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BRIEF COMMUNICATION

Photosynthesis and yield traits in different soybean lines in response to salt stress

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Abstract

To evaluate utility of different salt-tolerant lines, three soybean lines with different resistance to salt were planted in the field under control and salt-stress conditions for two years. The results showed that net photosynthetic rate (P_N) was significantly different among lines at the anthesis stage and decreased on average by 13.6–34.1% under conditions of salt stress. The stomatal conductance was a primary limiting factor for the reduction of P_N under salt stress. Meanwhile, the grain yield (GY) decreased on average by 14.0–35.3% among lines under salt stress. The salt-tolerant lines S111-9 and S113-6 showed higher P_N and GY under salt stress in comparison with the salt-sensitive cultivar Melrose. Regression analysis indicated that there was extremely significantly positive correlation between GY and P_N under field conditions. Therefore, P_N might be used as a physiological index for field resistance of soybean to salt stress.

Additional key words: chlorophyll fluorescence; cyclic electron flow; electron transport rate; nonphotochemical quenching; photochemical quenching; stomatal conductance.

Soil salinity becomes an increasingly prominent problem in agriculture. It is estimated that at least one third of the irrigated and arable land in the world is affected by salinity (Munns and Tester 2008, He *et al.* 2015). Soybean (*Glycine max* [L.] Merr.) is considered as an important grain crop that accounts for more than 54% of the world's oilseed production (USDA-FAS 2013, James *et al.* 2014). Soybean oil is the second major vegetable oil after palm oil in the total world supply (67%) in 2011–2012 and is the leading source of protein (USDA-FAS 2013). In addition, soybean productivity is significantly hampered by salt stress. The high salt concentration imposes negative impacts on growth, nodulation, agronomy traits, seed quality and quantity, and decreases the yield (Phang *et al.* 2008).

Salt stress decreases crop production by inhibition of photosynthesis, depression in PSII and electron transport activity (Mishra *et al.* 1991, Lu and Vonshak 2002), decline of content and activity of Rubisco, and limitation of ribulose-1,5-bisphosphate (RuBP) or inorganic phosphate regeneration capacity (Ziska *et al.* 1990). Nevertheless, other studies suggest that the limitation of photosynthesis is directly attributed to stomata closure (Mäkelä *et al.* 1999, Bayuelo-Jiménez *et al*. 2003, Karimi *et al.* 2005, Yang and Lu 2005). The salt-tolerant soybean descendants grow better than their cultivated parents. The resistant lines showed the sufficient dissipation of excess excitation energy by the cyclic electron flow that protects photosynthetic apparatus from the damage of reactive oxygen species (Yang *et al.* 2007). The salt-induced reduction in P_N occurs mainly due to lower g_s in the salt-tolerant line and lower Rubisco activity in the salt-

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Abbreviations: C_i – intercellular CO_2 concentration; Chl – chlorophyll; E – transpiration rate; ETR – electron transport rate; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; GY – grain yield; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient.

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sensitive cultivar, respectively (Lu *et al.* 2009). In addition, it has been shown that salt stress decreases P_N partially through Rubisco degradation. And salt stress induces chloroplast protrusions and production of many Rubisco-containing bodies responsible for degradation of Rubisco under salt stress (He *et al.* 2014).

During recent years some studies reported that salt stress significantly affected the progress of growth and development in soybean (Phang *et al.* 2008, Hao *et al.* 2011, Luo *et al.* 2013). However, limited data is available on the relationship between soybean photosynthesis and grain yield (GY) under salt stress conditions. The objective of the present research was to investigate the effect of salt stress on photosynthesis and yield traits of three soybean lines in the field. Thus, it could help elucidate and improve the salt tolerance of soybean varieties in the field.

