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The influence of ABA on the photosynthesis of the rare and endangered *Emmenopterys henryi* under salt stress

L.-J. CAI, X.-Y. JI, M.-F. HOU, Y.-F. HAO, Q. WU*, and L.-L. SONG*

School of Ecological Technology and Engineering, Shanghai Institute of Technology, Shanghai 201418, P.R.China

*Corresponding authors: E-mails: 1046143482@qq.com, songLL713@163.com

Abstract

Emmenopterys henryi Oliv., a monotypic genus in family *Rubiaceae* with high scientific and application value, is currently endangered. Adaptability of *E. henryi* to environment is important for its cultivation, management, and application. In this paper, the effect of abscisic acid (ABA) on the photosynthesis of *E. henryi* under salt stress was discussed. Results showed that 0.3 % (m/v) NaCl led to reduction of net photosynthetic rate (P_N), instantaneous carboxylation efficiency (ICE), and Rubisco activity but the increase of intercellular CO_2 concentration (c_i), which were remarkable relieved by ABA pretreatment. NaCl also induced reduction of the maximal efficiency of PS II photochemistry (F_v/F_m), the photochemical quenching (qP), the non-photochemical quenching (NPQ), the actual PS II efficiency [Y(II)], the regulated-energy dissipation [Y(NPQ)], whereas the increase of the unregulated energy dissipation [Y(NO)]. ABA application remarkably mitigated the depression of F_v/F_m, qP, Y(II) and the increase of Y(NO), but further promoted NPQ and Y(NPQ) in *E. henryi* due to high salinity. In addition, decrease of chlorophyll content, accumulation of MDA, and ion leakage in *E. henryi* due to high salinity were significantly alleviated by ABA pretreatment. Fluridone, an inhibitor of endogenous ABA synthesis, partially or completely reversed ABA mediated effects. These results suggested that ABA might improve the photosynthesis of *E. henryi* under salt stress *via* allocating more energy to photochemical reactions, or/and mitigating the decrease of Rubisco activity, or/and protecting photosynthetic apparatus by reinforcement of heat dissipation and alleviating oxidative damage.

Keywords: abscisic acid, chlorophyll fluorescence, *Emmenopterys henryi*, photosynthetic rate, salt stress.

Introduction

Soil salinization is becoming serious problem all over the world. Statistically, about 7 % of land area worldwide was threatened by salinity (Afzal *et al.* 2020), which is claiming about 300 m^2 of arable land every minute (Shabala *et al.* 2014). Salt stress results in severe reduction in crop production (Hanin *et al.* 2016) and economic losses annually (Morton *et al.* 2019) and thus brings challenge to food security with a growing population in the world (Morton *et al.* 2019). Salt stress brings about early occurring osmotic stress and a late ionic stress and subsequent oxidative stress in plants (Sewelam *et al.* 2014, Yang and Guo 2018), which leads to water deficit, nutrient imbalance, ROS accumulation, membrane interruption, photosynthesis reduction, growth inhibition, premature senescence (Muchate *et al.* 2016, Kwon *et al.* 2019), and even death of plants. Photosynthesis is among the primary processes to be affected by salt stress. Under salt stress, photosynthesis has been demonstrated to be adversely affected due to inhibition of leaf development (Hussain *et al.* 2016, Mijiti *et al.* 2017), disruption of chloroplast ultrastructure (Kwon *et al.* 2019, Zhu *et al.* 2019), as well as alterations in gene expression and related enzymes activities (Wang *et al.* 2019b, Afzal *et al.* 2020).

Abscisic acid (ABA) participates in signaling network related to maturation, dormancy, germination, fruit ripening, senescence, abscission (Liu *et al.* 2018), and acclimation to environmental stresses including high temperature, cold, heavy metals, aridity, and salinization

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Abbreviations: ABA - abscisic acid; c_i - intercellular CO_2 concentration; E - transpiration rate; Flu - fluridone; F_v/F_m - variable to maximum fluorescence ratio (the maximal efficiency of PS II photochemistry); g_s - stomatal conductance; ICE - instantaneous carboxylation efficiency; NPQ - non-photochemical quenching; P_N - net photosynthetic rate; qP - photochemical quenching; Y(II) - actual PS II efficiency; Y(NPQ) - regulated-energy dissipation.

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(Chen *et al*. 2020). Under salt stress, ABA biosynthetic related genes were found to be activated and endogenous content of ABA was increased (Zhu 2002, Kang *et al*. 2005). Exogenous ABA promoted high salt tolerance in plants (Yao *et al*. 2020). The hypersensitivity of the *Arabidopsis* mutant, *sahy9/apum23,* which contained lower ABA content than wild-type plants, was observed to be largely recovered by ABA application (Huang *et al*. 2018). Down-regulation of genes related to abscisic acid synthesis in *Arabidopsis* resulted in inhibition of endogenous ABA synthesis and decreased adaptability to high salt stress (Wang *et al*. 2019a). The above data provided genetic evidences for the participation of ABA in salt stress adaptation mechanism in plants.

