Adv. Hort. Sci., 2019 33(3): 409-416 DOI: 10.13128/ahs-24335

AHS
Advances in Horticultural Science

# Alleviation of salinity stress by hydrogen peroxide and nitric oxide in tomato plants

**B. Hajivar, M.R. Zare-Bavani (*)**
*Department of Horticultural Science, College of Agriculture, Agricultural Sciences and Natural Resources University of Khuzestan, Mollasani, Khuzestan, Iran.*

*Key words*: membrane stability, photosynthetic attributes, relative water content, salt tolerance.

**Abstract: Salinity is one of the major abiotic stress factors limiting plant growth and productivity, particularly in arid and semi-arid climates. Hydrogen Peroxide ($H_2O_2$) and Nitric Oxide (NO) are important signaling molecules in plant response to abiotic stress. In this research the effects of foliar sprays with $H_2O_2$ (10 mM) and NO (0.1 mM sodium nitroprusside, as a NO donor) on alleviation of Salinity stress (0, 25, 50 and 100 mM NaCl) were investigated in Tomato (*Solanum lycopersicum* L. cv. Falat). Photosynthetic attributes, plant-water relations, membrane stability index and growth parameters were decreased by NaCl treatments. Exogenous $H_2O_2$ and NO application enhanced salt stress tolerance in tomato plants by improving the photosynthetic efficiency and plant water status as measured by relative water content and membrane stability index. These results were positively reflected by the increase in plant growth under salinity stress conditions. The results of this study described that under the adverse conditions of salinity stress, $H_2O_2$ and NO could activate the photosynthetic system and improve the physiological attributes in plant growth.**



(*) **Corresponding author:**
mzarebavany@gmail.com

**Citation:**
HAJIVAR B., ZARE-BAVANI M.R., 2019 - *Alleviation of salinity stress by hydrogen peroxide and nitric oxide in tomato plants*. - Adv. Hort. Sci., 33(3): 409-416



**Data Availability Statement:**
All relevant data are within the paper and its Supporting Information files.

**Competing Interests:**
The authors declare no competing interests.

Received for publication 18 December 2018
Accepted for publication 15 May 2019

## 1. Introduction

Salinity in soil or water is a major problem affecting growth and productivity of many crops, especially under arid and semi-arid conditions. It was estimated that about 20% of the world's cultivated land area and 50% of all irrigated land are salt-affected (Hayat *et al.,* 2013). But, the area of soils with restrictions for vegetable crop production is certainly greater than the area of salinized soils, since a saline soil is generally defined as showing an electrical conductivity (EC) value of the saturation extract (ECe) in the root zone that exceeding 4 dS $m^{-1}$, while the majority of vegetable crops have a salinity threshold that is 2.5 dS $m^{-1}$ (Machado and Serralheiro, 2017).

Salinity negatively affects plants growth and development through: low osmotic potential of soil solution (water stress), nutritional imbalance, specific ion effect (salt stress) or a combination of these factors (Ashraf, 2004). All of these factors cause morphological, physiological and metabolic modifications in plants, such as a decrease in seed germination, shoot and root length, leaf area, cell membranes stability, inhibition of

different enzymatic activities and photosynthesis attributes (Sairam and Tyagi, 2004; Parida and Das, 2005).

Photosynthesis is one of the physiological processes that is affected by salinity stress (Munns *et al.,* 2006; Chaves *et al.*, 2009). Salinity stress may reduce the photosynthesis rate by decreasing in stomatal factors such as stomatal conductance (Bethke and Drew, 1992; Parida *et al.,* 2004), internal $CO_2$ partial pressure (Bethke and Drew, 1992; Iyenger and Reddy, 1996) and non-stomatal factors such as inhibition and degradation of photosynthetic pigments (Lee *et al.,* 2004; Chaves *et al.,* 2009), photosynthetic electron transport reactions, quenching ability of excessive energy through chlorophyll fluorescence (Lee *et al.,* 2004), efficiency of Rubisco for carbon fixation (Liu *et al.,* 2011), and photophosphorylation (Stoeva and Kaymakanova, 2008). Adverse effects of salinity on plant growth may also result from impairment of photosynthetic apparatus (Ashraf, 2004).

Hydrogen peroxide and Nitric oxide are bioactive molecule involved in the signaling process within plants (Leshem, 2000; Uchida *et al.,* 2002; Azevedo-Neto *et al.,* 2005; Hung *et al.,* 2005; Li *et al.,* 2011). Researches have shown that hydrogen peroxide and nitroxide at low concentrations, play an important role as signaling molecules (Gechev and Hille, 2005; Quan *et al.,* 2008). Studies have shown that hydrogen peroxide and Nitric oxide are involved in acclamatory signaling triggering tolerance against salt stress (Hayat *et al.*, 2013; Semida, 2016). Azevedo-Neto *et al.* (2005) reported that the pretreatment with $H_2O_2$ in nutrient solution induces acclimation to salinity stress in maize. Semida (2016) observed that exogenous $H_2O_2$ application enhanced salt stress tolerance in onion plants by improving the photosynthetic efficiency and plant water status as evaluated by relative water content and membrane stability index. The use of NO increased the resistance of *Pinus eldarica* to salinity and improved its growth characteristics (Zamani *et al.,* 2014). Uchida *et al.* (2002) reported that $H_2O_2$ and NO are the important signaling molecules in rice for resistance to salinity stress.

