Photosystem II efficiency of primed canola under salt stress

Zhara Karimi[1], Jalil Khara[1], Ghader Habibi[2]*

1. Department of Biology, Faculty of Sciences, Urmia University, Urmia, Iran
2. Department of Biology, Payame Noor University (PNU), 19395-3697 Tehran, Iran

Abstract

This experiment was conducted to investigate the role of priming in regulation of growth and photosynthesis in salt-acclimated canola plants. Salt stress caused a significant decrease in total dry mass, whereas seed priming with hydrogen peroxide (H_2O_2), nitric oxide (NO), or H_2O_2+NO mitigated the salt-induced inhibitory effects on the plant growth under acclimated conditions. The adverse effects of salinity on shoot and root lengths were alleviated only by combined H_2O_2 and NO priming in acclimated canola plants. Under salt-stress conditions, the contents of photosynthetic pigments were reduced in non-acclimated plants, whereas the priming with H_2O_2+NO alleviated the inhibitory effect of salinity on the chlorophyll *a* and carotenoids contents. Measuring the chlorophyll *a* fluorescence parameters indicated that NaCl markedly decreased the maximum quantum yield (F_v/F_m), the quantum yield of electron transport (Φ_{Eo}), and the oxygen-evolving complex efficiency of photosystem II (PSII) (F_v/F_o) in non-acclimated canola leaves showing photo-inhibition of PSII, but the priming with H_2O_2+NO improved these parameters under salt stress. Our results suggested that priming of canola seeds with H_2O_2+NO significantly increased photosynthetic pigment accumulation, which was associated with the improvement of the photochemical efficiency, resulting in better plant growth under salt stress.

Keywords: canola, carotenoids, electron transport, nitric oxide, priming, salt acclimation

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Introduction

Salinity stress represses plant growth and metabolism, which is correlated with increased osmotic stress and ionic toxicity (Munns and Tester, 2008). The osmotic stress induced by salt stress mainly stimulates the oxidative damage in plants due to overproduction of reactive oxygen species (ROS) as well as reactive nitrogen species (RNS) (Christou et al., 2014; Babitha et al., 2015). ROS can cause significant damage to membrane lipids, proteins, DNA, and photosynthetic pigments, resulting in significant decreases in photosynthetic capacity (Munns and Tester, 2008). Photosynthesis is significantly reduced in response to changes in environmental factors (Kalaji et al., 2017). Chlorophyll *a* fluorescence analysis is a sensitive method for the evaluation of the changes in the photosynthetic apparatus (Kalaji et al., 2017; Zivcak et al., 2017) as well as for tracking the salt-induced damage to photosystem II (PSII) (Mehta et al., 2010).

Plants have developed a well-organized antioxidative defense system in order to regulate

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** Corresponding Author*
E-mail Address: gader.habibi@gmail.com
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both ROS and RNS production and accumulation (Corpas and Barroso, 2013). The capacity of plants to accumulate compatible solutes, such as soluble sugars and free amino acids, and the adjustment of photosynthetic processes are also asumed to be closely correlated with plant tolerance to salinity in plants (Janda et al., 2016). In addition, it was reported that acclimation with low level of salt improves the salt tolerance of salt acclimated plants against subsequent salt stress via decrease in chlorotic symptoms and reduction in the impairment of the photosynthetic processes (Janda et al., 2016).

Different methodologies have been used aiming at enhancing multiple stress tolerance. Seed priming by sodium nitroprusside (SNP, as an NO donor) and H_2O_2 has been proposed as an effective method in enhancing plant tolerance to various abiotic stresses through enhancing antioxidative defense system, osmolyte accumulation, ionic homeostasis and photosynthetic adjustment (Savvides et al., 2016; Ali et al., 2017; Habibi, 2019). A number of studies on plants have revealed that pre-exposure to H_2O_2 and/or NO can increase salt stress tolerance through the modulation of photosynthesis and ROS detoxification (Ashfaque et al., 2014; Kilic and Kahraman, 2016).

We hypothesize that exogenously applied NO and H_2O_2 may alleviate salt-induced adverse effects in canola. Moreover, there have not been any studies about the combined effect of H_2O_2+NO on the photochemical efficiency of PSII under saline and non-saline conditions, where interplay between H_2O_2 and NO may be involved in inducing tolerance to salinity. Thus, in the current study, we investigated the effects of excessive NaCl on growth and photosynthesis of economically important canola plant, as well as the effects of NO and H_2O_2 priming on photosynthesis in NaCl-treated canola plants, which may enhance their resistance against salt stress.