Emmenopterys henryi Oliv. is a monotypic genus of *Rubiaceae* family and endemic to China (Zhang *et al*. 2019). Because of destruction of habitats, extensive deforestation, poor regenerative capacity, *E. henryi* is endangered. As a tall tree, *E. henryi* is excellent species for timber production and materials for papermaking as well as for pharmacological production. In addition, *E. henryi* is eminent ornamental species with various ecological functions and extremely wide prospect in urban greening. Adaptability of *E. henryi* to the environment is important for its possible cultivation, management, and application in landscaping. Our previous work has shown the acclimation mechanism of *E. henryi* to high irradiance (Hao *et al*. 2021). Little work has been done on the response of *E. henryi* to high salinity. In this work, we investigated the influence of high NaCl concentration on photosynthesis and chlorophyll fluorescence in *E. henryi*, which is important for the demonstration of adaptation mechanism of *E. henryi* to high salinity.

Materials and methods

Plants, cultivation, and treatments: The tissue-cultured seedlings of *Emmenopterys henryi* Oliv were obtained by organogenesis pathway. Leaves of *E. henryi* were used as explants and surface-sterilized in 75 % (v/v) ethanol for 15 s and then in 0.2 % (m/v) $HgCl_2$ for 10 min followed by rinsing with sterile water for five times. For embryonic calli induction, the sterilized leaves were cultured on 1/2 WPM medium supplemented with 2 mg dm^{-3} of benzyladenine, 0.5 mg dm^{-3} of 2,4 - dichlorophenoxyacetic acid, 2 % (m/v) of sucrose, and 6.0 g dm^{-3} of agar for four weeks. Then the embryonic calli were selected and transferred to shoot differentiation medium, namely, 1/2 WPM medium containing 2 mg dm^{-3} of 6-benzyladenine, 2 % (m/v) sucrose, and 6.0 g dm^{-3} agar. Four weeks later, the differentiated shoots were transferred to rooting medium, namely, 1/2 WPM medium supplemented with 1 mg dm^{-3} of indole-3-butyric acid, 0.3 mg dm^{-3} of activated charcoal, 2 % (m/v) sucrose, and 6.0 g dm^{-3} of agar. All cultured materials were incubated at 25 °C with a 16-h photoperiod, and an irradiance of 54 µmol m^{-2} s^{-1}. One month later, the rooted plantlets were transplanted into plastic pots (top side length, 10 cm; bottom side length, 7 cm; depth, 8.5 cm) containing substrate of peat soil: *Perlite* (2.5:1, v/v) and maintained at 25 °C in an incubator with a 16-h photoperiod, a relative humidity of 70 %, an irradiance of 54 µmol m^{-2} s^{-1}. The seedlings with 6 leaves were used in following experiments.

ABA and fluridone were dissolved with 95 % ethanol, respectively. Seedlings at the 6 leaves stage were sprayed with 100 cm^3 of distilled water, 50 mM ABA, and 25 µM fluridone, respectively, once daily for three days. Then the pretreated seedlings were subjected to salt stress treatment for 3 d, 5 d, and 7 d, respectively. Salt stress treatment was given by soaking the seedling pots in a container with 4 dm^3 of 0.3 % NaCl solution for 30 min once daily for three days. The distilled water sprayed and soaked seedlings were used as the control (CK). Six seedlings with similar development status were selected for each treatment.

Relative ion leakage of the third or fourth fully expanded leaves (from down to up) was determined according to Song *et al*. (2013). The leaves (0.2 g) were placed in 10 cm^3 of de-ionized water at 25 °C for 2 h. Then the conductivity of the bathing solution was determined (C1). Afterwards, the samples were boiled for 15 min and the conductivity was read again (C2). Relative ion leakage was calculated according to the equation: relative ion leakage [%] = C1/C2 × 100.

Lipid peroxidation of the third or fourth fully expanded leaves was measured in terms of MDA content following the method of Song *et al*. (2008). The leaves (0.5 g) were homogenized in 10 % (m/v) trichloroacetic acid (TCA) and then the homogenate was centrifuged at 4 000 *g* for 30 min. A 2 cm^3 aliquot of supernatant was mixed with 2 cm^3 of 10 % TCA containing 0.5 % (m/v) thiobarbituric acid. The mixture was heated at 100 °C for 30 min. The absorbance of the supernatant was measured at 532 nm, with a reading at 600 nm subtracted from it to account for non-specific turbidity. The amount of malonaldehyde was calculated using a coefficient of absorbance of 155 mM^{-1} cm^{-1}.