Tomato is one of the most important vegetable crop in the world. In Iran, the tomato also holds the number one position among vegetables, with almost 6.4 million metric tons of production (FAO, 2014). The cultivated tomato has been classified as moderately sensitive to salinity. Salinity affects tomato plant growth at various stages including seed germination, root and shoot development and fruit production (Cuartero and Fernandez-Munoz, 1999).

This research was undertaken to assess changes in plant growth, water relations, cell membrane stability and photosynthesis parameters in salt-treated tomato plants and to examine neutralizing effects of NO and $H_2O_2$ to exposure to salt.

## 2. Materials and Methods

*Plant material*

Tomato seeds, cv. Falat were surface-sterilized in 2.5% sodium hypochlorite for 10 min, followed by four washes with distilled water. Seeds were sown in the plastic tray filled with a silica sand in the greenhouse under controlled conditions (photoperiod of 16/8 h day/night, 60-65% humidity and 25-30°C temperature). Seeds were irrigated with tap water daily. Seedlings with 2 true leaves were transplanted to 25×25 cm pots (one plant per pot) maintained under similar conditions as the tray containing developing seedlings and fertilized alternate days with half-strength Hoagland solution (Hoagland and Arnon, 1950) until solution drainage occurred at the bottom of the pot at each fertigation.

*Treatment and experimental design*

Seven days after transplanting, uniform seedlings of tomato cultivars were sprayed to run off with distilled water, 10 mM $H_2O_2$ or 0.1 mM SNP in 0.025% Tween 20 (as a surfactant) at 6:30 am and then the sprays were repeated at 7 and 14 days later. The concentrations of $H_2O_2$ and SNP and the number and timing of sprays were based on results from a preliminary experiment (data not shown). After the last spraying, irrigation was done with half strength Hoagland solution supplemented with 0, 25, 50 and 75 mM of NaCl solution. The experimental procedures were completely randomized in 3 × 5 factorial design, with three foliar spray (sodium nitroprusside [SNP], $H_2O_2$ and distilled water) and four salt concentrations (0, 25, 50, and 100 mM NaCl in nutrient solution), performed in triplicate. The number of plants were six in each replicate. Plants were sampled at 90 day after seeding. Three samples were analyzed for each replication (9 samples in each treatment). The fully-expanded leaves were used for the determination of all experimental parameters.

*Determination of plant growth traits*

Ninety-day-old tomato plants were carefully removed from each pot and the leaves, stems and roots of plants were weighed to record their fresh

weights and then placed in an oven at 70°C till the constant weight to record their dry weights.

*Determination of relative water content (RWC)*

RWC was estimated using 2-cm-diameter fully-expanded leaf discs, excluding midrib according to the method of Hayat *et al*. (2013). The discs were weighted for fresh mass (FM) and immediately floated on double-distilled water in Petri dishes for 24 h, in the dark, to saturate them with water. Water adhering to discs was blotted and the turgid mass (TM) was measured. The dry mass (DM) of discs was recorded after dehydrating them at 70°C until the constant weight. The RWC was then calculated using the formula:

$$RWC = [(FM - DM)/(TM - DM)] \times 100.$$

*Determination of proline content*

Free proline content was determined according to the method of Bates *et al.* (1973). Samples (0.5 g) were homogenized in 5 ml 3% sulfosalicylic acid and extracts were centrifuged at 8000 x *g* for 15 min. The amount of 1 ml filtrate was mixed with equal volumes of acetic acid and ninhydrin reagent (1.25 g ninhydrin, 30 ml of glacial acetic acid, 20 ml 6 M $H_3PO_4$) and incubated for 1 h at 100°C. The reaction was stopped by placing the test tubes in ice cold water. The samples were vigorously mixed with 3 ml toluene. After 50 min, the light absorption of the toluene phase was estimated at 520 nm on a UV-VIS spectrophotometer. The proline concentration was determined using a standard curve. Free L- proline content was expressed as µg/g dry weight.

*Determination of total soluble sugar content*

Total soluble sugar content was determined by phenol-sulfuric acid according to the method of Dubois *et al.* (1956). Dry leaves sample (0.1 g) were extracted with 5 ml of 80% ethanol, by boiling the samples in glass tubes in a 95°C-water bath for 10 min. After extraction, the tubes were centrifuged at 500 x *g* for 5 min, and the supernatants of the extractions were used for sugar analysis. One hundred ml of sample was added to 900 ml of distilled water then the mixture was vortexed. One ml of 5% phenol and 5 ml of $H_2SO_4$ were added to 1 ml of sample and the mixture was stirred. After cooling under room temperature for 15 min, the absorbance of the sample was recorded at 490 nm.