Materials and Methods

Plant material and treatments

Seeds of canola (*Brassica napus* L. cv. Gabriella) were sown on top of the cylindrical plastic pots. For priming treatments, canola seeds were soaked in aerated solutions of sodium nitroprusside (SNP, as a NO donor) and H_2O_2 for 12 h. The concentrations of NO and H_2O_2 were chosen in a preliminary study (data not showed). In the preliminary study, we detected that 1000 µM NO and 20 mM H_2O_2 priming significantly promoted seed germination of canola. Pots were 17 cm in diameter and 25 cm in depth, filled with sandy loam soil (pH 7.2, organic carbon (OC) 1.22 %). After emergence, the seedlings were thinned to one plant per pot and irrigated with distilled water every 5 days to maintain 90% field capacity (FC). Nine weeks after sowing, half of the pots were irrigated with 50 mM NaCl solution dissolved in tap water for 7 days (salt acclimation). These plants are referred as “acclimated” in this study. After the acclimation period, the plants were irrigated with 200 mM NaCl (salt stress). Acclimation treatments were termed as control (non-acclimated, non-stressed), ST (non-acclimated, stressed) and ACC+ST (acclimated, stressed). The EC of control pots were 1.28 dS m^{-1}. Plants were grown under day/night temperature of 25-30/19-21 ℃, 16/8 h day/night cycle, relative humidity of 60-65% and daily photon flux density of about 350-400 µmol m^{-2} s^{-1} throughout the experimental period.

Shoots and roots were separated and washed with distilled water, blotted dry on filter paper and after determination of fresh weight (FW) they were dried for 48 h at 70 ℃ for determination of dry weight (DW). The length-width proportion method was used to measure the leaf area of the canola according to Ma et al. (2015). For the latter analysis, leaf samples were frozen immediately in liquid N_2 and stored in it until the assay. Chlorophyll fluorescence induction measurements were also carried out using intact leaves four weeks after treatment with 200 mM NaCl.

Chlorophyll *a* fluorescence measurement

Chlorophyll *a* fluorescence transients (*OJIP* transients) were calculated with a Packet-PEA chlorophyll fluorimeter (Plant Efficiency Analyzer, Hansatech Instruments Ltd., King’s Lynn, Norfolk, PE 32 1JL, England) in dark-adapted leaves for at least 20 min. We used the *JIP*-test to analyze chlorophyll a fluorescence rises. The parameters assayed using the *JIP*-test (Strasser et al., 2004) included the followings:

1. F_v/F_m, is the maximum PSII photochemical efficiency, namely the maximum quantum yield of primary photochemistry, where F_m or F_{max} is the maximal chlorophyll fluorescence intensity measured when all PSII reaction centers are closed, F_v is variable chlorophyll fluorescence (F_m-F_o), and F_o is minimal fluorescence (all PSII RCs are assumed to be open).

2. F_v/F_o is the efficiency of the water-splitting complex on the donor side of PSII, where F_v is variable chlorophyll fluorescence (F_m-F_o) and F_o is minimal fluorescence (all PSII RCs are assumed to be open).

3. PI_{abs} denotes the performance index calculated as:

   $(RC/ABS) \times (\varphi_{Po}/(1-\varphi_{Po})) \times (\psi_o/(1-\psi_o))$

   where RC is for reaction center, ABS represents absorption flux, φ_{Po} is maximal quantum yield for primary photochemistry, and ψ_o denotes the quantum yield for electron transport.

4. Φ_{Eo} is the quantum yield of electron transport.

Determination of total carotenoids and chlorophyll *a* and *b*

To determine chlorophyll and carotenoid concentrations of leaves, samples were homogenized in methanol according to Lichtenthaler and Wellburn (1983). After centrifugation at 1000 rpm for one minute, supernatants were used for determination of photosynthetic pigments, and the absorbance was read at 400-700 nm on a spectrophotometer. Chlorophylls and carotenoid contents of leaves were determined as:

Chl a = 15.65 A666 - 7.340 A653

Chl b = 27.05 A653 - 11.21 A666

Total carotenoids = 1000 A470 - 2.860 Ca - 129.2 Cb/245

Statistical Analysis

Experiments followed a complete randomized block design (RBD) with 10 independent replications. Chlorophyll fluorescence data were analyzed using PEA Plus V1.10 software. All data were subjected to one-way ANOVA and significant differences between means were determined by Tukey test ($P \leq 0.05$) using Sigma Stat (3.5).

