



Role of Triacantanol in Counteracting the Ill Effects of Salinity in Plants: A Review

Shaistul Islam¹ · Abbu Zaid¹ · Firoz Mohammad¹

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Abstract

Soil salinity is one among the common environmental threats to agriculture. It adversely affects the physio-biochemical processes of plants that eventually lead to the reduction in growth, development and crop productivity. To cope with such adverse conditions, plants develop certain internal mechanisms, but under severe conditions these mechanisms fail to tolerate the salt stress. To overcome this problem, various strategies have been employed that help plants to mitigate salinity effects. Among the various strategies, the application of plant growth regulators (PGRs) has gained significant attention to induce salt tolerance in plants. A number of PGRs have been used so far. Among these, triacantanol (TRIA), a new PGR is gaining a lot of importance to enhance the plant growth, productivity and salinity tolerance in different crops. The utility of TRIA is dependent on its applied concentration. Its lower concentrations generally alleviate the salinity effects. However, the knowledge of its biosynthesis, signalling and its role particularly to mitigate salinity effect remains scanty. In the present article, the focus has been given on the role of exogenous applications of TRIA in the regulation of physio-biochemical characteristics especially plant growth, photosynthesis, nutrient acquisition, oxidative stress, antioxidant systems, compatible solutes, yield attributes and its mode of action in plants under salinity conditions. The salient features of the review may provide new insights on the role of TRIA in countering the ill effect of salinity in different crop plants.

Keywords Soil salinity · Plant growth regulators · Triacantanol · Plant growth · Physio-biochemical processes · Salt tolerance

Introduction

Plants being sessile are encountered with a variety of environmental stresses, generally classified into abiotic (cold, drought, flooding, heavy metal, salinity, etc.) and biotic (insects, pathogens, etc.). Of the various environmental stresses, soil salinity is the most common abiotic stress and is responsible for a major problem for agriculture, adversely affecting crop growth, development and their productivity (Nadeem et al. 2016; Rahman et al. 2017). Worldwide, approximately 930 million hectares of arable land, representing more than 6% of total land area, are salt-affected and this percentage is increasing daily mainly by natural and anthropogenic activities (Hasanuzzaman et al. 2018).

Salinity leads to osmotic stress, ion toxicity, turgescence, metabolic imbalance, membrane disorganisation and reactive oxygen species (ROS) generation that affect the integrity of biological membranes, cause oxidative damage to cells and their metabolic processes and finally reduce crop yield (Babu et al. 2012; Chen et al. 2017; Kumar et al. 2017; Klein et al. 2018). In response to abiotic stress, plants have developed a unique and complex mechanism involving morpho-physiological, cellular and anatomical changes to mitigate the salt stress (Saud et al. 2014; Khan et al. 2019). One of the strategies for stress tolerance may be the use of phytohormones due to their prominent roles in plants.

Phytohormones are well known to regulate growth and development in plants. Phytohormones also play a vital role in the alleviation of abiotic stresses in plants by facilitating their growth, development, nutrient allocations and source/sink transitions (Hu et al. 2013; Fahad et al. 2015; Ahmad et al. 2019). The role of abscisic acid (ABA), gibberellins (GAs), brassinosteroids (BRs), ethylene (ET), jasmonic acid (JA), nitric oxide (NO) and salicylic acid (SA) in salinity

✉ Firoz Mohammad
Firoz_59@rediffmail.com

¹ Plant Physiology and Biochemistry Section, Department of Botany, Aligarh Muslim University, Aligarh 202002, India

tolerance are well defined (Iqbal et al. 2011; Khan et al. 2012; Gurmani et al. 2013; Colebrook et al. 2014; Ahmad et al. 2016; Noreen et al. 2017; Wani et al. 2017; Ahmadi et al. 2018); however, their mode of action varies under salt tolerance (Iqbal et al. 2014). Due to the pronounced roles in plants, there is a need for seeking the new plant growth regulators (PGRs) and their roles in modulating the different processes in plants (Keramat et al. 2017; Maresca et al. 2017). Triacontanol is a relatively new PGR, which regulates various physio-biochemical processes leading to mitigation of the ill effect of salinity in plants.