*Determination of membrane stability index (MSI)*

The MSI was determined according to methods of Sairam and Srivastava (2002). Leaf disc (0.2 g) were thoroughly washed in double distilled water and thereafter placed in a test tube containing 10 ml of double distilled water in two sets. One set was heated at 40°C in a water bath for 30 min and the electrical conductivity (EC1) of the solution was recorded using an electrical conductivity meter. Another set was boiled at 100°C for 10 min and their electrical conductivity was recorded as above (EC2). The MSI was calculated as:

$$MSI = [1-(EC1/EC2)] \times 100$$

*Determination of leaf photosynthetic pigments*

Chlorophyll a, b and total chlorophyll were extracted and determined (in mg/ g FW) following the procedure is given by Lichtenthaler and Buschmann (2001). Fresh leaf samples (0.2 g) were homogenized in 50 ml acetone (80%) and then centrifuged at 10,000 × *g* for 10 min. The absorbance of the acetone extract was measured at 663, 645 and 470 nm using a UV-visible spectrometer (Shimadzu, Kyoto, Japan).

*Determination of leaf photosynthetic attributes*

Photosynthetic attributes (stomatal conductance [gs], internal $CO_2$ concentration [Ci], transpiration rate [E], and net photosynthetic rate [Pn]) in intact leaves were measured by a infrared gas analyzer (CI-340, Photosynthesis system, CID Bio-Science, USA) between 10:00 and 12:00 h under a clear sky. Photosynthetic Pigments and Attributes were measured on three samples of leaves in each pot and three pot in each replication.

*Statistical analysis*

The experimental design was a completely randomized factorial, four salinity levels (0, 25, 50 and 100 mM NaCl) and two levels of $H_2O_2$ and SNP (10 and 0.1 mM respectively). All measurements were carried out in three replicates and data were subjected to one-way analysis of variance using SAS program (SAS 9.1; SAS Institute Inc., Cary, NC). Significant differences between means were determined by Tukey's tests. P values less than 0.05 were considered statistically significant.

## 3. Results

*Growth parameters*

Salinity markedly decreased fresh weight and dry weight of root, leaf and shoot (Fig. 1, A-H). However, the $H_2O_2$ and SNP spraying were able to reduce the

adverse effects of salt stress. Moreover, the fresh weight and dry weight of root, leaf and shoot from $H_2O_2$ and SNP-sprayed plants were higher than the ones stressed plants (Fig. 1).

*Relative water content (RWC)*

When salinity was absent, RWC was not significantly altered by $H_2O_2$ and SNP pretreated plants (Fig. 2, I). Under salinity condition, plants sprayed with SNP or $H_2O_2$ displayed higher RWC when compared to water sprayed ones. Plant pretreated with $H_2O_2$ was not significantly affected by salinity of 25 mM NaCl. Salinity did not promote any significant alteration in SNP pretreated plants in 25 and 50 mM NaCl stress. Under 100 mM NaCl stress conditions, the RWC was reduced in all evaluations (Fig. 2, I).

*Proline content*

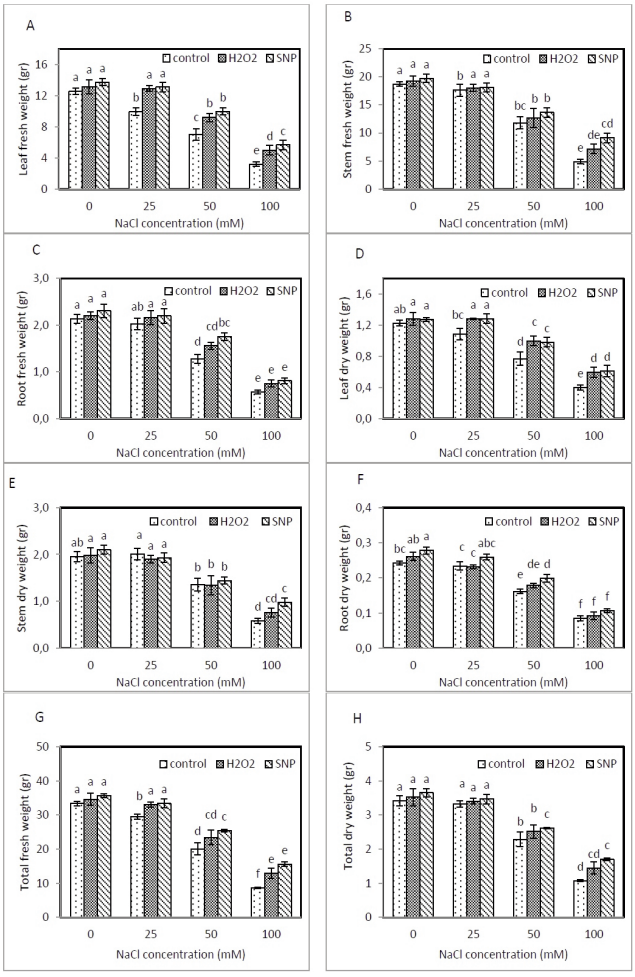


Fig. 1 - Effect of salt treatment and application of exogenous $H_2O_2$ and SNP on growth parameter of tomato plants. Leaf fresh weight (A), stem fresh weight (B), root fresh weight (C), leaf dry weight (D), stem dry weight (E), root dry-weight (F), total fresh weight (G), and total dry weight (H). Data shown are the mean (±SE) of three independent experiments. Significant differences among treatments were determined by Tukey's Test (P<0.05).