Chlorophyll content of the third or fourth fully expanded leaves was determined according to Wang *et al*. (2015). The leaf sample (0.25 g) was mashed with 80 % acetone (v/v) and the extract was filtered through two layers of nylon and centrifuged in sealed tubes at 15 000 *g* for 5 min. The supernatant was collected and read at 663 and 645 nm for chlorophyll determination. The total content of chlorophyll was calculated according to (8.02 A_{663} + 20.21 A_{645})/leaf area.

Rubisco activity assay: The activity of ribulose-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39) of the third or fourth fully expanded leaves was assayed by Rubisco assay kit (*Solarbio Life Sciences*, Beijing, China). The assay was completed in accordance with the manufacturer's description.

Gas exchange parameters analysis: Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2

concentration (c_i), and transpiration rate (E) of the third or fourth fully expanded leaves were determined with a *LI-COR 6400* portable photosynthesis system (*LI-COR*, Lincoln, NE, USA). The measurements were performed at a PAR of 400 μmol m^{-2} s^{-1}, CO_2 concentration of 400 μmol mol^{-1}, relative humidity of 70 %, air temperature of 25 °C, and a flow rate of 500μmol s^{-1}. The instantaneous carboxylation efficiency (ICE) was defined as P_N/c_i.

Chlorophyll fluorescence was determined with a pulse-amplitude modulated chlorophyll fluorometer (*PAM-2500*, *Walz*, Effeltrich, Germany). The third or fourth fully expanded leaves were dark-adapted for 20 min. The minimal fluorescence in the dark-adapted state (F_o) was assayed under irradiance of 0.8 μmol m^{-2} s^{-1}. The maximal fluorescence in the dark adapting leaves (F_m) was recorded under saturating pulse (8 000 μmol m^{-2} s^{-1}). The maximal fluorescence under irradiation (F_m') was determined by applying successive actinic light (50 μmol m^{-2} s^{-1}) and saturating pulse (8000 μmol m^{-2} s^{-1}). The steady-state yield of fluorescence under actinic light was termed as F_t. The minimal fluorescence during irradiation (F_o') was obtained after the actinic light was turned off and a far-red light was turned on. The maximum photochemical efficiency (F_v/F_m) was defined as $(F_m - F_o)/F_m$. The coefficient of photochemical quenching (qP) was defined as $(F_m' - F_t)/(F_m' - F_0')$. Non-photochemical quenching (NPQ) was calculated as $(F_m - F_m')/F_m'$. The actual PS II efficiency [Y(II)] was defined as $(F_m' - F_t)/F_m'$. The yield of regulated energy dissipation Y(NPQ) was defined as $F_t/F_m' - F_t/F_m$. The yield of non-regulated energy dissipation Y(NO) was defined as F_t/F_m.

Statistical analysis: The data presented are the average of three repeated experiments. Data analysis was performed by one-way analysis of variance (*ANOVA*) using *SPSS19* statistical software (*IBM SPSS Statistics*, Chicago, USA). The means were compared using Duncan's multiple range test at the 5 % level. Graphical presentation was carried out using *Origin 6.1* and *Adobe Photoshop 8.0.1*

Results

NaCl treatment led to significant increase of relative ion leakage on day 5 and 7 (Fig. 1*A*). ABA pretreatment significantly lessened the increase of ion leakage resulted from salt stress. In order to clarify the effect of endogenous ABA, fluridone (an inhibitor of ABA biosynthesis) was employed. Under salt stress, fluridone application caused more serious ion leakage, which on days 3, 5, and 7 reached 136.9, 207.3, and 374.4 % of the control (Fig. 1*A*).

As shown in Fig.1*B*, MDA content increased with NaCl treatment time, which attained 177.8, 261.1, and 342.1 % of the control on day 3, 5, and 7, respectively. Under salt stress, pretreatment with ABA obviously prevented the increase of MDA content induced by salt stress whereas fluridone application resulted in higher MDA content in comparison with that under salt stress alone.

Salt stress led to obvious decrease of chlorophyll content in leaves of *E. henryi*, which aggravated with salt stress time. ABA pretreatment evidently mitigated the degradation of chlorophyll due to salt stress. Under salt stress, fluridone pretreatment led to significant decline of the chlorophyll content (Fig. 2).

