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Full Length Research Paper

Effects of 24-epibrassinolide on photosynthesis of eggplant (*Solanum melongena* L.) seedlings under salt stress

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In this study, 24-epibrassinolide (EBR), an active brassinosteroid, was exogenously applied to investigate photosynthetic performance of salt-stressed eggplant (*Solanum melongena* L.). EBR, especially 100 nM, dramatically alleviated growth suppression caused by salt stress. Similarly, the application of 100 nM EBR, the most effective concentration, for salt-stressed plants significantly increased chlorophyll concentration, net photosynthetic rate (P_n), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i). In addition, maximal quantum efficiency of photosystem II (PSII) photochemistry (F_v/F_m), PSII maximum efficiency (F_v'/F_m'), photochemical quenching coefficient (*qP*), PSII operating efficiency (*ΦPSII*) and the fractions of light absorbed which is utilized in PSII photochemistry were also increased, while nonphotochemical quenching (*NPQ*) was reduced. However, higher concentrations (200 and 400 nM) of EBR reduced its effects or even caused a further reduction of photosynthetic capacity as compared to plants that received high salinity treatment alone. Furthermore, the changes in P_n at varying levels of EBR under salt condition were not accompanied by a significant corresponding change in C_i, suggesting that g_s was not the sole factor for EBR-induced changes in photosynthesis. Results obtained here demonstrate that EBR application could improve photosynthesis and alleviate the detrimental effects of salt stress on plant growth.

Key words: Chlorophyll fluorescence, eggplant, 24-epibrassinolide, photosynthetic gas exchange, salt stress, thermal energy dissipation.

INTRODUCTION

Soil salinity is considered as a major abiotic stress posing major challenges to the growth and production of crops around the world (Shabala and Cuin, 2008; Zhang et al., 2009). The decline in growth of plants under saline condition is often associated with decrease in their photosynthetic activity (Hajlaoui et al., 2006; Stepien and Klobus, 2006). The reduced photosynthesis is due to stomatal closure resulting in reduction of stomatal conductance (g_s), transpiration rate (T_r), intercellular CO_2 concentration (C_i) and net photosynthesis (P_n) (Wilson et al., 2006; Lu et al., 2009) or to non-stomatal limitations including the depression in photosystem II (PSII) activity, electron transport and photophosphorylation activity (Lu and Vonshak, 2002; Xia et al., 2004; das Neves et al., 2008). However, the mechanisms of inhibition of photosynthesis by salt stress remain poorly defined.

Brassinosteroids (BRs) are a novel group of phytohormones occurring in plant steroid hormones and are distributed throughout the plant kingdom (Krishna, 2003; Montoya et al., 2005). BRs play prominent roles in various physiologic processes, like cell division and expansion, xylem differentiation, stem elongation and root growth (Khripach et al., 2000; Cao et al., 2005; Kartal et al., 2009). Moreover, BRs are also reported to have an ameliorative effect on plants subjected to environmental stress such as cold stress (Yu et al., 2002; Hu et al., 2008; Liu et al., 2009), heat stress (Ogweno et al., 2008), oxidative

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damage (Cao et al. 2005) and pathogen infection (Nakashita et al., 2003; Zhou et al., 2004). Under salt stress, the effects of BRs were mainly focused on plant growth and antioxidant systems (Anuradha and Rao, 2001; Nunez et al., 2003; Ozdemir et al., 2004; Ali et al., 2008; Arora et al., 2008; Rady, 2011). Under salt stress, few studies have been conducted on the effects of BRs on photosynthesis and PSII photochemistry.

The potential application of BRs in agriculture and horticulture is based on their ability to increase crop yield, also due to stress amelioration. Eggplant (*Solanum melongena* L.), an important horticultural crop worldwide, is moderately sensitive to salinity. Until now, however, very little study has been done on the influence of BRs on eggplant under salt stress, especially on photosynthetic performance. Therefore, this study was designed to investigate the effects of varying concentrations (0, 50, 100, 200 and 400 nM) of 24-epibrassinolide (EBR) on the growth, photosynthetic pigment composition, gas exchange parameters and PSII photochemistry in eggplant under salinity conditions in order to improve our understanding of the mechanisms regarding the alleviation of salt toxicity.