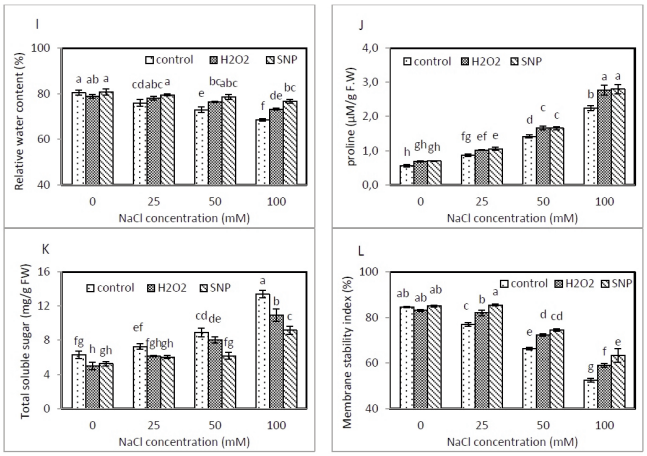


Fig. 2 - Effect of salt treatment and application of exogenous $H_2O_2$ and SNP on relative water content (I), proline (J), total soluble sugar (K) and membrane stability index (L). Three plants were analyzed for each treatment. Data shown are the mean (±SE) of three independent experiments. Significant differences among treatments were determined by Tukey's Test (P<0.05).

The proline-specific increase in plants exposed to NaCl (Fig. 2, J). Pretreatment to either $H_2O_2$ or SNP resulted in an increase in proline levels of plants under salinity stress. Interestingly, among unstressed plants, treatment of $H_2O_2$ and SNP also increased the proline levels (Fig. 2, J).

*Total soluble sugar content (TSSC)*

Salinity stress significantly increased the TSSC (Fig. 2, K). Pretreatment of $H_2O_2$ or SNP significantly decreased the TSSC compared to water sprayed plants. The highest amount of TSSC was observed with 100 mM NaCl without $H_2O_2$ or SNP, while the lowest amount of TSSC was observed with SNP and $H_2O_2$ application without salinity (Fig. 2, K).

*Membrane stability index (MSI)*

Under non saline conditions, the MSI were not affected by $H_2O_2$ and SNP spraying (Fig. 2, L). Although salinity had decreased the leaf MSI, it did not promote any significant alteration in $H_2O_2$ and SNP sprayed plants in 25 mM NaCl stress compared to non saline conditions. The MSI was significantly decreased by 50 and 100 mM NaCl stress, however, plants treated with $H_2O_2$ and SNP were less affected by salinity stress compared to water sprayed plants. The SNP-sprayed plants showed values of MSI higher than the stressed plants sprayed with water and $H_2O_2$ (Fig. 2, L).

*Leaf photosynthetic pigments*

There were significant decreases in the chlorophyll a, b and total chlorophyll contents in salt-stressed plants. Plants treated with $H_2O_2$ and SNP

spray had higher values compare to the water-sprayed plants (Fig. 3, M-O). The chlorophyll content (a, and total chlorophyll) in the water-sprayed plants and plants receiving $H_2O_2$ and SNP were similar in 0 and 25 mM NaCl treatment (Fig. 3, M and O).

*Leaf photosynthetic attributes*

The $H_2O_2$ and SNP-sprayed plants showed higher Net photosynthesis (Pn), Stomatal conductance (gs) and intercellular $CO_2$ concentration (Ci) than the water-sprayed plants under non saline conditions (Fig. 1A-1C). Although the Pn, E, gs and Ci were strongly decreased by salinity stress, plants sprayed with $H_2O_2$ and SNP were less affected than the water-sprayed ones. The Pn in the plants receiving $H_2O_2$ and SNP were higher at 25 mM NaCl treatment compared with the water-sprayed ones. Plants receiving 100 mM NaCl had lower Pn, gs, Ci and E than other treatment.