The study site, the Gulf of Hangzhou, new district in Zhejiang province of China (30°2912'N, 121°1381'E and 30°2913N, 121°1385'E), is characterized by a subtropical monsoon climate with a mean annual temperature of 16°C, a mean annual precipitation of 1,272 mm, and a mean annual sunshine of 2,038 h. The soluble NaCl content of control soil was 0.59%(NaCl) kg^{-1}(soil) and the soluble salt content in the field was 1.29%(NaCl) kg^{-1}(soil). Two fields were used in the present experiment and the study was carried out during 2012–2013. The average nutrient contents in soil were as follows: 23.72 mg(total N) kg^{-1}, 22.55 mg(total P) kg^{-1}, and 202.37 mg(total K) kg^{-1}.

Three soybean lines, Melrose (salt-sensitive), S111-9 and S113-6 (salt-tolerant) (Yang *et al.* 2007), were used in the present experiment. The soybeans were planted manually in plots and plant distance in each plot was 0.5 m at the beginning of April in both years. The plot size was 8 m^2 (4 m× 2 m) and the plots in two fields were arranged in a completely randomized design with three replicates, respectively. Twelve plants were used for analysis from control and salt fields, respectively.

Gas-exchange parameters, such as the net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration (E) were measured at the anthesis and pod-bearing stage in the middle of June. Measurements were performed on the full-expanded third leaf (from top) between 09:00 and 12:00 h using a portable photosynthesis system (*Licor-6400*, *LICOR Inc.*, Lincoln NE, USA) equipped with a LED red and blue light source in all plots. All measurements were carried out at a PPFD of 1,200 μmol m^{-2} s^{-1}, a leaf temperature of 25°C, and a CO_2 concentration of 400 μmol mol^{-1} in the sample chamber.

Chl fluorescence was measured with an integrating Chl fluorometer (*Licor-6400*, *LICOR Inc.*, Lincoln NE, USA) according to the method described by Yang *et al.* (2007). Minimal Chl fluorescence (F_0) and maximal fluorescence (F_m) were measured in all plants after 30 min of dark adaptation. The F_v parameter was calculated as ($F_m - F_0$). Following this, another saturation flash was applied and then the maximal fluorescence yield (F_m') during actinic illumination was determined. The actinic light was removed after the flash. Then a far-red light was given, and the minimal fluorescence yield (F_0') was determined. The maximal quantum yield of PSII photochemistry (F_v/F_m) was determined as a ratio of F_v to F_m. NPQ and q_P were calculated as NPQ = $(F_m - F_m')/F_m'$ and $q_P = (F_m - F_m')/(F_m' - F_0')$. ETR was calculated as ETR = PPFD × Φ_{PSII} × 0.85 × 0.5.

Post-illumination transient increase in Chl fluorescence was determined according to the procedure described previously (Mi *et al.* 1995, Shikanai *et al.* 1998) using a *Dual-PAM 100* Chl fluorescence analyzer (*Heinz Walz, Effeltrich*, Germany) as described in Wang *et al.* (2006). Weak modulated irradiation [<0.1 μmol (photon) m^{-2} s^{-1}] was used to determine F_0. Subsequently, a saturating light [>7,000 μmol(photon) m^{-2} s^{-1}] flash was given to determine F_m, and then actinic light [1,000 μmol(photon) m^{-2} s^{-1}] was turned on. After 3 min, the actinic light was turned off and fluorescence yield changes were continuously recorded (Yang *et al.* 2007).

The number of branches, pods, and seeds from 20 plants per each plot was measured at maturity (17 July 2012 and 22 July 2013). The plants were harvested from the middle to the end of July when over 95% of the plants showed visible yellow leaves and over 80% of soybean pod showed yellow. The harvested seeds were dried under the sunlight till stable mass for measurement of GY and 100-seed mass.

Two-year data were analyzed, the means and calculated standard deviations (SD) were shown. For multiple comparisons, the data were first analysed by one-way analysis of variance (*ANOVA*) in order to check the equality of variance (*Levene*'s test), then the *Tukey*'s multiple comparison tests were used to determine the significant difference ($P<0.05$) of means with the *SAS 8.0* statistical software package (*SAS Institute, Inc.*, Cary, NC, 2000).

