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Cyclic electron flow around photosystem 1 is required for adaptation to salt stress in wild soybean species *Glycine cyrtoloba* ACC547

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Abstract

A wild soybean species *Glycine cyrtoloba* ACC547 was found to possess a high salinity resistance trait. It maintained higher net photosynthetic rate (P_N) and maximal photochemical efficiency (F_v/F_m) than the soybean *Glycine max* cultivar Melrose under salt stress. Saline treatment enlarged the post-illumination transient increase in chlorophyll fluorescence in ACC547 much more than that in Melrose, indicating that its cyclic electron flow around photosystem 1 (CEF1) was accelerated more by salt stress. Additionally, ACC547 maintained higher nonphotochemical dissipation of excitation energy than Melrose under salt stress. It is suggested that the salinity resistance of ACC547 might be due to the CEF1-coupled dissipation of excess excitation energy.

Additional key words: chlorophyll fluorescence, dissipation of excitation energy, NaCl, nonphotochemical quenching, photosynthesis.

Introduction

Salinity is a major factor in reducing crop production worldwide and one of the most important reasons is the drastic inhibition of photosynthesis. Some studies have shown that the decrease in photosynthesis is related directly to the salinity-induced stomata closure and the coupled reduction in intercellular CO_2 concentration (Bayuelo-Jiménez *et al.* 2003, Karimi *et al.* 2005). Additionally, salt stress causes the decrease in chlorophyll (Chl) content (Baek *et al*. 2005, Karimi *et al.* 2005), the changes in chloroplast ultrastructure (Stoynova-Bakalova and Toncheva-Panova 2003/4), the depression in photosystem (PS) activity and electron transport (Kirst 1990), and the decline in the activity and content of Rubisco (Ziska *et al*. 1990). All these non-stomatal limitations also make great contribution to the photosynthetic attenuation in salt stressed plants.

The salinity-induced limitation of photosynthetic capacity results in the accumulation of excess energy, which, if not safely dissipated, is harmful to photosynthetic apparatus (Demmig-Adams and Adams 1992, Demmig-Adams *et al*. 1996). For example, the excess energy can lead to the generation of the reactive oxygen species, which, in turn, can seriously aggravate the decrease in photo-synthesis through oxidative damage to membranes, photosynthetic pigments and enzymes. Researches have revealed that in many plants salt stress elevates the production of the reactive oxygen species and the activities of the antioxidant enzymes are

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Abbreviations: CEF1 - cyclic electron flow around PS1; Chl - chlorophyll; c_i - intercellular CO_2 concentration; E_{QA} - the estimate of redox potential of Q_A; F_m, F_o and F_v - maximal, minimal and variable Chl fluorescence yield for dark-acclimated samples, respectively; F_m', F_o' and F_s - maximal, minimal and steady-state Chl fluorescence yield for light-acclimated samples, respectively; F_p - height of the post-illumination Chl fluorescence peak; F_v/F_m - maximal photochemical efficiency; g_s - stomatal conductance to water vapour; NPQ - non-photochemical quenching; P_N - net photosynthetic rate; PS - photosystem; Q_A - primary quinone electron accepter of PS2; q_E - high-energy state nonphotochemical quenching; q_P - photochemical quenching; q_T - nonphotochemical quenching due to state transitions.
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correspondingly up-regulated for scavenging them (Agarwal and Pandey 2004, Ghorbanli *et al.* 2004, Rahnama and Ebrahimzadeh 2005).

Through long-term natural selection, halophytes have survived under high salinity and thus obtained some traits for adaptation to salinity. Some halophytes can compartmentalize toxic ions into vacuole or exclude them through glands and bladders (Hasegawa *et al.* 2000). Others improve their salt resistance by accumulation of compatible solutes such as proline, glycinebetaine and sugars (Niknam *et al.* 2004, Karimi *et al.* 2005). As for the excess excitation energy induced by salt stress, some halophytes have developed certain photoprotective mechanisms to effectively dissipate the surplus energy. Chen *et al.* (2004) have suggested that Mehler-peroxidase reaction serves as a sink to excess light energy in salt-stressed halophyte *Rumex* K-1. In another typical halophyte *Atriplex centralasiatica*, xanthophylls cycle-dependent nonradiative energy dissipation has been suggested as an important mechanism to dissipate surplus energy for tolerance to salt stress (Qiu *et al.* 2003).

However, halophytes seem to lack unique mechanism for resistance to salt stress and, despite an increasing number of studies, the data concerning effects of salt stress on photosynthesis are still fragmentary. *Glycine cyrtoloba* ACC547, a wild soybean species native to saline soils in Australian beach, is a typical halophyte. So it can be used as a good material for research on the mechanism of resistance of halophytes to salinity. The primary aim of this study is to investigate the different influences of salinity on ACC547 and *Glycine max* Melrose, a high-yielding cultivar.