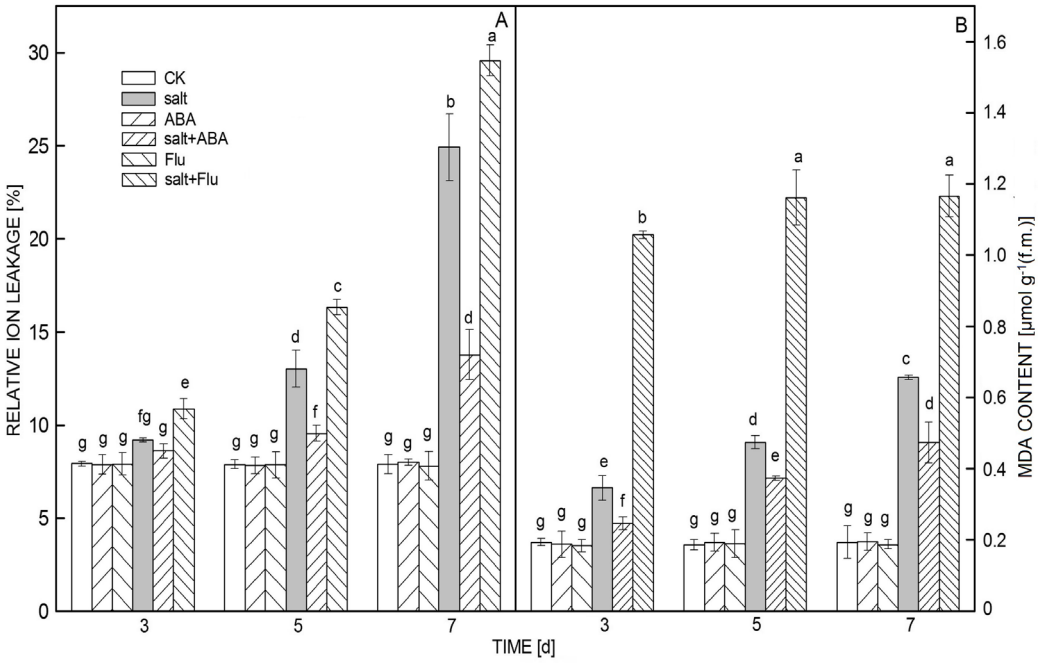

Fig. 1. Influence of ABA on relative ion leakage (*A*) and malondiadehyde (MDA) content (*B*) under salt stress. *Emmenopterys henryi* Oliv. seedlings were sprayed with distilled water (CK), 50 mM abscisic acid (ABA), and 25 μM fluridone (Flu) for 3 d and then subjected to 0.3 % NaCl treatment for 3, 5, and 7 d. The data presented are the average of three repeated experiments. Different letters mean significant difference between different treatments at $P < 0.05$.

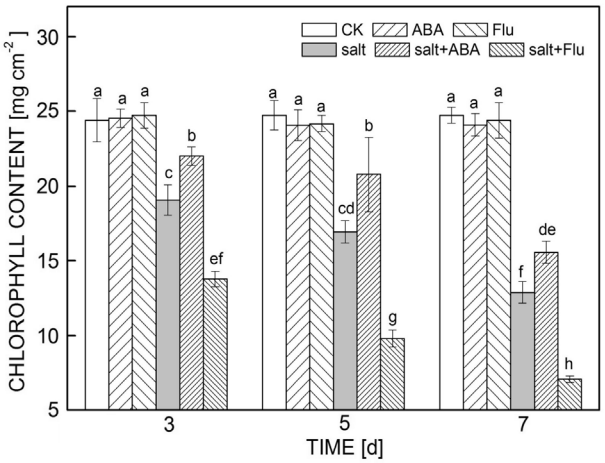

Fig. 2. Influence of ABA on chlorophyll content under salt stress. *Emmenopterys henryi* seedlings were sprayed with distilled water (CK), 50 mM abscisic acid (ABA), and 25 μM fluridone (Flu) for 3 d and then subjected to 0.3 % NaCl treatment for 3, 5, and 7 d. The data presented are the average of three repeated experiments. Different letters mean significant difference between different treatments at $P < 0.05$.