MATERIALS AND METHODS

Plant culture and treatments

Seeds of eggplant (*S. melongena* L.cv. Huqie '08-9') used in this study, obtained from Shanghai Academy of Agricultural Sciences were rinsed thoroughly with distilled water and germinated on moist filter paper in an incubator at 28°C. Uniformly germinated seeds were selected, and planted in plastic pots filled with a 1:1 mixture of peat and vermiculite, one plant per pot. Seedlings were grown in greenhouse at average day/night temperature of 25/20°C and relative humidity of 65 to 70%. The photoperiod was maintained at 12 h, with a photosynthetic photon flux density (PPFD) of 800 to 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$. All plants were irrigated with half strength Hoagland nutrient solution every two days. When eggplant seedlings were at the fourth or fifth-true leaf stage, salinity treatment began by the addition of 90 mM NaCl (preliminary studies using various concentrations of NaCl (60 to 180 mM) showed that 90 mM NaCl was the critical concentration) with different concentration of EBR treatment (Sigma, USA). EBR was dissolved in a minimal volume of ethanol and then made to volume with distilled water. The experiments consisted of six treatments: (1) control (S0); (2) 90 mM NaCl and 0 nM EBR (S1); (3) 90 mM NaCl and 50 nM EBR (S2); (4) 90 mM NaCl and 100 nM EBR (S3); (5) 90 mM NaCl and 200 nM EBR (S4) and (6) 90 mM NaCl and 400 nM EBR (S5). Each treatment was replicated three times, every time with four plants. After 10 days of exposure to treatment, plants were collected to determine plant growth.

For determination of fresh weight, plants were harvested and divided into shoots and roots, all materials were rinsed three times in distilled water after disinfecting with non-ionic detergent, then blotted on filter paper and weighed.

Chlorophyll quantification

Chlorophyll content was measured as SPAD value on the intact topmost fully expanded leaf using a chlorophyll meter (Minolta, Japan) which provides a rapid, accurate and non-destructive estimate of leaf chlorophyll content, and replicated at least eight times (Wu et al., 1998).

Gas-exchange parameters

P_n, g_s, T_r and C_i were measured in four plants per treatment by a photosynthesis system (LI-6400, LICOR Inc., Lincoln, NE, USA). During the measurements, photosynthetic photon flux density was set to 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the air relative humidity was about 80%, the leaf temperature was maintained at 25°C and the ambient CO_2 concentration was about 400 $\mu L \cdot L^{-1}$. Measurement of photosynthesis was measured once for each leaf and for five different leaves per treatment. The water use efficiency (WUE) was calculated as the P_n/T_r ratio.

Chlorophyll fluorescence

Chlorophyll fluorescence was measured with a PAM-2100 pulse modulated fluorometer (Walz, Effeltrich, Germany). The fluorescence parameters were recorded from the same leaves used for measurement of photosynthesis. Before each measurement, leaves were dark-adapted for at least 30 min. The minimal fluorescence (F_o) was determined by a weak modulated light which was low enough not to induce any significant variable fluorescence. A 0.8 s saturating light of 8000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was used on dark-adapted leaves to determine the maximal fluorescence (F_m). Then the leaf was illuminated with actinic light (red led light) of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. When the leaf reached steady-state photosynthesis, the steady-state fluorescence (F_s) was recorded and a second 0.8 s saturating light of 8000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was applied to determine the maximal fluorescence (F_m') in the light adapted state. When the actinic light was turned off, the minimal fluorescence in the light-adapted state (F_o') was determined by the illumination with 3 s far-red light, and photochemical quenching coefficient (*qP*) was measured. PSII operating efficiency ($\Phi PSII$), PSII maximum efficiency of open centers (F_v'/F_m') and non-photochemical quenching (*NPQ*) were calculated as $(F_m' - F_s)/F_m'$, F_v'/F_m' and $F_m/F_m' - 1$, respectively (Genty et al., 1989; van Kooten and Snel, 1990; Yu et al., 2004). The ratio $(1 - qP)/NPQ$ was used as an estimation of photon excess and therefore, as the susceptibility of PSII to high irradiance (Park et al., 1995).