In S111-9, the decline of P_N in the salt field was 13.5% compared with the control field (Table 1). This decrease was 26.6% in the S113-6 plants and 34.1% in Melrose plants. g_s was significantly reduced by 26.5, 55.3, and 61.8% in S111-9, S113-6, and Melrose plants, respectively. For F_v/F_m and NPQ, there was no obvious difference between three lines with or without salt stress. Concerning q_P and ETR, the Melrose plants showed quite different tendencies compared to the S111-9 and S113-6 plants. The increase of 51.1% in q_P and no change in ETR were observed only in the Melrose plants under salt-stress conditions, but none of it in the S111-9 and S113-6 plants.

Table 1. Effects of salt stress on photosynthetic indexes and yield indexes in three lines. Means followed by *the same letter* within the same parameter were not significantly different at $P>0.05$. *Different letter* indicates significantly difference at $P<0.05$. CF – control field; SF – salt field.

Parameter	Field	S111-9	S113-6	Melrose
P_N [μmol(CO_2) m^{-2} s^{-1}]	CF	22.59 ± 1.96^{a}	21.09 ± 1.77^{ab}	18.36 ± 1.11^{d}
	SF	19.53 ± 1.92^{b}	15.49 ± 1.18^{c}	12.11 ± 1.09^{e}
SF/CF [%]		86.5	73.4	66.0
g_s [mol(H_2O) m^{-2} s^{-1}]	CF	0.34 ± 0.06^{a}	0.38 ± 0.09^{a}	0.34 ± 0.06^{a}
	SF	0.25 ± 0.05^{b}	0.17 ± 0.04^{c}	0.13 ± 0.06^{d}
SF/CF [%]		73.5	44.7	38.2
C_i [μmol(CO_2) mol^{-1}]	CF	248.7 ± 9.3^{b}	263.0 ± 16.5^{a}	259.2 ± 14.4^{a}
	SF	243.4 ± 12.3^{b}	222.8 ± 13.3^{c}	188.6 ± 13.1^{d}
SF/CF [%]		97.9	84.7	72.7
E [mmol(H_2O) $^{-2}$ s^{-1}]	CF	6.07 ± 0.32^{a}	6.28 ± 0.63^{a}	5.27 ± 0.46^{b}
	SF	5.41 ± 0.36^{b}	4.42 ± 0.65^{c}	3.09 ± 0.79^{d}
SF/CF [%]		89.1	70.4	58.6
F_v/F_m	CF	0.830 ± 0.006^{a}	0.821 ± 0.006^{ab}	0.820 ± 0.010^{ab}
	SF	0.832 ± 0.010^{a}	0.825 ± 0.008^{a}	0.777 ± 0.035^{b}
SF/CF [%]		100	100	93.9
NPQ	CF	1.51 ± 0.15^{bc}	1.81 ± 0.41^{ab}	1.97 ± 0.12^{a}
	SF	1.20 ± 0.19^{d}	1.39 ± 0.31^{cd}	1.22 ± 0.15^{d}
SF/CF [%]		79.5	76.8	62.9
q_P	CF	0.70 ± 0.02^{a}	0.67 ± 0.03^{a}	0.45 ± 0.12^{c}
	SF	0.64 ± 0.06^{ab}	0.61 ± 0.06^{b}	0.68 ± 0.04^{a}
SF/CF [%]		91.4	91.0	151.1
ETR [μmol m^{-2} s^{-1}]	CF	217.7 ± 10.5^{a}	200.3 ± 6.6^{b}	170 ± 8.3^{c}
	SF	193 ± 14.4^{b}	176.1 ± 10.5^{c}	174.9 ± 7.2^{c}
SF/NF [%]		88.7	87.9	102.9
Branch number [per plant]	NF	4.93 ± 0.59^{a}	4.72 ± 0.44^{ab}	4.54 ± 0.52^{ab}
	SF	4.86 ± 0.29^{ab}	5.05 ± 0.32^{a}	3.06 ± 0.46^{c}
SF/CF [%]		98.6	107.0	67.4
Pod number [per plant]	CF	68.7 ± 8.6^{a}	42.4 ± 6.3^{b}	29.7 ± 2.5^{d}
	SF	37.0 ± 7.8^{bc}	27.1 ± 2.6^{d}	17.9 ± 4.4^{e}
SF/CF [%]		53.9	63.9	60.3
Seed number [per plant]	CF	167.1 ± 10.5^{a}	107.3 ± 16.8^{b}	73.5 ± 3.9^{d}
	SF	83.8 ± 6.5^{c}	67.9 ± 5.7^{d}	35.7 ± 11.2^{e}
SF/CF [%]		50.1	63.3	48.6
Mass [g per 100 seeds]	CF	17.4 ± 0.62^{a}	17.2 ± 0.86^{a}	16.3 ± 0.18^{b}
	SF	15.5 ± 0.55^{bc}	15.0 ± 0.61^{c}	14.4 ± 0.32^{d}
SF/CF [%]		89.1	87.2	88.2
Grain yield [kg ha^{-1}]	CF	$2{,}498.8 \pm 102.3^{a}$	$1{,}934.2 \pm 128.1^{b}$	$1{,}547.2 \pm 169.5^{c}$
	SF	$1{,}892.3 \pm 147.4^{b}$	$1{,}662.7 \pm 136.2^{c}$	$1{,}000.3 \pm 156.4^{d}$
SF/CF [%]		75.7	86.0	64.7