Results

Under non-saline conditions, H_2O_2+NO-primed plants exhibited higher dry weight than the non-primed plants (Fig. I). Total dry weight was

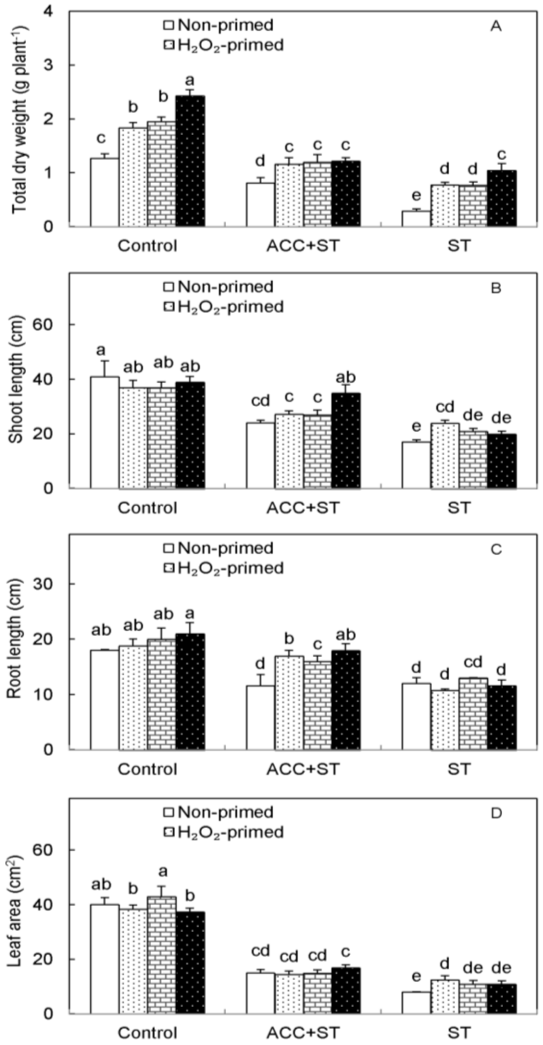

Fig. I. Effects of salt stress (200 mM NaCl) on total dry weight, shoot length, root length, and leaf area of canola plants acclimated with 50 mM salt and primed with 20 mM H_2O_2 and 1000 µM NO; Error bars indicate the standard deviation. Acclimation treatments included control (non-acclimated, non-stressed), ST (non-acclimated, stressed), and ACC+ST (acclimated, stressed).

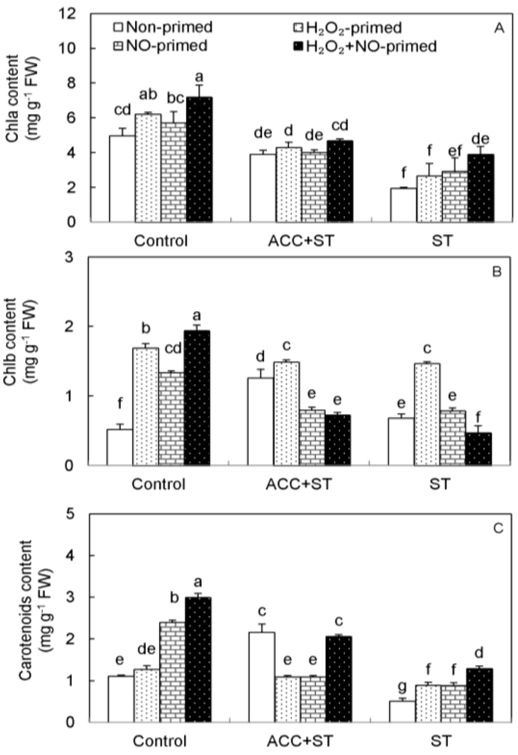

Fig. II. Effects of salt stress (200 mM NaCl) on the chlorophyll *a*, *b* and total carotenoid contents of canola plants acclimated with 50 mM salt and primed with 20 mM H_2O_2 and 1000 µM NO; error bars indicate the standard deviation. Acclimation treatments included control (non-acclimated, non-stressed), ST (non-acclimated, stressed), and ACC+ST (acclimated, stressed).

significantly decreased by salinity under both acclimated and non-acclimated conditions. Priming seeds with H_2O_2, NO, or H_2O_2+NO mitigated the adverse effects of salinity under acclimated conditions. However, total dry weight was improved only by H_2O_2+NO priming in non-acclimated canola plants under salt stress conditions. In this study, shoot and root lengths were inhibited by salt stress in acclimated and non-acclimated canola plants (Fig. I). The adverse effects of salinity on shoot and root lengths were alleviated only by H_2O_2+NO priming in acclimated canola plants. The leaf area parameter showed a significant decrease in response to salinity under both acclimated and non-acclimated conditions while it was not affected by exposure to H_2O_2 and NO alone, or by the combination of H_2O_2 and NO.