To get more information about the divergent parameters, we calculated the fractions of the excitation energy absorbed in the PSII antennae allocated to PSII photochemistry (*P*), thermal dissipation (*D*) and excess excitation (*X*) according to Demmig-Adams et al. (1996). The fractions of the absorbed light dissipated in the PSII antennae (*D*) and those utilized in PSII photochemistry (*P*) were estimated as $1 - (F_v'/F_m')$ and $(F_v'/F_m') \times qP$, respectively. The fraction of absorbed light by PSII, which was neither used in photochemistry nor dissipated in the PSII antenna (*X*) was estimated as $(F_v'/F_m') \times (1 - qP)$.

Statistical analysis

All data presented are the mean values. Each value was presented as the mean ± standard deviation with a minimum of five replicates. Differences between treatments were considered statistically significant when $p<0.05$ with the least significant difference (LSD) test.

RESULTS

Effects of EBR on the growth of eggplant seedlings under salt stress

Salt stress caused a significant reduction in plant growth

Table 1. Effects of 24-epibrassinolid (EBR) on the growth of eggplant seedlings under salt stress.

Treatment	Plant height (cm)	Stem diameter (cm)	Shoot fresh mass (g)	Root fresh mass (g)
S0	20.48 ± 1.39^{a}	4.27 ± 0.18^{a}	8.84 ± 0.28^{a}	4.81 ± 0.32^{a}
S1	17.46 ± 0.91^{b}	3.55 ± 0.23^{b}	6.36 ± 0.36^{c}	3.43 ± 0.30^{b}
S2	20.09 ± 0.42^{a}	3.92 ± 0.34^{ab}	6.73 ± 0.23^{bc}	4.23 ± 0.46^{a}
S3	20.29 ± 2.16^{a}	4.10 ± 0.34^{a}	7.13 ± 0.29^{b}	4.27 ± 0.29^{a}
S4	18.67 ± 0.74^{ab}	3.98 ± 0.14^{ab}	6.96 ± 0.57^{bc}	3.47 ± 0.17^{b}
S5	17.53 ± 1.42^{b}	4.01 ± 0.21^{ab}	6.38 ± 0.51^{c}	3.55 ± 0.29^{b}

Different letters in each column indicate significant difference ($P < 0.05$) between them. Data were presented as mean values ± SD obtained from measurements of five replicates.

on day 10 after treatment. Under salt stress, plant height, stem diameter, shoot fresh mass and root fresh mass decreased by 14.8, 16.9, 28.1 and 28.7%, respectively as compared to the control (Table 1). However, exogenously application of EBR dramatically alleviated the decrease in growth caused by salt stress. Application of 50 and 100 nM EBR had a significant positive effect on plant height and root fresh mass, while only 100 nM EBR caused a markedly induction on stem diameter and shoot fresh mass when compared with salt-treated plants (Table 1). In the presence of 100 nM EBR under salt stress, the reduction in plant height, stem diameter, shoot fresh mass and root fresh mass declined to 1.0, 4.0, 19.3 and 11.2%, respectively.

Effects of EBR on gas exchange parameters and chlorophyll pigments of eggplant seedlings under salt stress

To examine how EBR regulate photosynthetic capacity under salt treatment, we determined the effects of EBR application on gas exchange parameters. Photosynthetic gas-exchange parameters such as P_n, g_s, T_r and C_i were significantly reduced due to salt stress, while *WUE* was increased (Figures 1A to E). Furthermore, addition of 50 and 100 nM EBR caused a significant increase in P_n, but addition of 200 and 400 nM EBR caused a significant decrease in P_n (Figure 1A) as compared to the S1 treatment. In contrast, addition of 50 and 100 nM EBR caused a markedly increase in g_s and C_i, whereas 200 nM EBR did not affect these parameters but 400 nM EBR significantly reduced g_s (Figures 1B and C). Furthermore, T_r was significantly reduced under saline conditions, and the reduction was alleviated by 50 and 100 nM EBR, while it was significantly decreased by 200 and 400 nM EBR (Figure 1D). *WUE* was significantly enhanced by salt stress, and the enhancement was not significantly increased by different levels of EBR (Figure 1E). Chlorophyll content was significantly reduced by salt stress, while the reduction was alleviated by different concentration of EBR. Specifically, 50 to 200 nM EBR caused a marked increase in chlorophyll content, while 400 nM EBR had no significant effect on it when compared with salt stress (Figure 1F).