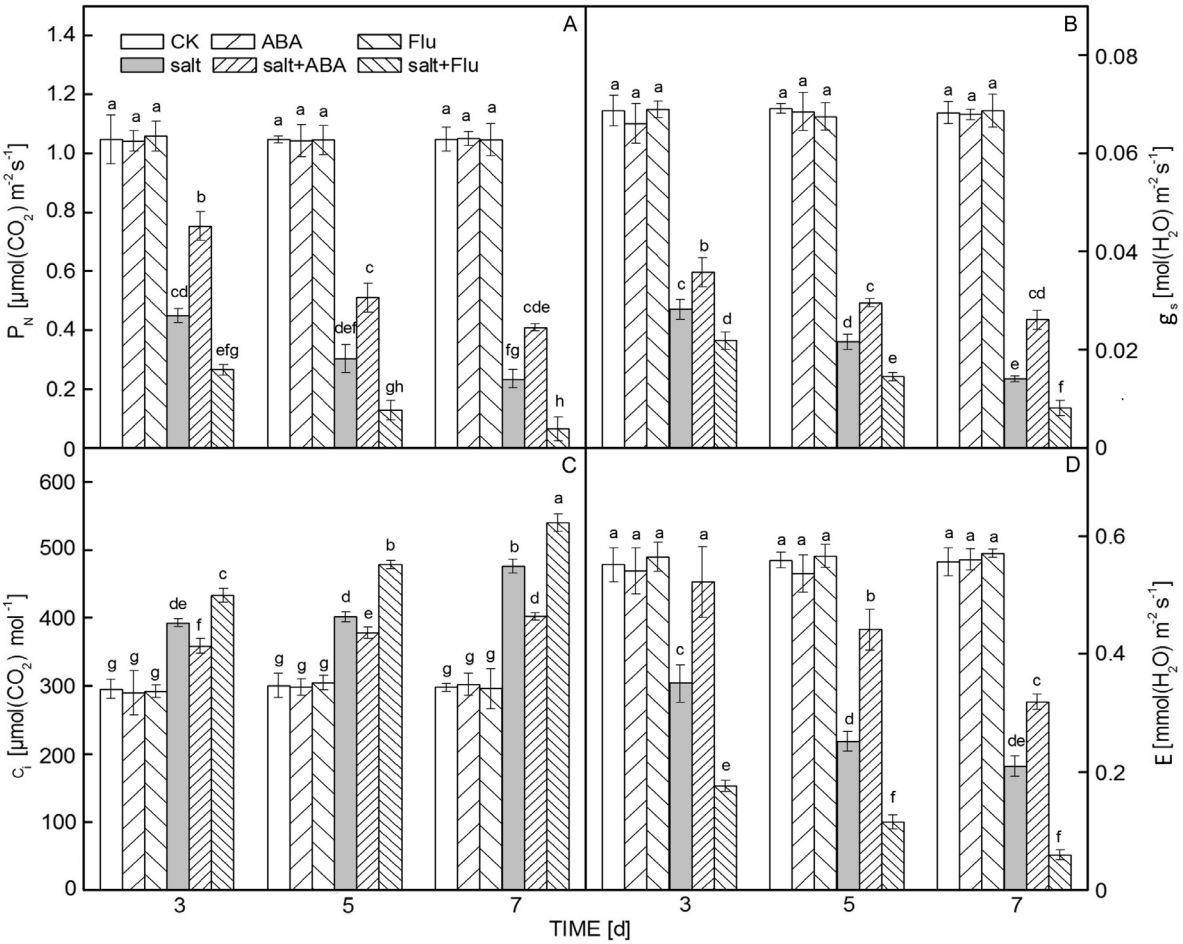

Fig. 3. Influence of ABA on net photosynthetic rate (P_N) (*A*); stomatal conductance (g_s) (*B*); intercellular CO_2 concentration (c_i) (*C*), and transpiration rate (E) (*D*) under salt stress. *Emmenopterys henryi* seedlings were sprayed with distilled water (CK), 50 mM abscisic acid (ABA), and 25 μM fluridone (Flu) for 3 d and then subjected to 0.3 % NaCl treatment for 3, 5, and 7 d. The data presented are the average of three repeated experiments. Different letters mean significant difference between different treatments at $P < 0.05$.

The net photosynthesis rate (P_N) decreased to 42.9, 28.8, and 18.5 % of the control after exposure to NaCl treatment for 3, 5, and 7 d, respectively. ABA application evidently mitigated the reduction of P_N caused by salt stress (Fig. 3*A*). However, P_N in seedlings exposed to fluridone application were obviously lower than that under