Chlorophyll *a* and *b*, and carotenoid contents were significantly increased by H_2O_2, NO, and H_2O_2+NO priming under non-saline conditions (Fig. II). Results also indicated that the plants under ACC + ST had relatively higher photosynthetic pigment concentrations (chlorophyll *b* and carotenoids) than the control plants. By contrast, the concentration of photosynthetic pigments (Chlorophyll *a* and *b* and carotenoids) was depressed by single ST treatment, whereas priming with H_2O_2+NO alleviated the inhibitory effects of salinity on the chlorophyll a and carotenoid contents. No significant differences in the maximum quantum yield (F_v/F_m), quantum yield of electron transport (Φ_{Eo}), and the efficiency of the water-splitting complex on the donor side of PSII (as inferred from F_v/F_o) were detected in plants grown with or without H_2O_2 and NO under non-salt stress conditions (Fig. III). However, NaCl

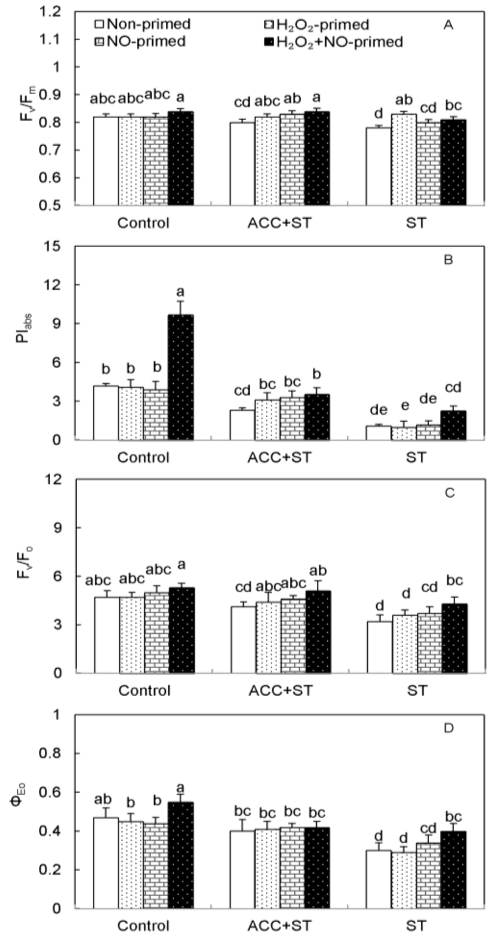

Fig. III. Effects of salt stress (200 mM NaCl) on the maximum quantum yield (F_v/F_m), performance index (PI_{abs}), oxygen-evolving complex efficiency of PSII (F_v/F_o), and the quantum yield of electron transport (Φ_{Eo}) of canola leaves acclimated with 50 mM salt and primed with 20 mM H_2O_2 and 1000 µM NO; error bars indicate the standard deviation. Acclimation treatments included control (non-acclimated, non-stressed), ST (non-acclimated, stressed), and ACC+ST (acclimated, stressed).