Effects of EBR on chlorophyll fluorescence parameters

The maximal quantum yield of PSII photochemistry F_v/F_m was significantly reduced under salt stress. However, the decline in F_v/F_m, was significantly alleviated by 100 and 200 nM EBR, but was not markedly influenced by 50 or 400 nM EBR when compared with salt stress (Figure 2A). *ΦPSII*, *qP* and F_v'/F_m' were significantly reduced by salt treatment. The reduction of *ΦPSII* was attributed to decreases in both *qP* and F_v'/F_m' (Zhou et al., 2004). Application of EBR at 50, 100 and 200 nM had significant effects on increase in *ΦPSII*, *qP* and F_v'/F_m' particularly at 100 nM, while 400 nM EBR significantly improved *ΦPSII* but not *qP* and F_v'/F_m' (Figures 2B, C and D) as compared to the S1 plants.

NPQ was sharply increased due to salt stress, while it was markedly decreased by application of 50 and 100 nM EBR, and not affected by other concentrations of EBR when compared with salt stress (Figure 2E). The (1–*qP*)/NPQ ratio which estimates the excess of light during photosynthesis induction was significantly increased by salt stress. Application of 100 and 200 nM EBR, however, caused a significant reduction in the ratio, while 50 and 400 nM EBR slightly reduced it when compared with the S1 plants (Figure 2F).

Effects of EBR on distribution of absorbed energy

The fraction of *P* was remarkably reduced by salt stress, and the reduction was accompanied by a significant induction in *D*, while excess excitation (*X*) had no significant reduction due to salt stress. The reduction of *P* caused by salt stress was alleviated by different concentrations of EBR. Addition of 50, 100 and 200 nM EBR had significant effects on *P*, but addition of 400 nM had little effects on it (Table 2). In contrast, all the concentrations of EBR had no marked effects on *X* when compared with salt stress. The increase in *D* due to salt stress was restrained significantly by 50, 100 and 200 nM