Materials and methods

Seeds of *Glycine cyrtoloba* Tind. ACC547 and *Glycine max* (L.) Merr. cv. Melrose were sterilized with 0.1 % (m/v) formaldehyde solution and germinated in quartzes. When the first pair of leaves fully expanded, the well-grown seedlings were transplanted in complete nutrient solution (Neumann *et al.* 1999) and grown in green house at Hua-jia-chi Campus of the Zhejiang University. Its daily temperature was about 25 °C and relative humidity approximately 60 % with 12-h photoperiod and the maximum irradiance reaching 1300 μmol m^{-2} s^{-1}. When the 7th leaf grew out, plants were subjected to 0 (control), 50 and 100 mM NaCl, respectively. The nutrient solutions were renewed twice a week and the pH was adjusted to about 5.5 during the culture period.

All the measurements were conducted in the 6th leaves of the main stem. Gas exchange and Chl fluorescence were measured by the method previously described (Huang *et al.* 2004) with a portable photosynthesis system (*LICOR-6400*, *LI-COR*, Lincoln, USA) and its integrating fluorescence fluorometer (*LI-6400-40* leaf chamber fluorometer). Q_A is the first and stable quinone electron accepter of the photosystem 2 (PS 2) reaction center. Its redox potential (E_{QA}) was estimated by the Nernst equation (Pfannschmidt 2003):

$$E_{QA} = [E_m - (R \times T)/(n \times F)] \times \ln [Q_A(red.)/Q_A(ox.)],$$

where E_m is the mid-point potential, T is the temperature in Kelvin degree, and n is the number of transferred electrons. R and F are the universal gas constant and the Faraday constant, respectively. Q_A(red.) and Q_A(ox.) are the reduced and oxidized forms of Q_A, respectively, and the ratio $Q_A(red.)/Q_A(ox.)$ was estimated from equation:

$$Q_A(red.)/[Q_A(red.) + Q_A(ox.)] \approx 1 - q_P$$

(Dietz *et al.* 1985, Huner *et al.* 1996). With rearrangement of the second equation, $Q_A(red.)/Q_A(ox.)$ could be expressed as:

$$Q_A(red.)/Q_A(ox.) \approx (1/q_P) - 1$$

where q_P is the photo-chemical quenching coefficient and was calculated as:

$$q_P = (F_m' - F_s)/(F_m' - F_o')$$

where F_o', F_m' and F_s are the minimal, maximal and steady-state fluorescence yield for light-acclimated samples, respectively (Huang *et al.* 2004).

The post-illumination transient increase in Chl fluorescence was recorded according to the procedure described by Mano *et al.* (1995) and Mi *et al.* (1995). After dark-adaptation of the sample for 1 h, a weak modulated irradiation (< 0.1 μmol m^{-2} s^{-1}) was on to determine the minimal fluorescence yield (F_o). Subsequently, a 600-ms saturating light (> 7000 μmol m^{-2} s^{-1}) flashed to determine the maximal fluorescence yield (F_m), and an actinic light (1000 μmol m^{-2} s^{-1}) was then turned on. After 30 s, the actinic light was turned off and fluorescence yield was continuously recorded.

High-energy state nonphotochemical quenching (q_E) and state transition nonphotochemical quenching (q_T) were measured and calculated as previously described by Quick and Stitt (1989). The soybean leaf was kept in dark for 1 h. After the weak measuring beam, an actinic light was turned on, and saturating pulses were then applied every 60 s. After 10 min, the actinic light was turned off for the dark relaxation of nonphotochemical Chl fluorescence quenching. The saturating pulses were continuously applied every 60 s, and the whole record of the fluorescence yield lasted for around 60 min.

Results and discussion

NaCl stress strongly reduced photosynthesis in Melrose. As compared to the control, net photosynthetic rate (P_N) in Melrose declined when treated with 50 mM NaCl for 1 d and as the stress progressed, P_N was decreased more dramatically. However, not until the 15th day did P_N in ACC547 decline significantly. Similarly, the decrease of P_N in ACC547 was also less than that in Melrose at 100 mM NaCl (Table 1). On the 10th day after treatment, P_N in ACC547 was increased by 5.4 % at 50 mM NaCl and decreased by 29.2 % at 100 mM NaCl (Table 1). While P_N in Melrose was decreased by 41.9 and 66.5 %, respectively, when stomatal conductance (g_s) was decreased by 49.6 and 60.7 % (Table 2), indicating that the stomatal limitation in Melrose made great contribution to the inhibition of photosynthesis. In parallel with the attenuation in g_s, there was not simultaneous decline but increase in intercellular CO_2 concentration (c_i) (Table 2). These results suggested that non-stomatal limitation might also partly inhibit the photosynthesis in Melrose, which was supported by the decline in maximal photochemical efficiency (F_v/F_m), a parameter indicating the activity of PS 2. In comparison to Melrose, ACC547 exhibited slight decline in F_v/F_m (Table 2).