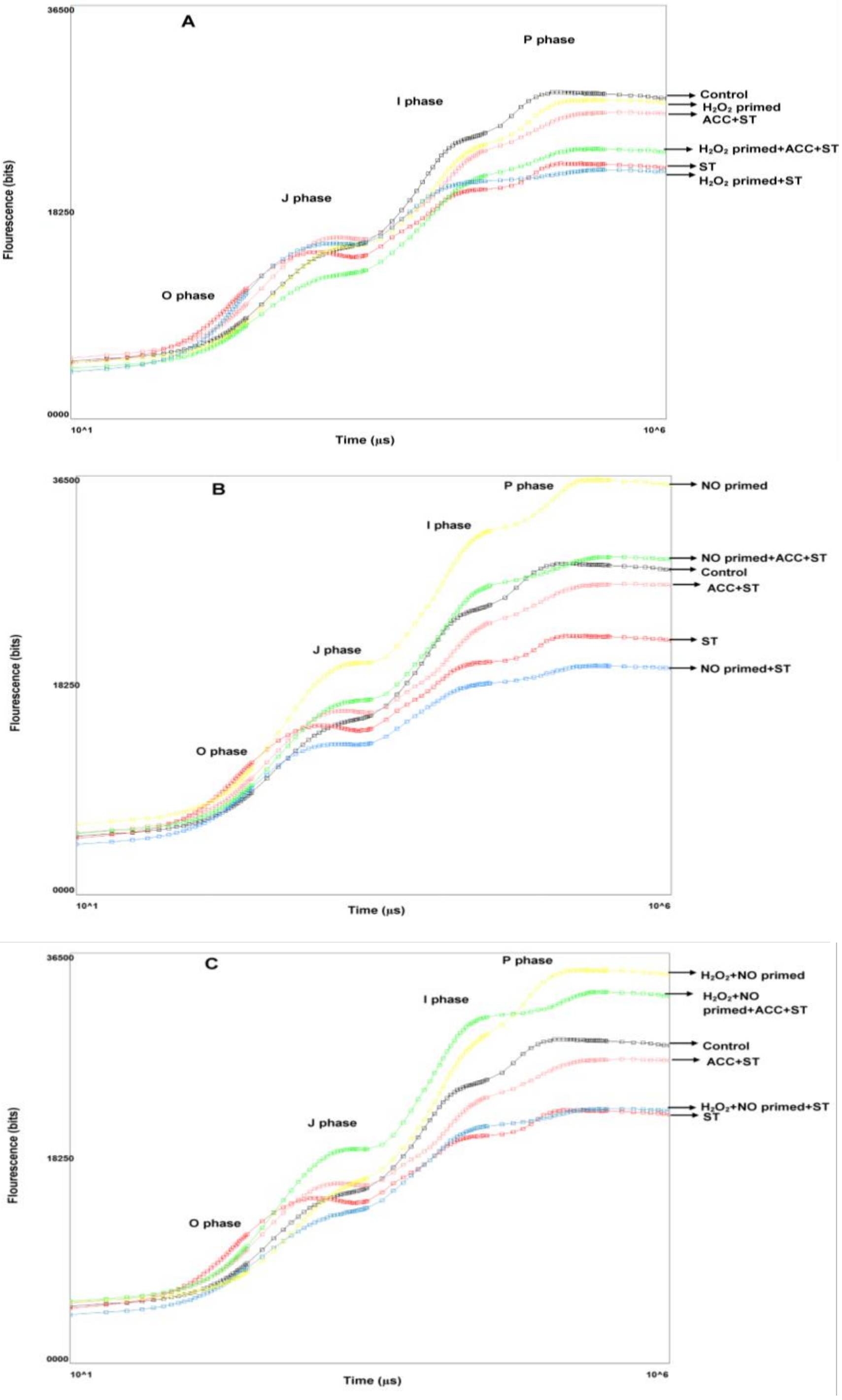

Fig. IV. Effects of salt stress (200 mM NaCl) on the chlorophyll *a* fluorescence induction curve of canola leaves acclimated with 50 mM salt and primed with 20 mM H_2O_2 (a), 1000 µM NO (b), or H_2O_2+NO (c); acclimation treatments included control (non-acclimated, non-stressed), ST (non-acclimated, stressed), and ACC+ST (acclimated, stressed).

markedly decreased F_v/F_m, Φ_{Eo} and F_v/F_o in canola leaves under non-acclimated conditions while priming with H_2O_2+NO improved these parameters under salt stress. Results showed that in H_2O_2+NO-primed plants, PI_{abs} was higher than other treatments under non-saline conditions. Besides, PI_{abs} was greatly depressed by salt stress in acclimated and non-acclimated plants, but remained unaffected by H_2O_2+NO priming. Measuring the typical OJIP chlorophyll a fluorescence transients using the JIP-test revealed a noticeable change in the shape of the transients under salt-stress conditions (Fig. IV). Analysis of fluorescence transient showed a larger decrease in the O–J part of the fluorescence rise in non-acclimated salt-stressed plants, which reflects the closure of some of the PSII reaction centers. Additionally, under non-saline conditions, NO pretreatment affected the shape of the O–J–I–P curve, increasing both O-J (F_o) and I-P (F_m) phases.