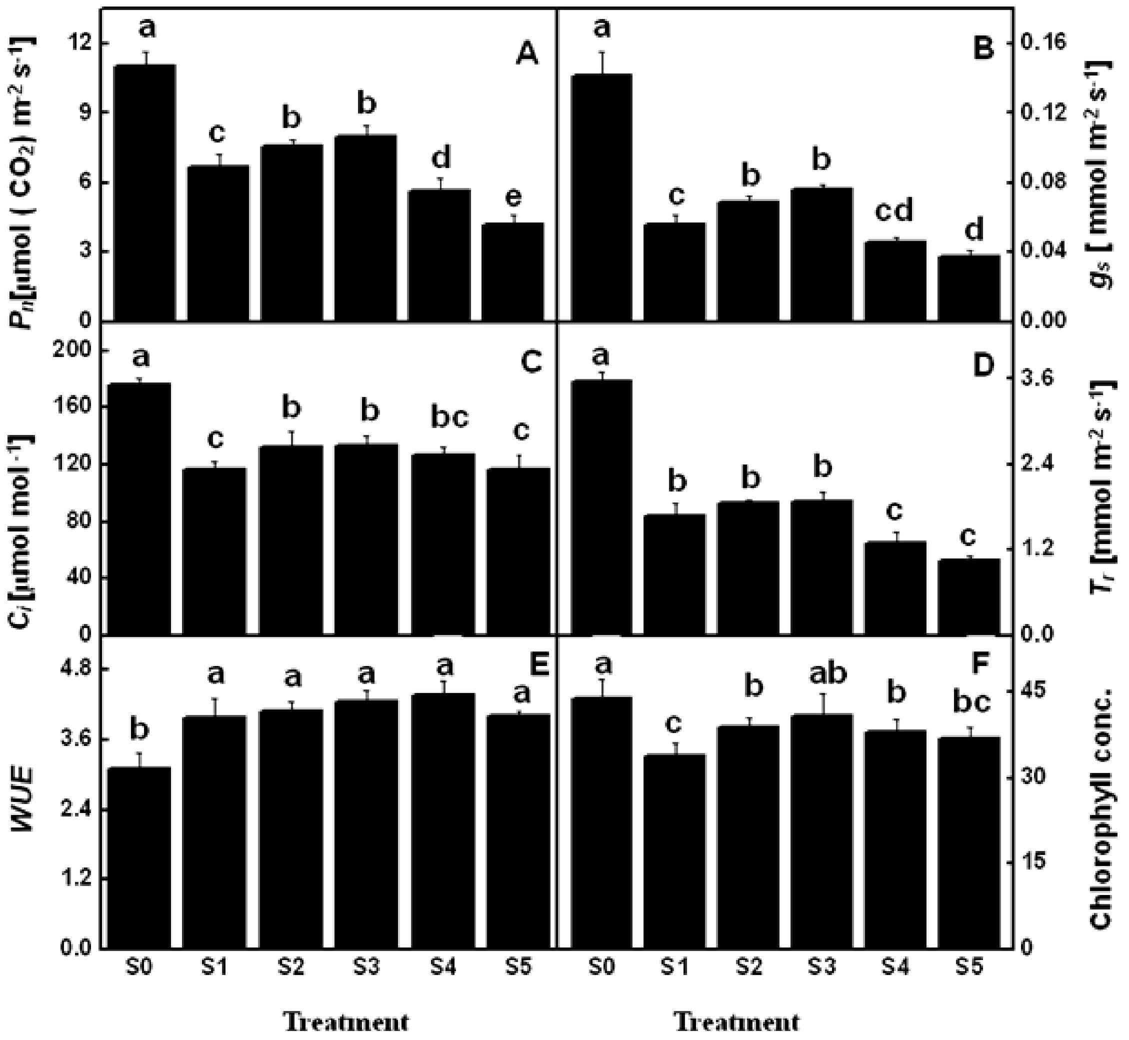

Figure 1. Effects of 24-epibrassinolide (EBR) on photosynthetic rate (*P_n*) (A), stomatal conductance (*g_s*) (B), intercellular CO$_2$ concentration (*C_i*) (C), transpiration rate *(T_r)* (D), water use efficiency (*WUE*) (E), and chlorophyll contents (F) of the leaves of eggplant seedlings under salt stress. Data are the mean of three independent measurements of 15 plants ± standard deviation shown by vertical error bars. Columns marked with the same lower case letters are not significantly different by the LSD test at $P<0.05$. LSD, Least significant difference.

EBR, but was not affected by 400 nM EBR (Table 2).

DISCUSSION

Salinity affects various physiological and biochemical mechanisms related with plant growth and development. Naeem et al. (2010) reported that salinity decreased the growth of *Brassica napus*, and decreased leaf water potential and chlorophyll concentration. BRs, as a new kind of phytohormones, are newly defined to play an essential role in various biotic and abiotic stresses (Krishna, 2003). Recent studies reported an increase in the tolerance of plants to salinity due to BRs application (Nunez et al., 2003; Arora et al., 2008). In the present study, salt stress significantly reduced plant height, stem diameter, shoot fresh mass and root fresh mass in eggplant. These reductions in growth traits were alleviated by 50 and 100 nM EBR. Moreover, we found that the most effective dose of EBR in improving the growth was 100 nM (Table 1). These results can be related to some earlier studies in which it has been observed that EBR play positive roles in growth of rice (Anuradha and Rao, 2001; Ozdemir et al., 2004), wheat (Ali et al., 2008; Shahbaz et al., 2008) and *Phaseolus vulgaris* (Rady, 2011) under saline conditions.

The inhibition of photosynthetic capacity under salinity might be due to the stomatal closure, which limits photosynthetic CO$_2$ assimilation (Downton et al., 1990; Yang and Lu, 2005). Lu et al. (2009) showed that salt stress induced a significant decrease in the P_n, and the decrease in P_n was positively related to the decrease in g_s

