

The Eq. (4) is based on CO_2 balance. This is shown in Eq. (5) based on electron transport rate:

$$\mathrm{ETR} = \mathrm{kc}\ T_c + 2.06\ \mathrm{kc}\ R_P \tag{5}$$

where ETR is the total electron transport; and kc T_c and 2.06 kc R_P indicate the electron transport rates used for CO_2 fixation and photoresiratory CO_2 release, respectively. The number of electrons required to release 1 mol CO_2 in the photorespiration is 2.06 times that required for reducing 1 mol CO_2 in the Calvin cycle (Oliver 1994).

From Eqs. (4) and (5), Eq. (6) is obtained:

$$T_c = 2.06\ \mathrm{kc}\ P_G\,\mathrm{ETR}/3.06\ \mathrm{kc} \tag{6}$$

The value of R_P used here is obtained from Eq. (4). The photorespiration ratio was calculated as R_P/T_c.

Non-photochemical quenching was calculated by the Eq. (7):

$$\mathrm{NPQ} = (F_m - F'_m)/F'_m \tag{7}$$

Results and discussion

Dry matter production (ΔM), top and root mass ratio (T/R), and leaf area (LA) in plants grown under the control and drought conditions are shown in Table 1. The ΔM was the dry matter gain during the 16-d treatment. The other two parameters were values from the final samples. By the drought treatment, the averages of ΔM and LA of the four cultivars decreased to 40.0 and 45.3 % of those of control plants, respectively, while T/R slightly increased in the drought treatment. Both KOG and OKI showed a low value of T/R; on the other hand, BEN and TSU had a significantly high T/R in both control and drought conditions.

Table 1. Differences in increase in dry mass, ΔM [g per plant], leaf area, LA [m^3 per plant], and ratio of top and root dry mass, R/T, in four cultivars (KOG = Kaganesengan, BEN = Beniaka, OKI = Okinawa, TSU = Tsurunasigenji) grown under the control and drought conditions.

		ΔM	T/R	LA
Control	KOG	41.2 (100)	1.06 (100)	0.60 (100)
	BEN	20.0 (100)	2.59 (100)	0.20 (100)
	OKI	46.1 (100)	1.54 (100)	0.30 (100)
	TSU	34.8 (100)	5.11 (100)	0.67 (100)
	mean	35.5 (100)	2.58 (100)	0.44 (100)
Drought	KOG	17.8 (43.2)	1.12 (105.7)	0.20 (33.3)
	BEN	8.6 (43.0)	2.66 (102.7)	0.13 (65.0)
	OKI	11.0 (23.8)	1.87 (121.4)	0.13 (43.3)
	TSU	19.2 (55.2)	6.25 (122.3)	0.35 (52.2)
	mean	14.2 (40.0)	2.98 (115.5)	0.20 (45.5)

A large difference was found in matter production among the cultivars (Table 1). Of the four cultivars, KOG and TSU had a largest value of LA, but their response of LA to the drought was different: KOG was the most sensitive to the drought and TSU was the least. LA is one of the important determinants for dry matter production, but the change in LA of the four cultivars at drought was not always parallel to the change in ΔM. This predicts that in addition to LA, the leaf photosynthetic ability and its response to drought may differently restrict the production of cultivars.

Table 2 shows the parameters related to leaf photosynthesis and PS2 electron transport in the four cultivars grown under the control and drought conditions. For each cultivar, mean values of the measurements with the 6th, 12th, 18th, and 24th leaves are shown. The soil water potential of pots was –0.31 and –3.94 MPa on average under the control and drought conditions, respectively. The average leaf water potential of the four cultivars under the drought stress was –1.32 MPa, and that of the control was –0.51 MPa. A leaf water potential of –1.32 MPa reached probably the level at which sweet potato plants suffer a relatively strong drought stress (Kubota *et al.* 1993).

As shown in Table 2, the average value of P_G of the four cultivars was 14.58 µmol(CO_2) m^{-2} s^{-1} in the control and 4.55 µmol(CO_2) m^{-2} s^{-1} in the drought condition. The cultivar difference in P_G observed in the control was more expanded at drought stress. KOG showed the highest P_G and g_s in the control, and also these parameters were relatively high under drought stress. Kubota *et al.* (1991) suggested that keeping a large stomata openness was one of the features unique to KOG. The increased P_G in KOG may greatly depend on the gas exchange promotion caused by a large stomata aperture. On the other hand, OKI showed a highly sensitive response in P_G and g_s to the drought.

The average values of Φ_e and R_P of the four cultivars decreased under drought to 47.5 and 75.9 %, respectively, but the decrease was not as large as those of P_G and g_s (Table 2). On the other hand, R_P/T_c doubled under the drought. The cultivar differences of these parameters were also increased by drought.