Discussion

Combined hydrogen peroxide and nitric oxide priming improved growth of canola under salt stress

Canola is a moderately salt-sensitive crop, and its growth is reduced at high salinity (Kholghi et al., 2018). In this study, total dry weight was significantly reduced by salinity under both acclimated and non-acclimated conditions. Similar results were obtained by Kholghi et al. (2018), who reported that the growth of canola decreased under salinity.

Like negative effects of salinity on total dry weight, significant decreases in shoot and root lengths were observed in this study, which was consistent with the findings of Benincasa et al (2013) and Rasheed et al. (2014), who showed that a high NaCl concentration significantly reduced the shoot and root lengths of canola cultivars. In the present study, the growth inhibition of salt-stressed canola plants was mitigated by the H_2O_2 and NO priming. Our results are consistent with the findings of Ali et al. (2017) for wheat cultivars and Kilic and Kahraman (2016) for barley seedlings, who reported that the growth inhibition of salt-stressed plants was mitigated by seed priming with NO.

Combined hydrogen peroxide and nitric oxide priming enhanced carotenoids and alleviated the adverse effects of salt stress on the PSII functioning

Our results showed that chlorophyll and carotenoid contents improved in salt-acclimated plants under salt stress, which can lead to an increase in the photosynthetic capacity of canola plants under salt stress (Acosta-Motos et al., 2017). Janda et al. (2016) found similar results in wheat and observed a significant rise in the carotenoid content in salt-acclimated plants. Furthermore, this study revealed that salt stress caused further decreases in chlorophyll content of salt-exposed non-acclimated plants, whereas priming with H_2O_2+NO alleviated these inhibitory effects. Recent studies have revealed that pretreatment of Seeds with H_2O_2 and NO improves leaf chlorophyll contents under abiotic stress (Yildiz et al., 2013; Wang et al., 2016; Khan et al., 2017). In agreement with our results, Gondim et al. (2013) reported that under salinity condition exogenously applied H_2O_2 significantly improved leaf chlorophyll contents of *Zea mays* plants.

In addition, priming of canola seeds with H_2O_2+NO significantly increased the leaf content of carotenoids under the salt stress. Owing to the protective effects of carotenoids in the dissipation of absorbed light energy as thermal energy as well as its function as a non-enzymatic antioxidant during exposure to stress (Miura and Tada, 2014; Habibi and Ajory, 2015; Habibi, 2017), this higher accumulation of carotenoids may be an important protection mechanism for photosynthetic primary reactions of canola leaves under salt stress. To further study the effects of H_2O_2 and NO priming on photosystem II (PSII) electron transport chain components of canola leaves under salt stress, we assayed the typical OJIP chlorophyll *a* fluorescence transients. While the F_v/F_m remained unchanged under salt-acclimated conditions, in parallel to the decrease in photosynthetic pigment contents, salt stress (200 mM NaCl) caused a significant decrease in the F_v/F_m and PI_{abs}, showing photo-inhibition of PSII in non-acclimated plants. However, when H_2O_2+NO-pretreated plants were subjected to 200 mM NaCl, the degree of reduction in F_v/F_m and Φ_{Eo} was smaller than the non-primed plants, suggesting that priming with H_2O_2+NO enhances the salt tolerance of canola by improving PSII photochemical efficiency. In addition, salt stress under non-acclimated conditions affected the shape of the O–J–I–P curve, and caused a significant increase in F_o which may be related to the dissociation of LHCII and PSII (Mathur et al. 2011; Kalaji et al. 2016). Confirming this, there was a significant decrease in F_v/F_o in salt-stressed plants under non-acclimated conditions, which reflects the damage caused by 200 mM NaCl at the donor side of PSII (Mehta et al., 2010 Kalaji et al., 2016). However, in H_2O_2+NO-treated plants, the degree of reduction in F_v/F_o

was lower than the non-primed plants under ST conditions, suggesting that PSII reaction centers behave almost normally (Zhang et al., 2014). Interestingly, NO pretreatment caused distinct O-J-I-P changes under non-saline conditions; however, further analyses are required to understand the effects of NO priming on the photochemical processes as well as fast chlorophyll *a* fluorescence kinetics.

Conclusion

Canola growth significantly decreased under salinity in both acclimated and non-acclimated conditions. Maximum amelioration of salt stress was found by only H_2O_2+NO priming, which is attributed to the improved photochemical processes as well as fast chlorophyll *a* fluorescence kinetics. This improved PSII activity coupled with the higher carotenoid accumulation, resulting in higher photosynthesis in canola seedlings under salinity.

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