Triacontanol (TRIA) is a naturally occurring plant growth regulator (Ries et al. 1977; Taştan et al. 2016) and is found in epicuticular waxes of plants (Kolattukudy and Walton 1973; Digruber et al. 2018). Its exogenous application increases plants biomass, nutrient and water uptake, photochemical pigments, photosynthetic rate, transpiration rate, internal carbon dioxide concentration, water use efficiency, carbonic anhydrase, nitrate reductase activity, sugars, soluble proteins, free amino acids, nitrogen-fixation, crop yield, essential oil and active constituents (Aftab et al. 2010; Naeem et al. 2014, 2017; Li et al. 2016; Sharma et al. 2018). TRIA is known to be effective in regulating physio-biochemical processes of plants under varying environments (Borowski and Blamowski 2009; Naeem et al. 2012; Perveen et al. 2014). Under abiotic stresses, including salinity stress, exogenously applied triacontanol alleviates the toxic effects in plants by increasing growth, dry mass, photosynthetic pigments, rate of photosynthesis, compatible osmolytes and antioxidant enzyme activities (Shahbaz et al. 2013; Zulfiqar and Shahbaz 2013; Perveen et al. 2014, 2017). Due to diverse physiological and biochemical roles of TRIA in plants under salt stress conditions, it is highly desirable to review its role and mode of action in them.

Mode of Action of Triacontanol in Plants

Researchers have elucidated the mechanism of action of TRIA for its beneficial effect on various metabolic processes, including photosynthesis, nutrient (micro and macronutrient) uptake and enzyme activities in plants. Overwhelming assumptions led to the identification of a secondary messenger of TRIA (abbreviated as TRIM) in the form of 9- β -L(+)-adenosine, i.e. 9H-purine-6-amine, 9- β -L-ribofuranosyl (Ries and Wert 1988; Ries et al. 1990, 1993; Ries 1991). L(+)-adenosine acts as a secondary messenger to be elicited by TRIA (Naeem et al. 2012). TRIM was found to affect the metabolic processes similar to TRIA at a nanomolar concentration in rice (Ries 1991). The ratio of L(+) adenosine to its isomer D(-)adenosine was found to be rapidly increased by TRIA, probably in the tonoplast (Ries, 1991). Adenosine monophosphate (AMP) derived