In order to compare such a discrepancy in Chl fluorescence, a transient increase in Chl fluorescence was measured in three lines. Although there was no significant difference between them at the control field, the increase of Chl fluorescence in S111-9 plants was remarkably higher than that of the S113-6 and Melrose plants under salt stress (Fig. 1*A*,*B*). It implied that downregulation of linear photosynthetic electron flow (Table 1, q_P and ETR) and upregulation of cyclic electron flow in the S111-9 plants occurred under salt-stressed field conditions.

Salt stress decreased a branch number per plant by 32.6% in Melrose in the field, while there was no significant change in the S111-9 and S113-6 plants (Table 1). In addition, salt stress also decreased pod and seed numbers per plant of all lines by about 46.1 and 49.9% for S111-9, respectively, 36.1 and 36.7% for S113-6, respectively, 39.7 and 51.4% for Melrose, respectively. The decrease in the mass per 100 seeds was not significant under the salt-stressed field conditions (Table 1). Although there were significant declines in the pod and seed numbers per plant for all lines under salt-stressed field compared with control field, the pod and seed numbers of S111-9 plants under the salt-stressed field were also higher than those of S113-6 and Melrose plants. Therefore, the branch number per plant might be the primary responsible component for GY under salt-stressed field.

In order to understand better which factor was the primary limiting factor for the yield and P_N under salt