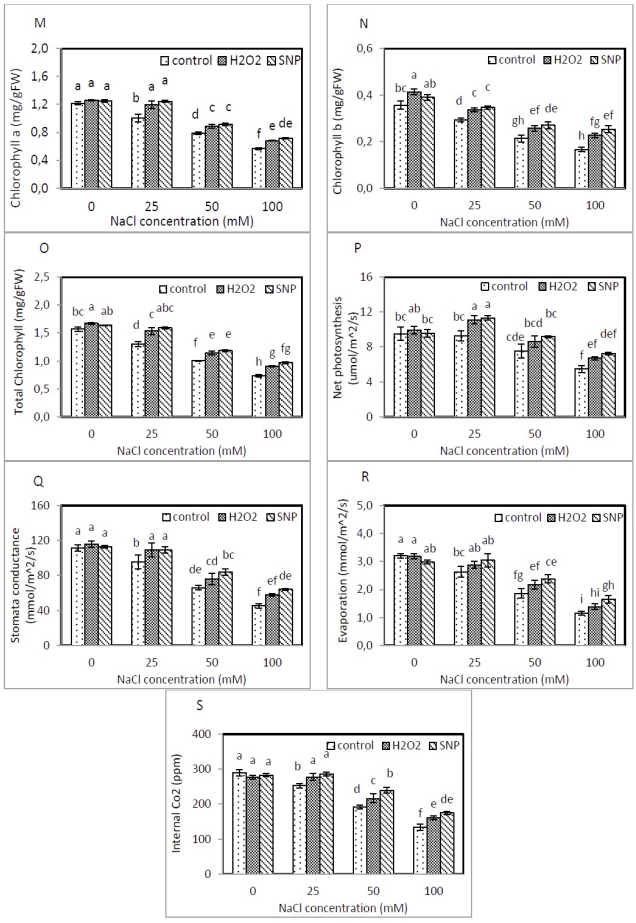


Fig. 3 - Effect of salt treatment and application of exogenous $H_2O_2$ and SNP on photosynthesis pigment and attributes of tomato plants. Chlorophyll a (M), chlorophyll b (N), total chlorophyll (O), Photosynthetic rate (P), stomatal conductance (Q), transpiration (R) and intercellular $CO_2$ concentration (S). Data shown are the mean (±SE) of three independent experiments. Significant differences among treatments were determined by Tukey's Test ($P<0.05$).

## 4. Discussion and Conclusions

Salt stress is a major abiotic stress that imposes osmotic and toxicity stress to plants and consequently induces a reduction in plant photosynthesis and growth (Acosta-Motos *et al.,* 2017). In this study, our results confirmed that salinity at the tested concentrations inhibited the growth of tomato plants (Fig. 1, A-H). $H_2O_2$ and NO are bioactive molecules that are known as important signals not only in plant disease resistance, but also in the process of growth, development, and responses against abiotic stress (Mazid *et al.,* 2011; Niu and Liao, 2016). Salinity stress is known detrimental effect on the overall growth and productivity of plants (Ashraf, 2004) and may inhibit plant growth due to reduction of water uptake by plants (Kaya *et al.*, 2003). Several studies have shown the beneficial effects of $H_2O_2$ and SNP pretreatment on salt tolerance in plants (Uchida *et al*., 2002; Azevedo-Neto *et al.*, 2005; Wahid *et al.*, 2007). Potikha *et al.* (1999) suggested that $H_2O_2$ increases cell division and is involved in the differentiation of the cell wall. Our results are in agreement with those previously reported for maze (Azevedo-Neto *et al.*, 2005; Gondim *et al.,* 2013), rice (Sathiyaraj *et al.,* 2014), cotton, cowpea and sorghum (Freitas *et al.*, 2011). Terasaki *et al.* (2001) noted that SNP possibly enhances exo- and endo-β-D-glucanase activities in cell walls, where the glycosidic linkage between glucose units within cell walls is broken by these enzymes (Zhang *et al.,* 2003), and growth enhance by increasing internal turgor pressure and water content. Similarly to our results, growth stimulation by exogenous NO was demonstrated in tomato (Wu *et al.,* 2010; Hayat *et al.,* 2013).

In this study $H_2O_2$ or NO resulted in higher increase of relative water content, proline and membrane stability index in leaf of tomato plant and decrease of total soluble sugar content (Fig. 2, I-L) which could promote plant growth under salt stress (Duan *et al.,* 2007) and non saline conditions (Zhang *et al.,* 2005), indicating that $H_2O_2$ and NO are involved in the intrinsic mechanism of growth under different conditions. The higher relative water content in $H_2O_2$ and SNP-sprayed stressed plants (Fig. 2, I) appears to be the result of $H_2O_2$ and NO-induced increased levels of compatible solutes under salt-induced osmotic stress (Tan *et al.,* 2008; Hayat *et al.,* 2013), which resulted in better growth of stressed plants. Proline accumulation is an essential indicator for plant response to salinity stress (Sathiyaraj *et al.,* 2014). The $H_2O_2$ and SNP-pretreated plants showed a signifi-

cantly higher amount of proline than the salt-stressed ones (Fig. 2, J). stress-induced proline accumulation in plants help in osmotic adjustment (Sathiyaraj *et al.,* 2014). In addition to the role as a compatible osmolyte, proline can also increase membrane stability, confer enzyme protection and help in non-enzymatic free radical detoxifications (Khan *et al.,* 2002; Sathiyaraj *et al.,* 2014). Thus, the increase of proline may trigger tolerance to salt stress in tomato plants.

The salt stressed plant showed an increase in Total soluble sugar content, but $H_2O_2$ and SNP sprayed plants showed a significantly decreased of TSSC compared with the water-sprayed plants (Fig. 2, K). The reduction in TSSC by $H_2O_2$ and NO application in this experiment (Fig. 2, K) may be attributed to the crucial role of $H_2O_2$ and NO in mitigating the negative effect of salinity stress (Semida, 2016). Similarly, TSSC reduction by exogenous $H_2O_2$ was demonstrated in onion (Semida, 2016).

$H_2O_2$ and SNP sprayed plants showed a significantly increased of Membrane Stability Index compared with the water-sprayed ones (Fig. 2, L). The salt stressed plant showed an decreas in MSI, and the decrease in MSI reflects the extent of lipid peroxidation caused by active oxygen species. The rate of lipid peroxidation has been widely used as an indicator of oxidative damage (Sathiyaraj *et al.,* 2014). Result showed exogenous $H_2O_2$ and SNP treatment are able to prevent lipid peroxidation and thus protect the cells from the damage of salinity stress.