from adenosine diphosphate/adenosine triphosphate acts as a portable source for L(+)-adenosine in plants (Olsson and Pearson 1990). Studies with adenosine deaminase indicated that L(+)-adenosine in untreated plants might exist in inactive racemic mixture with D(-)-adenosine and the remaining adenosine (~ 99%) exists as the D(-)-isomer. After treatment with TRIA, non-racemic L(+)-adenosine (~ 11%) seemed to be released to affect the plant processes (Ries 1991). Ries et al. (1990) extracted TRIM from TRIA-treated plants, which was similar to that extracted from control plants. L(+)-adenosine structurally similar to cytokinins obtained from triacontanol-treated plants at 10 μ g/L was found to stimulate the rice plant growth only, while other forms including D(-)-adenosine did not stimulate the growth at such concentration (Ries et al. 1990). Application of L(+)-adenosine elicits many physiological responses like malate dehydrogenase activity and plant growth (Ries and Wert 1992; Savithiry et al. 1992). Further, Ries et al. (1993) reported that L(+)-adenosine increased the content of Ca^{2+} , Mg^{2+} and K^{+} in tomato, cucumber and maize plants. TRIA quickly moves to the plasma membrane of epidermal cells through leaf cuticle and elicits the formation of L(+)-adenosine, which is a form of TRIM (Ries 1991). L(+)-adenosine induced the influx of Ca^{2+} , Mg^{2+} and K^{+} ions in the cytosol by opening ion channels in the plasma membrane (Lesnaik et al. 1986; Perveen et al. 2014). The elevated Ca^{2+} level may result in its binding to sensor proteins, i.e. calcium calmodulin in a similar way, as suggested by Reddy et al. (2011). Mg^{2+} and K^{+} ions may regulate various metabolic processes by way of becoming an activator of enzymes. Activated calmodulin protein may directly modulate transcription factors (CAMTA₃, GTL, MYB₂, etc.) and actuate activities of phosphatases and kinases leading to gene expression (Viridi et al. 2015) that leads to enhanced growth and development of TRIA-treated plants (Fig. 1). Several studies demonstrated that exogenous application of TRIA plays a pivotal role in alleviating salinity damage and improves salinity tolerance in plants as depicted in Fig. 2. TRIA elicits TRIM which down-regulates the stress-related genes while up-regulates the photosynthesis regulating genes such as (rbcS, pbsO, GDC and SHMT), enhances water uptake and mineral nutrient acquisition, stimulates synthesis of organic compounds, as well as enhances antioxidant enzyme activities for proper metabolic processes. These ameliorating effects of TRIA on various processes may lead to alleviate the harmful effects of salinity in plants (Chen et al. 2002, 2003; Perveen et al. 2014, 2017; Aziz and Shahbaz 2015). However, the detailed mechanism of TRIM to alleviate salt stress is not yet to be addressed.