Table 1. The effects of NaCl at different concentrations on P_N [μmol(CO_2) m^{-2} s^{-1}] in the leaves of Melrose and ACC547 during 20 d. Means ± SE of three to six replications. Means with same letters are not significantly different ($P < 0.05$) within the same genotype by Tukey's test. nd - not detectable.

Genotype	Time [d]	0 mM	50 mM	100 mM
Melrose	0	15.2 ± 0.4bc	15.0 ± 0.5bc	15.3 ± 0.3bc
	1	15.7 ± 0.6bc	15.1 ± 1.9bc	15.6 ± 1.0bc
	5	19.5 ± 1.1a	13.1 ± 1.6cd	8.6 ± 1.1ef
	10	17.9 ± 0.7ab	10.4 ± 0.7de	6.0 ± 0.3fg
	15	8.6 ± 1.4ef	3.3 ± 0.9gh	0.9 ± 0.1hi
	20	6.4 ± 1.3f	1.2 ± 0.2hi	nd
ACC547	0	10.4 ± 0.2de	10.5 ± 0.2cde	10.9 ± 0.6cde
	1	12.6 ± 0.2abcd	12.7 ± 0.4abc	12.3 ± 0.4bcd
	5	14.8 ± 0.5a	14.8 ± 0.5a	12.7 ± 0.6abc
	10	14.0 ± 0.2ab	14.7 ± 1.8a	9.9 ± 1.2e
	15	10.6 ± 0.5cde	7.1 ± 0.2f	4.0 ± 0.7g
	20	7.3 ± 0.6f	4.6 ± 0.9g	0.5 ± 0.2h

There is now broad agreement that a close relationship exists between the post-illumination transient increase in Chl fluorescence and the cyclic electron flow around PS 1 (CEF1). Ye *et al.* (1997) have reported that the Chl fluorescence increase reflects the transport of electron from NADPH (formed by the photoreduction of $NADP^+$) back to the oxidized PQ through CEF1 after illumination. Mi *et al.* (1995) have also proved that this phenomenon is mainly related to CEF1 mediated by NAD(P)H dehydrogenase complex. In the present experiment, treatment with NaCl slightly increased the height of the post-illumination Chl fluorescence peak (F_p) in Merose, which was increased by 9.9 and 5.7 % at 50 mM and 100 mM, respectively, but no statistically

Table 2. The effects of NaCl with different concentrations on the physiological parameters in Melrose and ACC547 on the 10th day after treatment. Means ± SE of three to six replications. In last two columns the data are expressed as percentage of control. Means with same small letters are not significantly different ($P < 0.05$) within the same parameter by Tukey's test. The significant difference ($P < 0.05$) of means (% of control) is indicated with different capital letters.

Parameter	Genotype	0 mM	50 mM	100 mM	50 mM [%]	100 mM [%]
g_s [mol(H_2O) m^{-2} s^{-1}]	Melrose	0.372 ± 0.082a	0.187 ± 0.021b	0.146 ± 0.043b	50.40 ± 5.70BC	39.30 ± 11.5C
	ACC547	0.222 ± 0.055b	0.248 ± 0.047ab	0.168 ± 0.052b	111.7 ± 21.0A	75.70 ± 22.4B
c_i [μmol(CO_2) mol^{-1}]	Melrose	255.7 ± 11.60b	264.6 ± 5.100ab	292.7 ± 11.60a	103.5 ± 2.00B	114.5 ± 4.50A
	ACC547	234.7 ± 20.60b	237.5 ± 11.100b	248.7 ± 14.50b	101.2 ± 4.70B	106.0 ± 6.20AB
F_v/F_m	Melrose	0.785 ± 0.003a	0.744 ± 0.005c	0.688 ± 0.013d	94.70 ± 0.60B	87.60 ± 1.60C
	ACC547	0.786 ± 0.006a	0.771 ± 0.005ab	0.754 ± 0.000bc	98.10 ± 0.70A	95.90 ± 0.00AB
F_p	Melrose	30.90 ± 0.400c	34.00 ± 1.000bc	32.70 ± 2.300c	109.9 ± 3.20B	105.7 ± 7.30B
	ACC547	36.50 ± 0.800b	56.70 ± 0.500a	59.30 ± 1.100a	155.3 ± 1.30A	162.5 ± 2.90A
E_{QA} [-V]	Melrose	0.147 ± 0.001a	0.161 ± 0.001c	0.196 ± 0.003e	109.7 ± 0.70C	133.4 ± 1.80A
	ACC547	0.146 ± 0.001a	0.155 ± 0.001b	0.179 ± 0.000d	106.2 ± 0.70D	122.6 ± 0.20B
NPQ	Melrose	1.805 ± 0.035c	1.617 ± 0.034d	1.163 ± 0.030e	89.60 ± 1.90C	64.40 ± 1.60D
	ACC547	1.859 ± 0.040c	2.112 ± 0.019a	2.014 ± 0.033b	113.6 ± 1.00A	108.3 ± 1.80B
q_E	Melrose	0.571 ± 0.023bc	0.444 ± 0.032d	0.418 ± 0.017d	77.80 ± 5.60B	73.20 ± 2.90B
	ACC547	0.498 ± 0.004cd	0.685 ± 0.069a	0.650 ± 0.007ab	137.5 ± 13.8A	130.4 ± 1.30A
q_T	Melrose	0.306 ± 0.007e	0.348 ± 0.017cd	0.341 ± 0.016d	113.8 ± 5.40B	111.5 ± 5.30B
	ACC547	0.380 ± 0.007c	0.520 ± 0.012a	0.427 ± 0.010b	136.8 ± 3.00A	112.2 ± 2.60B