$H_2O_2$ and NO are known to enhance chlorophyll content in plant (Gondim *et al.,* 2013; Hayat *et al.,* 2013). In this experiment, the chlorophyll content was negatively affected by salinity (Fig. 3, M- O). Singh and Dubey (1995) showed that the loss of chlorophyll content could be related to photoinhibition or oxidative damages that acts as a cellular marker of salinity stress. Therefore, the pretreatment with $H_2O_2$ and SNP was effective to reduce the detrimental effects of salinity in chlorophyll content (Fig. 1A).

Salinity stress is also known to reduce photosynthesis, due to an increase in reactive oxygen species formation, water status alteration, and a decrease in chlorophyll content and $CO_2$ diffusion through stomatal guard cells (Chaves and Oliveira, 2004; Munns and Tester, 2008). Silva *et al.* (2011) reported that reduction in photosynthesis by stomatal closure occurs during early exposure to salinity stress, while biochemical limitations concern due to long-term NaCl exposure. Thus, the reduction of photosynthesis in plants was caused by reduction in stomatal conductance, decreasing the intercellular $CO_2$ concentration for Rubisco activity (Shahbaz *et al.*, 2010). Some studies reported the maintenance of gas exchange correlate with salt tolerance in plants (James *et al.*, 2006; Munns and Tester, 2008). In this experiment, results showed all gas exchange parameters were less affected by salinity in plants previously treated with $H_2O_2$ and SNP (Fig. 3, P-S). Therefore, our data indicate that $H_2O_2$ and NO-pretreatment increased stomatal conductance, which enabled high net photosynthetic rate and
improved growth parameters. In addition, the higher leaf MSI induced by the $H_2O_2$ and SNP pretreatment in NaCl stressed plants is an evidence that plants were able to control oxidative damages caused by ROS in the photosynthetic apparatus and maintain leaf gas exchange (Fig. 2, L). Similarly, it is observed that that the $H_2O_2$ and SNP-pretreatment caused increases in net photosynthetic rate, transpiration rate, stomatal conductance and intercellular $CO_2$ concentration in plants subjected to salinity when compared to non-treated seedlings (Wahid *et al.*, 2007; Gondim *et al.,* 2013; Hayat *et al.,* 2013).

As a whole, exogenous $H_2O_2$ and NO are able to improve plant growth of tomato and 0.1 mM SNP produces the most effective improvement. Exogenous $H_2O_2$ and NO greatly alleviated the oxidative stress induced by salt stress in tomato plant. Therefore, exogenous $H_2O_2$ and NO treatment on tomato seedling may be an option to improve photosynthesis and growth under saline conditions. Foliar application of $H_2O_2$ and SNP provides an easy, low cost, and effective strategy to overcome environmental stress problems. Exogenous $H_2O_2$ and SNP application is a convenient and effective approach to increase salt tolerance of crops and eventually improving crop growth and, productivity under salinity condition.

**References**

ACOSTA-MOTOS J.R., ORTUNO M.F., BERNAL-VICENTE A., DIAZ-VIVANCOS P., SANCHEZ-BLANCO M.J., HERNANDEZ J.A., 2017 - *Plant responses to salt stress: adaptive mechanisms*. - Agronomy, 7(18): 1-38.

ASHRAF M., 2004 - *Some important physiological selection criteria for salt tolerance in plants*. - Flora, 199(5): 361-376.

AZEVEDO-NETO A.D., PRISCO J.T., ENEAS-FILHO J., ROLIM MEDEIROS J.V., GOMES-FILHO E., 2005 - *Hydrogen peroxide pre-treatment induces salt-stress acclimation in maize plants*. - J. Plant Physiol., 162(10): 1114-1122.

BATES L.S., WALDREN R.P., TEAR I.D., 1973 - *Rapid determination of free proline for water-stress studies*. - Plant Soil., 39(1): 205-207.

BETHKE P.C., DREW M.C., 1992 - *Stomatal and nonstomatal components to inhibition of photosynthesis in leaves of* Capsicum annum *during progressive exposure to NaCl salinity*. - Plant Physiol., 99(1): 219-226.

CHAVES M.M., FLEXAS J., PINHEIRO C., 2009 - *Photosynthesis under drought and salt stress: Regulation mechanism of whole plant to cell*. - Ann. Bot., 103(4): 551-568.

CHAVES M.M., OLIVEIRA M.M., 2004 - *Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture*. - J. Exp. Bot., 55(407): 2365-2384.

CUARTERO J., FERNANDEZ-MUNOZ R., 1999 - *Tomato and salinity*. - Sci. Hortic., 78(1-4): 83-125

DUAN P., DING F., WANG F., WANG B.S., 2007 - *Priming of seeds with nitric oxide donor sodium nitroprusside (SNP) alleviates the inhibition on wheat seed germination by salt stress*. - J. Plant Physiol. Mol. Biol., 33(3): 244-250.

DUBOIS M., GILLES K.A., HAMILTON J.K., REBERS P.A., SMITH F., 1956 - *Colorimetric method for determination of sugars and related substances*. - Anal. Chem., 28: 350-356

FAO, 2014 - *FAO statistics*. - Food and Agriculture Organization of United Nations, Rome, Italy.