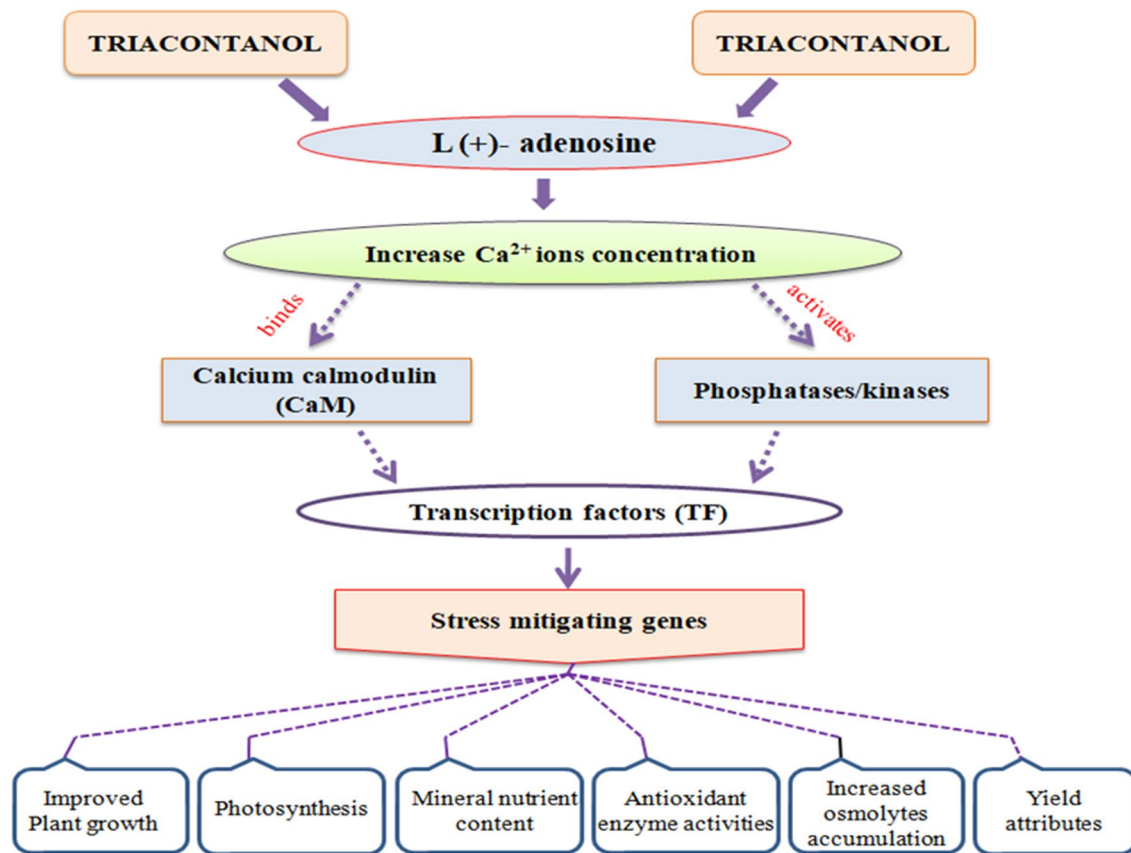


Fig. 1 Proposed model of TRIA action in plants under salt stress conditions

Triacontanol and Salt Stress

The survey of the literature reveals that the application of triacontanol results in significant effects on physiological and biochemical characters of plants under salt stress conditions (Table 1). The findings of various workers regarding the roles of TRIA in mitigating the ill effect of salt stress on the performance of various plants are summarised below.

Plant Growth

Salinity stress induces metabolic perturbation by generating ROS, leading to oxidative stress in plants that reduces the enzyme activities, causes lipid peroxidation, DNA damage, and finally hampering the crop growth (Hayat et al. 2010; Khan et al. 2010; Parihar et al. 2015; Machado and Serralheiro 2017). Krishnan and Kumari (2008) reported that soybean receiving spray treatment of 10 mM n-triacontanol under 20 mM NaCl was capable of restoring the metabolic processes in plants by substantially increased relative water content (RWC), specific leaf area (SLA), leaf weight ratio and decreased leaf osmotic potential. *Helianthus annuus* L.

cultivars receiving sprays of 50 and 100 μ M TRIA showed marked values for root and shoot lengths, fresh weights, under 150 mM salt regimes (Aziz et al. 2013). In contrary to this, pre-seed treatment of TRIA shows a non-significant effect on shoot fresh and dry weight, root fresh and dry weight, shoot and root length, and leaf area under saline conditions (Perveen et al. 2010, 2012b; Shahbaz et al. 2013). Wheat cultivars MH-97 and S-24 cultivars of wheat receiving foliar spray of 10 and 20 μ M TRIA particularly at vegetative + boot stages under 150 mM saline conditions proved effective in reducing the toxic effects of salt regimes on the root, shoot dry biomass and leaf area (Perveen et al. 2014). Similarly, Aziz and Shahbaz (2015) also noticed that foliar spray of 50 and 100 μ M TRIA at vegetative stage ameliorated the salt-induced effects in terms of root and shoot dry weights in SMH-907, SMH-917 cultivars of sunflower (*Helianthus annuus* L.). Moreover, MMRI-Yellow and Hybrid S-515 cultivars of maize receiving four sprays of 0–5 μ M TRIA prompted shoot and root fresh weight, shoot length and increased leaf area under 100 mM salt stress conditions (Perveen et al. 2017). Besides, Khanam and Mohammad (2018) reported that two spray treatments of 1 μ M TRIA proved effective in mitigating salinity effect on *Mentha*