In many plants, the reduction of leaf water potential induced by the decline of soil water potential affects stomata movement and gas exchange. Thus stomata

Table 2. Parameters of gas exchange and electron transport in four cultivars (KOG = Kaganesengan, BEN = Beniaka, OKI = Okinawa, TSU = Tsurunasigenji) grown under the control and drought conditions. SWP = soil water potential [MPa], LWP = leaf water potential [MPa], P_G = gross photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}], g_s = stomatal conductance [mol(CO_2) m^{-2} s^{-1}], Φ_e = PS2 quantum yield, R_P = photorespiration rate [μmol(CO_2) m^{-2} s^{-1}], R_P/T_c = ratio of photorespiration rate/total CO_2 fixation rate [%].

		SWP	LWP	P_G	g_s	Φ_e	R_P	R_P/T_c
Control	KOG	-0.27	-0.43	17.00	0.175	0.572	3.00	15.3
	BEN	-0.27	-0.75	13.20	0.131	0.536	3.00	18.8
	OKI	-0.34	-0.47	14.90	0.168	0.569	2.70	14.8
	TSU	-0.34	-0.45	13.20	0.131	0.529	2.80	17.3
	mean	-0.31	-0.51	14.58 (100)	0.151 (100)	0.552 (100)	2.90 (100)	16.6 (100)
Drought	KOG	-3.88	-1.39	8.60	0.070	0.382	2.70	25.6
	BEN	-3.88	-1.41	4.60	0.023	0.311	2.80	38.9
	OKI	-4.02	-1.19	2.00	0.013	0.151	1.40	38.6
	TSU	-4.02	-1.28	2.98	0.013	0.205	1.80	38.4
	mean	-3.94	-1.32	4.55 (31.2)	0.029 (19.2)	0.262 (47.5)	2.20 (75.9)	35.4 (213.3)

movements may depend on factors such as the signal from roots (Davies and Zhang 1991), phytohormones related to turgor pressure in guard cells (Raschke 1975, Collatz *et al.* 1991), and the vapour pressure gradient between leaf and air (Turner *et al.* 1984). In our experiment, KOG was able to keep the stomata open under drought as mentioned. This is an important cause to characterise the growth responses to environment in this cultivar.

The value of Φ_e was the largest in KOG in both the control and drought variant (Table 2). The promotion of gas exchange rate by a large stomata aperture is related to the increased Φ_e, and is also effective in preventing the physiological inhibition caused by the excessive accumulation of photon energy supplied from the photosystem. R_P/T_c in KOG is low because the relative activity of RuBP oxidase to RuBP carboxylase is considered to decrease by high CO_2 concentration in intercellular spaces under a large stomata aperture.

Many leaves of different ages usually carry out the production of sweet potato plants grown in the field. Hence, it is important to clarify the effect of leaf age on the photosynthetic activity, in order to obtain a deeper evaluation of leaf photosynthesis and its cultivar variation (O`Neil 1983, Jordi *et al.* 2000, Haimeirong and Kubota 2001). Fig. 1 shows changes in P_G and g_s of the four cultivars with leaf number under the control and drought conditions. In the control (Fig. 1*A*), P_G of KOG kept a high value from the 6th to the 24th leaf, being less affected by leaf age. P_G of OKI was the second highest; however, it rapidly decreased with leaf age. In the drought treatment, P_G of the four cultivars dropped as shown in Fig. 1*B*, but that of KOG showed relatively high values in young leaves.

The value of g_s decreased with leaf age and dropped further in the drought treatment as shown in Fig. 1*C,D*. This response was almost similar to that of P_G. The reduction of leaf photosynthesis with age is also considered to relate with g_s or stomata aperture. That is, we may predict here that the photosynthetic activity of cultivars with small stomata aperture is more quickly reduced because the energetic imbalance is more seriously brought about in leaves by the restriction of CO_2 fixation rate (Haimeirong and Kubota 2001).

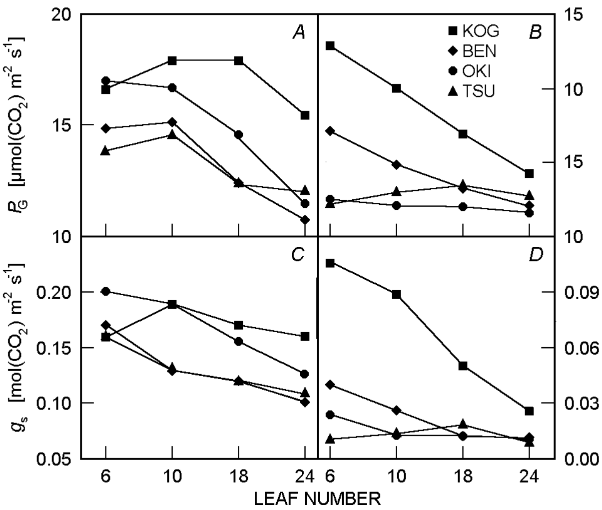

Fig. 1. Changes in gross photosynthetic rate (P_G) and stomatal conductance (g_s) with leaf age in four cultivars (■, KOG = Kaganesengan; ◆, BEN = Beniaka; ●, OKI = Okinawa; ▲, TSU = Tsurunasigenji) grown under the control (*A, C*) and drought (*B, D*) conditions.