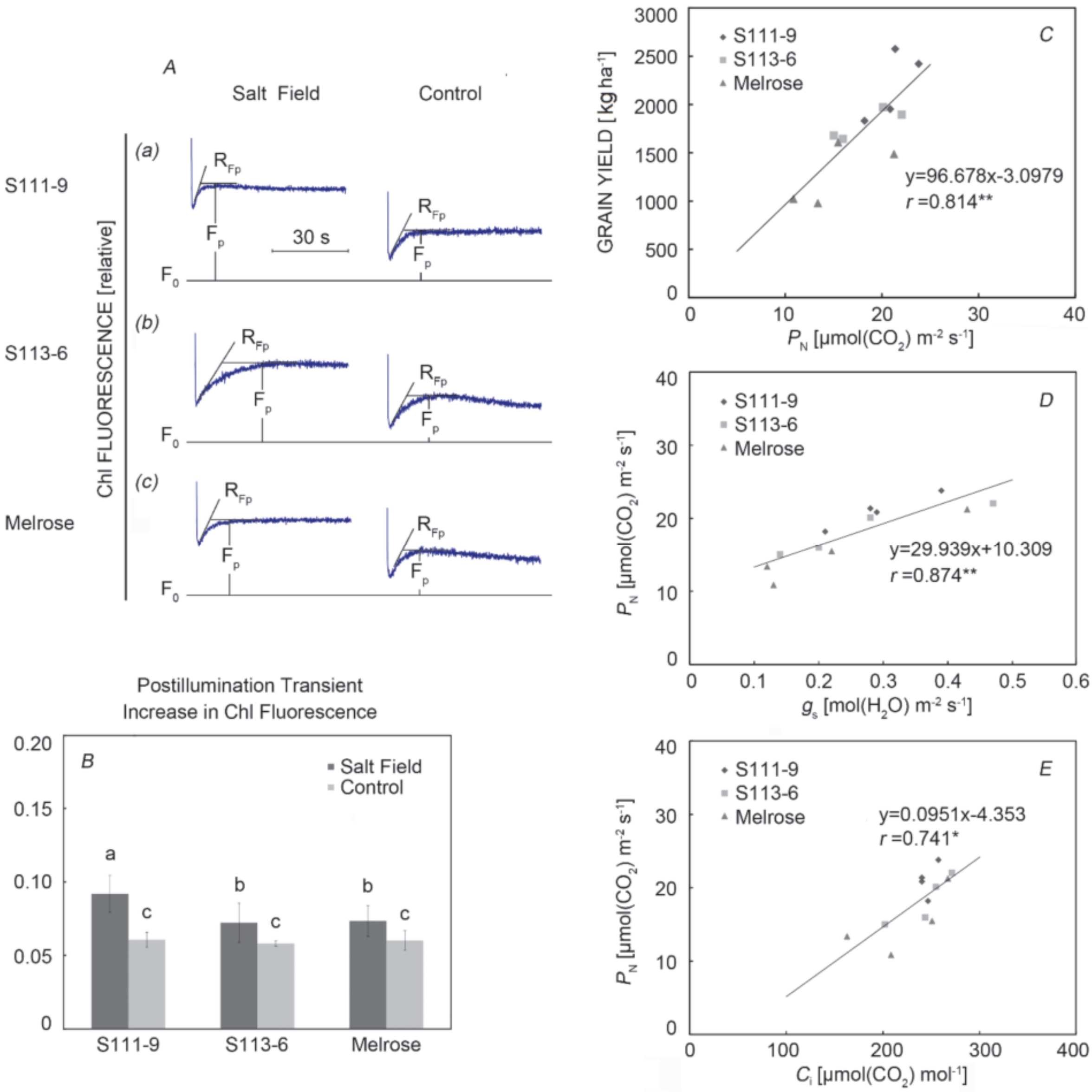

Fig. 1. Effects of salt stress on Chl fluorescence and the correlation between GY and P_N, or P_N and g_s, or P_N and C_i. (*A*) A typical postillumination transient increase induction curve in S111-9 (*a*), S113-6 (*b*), and Melrose (*c*); dark fluorescence level (F_0); the height of postillumination fluorescence increase (F_p); the rising rate of postillumination fluorescence increase (R_{Fp}). (*B*) The effects of salt stress on the height of postillumination fluorescence increase in S111-9, S113-6, and Melrose. Bars represent the mean ± SD of six independent experiments. *Different letters* indicate a significant difference between lines or salt-treatment time ($P<0.05$) by *Tukey*'s test. Correlation analysis between P_N and grain yield (*C*), or P_N and g_s (*D*), or P_N and C_i (*E*) in the control and salt-stressed field ($n = 12$). * – significant difference ($P<0.05$), ** – extremely significant difference ($P<0.01$).

stress, regression analysis was carried out between GY and the photosynthetic parameters. The results indicated a significant positive correlation between GY and P_N (Fig. 1*C*). Meanwhile, P_N was significantly positive correlated with g_s (Fig. 1*D*) and C_i (Fig. 1*E*).