FREITAS V.S., ALENCAR N.L.M., LACERDA C.F., PRISCO J.T., GOMES-FILHO E., 2011 - *Changes in physiological and biochemical indicators associated with salt tolerance in cotton, sorghum and cowpea*. - Afr. J. Biochem. Res., 5(8): 264-271.

GECHEV T.S., HILLE J., 2005 - *Hydrogen peroxide as a signal controlling plant programmed cell death*. - J. Cell Biol., 168(1): 17-20.

GONDIM F.A., MIRANDA R.S., GOMES-FILHO E., PRISCO J.T., 2013 - *Enhanced salt tolerance in maize plants induced by $H_2O_2$ leaf spraying is associated with improved gas exchange rather than with nonenzymatic antioxidant system*. - Theor. Exp. Plant Physiol., 25(4): 251-260.

HAYAT S., YADAV S., ALYEMENI M.N., IRFAN M., WANI A.S., AHMAD A., 2013. - *Alleviation of salinity stress with sodium nitroprusside in tomato.* - Int. J. Veg. Sci., 19(2): 164-176.

HOAGLAND D.R., ARNON D.J., 1950 - *The water culture method for growing plants without the soil*. - California Agricultural Experiment Station, Circular no. 347.

HUNG S.H., YU C.W., LIN C.H., 2005. - *Hydrogen peroxide function as a stress signal in plants*. - Bot. Bull. Acad. Sinica, 46: 1-10.

IYENGER E.R.R., REDDY M.P., 1996 - *Photosynthesis in highly salt-tolerant plants*, pp. 897-909 - In: PESSARAKI M., (ed.). *Handbook of photosynthesis.* Marcel Dekker Inc., New York, USA, pp. 989.

JAMES R.A., MUNNS R., VON CAEMMERER S., TREJO C., MILLER C., CONDON T.A.G., 2006 - *Photosynthetic capacity is related to the cellular and subcellular partitioning of Na+, K+ and Cl- in salt-affected barley and durum wheat*. - Plant Cell Environ., 29(12): 2185-2197.

KAYA D.M., IPEK A., ÖZTÜRK A., 2003 - *Effects of different soil salinity levels on germination and seedling growth of safflower (*Carthamus tinctorius *L.).* - Turk. J. Agr., 27(4): 221-227.

KHAN M.H., SINGHA L.B., PANDA S.K., 2002 - *Changes in antioxidant levels in* Oriza sativa *L. roots subjected to NaCl-salinity stress*. - Acta Physiol. Plant., 24: 145-148.

LEE G.J., CARROW R.N., DUNCAN R.R., 2004 - *Photosynthetic responses of salinity stress of halophytic seashore paspalum ecotypes*. - Plant Sci., 166(6): 1417-1425.

LESHEM Y.Y., 2000 - *Nitric oxide in plants: Occurrence, function and use*. - Springer, Kluwer, Dordrecht, The Netherlands, pp. 154.

LI J.T., QUI Z.B., ZHANG X.W., WANG L.S., 2011 - E*xogenous hydrogen peroxide can enhance tolerance of wheat seedlings to salt stress.* - Acta Physiol. Plant., 33(3): 835-842.

LICHTENTHALER H.K., BUSCHMANN C., 2001 - *Chlorophylls and carotenoids: Measurement and characterization by UV-VIS Spectroscopy,* pp. F4.2-F4.2.6. - In: WROLSTAD R.E., T.E. ACREE, H. AN, E.A. DECKER, M.H. PENNER, D.S. REID, S.J. SCHWARTZ, C.F. SHOEMAKER, and P. SPORNS (eds.) *Current protocols in food analytical chemistry (CPFA)*. John Wiley and Sons, New York, USA, pp. 1000.

LIU Y., DU H., WANG K., HUANG B., WANG Z., 2011 - *Differential photosynthetic responses to salinity stress between two perennial grass species contrasting in salinity tolerance*. - Hort Sci., 46(2): 311-316.

MACHADO A.R.M., SERRALHEIRO R.P., 2017 - *Soil salinity: effect on vegetable crop growth. Management practices to prevent and mitigate soil salinization*. - Hortic., 3 (2): 30

MAZID M., KHAN T.A., MOHAMMAD F., 2011 - *Potential of Nitric oxide and Hydrogen peroxide as signalling molecules in tolerance to abiotic stress in plants*. - J. Industrial Res. Technol., 1(1): 56-68.

MUNNS R., JAMES R.A., LAUCHLI A., 2006 - *Approaches to increasing the salt tolerance of wheat and other cereals*. - J. Expt. Bot., 57(5): 1025-1043.

MUNNS R., TESTER M., 2008 - *Mechanisms of salinity tolerance*. - Annu. Rev. Plant Biol., 59: 651-681

NIU L., LIAO W., 2016 - *Hydrogen peroxide signaling in plant development and abiotic responses: crosstalk with nitric oxide and calcium*. - Front. Plant Sci., 7(230): 1-14.

PARIDA A.K., DAS A.B., 2005 - S*alt tolerance and salinity effects on plants: A review*. - Ecotoxicol. Environ. Safety, 60(3): 324-349.

