Ecotoxicology and Environmental Safety 147 (2018) 1010–1016

Contents lists available at ScienceDirect

Ecotoxicology and Environmental Safety

journal homepage: www.elsevier.com/locate/ecoenv

How can salicylic acid and jasmonic acid mitigate salt toxicity in soybean plants?

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ARTICLE INFO

Keywords:
Jasmonic acid
Oxidative stress
Salicylic acid
Salt toxicity
Soybean

ABSTRACT

This research was undertaken to assess the impact of 1 mM salicylic acid (SA) and 0.5 mM jasmonic acid (JA) on alleviation of oxidative, ionic and osmotic stresses of different levels of salinity (0, 4, 7, 10 dS m^{-1} NaCl, respectively). Salinity increased the contents of glycine betaine, proline, soluble sugars, proteins and the activities of peroxidase, catalase, superoxide dismutase, ascorbate peroxidase, and the amount of malondialdehyde and sodium ion of soybean leaves, but decreased the leaf water content, membrane stability index, potassium and calcium ions, chlorophylls content, chlorophyll stability index, plant biomass and seed yield. Foliar spray of JA reduced Na^+ entry to the cells, while enhancing the glycine betaine and soluble proteins content, antioxidant enzymes activity, membrane stability index and leaf water content. This treatment had no effect on potassium and the calcium ions content, chlorophyll contents, chlorophyll stability index, soluble sugars, plant biomass and seed yield. In contrast, SA enriched the leaf cells with potassium and calcium ions under different levels of salt stress and increased glycine betaine, soluble sugars, proteins, antioxidant enzymes, leaf water content, membrane stability index, chlorophyll content and chlorophyll stability index, but reduced proline content. These superiorities of SA treatment led to considerable improvement in plant biomass (10%) and seed yield (17%) of soybean.

1. Introduction

The High level of salt stress (specially induced by NaCl) is the most important environmental factor, limiting plant production on at least 20% of irrigated farms worldwide (Mahajan and Tuteja, 2005; Sytar et al., 2017). Salt toxicity inhibits the plant growth and development and can also lead to physiological water limitation and ion imbalance (Zhu, 2002; Puyang et al., 2015; Xu et al., 2016; Lin et al., 2017). So, the basic physiology and biochemistry of severe salinity and water limitation overlaps with each other as a severe salt deposition in rhizosphere causing a low osmotic potential. Plants can maintain an osmotic equilibrium by the synthesis of compatible solutes such as prolines, glycine betaine, proteins and soluble carbohydrates (Munns and Tester, 2008; Farhangi-Abriz and Torabian, 2017).

The next adverse effect of salt toxicity in plant cells is the ion-specific stress resulting in a changed K^+/Na^+ ratio. The sodium ions (Na^+) can adversely influence the intracellular content of potassium ions (K^+) (Ghassemi-Golezani and Nikpour-Rashidabad, 2017). The role of active transmission of cations through tonoplasts is an essential reason affecting the homeostasis of sodium and chloride in plants (Conde et al., 2011). This ability has been indicated by the high activities of H^+–ATPase and H^+–PPiase in the vesicles of root tonoplasts of salt-tolerant soybean cultivars for pumping protons into the vacuoles (Luo et al., 2005). The harmful effect of Na^+ toxicity is expressed on whole crop, and appears in all growing phases, including germination, seedling emergence and vegetative stages. Salinity increases ion toxicity and decreases photosynthesis (Kaya et al., 2013; Lin et al., 2017). The reduction in photosynthesis under Na^+ toxicity could be attributed to a reduction in chlorophyll content (Jamil et al., 2007). High level of Na^+ can affect chlorophyll production by preventing chlorophyll synthesis or by accelerating its degradation (Reddy and Vora, 1986). High level of Na^+ content causes an augmentation in reactive oxygen species (ROS) levels, leading to a variation in the cellular redox metabolism. Extreme exposure of crops to Na^+ toxicity can lead to the production of ROS such as $O_2^{\bullet -}$ (superoxide radical), H_2O_2 (hydrogen peroxide), $^{\bullet}OH$ (hydroxyl radical) and $^1O_2$ (singlet oxygen). Extra ROS generation is a basis of toxic responses like lipid peroxidation, DNA mutation and protein degradation (Ahmad et al., 2008). In plant cells, these ROS are generated due to oxidative damage to cells during salt stress in the chloroplasts, cytosol, mitochondria, and the apoplectic space (Mittler, 2002; Shalata et al., 2001).