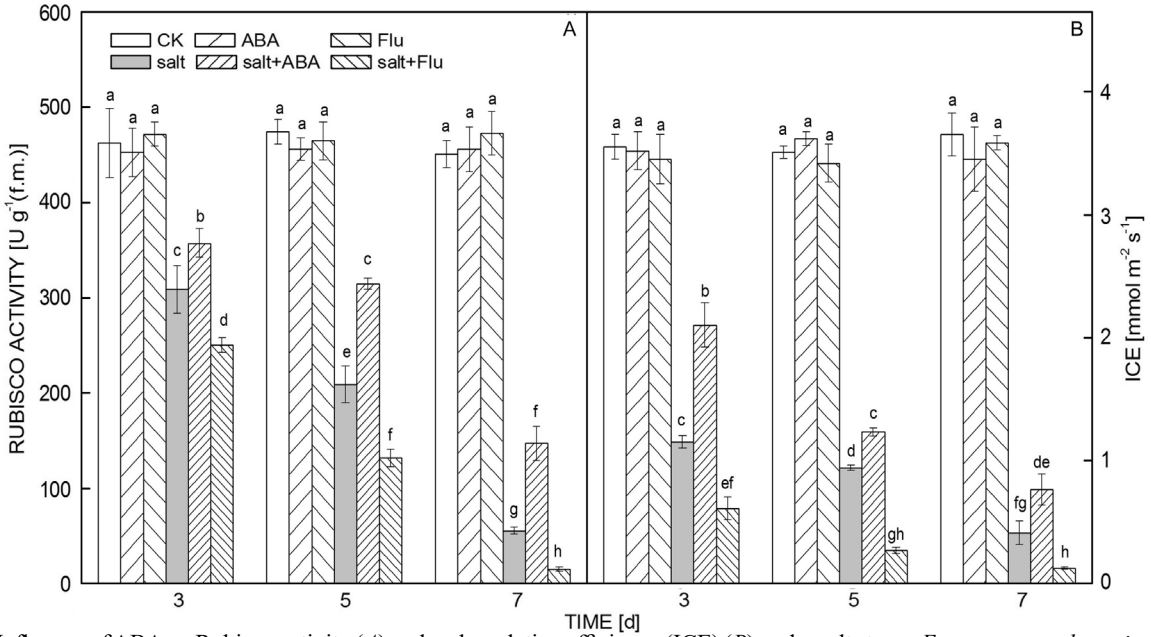

Fig. 4. Influence of ABA on Rubisco activity (*A*) and carboxylation efficiency (ICE) (*B*) under salt stress. *Emmenopterys henryi* seedlings were sprayed with distilled water (CK), 50 mM abscisic acid (ABA), and 25 μM fluridone (Flu) for 3 d and then subjected to 0.3 % NaCl treatment for 3, 5, and 7 d. The data presented are the average of three repeated experiments. Different letters mean significant difference between different treatments at $P < 0.05$.

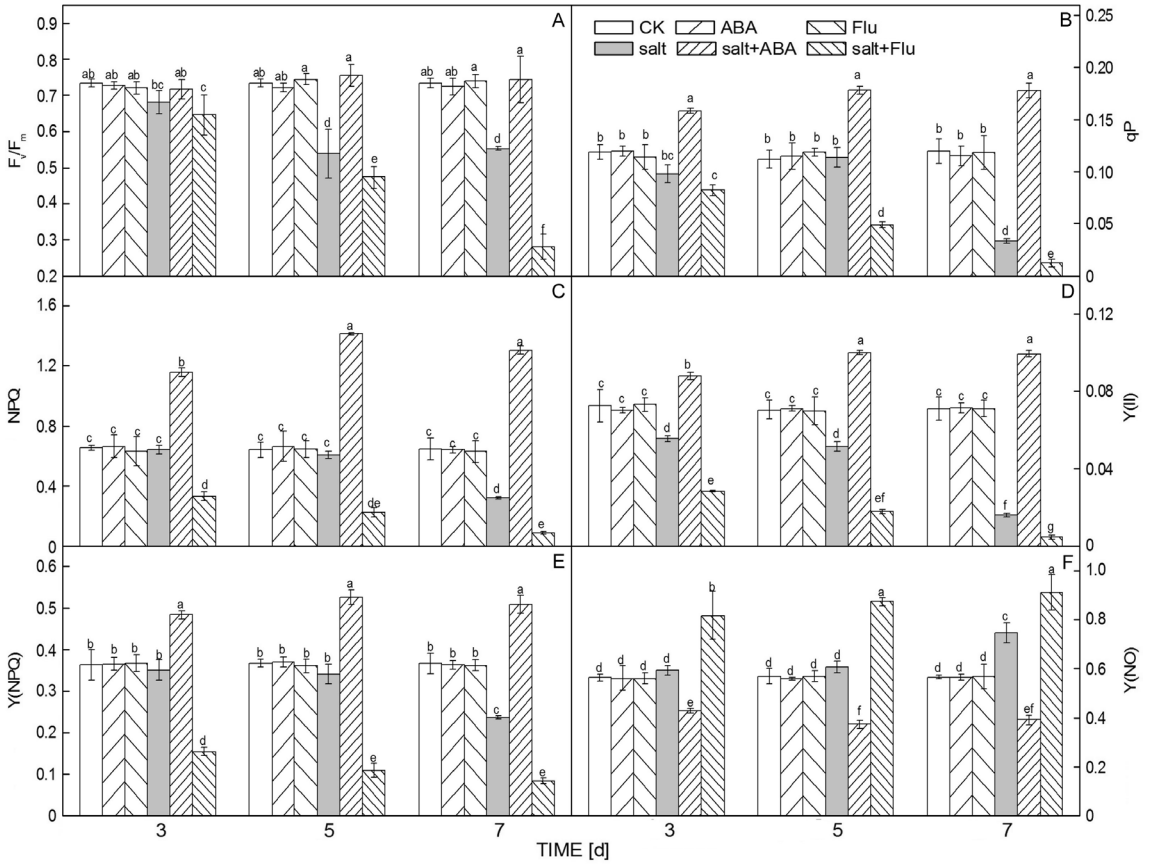

Fig. 5. Influence of ABA on the maximal efficiency of PS II photochemistry F_v/F_m (*A*), the photochemical quenching qP (*B*), the proportion of excess energy dissipation by nonradiative processes NPQ (*C*), the actual PS II efficiency Y(II) (*D*), the quantum yield of non-photochemical fluorescence quenching Y(NPQ) (*E*), and the unregulated energy dissipation Y(NO) (*F*) under salt stress. *Emmenopterys henryi* seedlings were sprayed with distilled water (CK), 50 mM abscisic acid (ABA), and 25 μM fluridone (Flu) for 3 d, and then subjected to 0.3 % NaCl treatment for 3, 5, and 7 d. The data presented are the average of three repeated experiments. Different letters mean significant difference between different treatments at $P < 0.05$.

salt stress alone (Fig. 3*A*).