The value of F_v/F_m, which is used widely as an indicator of functional activity of PS2, exerted large cultivar differences (Fig. 2*A*). Both leaf age and drought less affected F_v/F_m of KOG, which had a high value of about 0.8 in all the leaves. This may mean that the functional damage in the photosystem did not occur in these leaves. On the other hand, F_v/F_m in BEN rapidly decreased with leaf age, and in both OKI and TSU this parameter was considerably low.

The operation of PS2 is believed to play a key role in characterising the response of leaf photosynthesis to environmental stresses (Baker 1991), and its functional deterioration has been regarded as a criterion of photoinhibition damage (Masojídek *et al.* 1991, Barber and Andersson 1992, van Rensburg and Krüger 1993). The value of F_v/F_m was reduced with leaf senescence (Šesták 1996, Haimeirong and Kubota 2001). In leaves of sweet potato cultivars, the behaviour of stomatal movement significantly differed with leaf age particularly under the drought (Fig. 1*D*), and this should strongly affect the energy flow from photochemical system to the CO_2 fixation site. The stomata behaviour is one of the important causes of creating the cultivar differences in leaf functional responses to age and drought stress.

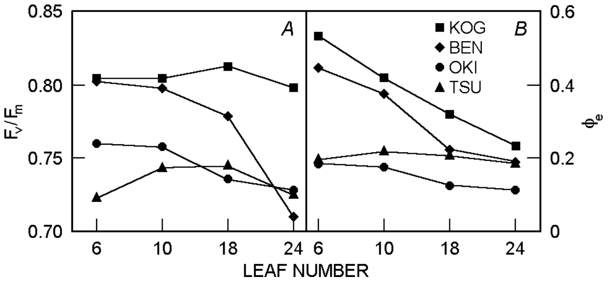

Fig. 2. Changes in F_v/F_m (*A*) and Φ_e (*B*) with leaf age in four cultivars grown under the drought condition.

The general relationship between g_s and Φ_e or NPQ through all the four cultivars is shown in Fig. 3. The values of NPQ and Φ_e exponentially decreased and increased with an increase in g_s, respectively, and both regression curves showed a statistically high significance. This fact may suggest that g_s plays a common role in the energy dissipation through all differently aged leaves in different cultivars grown under different water conditions. When g_s decreased below about 0.05 mol(CO_2) m^{-2} s^{-1}, its effects on Φ_e and NPQ greatly increased. The g_s of about 0.05 mol(CO_2) m^{-2} s^{-1} may be a limiting point for preventing damage of the leaf physiological function. In cultivars with low g_s or insufficient stomata aperture, the restriction of gas exchange induces accumulation of excessive energy, which may cause the leaf senescence promotion and functional depression under drought. As mentioned above, only KOG has such beneficial characteristics as keeping photosynthetic activity from young to aged leaves under the drought. Although many physiological factors may relate to this cultivar feature, the stomata aperture, or g_s, was identified as one of the important factors realising an advantageous production. On the other hand, we may predict that the cultivar characterised by large g_s is not beneficial from the viewpoint of water utilisation efficiency, but as described here, the characteristic of keeping stomata aperture is important to prevent the leaf senescence and photoinhibition even under the drought stress. For the genetic improvement of sweet potato leading to a high and long-life photosynthetic activity under the stress, the stomata movement is one of the important criteria.

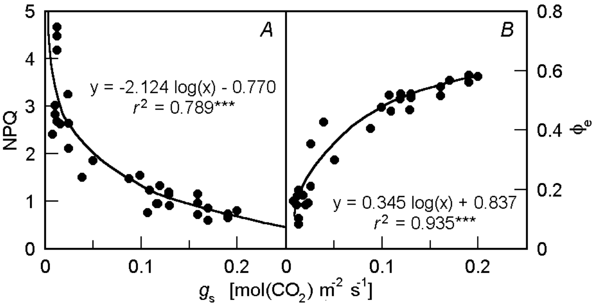

Fig. 3. Relationship between NPQ (*A*) and Φ_e (*B*) in four cultivars grown under the control and drought conditions. ***statistically significant at $p<0.001$.

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