Plants have an efficient system for scavenging ROS that defend them

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http://dx.doi.org/10.1016/j.ecoenv.2017.09.070
Received 14 June 2017; Received in revised form 25 September 2017; Accepted 28 September 2017

from damaging oxidative reactions (Foyer et al., 1994). As part of this system, the most essential key elements in the protection mechanisms are anti-oxidative enzymes. Salt stress induction of ROS accumulation is defused by antioxidant enzyme systems such as catalase (CAT), peroxidase (POX), superoxide dismutase (SOD), ascorbate peroxidise (APX) and polyphenol oxidase (PPO) (Mittler et al., 2004). High production of antioxidant enzymes in plant cells have been reported to lead to superior resistance to oxidative stress (Spychalla and Desborough, 1990). Foliar application of growth regulators such as salicylic acid (SA) and jasmonic acid (JA) is a useful strategy to mitigate the harmful effects of salt toxicity in plants (Qiu et al., 2014. Pirasteh-Anosheh et al., 2017).

SA is one of the most important phenolic compounds that can act as a growth regulator and has been reported to prompt important effects on different biological features in crops (Shakirova et al., 2003; Horvath et al., 2007; Hayat et al., 2010; Singh et al., 2017). SA stimulates a range of various processes in plants, such as seed germination (Cutt and Klessig, 1992), cation uptake and transport (Harper and Balke, 1981), photosynthetic activities and growth rate (Khan et al., 2003). Several new roles have been reported for SA. These include, mediation of the response to different environmental stresses such as salinity and drought (Ghassemi-Golezani and Hosseinzadeh-Mahootchi, 2015; Farhangi-Abriz and Ghassemi-Golezani, 2016). Foliar spray of SA enhances photosynthetic activity and plant growth under salinity (Khan et al., 2014). Exogenous SA improves the resistance of wheat plants to salt stress via increasing proline and abscisic acid (ABA) contents (Shakirova et al., 2003).

JA was identified by Demole et al. (1962) in the essential oil of jasmin plants. JA has a key role in physiological and biochemical responses of plants to environmental conditions. Many reports suggest that exogenous JA could alleviate salt toxicity via stimulating antioxidant activities. Foliar spray of JA on different plants reduces the harmful effects of salt toxicity and improves plant performance and yield through induction of ROS scavenging enzymes and ion absorption (Kang et al., 2005; Walia et al., 2007; Qiu et al., 2014). Anjum et al. (2011) stated that exogenous JA has a key role in improving water potential in plant cells with enhancing the synthesis of some osmoregulators in soybean.

Since soybean is an important farm crop, it would be valuable to evaluate the responses of this crop to various environmental conditions such as salt stress. Exogenous applications of SA and JA may be useful for decreasing the harmful effects of salt stress on soybean performance, but some of the mechanisms of action of these hormones are still poorly understood. Therefore, this research was laid out to investigate the impact of foliar sprays of salicylic acid and jasmonic acid on alleviation of oxidative, ionic and osmotic stresses of salt toxicity in soybean plants.