PARIDA A.K., DAS A.B., MITTRA B., 2004 - *Effects of salt on growth, ion accumulation, photosynthesis and leaf anatomy of the mangrove,* Bruguiera parviflora. -

Trees, 18(2): 167-174.
POTIKHA T.S., COLLINS C.C., JOHNSON D.I., DELMER D.P., LEVINE A., 1999 - *The involvement of hydrogen peroxide in the differentiation of secondary walls in cotton fibers.* - Plant Physiol., 119(3): 849-858.
QUAN L.J., ZHANG B., SHI W.W., LI H.Y., 2008 - *Hydrogen peroxide in plants: a versatile molecule of the reactive oxygen species network.* - J. Integr. Plant Biol., 50(1): 2-18.
SAIRAM R.K., SRIVASTAVA G.C., 2002 - *Changes in antioxidant activity in sub-cellular fractions of tolerant and susceptible wheat genotypes in response to long term salt stress*. - Plant Sci., 162(6): 897-904.
SAIRAM R.K., TYAGI A., 2004 - *Physiology and molecular biology of salinity stress tolerance in plants.* - Curr. Sci., 86(3): 407-421.
SATHIYARAJ G., SRINIVASAN S., KIM Y.J., LEE O.R., PARVIN S., BALUSAMY R.D., KHOROLRAGCHAA A., YANG D.C., 2014 - *Acclimation of hydrogen peroxide enhances salt tolerance by activating defense-related proteins in* Panax ginseng *C.A. Meyer* - Mol. Biol. Rep., 41(6): 3761-3771.
SEMIDA W.M., 2016 - *Hydrogen peroxide alleviates salt-stress in two onion (*Allium cepa *L.) cultivars*. - Am.-Eurasian J. Agric. Environ. Sci., 16(2): 294-301.
SHAHBAZ M., ASHRAF M., AKRAM N.A., HANIF A., HAMEED S., JOHAM S., REHMAN R., 2010 - *Salt-induced modulation in growth, photosynthetic capacity, proline content and ion accumulation in sunflower (*Helianthus annuus *L.).* - Acta Physiol. Plant., 33(4): 1113-1122.
SILVA E.N., RIBEIRO R.V., FERREIRA-SILVA S.L., VIÉGAS R.A., SILVEIRA J.A.G., 2011 - *Salt stress induced damages on the photosynthesis of physic nut young plants*. - Sci. Agric., 68(1): 62-68.
SINGH A.K., DUBEY R.S., 1995 - *Changes in chlorophyll a and b contents and activities of photosystems I and II in rice seedlings induced by NaCl*. - Photosynthetica, 31(4): 489-499.
STOEVA N., KAYMAKANOVA M., 2008 - *Effect of salt stress on the growth and photosynthesis rate of bean plants*. - Agriculture, 9(3): 385-392.
TAN J.F., ZHAO H.J., HONG J.P., HAN Y.L., LI H., ZHAO W.C., 2008 - *Effects of exogenous nitric oxide on photosynthesis, antioxidant capacity and proline accumulation in wheat seedlings subjected to osmotic stress*. - World J. Agr. Sci., 4(3): 307-313.
TERASAKI S., SAKURAI N., WADA N., YAMANISHI T., YAMAMOTO R., NEVINS D.J., 2001 - *Changes in cell wall polysaccharides of kiwifruit and the viscoelastic properties detected by laser Doppler method.* - J. Jpn. Soc. Hort. Sci., 70(5): 572-580.
UCHIDA A., JAGENDORF A.T., HIBINO T., TAKABE T., TAKABE T., 2002 - *Effect of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice.* - Plant Sci., 163(3): 515-523.
WAHID A., PERVEEN M., GELANI S., BASRA S.M.A., 2007 - *Pretreatment of seed with $H_2O_2$ improves salt tolerance of wheat seedlings by alleviation of oxidative damage and expression of stress proteins.* - J. Plant Physiol., 164(3): 283-294.
WU X.X., DING H.D., CHEN J.L., ZHANG H.J., ZHU W.M., 2010 - A*ttenuation of salt-induced changes in photosynthesis by exogenous nitric oxide in tomato (*Lycopersicon esculentum *Mill.) seedlings*. - African J. Biotechnol., 9(46): 7837-7846.
ZAMANI M., HAKIMI M.H., MOSLEH A., KIANI B., RASHTIAN A., 2014 - *The effects of salicylic acid (SA) and sodium nitroprusside (SNP) on physical and growth characteristics of* Pinus eldarica. - Bull. Env. Pharmacol. Life Sci., 3(3): 31-35.
ZHANG H., SHEN W.B., ZHANG W., XU L.L., 2005 - *A rapid response of b-amylase to nitric oxide but not gibberellins in wheat seeds during the early stage of germination*. - Planta, 220(5): 708-716.
ZHANG M., AN L., FENG H., CHEN T., CHEN K., LIU Y., TANG H., CHANG J., WANG X., 2003 - *The cascade mechanisms of nitric oxide as a second messenger of ultraviolet-B in inhibiting mesocotyl elongations.* - Photochem. Photobiol., 77(2): 219-225.