Salt stress significantly affected P_N and F_v/F_m in soybean according to Yang *et al.* (2007), Lu *et al.* (2009), and He *et al.* (2014). In addition, Kao *et al.* (2003) compared the responses of photosynthetic gas exchange and Chl fluorescence of three wild soybeans and found that P_N, g_s, ETR, and Chl fluorescence parameters decreased dramatically when plants were exposed to salt stress for a long time. Meanwhile, these reductions increased with increasing concentration of salt stress. However, all these studies were carried out in the greenhouse or under growth chamber conditions.

In present study, we found that the decreases of P_N, g_s, C_i, *E*, and NPQ in the S111-9 plants induced by salt stress were slighter than those in the S113-6 and Melrose plants (Table 1). There was no significant change in F_v/F_m in S111-9 and S113-6, implying that they showed better integrity of photosynthetic apparatus than the Melrose plants. The decrease of ETR in the S111-9 and S113-6 plants under salt stress was about 10% compared with that under control field, but ETR in the Melrose plants was not affected under control or salt-stress conditions (Table 1). Moreover, the enhancements of cyclic electron flow around PSI under salt stress was in favor of the improvement of salt tolerance that have been already reported (Yang *et al.* 2007, Lu *et al.* 2009). The increase in Chl fluorescence of the S111-9 plants was also significantly higher than that of S113-6 and Melrose plants under salt stress (Fig. 1*B*), suggesting that S111-9 plants showed stronger cyclic electron flow than that of the S113-6 and Melrose plants. Therefore, it indicates that the S111-9 plants could show better photosynthetic traits of salt tolerance enabling them to adapt to the salt environments.

Soybean is classified as a moderately salt-tolerant crop and the final yield of soybean is reduced when soil salinity exceeds about 60 mM NaCl concentration (Ashraf and Wu 1994). Many studies have been reported that high salt imposes negative impacts on the growth of nodulation, agronomic traits, seed quality and quantity, and thus reduces the yield of soybean (Chang *et al.* 1994, Abd-Alla *et al.* 1998, Phang *et al.* 2008). In order to further elucidate whether the excellent photosynthetic traits of the S111-9 plants could contribute to the improvement of the yield traits under salt stress in the field, the yield indexes of the three lines under control and salt field were studied in the 2-year experiment. Although the branch numbers could be severely affected by high salinity (Chang *et al.* 1994), the reduction in a branch number was observed only in the Melrose plants, but not in S111-9 and S113-6 plants under control or salt stress conditions (Table 1). Accordingly, for S111-9 and S113-6 plants, the salt-tolerant lines, the reduction in the pod number and seed number per plant became a critical factor for the salt stress-induced decrease in the yield. Although salt stress induced the decrease of grain yield in all three varieties (Table 1), the grain yield of the S111-9 plants was higher than that ot the S113-6 and Melrose plants. Our results further indicated that the high grain yield of S111-9 plants might partly result from its better photosynthetic traits of salt tolerance.

The photosynthetic and yield traits of soybean could be severely affected by high salinity, including a reduction in P_N, g_s, leaf size, number of branches, number of pods and mass per 100 seeds (Chang *et al.* 1994, Phang *et al.* 2008, Lu *et al.* 2009). Based on the comparison of photosynthesis and yield traits in the considered soybean lines for the 2-year experiment, our results indicated that the photosynthetic traits of the S111-9 plants did not only prevent its photosynthetic apparatus from salt stress-induced damage but the S111-9 plants exhibited better yield traits than that of the S113-6 and Melrose plants. The regression analysis suggested that GY was significantly correlated with P_N, which could be considered as an important index for the yield of soybean under salt stress. The g_s was a primary limiting factor for P_N under salt stress. Moreover, the high increase in Chl fluorescence of S111-9 plants also contributed to its excellent photosynthetic performance and further enhanced the salt tolerance of the S111-9 plants.

Therefore, achieving synchrony between the improvement of soybean photosynthesis and the enhancement of salt tolerance is the key to optimizing tradeoff among photosynthesis efficiency, yield, and salt tolerance in the breeding of new soybean varieties.

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