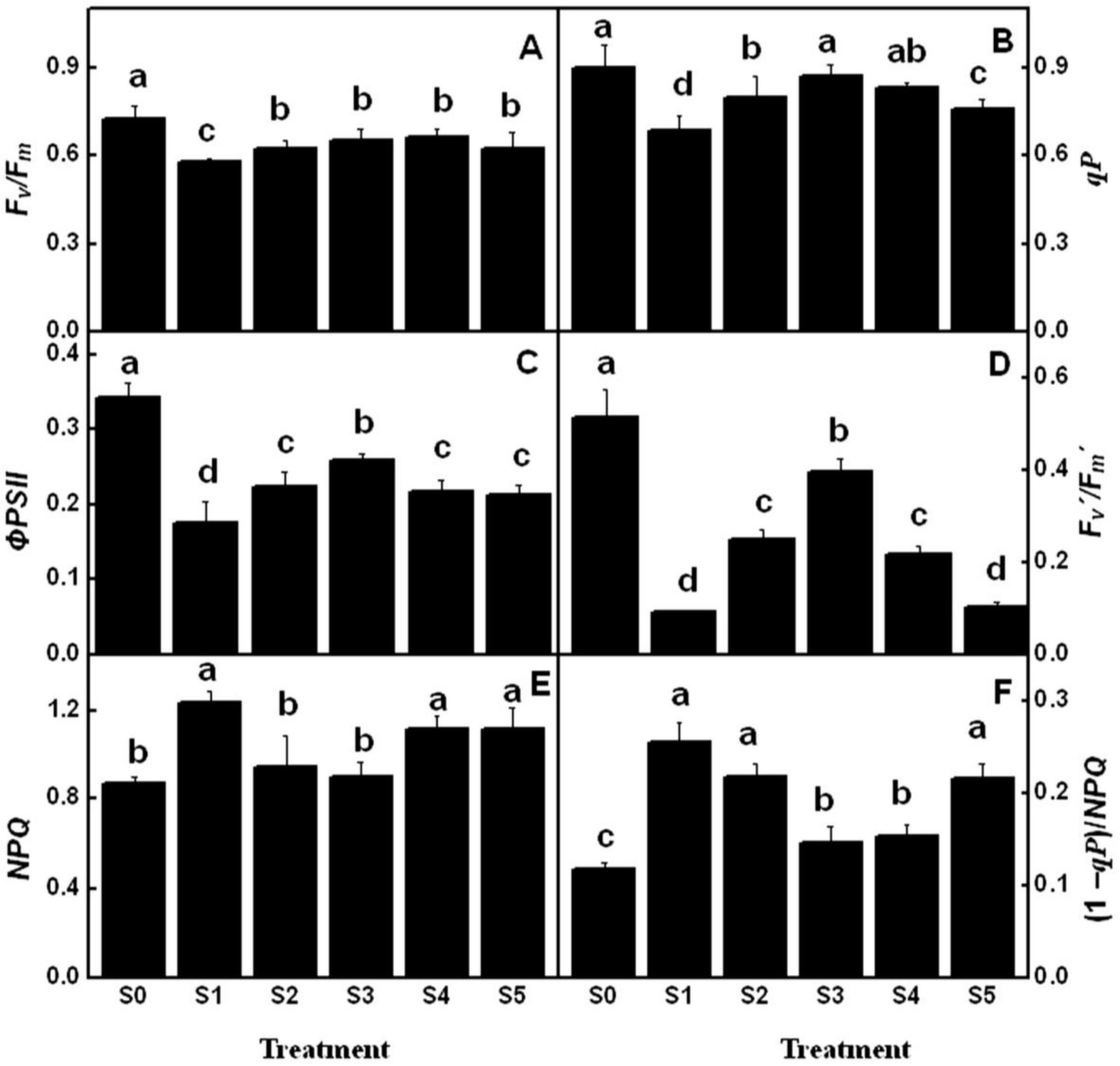

Figure 2. Effects of 24-epibrassinolide (EBR) on maximum quantum efficiency of PSII photochemistry (F_v/F_m) (A), photochemical quenching coefficient (qP) (B), PSII operating efficiency ($\Phi PSII$) (C), PSII maximum efficiency (F_v'/F_m') (D), non-photochemical quenching (NPQ) (E) and ($1 - qP$)/NPQ (F) of the leaves of eggplant seedlings under salt stress. Data are the mean of three independent measurements of 15 plants ± standard deviation shown by vertical error bars. Columns marked with the same lower case letters are not significantly different by the LSD test at $P<0.05$. LSD, Least significant difference; PSII, photosystem II.

and C_i. In this study, 90 mM NaCl stress induced reduction of P_n, C_i and T_r accompanied with a pronounced reduction of g_s, indicating that the effect of salinity on P_n can be due to stomatal factors (Figure 1). However, an increase or decrease in P_n at varying levels of EBR under saline conditions was not accompanied by a significant corresponding change in C_i, suggesting that stomatal conductance was not the sole factor for EBR-induced changes in photosynthesis (Figure 1).