significant difference was noted between treatments and the control. However, both 50 and 100 mM NaCl significantly increased Fp in ACC547, by 55.3 and 62.5 %, respectively (Table 2). These results indicated that ACC547 performed CEF1 at higher rate than Melrose in response to salt stress.

Limitation of photosynthetic capacity can result in over-accumulation of excess electrons in the electron chain. The E_{QA} in both Melrose and ACC547 dropped significantly (Table 2), indicating that salt stress considerably affected electron transport in both soybean genotypes. But the data revealed that the electrons accumulated in Q_A of Melrose more than that of ACC547. If the surplus excitation energy cannot be safely dissipated, the photosynthetic apparatus may be damaged (Demmig-Adams and Adams 1992, Demmig-Adams *et al.* 1996). It is now widely accepted that nonradiative dissipation of excitation energy occurs in plants as an internal mechanism for photoprotection of photosynthetic apparatus (Demmig-Adams *et al.* 1996, Horton *et al.* 1996, Qiu *et al.* 2003). In the present study, compared with the control, non-photochemical quenching (NPQ) in Melrose was decreased by 10.4 and 35.6 % at 50 and 100 mM NaCl, respectively (Table 2). This suggested that salt stress impaired the efficient dissipation of excess energy in Melrose. With a reverse trend, NPQ in NaCl-stressed ACC547 was increased by 13.6 and 8.3 % (Table 2), indicating that ACC547 possessed certain mechanisms for the efficient dissipation of excess energy. These results are in agreement with the observations in rice subjected to salt stress as reported by Baek *et al.* (2005). Since zeaxanthin was proposed to be able to dissipate excess excitation as heat in the PS 2 antennae for the first time by Demmig *et al.* (1987), xanthophylls cycle-dependent q_E has been extensively accepted as an important mechanism for nonradiative energy dissipation. q_E and xanthophylls cycle highly depend on the pH gradient across thylakoid membrane (Horton *et al.* 1996), and CEF1 contributes to the generation of the pH gradient, so CEF1 may be necessary for q_E. In this work, q_E in Melrose subjected to 50 and 100 mM NaCl was decreased by 22.2 and 26.8 % (Table 2). Consistent with the change in NPQ, salinity severely impaired q_E in Melrose, which was evidenced by the observation that high salt treatment eliminated the H^+ domain in light-harvesting complex (Renganathan and Dilley 1994). On the contrary, NaCl prominently increased q_E in ACC547 (37.5 % and 30.4 % at 50 and 100 mM NaCl, respectively) (Table 2). It might be the salinity-accelerated CEF1 that stimulated the higher q_E in ACC547. Another important nonradiative energy dissipation is q_T, which is associated with excitation energy redistribution between two photosystems (state transitions). In comparison with the control, 100 mM NaCl enhanced q_T by 11.5 and 12.2 % in Melrose and ACC547, respectively. At 50 mM NaCl, q_T in ACC547 (36.8 %) was enhanced much more than that in Melrose (13.8 %) (Table 2). The light energy redistributed to PS1 under NaCl stress might correspond with the increase in the rate of CEF1. On the other hand, Schreiber *et al.* (1995) have reported that CEF1 is involved in q_T. Despite little information on the detailed functions of CEF1 in q_T, CEF1-inactive mutants lost q_T and was locked into "state 1". So salt-stimulated CEF1 might also be an important reason for the increased q_T in ACC547 under NaCl stress.

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