The stomatal conductance decreased to 41.1, 30.4, and 20.6 % of the control after exposure to NaCl treatment for 3, 5, and 7 d, respectively. ABA application effectively inhibited the reduction of stomatal conductance due to salt treatment. Conversely, fluridone pretreatment aggravated the decline of g_s induced by salinity (Fig. 3*B*).

Salt stress resulted in distinct augmentation of intercellular CO_2 concentration, which was 32.9, 33.5, and 59.9 % higher than the control on the third, fifth, and seventh day, respectively. ABA treatment remarkably depressed the promotion of intercellular CO_2 concentration. Instead, the increase of c_i in the presence of fluridone application was greater than under salt treatment alone (Fig. 3*C*).

Under salt stress, the transpiration rate dropped to 63.5, 45.4 and 38.1 % of the control on the third, fifth, and seventh day, respectively. Exogenous ABA evidently lightened the decrease of E in response to salt stress. Fluridone pretreatment further intensified the depression of E induced by salt stress (Fig. 3*D*).

Salt stress brought about notable decline of the Rubisco activity, which descended from 66.7 % of the control on day 3 to 44.0 % on day 5, and 12.2 % on day 7. ABA application significantly alleviated the reduction of Rubisco activity due to salt stress (Fig. 4*A*).

Under salt stress, carboxylation efficiency descended gradually to 32.3, 26.8, and 11.2 % of the control on the third, fifth, and seventh day, respectively. Exogenous ABA remarkably relieved the reduction of ICE caused by salt stress whereas under fluridonce application, the decrease of ICE due to high salinity was more serious than that under NaCl alone (Fig. 4*B*).

The maximal efficiency of PS II photochemistry (F_v/F_m) reduced by 8.8, 27.3, and 24.6 % after exposure to NaCl treatment for 3, 5, and 7 d, respectively, while application of ABA completely inhibited this decline of F_v/F_m (Fig. 5*A*). Under salt stress, photochemical quenching (qP) and non-photochemical quenching (NPQ) kept stable during the first 5 days and then decreased to 25.0 and 49.2 % of the control on the seventh day, respectively. Under ABA treatment, qP increased to 133.5, 154.5, and 149.5 % of the control (Fig. 5*B*) while NPQ rose to 176.1, 220.3 and 203.1 % on day 3, 5, and 7, respectively (Fig. 5*C*). Instead, fluridone pretreatment intensified the decline of qP and NPQ induced by salt stress. High salinity led to decrease of Y(II) (Fig. 5*D*). During the first 5 d of NaCl treatment, Y(NPQ) remained stable and then declined to 65.8 % of the control on day 7 (Fig. 5*E*). Meanwhile, Y(NO) increased to 132.1 % of the control on day 7 (Fig. 5*F*). Application of ABA effectively relieved the decline of Y(II) and Y(NPQ) and increase of Y(NO) due to salt stress. Under fluridone treatment, the depression of Y(II) and Y(NPQ) and augmentation of Y(NO) induced by NaCl became more serious.

Discussion

Salinity-induced reductions in photosynthesis might attribute to stomatal or/and non-stomatal limitations (Farooq *et al*. 2015). In our work, the decrease of P_N and E in *E. henryi* under salt stress, whereas increase of c_i suggested that the inhibition of P_N was primarily due to nonstomatal limitation, which was further approved by the significant decrease of Rubisco activity and ICE. ABA pretreatment obviously relieved the depression of P_N, g_s, and E, which agreed with the results in *Toona sinensis* (Yao *et al*. 2020) and *Santalum album* (Liu *et al*. 2016). The effects of ABA on P_N, g_s, and E was not observed under fluridone treatment, proving the protection of ABA on photosynthesis under stress conditions. ABA might ameliorate photosynthesis by alleviating the decrease of Rubisco activity. Endogenous ABA content varied with the stress intensity, its duration, as well as species (Prerostova *et al*. 2017). In *Brassica juncea* and apple rootstocks, increase of endogenous ABA content under salt stress led to stomatal closure and subsequent decrease of P_N (Gupta *et al*. 2017, Zhu *et al*. 2019). Also, endogenous ABA content in the salt-tolerant species was found to be lower than that in the salt-sensitive species under salt stress, in which ABA was demonstrated to be involved in inhibition of photosynthesis and growth (He and Cramer 1996, Ryu and Cho 2015, Zhu *et al*. 2019). Instead, in other cases, endogenous ABA content in tolerant cultivar was higher than that in sensitive cultivar under high salinity and ABA was proved to play a positive growth-promoting role (De Costa *et al*. 2007, Farooq *et al*. 2015, Prerostova *et al*. 2017). The roles of endogenous and exogenous ABA in salt stress acclimation in plants are worth further exploration.