Salinity induced a serious decline in chlorophyll content and PSII activity in many plants (Nishihara et al., 2003; Naeem et al., 2010). In our study, salt stress significantly reduced the SPAD value, as well as affect parameters of PSII photochemistry of eggplant leaves. F_v/F_m was significantly reduced under NaCl stress, suggesting the development of photoinhibition (Figure 2A). F_v'/F_m', qP and $\Phi PSII$ exhibited a change pattern similar to that of F_v/F_m and EBR, showing their most significant effects on increasing F_v/F_m at 100 and 200 nM and F_v'/F_m', qP and $\Phi PSII$ at 50 to 200 nM, particularly at 100 nM (Figures 2B, C and D), indicating that EBR decreased the susceptibility to photoinhibition, probably because EBR reduced the fraction of reduced Q_A (Q_A^-) of PSII (Lu and Lu, 2004). In contrast, NPQ was increased markedly in salt-stressed leaves, and sharply decreased by application of 50 and 100 nM EBR (Figure 2E). These results suggest that application of EBR protected the PSII against over-excitation, perhaps from a loss of integrity in the thylakoid

Table 2. Effects of 24-epibrassinolid (EBR) on the fractions of light absorbed by PSII antennae used in PSII photochemistry (*P*), thermal energy dissipation (*D*) and excess PSII excitation (*X*) under salt stress.

Treatment	P	D	X
S0	0.464 ± 0.031^a	0.487 ± 0.039^d	0.049 ± 0.033^a
S1	0.064 ± 0.001^d	0.907 ± 0.020^a	0.029 ± 0.002^a
S2	0.202 ± 0.021^c	0.749 ± 0.037^b	0.050 ± 0.001^a
S3	0.343 ± 0.021^b	0.603 ± 0.055^c	0.054 ± 0.002^a
S4	0.178 ± 0.001^c	0.785 ± 0.038^b	0.037 ± 0.009^a
S5	0.079 ± 0.003^d	0.897 ± 0.014^a	0.024 ± 0.002^a

Different letters in each column indicate significant difference ($P < 0.05$) between them. Data were presented as mean values ± standard deviation (SD) obtained from measurements of 15 replicates.

membrane (Ogweno et al., 2008).

The contribution of photochemical and non- photochemical quenching to the photoinactivation of PSII can be conveniently assessed by the (1–*qP*)/*NPQ* ratio. Salt stress resulted in a significant increase with respect to the control, however, was significantly alleviated by treatment with 100 and 200 nM EBR (Figure 2F), preventing PSII damage (Calatayud and Barreno, 2004). The decrease in *P* was also associated with a drastic increase in *D*, *X* had no significant change under salt stress, 50 to 200 nM EBR significantly alleviated the decrease of *P* and the increase of *D*, and had no impact on *X*. Moreover, we found that *P* and *D* as the main components of energy dissipation were complementary to each other, and *X* was unchanged with different concentrations of EBR treatment under salt stress (Table 2). These results suggest that application of EBR reduced salt-induced photoinhibition by protecting PS II.

In conclusion, salinity stress affected gas-exchange and chlorophyll fluorescence parameters and decreased the growth of eggplant seedlings, and EBR, especially 100 nM, alleviated the detrimental effects of salinity by improving the photosynthetic capacity of eggplant. However, the mechanism is still obscure. Hence, it is importance to further study the mechanisms by which BRs regulate photosynthesis under salt stress at the molecular and physiological level.

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Abbreviation

BR, Brassinosteroid; C_i**,** intercellular CO_2 concentration; **EBR,** 24-epibrassinolide; F_o**,** minimal fluorescence at the dark-adapted state; $F_o{'}$**,** minimal fluorescence at the light-adapted state; F_m**,** maximal fluorescence at the dark-adapted state; $F_m{'}$**,** maximal fluorescence at the light-adapted state; F_s**,** steady-state level fluorescence; F_v**,** variable fluorescence at the dark-adapted state; F_v/F_m**,** maximum quantum yield of PSII photochemistry; $F_v{'}/F_m{'}$**,** PSII maximum efficiency; g_s**,** stomatal conductance; ***NPQ*,** nonphotochemical quenching; P_n**,** net photosynthetic rate; ***ΦPSII*,** PSII operating efficiency; ***qP*,** photochemical quenching coefficient; T_r**,** transpiration rate.

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