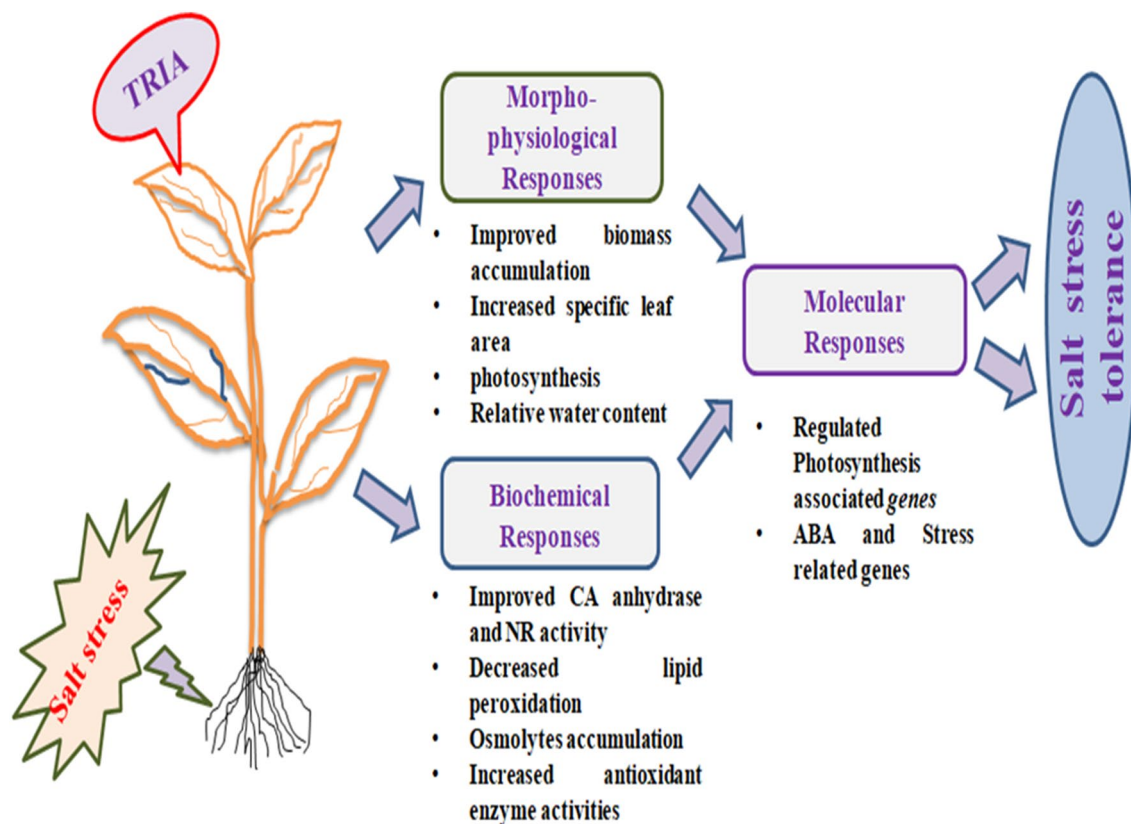


Fig. 2 Role of Triacontanol in making salt tolerance in plants

piperita L. by enhancing the overall growth attributes such as shoot length, root length, leaf area and leaves per plant, shoot fresh and dry weight, root fresh and dry weight. Triacontanol maintained plant water/nutrient relations and synthesis/accumulation of organic compounds and influenced signal transduction that up-regulated various metabolic processes resulting in improving the growth attributes under normal and varying environmental conditions in plants (Krishnan and Kumari 2008; Naeem et al. 2012; Perveen et al. 2014).

Photosynthesis

Photosynthesis is vital physiological process operating in green plants and generally depends on photosynthetic pigments, gas exchange parameters, photosystems, components of electron transport systems and enzymes involved in carbon metabolism (Rahman et al. 2017). Various reports suggested that salt stress decreases the process of photosynthesis. The decrease in the process results in reduced growth and development of crop plants (Chaum et al. 2009; Shelke et al. 2017). Krishnan and Kumari (2008) noticed that in salt-induced soybean, the leaf-applied 10 mM triacontanol