Chlorophyll fluorescence measurement has been used to assess the photosynthetic performance of plants in response to environmental stresses. F_v/F_m is indicator of the maximal photochemistry efficiency of PS II. In the work, decrease of F_v/F_m under salinity revealed occurrence of photoinhibition, which was similar to results in sweet potato (Xiao *et al*. 2016) and *Helianthus tuberosus* (Bian *et al*. 2020). Under ABA treatment, significant alleviation of the decrease of F_v/F_m imposed by salinity elucidated the protection of ABA for PS II reaction center, which was consistent with the situation in Chinese cabbage (Zhang *et al*. 2009). In *E. henryi*, qP gradually declined with the salt treatment time, indicating the decrease in energy used in photochemistry. The influence of salinity on NPQ was differently depending on plant species and its acclimation ability. In maize, NPQ was observed to decrease continuously with increased salt concentration (Qu *et al*. 2012). In *Helianthus tuberosus* and *Acer palmatum* (Tang *et al*. 2015, Bian *et al*. 2020), which are somewhat resistant to salinity, NPQ increased significantly under 1ow salt concentration and then decreased with the increase in NaCl concentration. In *E. henryi*, NPQ kept stable during the first 5 d and declined evidently on day 7 under salt stress, indicating gradual loss of self-preservation ability of PS II with the stress time. ABA application obviously alleviated the reduction of qP and NPQ in *E. henryi*, suggesting that ABA might ameliorate photosynthesis by allocating more energy to photochemistry and protected photosynthetic apparatus by heat emission, which agreed with the work in maize (Wu *et al*. 2006). Y(II), Y(NPQ), and Y(NO) have been frequently used as parameters of

damage of photosynthetic apparatus. In *E. henryi*, obvious reduction of Y(II) and Y(NPQ) whereas increase of Y(NO) under salt stress suggested that more energy was allocated to unregulated energy dissipation Y(NO) instead of photochemistry and regulated-energy dissipation, indicating weak photoprotection ability in *E. henryi* and the emergence of harm to the photosynthetic apparatus under salt stress. Differently, in *Forsythia*, severe salt stress resulted in decrease of Y(II) while increase of Y(NPQ) and Y(NO), indicating higher photoprotection ability in this species (Wu *et al*. 2016) and different response of NPQ to salinity in diferent species. Prominent elevation of Y(II) and Y(NPQ), and repression of Y(NO) in *E. henryi* owing to ABA pretreatment under salt treatment proved that ABA might keep higher photochemical efficiency by distributing more energy to photochemical reaction and protect photosynthesis apparatus by increase of heat dissipation.

Chlorophyll is important for photosynthesis (Rattan 2017). The decline of the net photosynthesis rate under salt stress might be associated with chlorophyll degradation (Farooq *et al*. 2015, Zhu *et al*. 2019). In *E. henryi,* the significant decrease of chlorophyll content under high salinity was alleviated by exogenous abscisic acid pretreatment, which is similar to the situation in soybean, sandal wood, and *Suaeda maritima* (Zhang *et al*. 2009, Liu *et al*. 2016, Anbarasi and Somasundaram 2020). However, in apple rootstocks, the increase of endogenous ABA was found to induce the accumulation of two chlorophyll-degrading enzymes, pheophytinase and pheophorbide a monooxygenase, and result in degradation of chlorophyll and decrease of P_N (Zhu *et al*. 2019). The contradictory effects of exogenous ABA and endogenous ABA under salt stress deserve deep research.

Salt stress resulted in high ROS production and induces oxidative stress in plants (Yang and Guo 2018, Zhu *et al*. 2019), which resulted in membrane lipids peroxidation, chloroplast ultrastructure damage, and decrease of photosynthesis (Eraslan *et al*. 2007, Zhang *et al*. 2009, Yao *et al*. 2020). In *E. henryi*, evident accumulation of MDA and ion leakage induced by salt stress was discovered to be effectively ameliorated by ABA application. The protection effect of ABA in *E. henryi* was consistent with previous results in soybean, sweet potato, and *Toona sinensis* (Zhang *et al*. 2009, Xiao *et al*. 2016, Yao *et al*. 2020).

In conclusion, photosynthesis inhibition in *E. henryi* under salt stress resulted from decrease of photochemical activity, reduction of carbon assimilation efficiency, and chloroplast ultrastructure damage induced by oxidative stress. ABA might ameliorate photosynthesis in *E. henryi* under high salinity by improving photochemistic reactions, or/and alleviating the decrease of Rubisco activity, or/and abating oxidative damage.

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