2. Materials and methods

2.1. Experimental conditions

A pot experiment was undertaken as factorial on the basis of randomized complete block design with four replicates in a glass greenhouse at the University of Tabriz, to investigate the effects of 1 mM SA and 0.5 mM JA on mitigation of salt toxicity (0, 4, 7 and 10 dS m^{-1} of NaCl salinity) in soybean plants. Specific amounts of NaCl were solved in water with a pH of 7.2 and electrical conductivity of 0.8 dS m^{-1} to achieve these levels of salinities. Each pot was filled with 1 kg perlite and then soybean seeds (30 seeds of cultivar M7) were sown in 3 cm depth of each pot. All 48 pots were placed in a glass greenhouse with natural light and photoperiod, day-night mean temperatures of 28–26 °C and relative humidity of 35–40%. Plants were thinned and reduced to 10 plants per pot after establishment. During plant growth and development (109 days), Hoagland solution (electrical conductivity = 1.3 dS m^{-1}, pH 6.7–7.2), was added to the pots according to the field capacity (FC). For avoiding the further increase in electrical conductivity, due to adding the Hoagland solution, perlites within pots were washed every 30 days, and non-saline and salinity treatments were reapplied. The hormones were sprayed on plants up to runoff from leaves, at vegetative (V3, third trifoliate; 28 days after sowing) and full flowering (R2; 51 days after sowing) stages (Purcell et al. 2014) in accordance with the treatments. A week after the last treatment, a plant from each pot was harvested and laboratory tests were performed.

2.2. Seed yield and plant biomass

At maturity (R8; 109 days after sowing), two plants from each pot were harvested and the seeds were separated from the pods and weighed (with about 15% moisture content). Plant biomass was determined after drying the plants at 80 °C for 48 h.

2.3. Cation analysis

About 100 mg of dried leaves of soybean were used to measure the sodium (Na^+), potassium (K^+) and calcium (Ca^{2+}) ions. The leaves were dried at 550 °C for 7 h in an electric furnace and then the powdered materials digested in 5 M HNO_3 at 25 °C for 24 h. Thereafter, the samples were transferred to a hot plate (120 °C) and kept there for 1 h. The digested samples were filled with 50 ml double-distilled water and was tested for cation contents (mg g^{-1} dry weight) by an atomic absorption spectrophotometry (Shimadzu model: AA-7000, Kyoto, Japan).

2.4. Chlorophyll content

The contents of Chl a, b and total chlorophyll in leaves were measured by the method of Arnon (1949). The fresh leaf samples (0.2 g each) were cut and placed in tubes containing 10 ml of 80% acetone at −4 °C for 24 h. The extracted samples were centrifuged at 10,000 g for 5 min. Absorbance of the upper layer (supernatant) was recorded at 645 and 663 nm, using a spectrophotometer (Model Analytikjena Spekol 1500 Germany). The chlorophyll stability index (ChSI) was also estimated by applying the method of Koleyoreas (1958).

2.5. Measurement of osmolytes

The method of Bates et al. (1973) was used to measure proline content of soybean leaves. Initially 500 mg of leaf sample was homogenized in 5 ml of 3% sulphosalycylic acid and after that, 2 ml of the extracted sample was poured into a plastic tube and then 2 ml of glacial acetic acid and 2 ml of ninhydrin were added to this mixture. The prepared samples were heated at 100 °C for 1 h in a Bain marie (BM-15 Bain Marie, Magapor SL, Spain). Then the samples were cooled in room temperature and the mixture was extracted with toluene, and the absorbance of upper phase was recorded at 520 nm. Proline content of leaves was determined with the calibration curve of pure proline and expressed as mg g^{-1} fresh weight (FW).

For measuring the glycine betaine content in leaves, 500 mg of leaf samples were ground and mixed with 5 ml of toluene-water mixture (0.05% toluene) in a 20 ml plastic tube. All of the tubes were shaken for 24 h at room temperature (25 °C). A 1 ml of 2 N HCl and 0.1 ml of potassium tri-iodide solution was added to 0.5 ml of prepared sample and shaken in an ice cold water bath for 90 min. Upper aqueous layer was discarded and optical density of organic layer was read at 365 nm. Glycine betaine content was stated as mg g^{-1} dry weight (DW) (Grieve and Grattan, 1983). The soluble sugar content of leaves was measured by the method of phenol sulphuric acid (Kochert, 1978). The soluble sugar content of soybean leaves was expressed as mg g^{-1} DW, by a calibration curve of pure glucose.