considerably increased the level of photosynthetic pigments such as Chl *a* and Chl *b*, soluble sugar, proteins and nucleic acids (DNA as well as RNA). Pre-treatment of *Triticum aestivum* L. seeds with 10 μM TRIA substantially increased CO_2 assimilation and transpiration under saline conditions (Perveen et al. 2010). In another study, Perveen et al. (2013) reported that spray treatments of 10 and 20 μM TRIA at vegetative and boot stage alleviate the effects of salinity stress on two wheat cultivars (MH-97 and SU-24) by modulating the chlorophyll contents, photosynthetic rate, transpiration rate, stomatal conductance, electron transport rate and relative membrane permeability. In sunflower, spray treatments of 50 and 100 μM TRIA increased net CO_2 assimilation rate, transpiration rate, water use efficiency, but was unable to alter the chlorophyll fluorescence attributes except for Fv/Fm efficiency of PS II (Aziz et al. 2013). Shahbaz et al. (2013) also observed the similar findings on *Brassica napus* L. when TRIA was applied as pre-seed treatment (soaking of seeds with some sort of chemical solution before sowing) under salt stress conditions. They noticed a slight increase in photochemical quenching, electron transport rate and water use efficiency, and non-significant effect on chlorophyll content, Fv/Fm efficiency of PSII and non-photochemical quenching under saline conditions in canola. Moreover,

Table 1 Response of various crops to the application of TRIA under salt stress

S. no	Types of crop	Plant species	Family	TRIA conc. applied	Plant responses	References
1	Cereals	<i>Zea mays</i> L.	<i>Poaceae</i>	11.2 μ M	Increased roots and leaves fresh weight, SPAD index, root and leaf protein content, the increased potassium content of leaf and roots, K/Na ratio, decreased roots and leaf sodium content	Ertani et al. (2013)
2	Oil seeds	<i>Glycine max</i> L.	<i>Leguminosae</i>	10 mM	Increased relative water content, specific leaf area, leaf weight ratio, enhanced level of photosynthetic pigments, soluble sugars, proteins and nucleic acids	Krishnan and Kumari (2008)
		<i>Helianthus annuus</i> L.	<i>Asteraceae</i>	0, 50 and 100 μ M	Enhanced dry biomass of shoot and roots, Glycinebetaine and proline accumulation, Superoxide dismutase, peroxidase, and GR activity	Aziz and Shahbaz (2015)
3	Vegetables	<i>Raphanus sativus</i> L.	<i>Brassicaceae</i>	10 μ M	Increased cuticle thickness, cortex zone thickness, epidermis cell width and length, stem diameter, vascular bundle width, cambium thickness, xylem and phloem width, trachea diameter	Çavuşoğlu et al. (2008)
		<i>Cucumis sativus</i> L.	<i>Cucurbitaceae</i>	0,25 and 50 μ M	Improved emergence index and the final emergence of seeds, root/shoot length, dry weight of seedlings and chlorophyll content, Increased Stomatal conductance (gs), photosynthetic rate (Pn), water use efficiency, transpiration (E), and proline content	Sarwar et al. (2017)
4	Medicinal plants	<i>Coriander sativum</i> L.	<i>Apiaceae</i>	0, 10 and 20 μ M	Increased dry biomass of roots and shoots, decreased lipid peroxidation level and hydrogen peroxide content, modulating antioxidant system	Karam and Keramat (2017)

Table 1 (continued)

S. no	Types of crop	Plant species	Family	TRIA conc. applied	Plant responses	References
		<i>Mentha piperita</i> L.	<i>Lamiaceae</i>	1 μ M	Enhanced plant biomass, chlorophyll content, Stomatal conductance (gs), photosynthetic rate (Pn), transpiration (E), internal carbon dioxide concentration, proline accumulation, increased superoxide dismutase, peroxidase and catalase activity, leaf nitrogen, phosphorus, potassium and menthol and essential oil content	Khanam and Mohammad (2018)
5	Ornamentals	<i>Erythrina variegata</i> L.	<i>Fabaceae</i>	1 mg/kg	Promoted plant biomass, improved chlorophyll and carotenoids content, enhanced protein, saccharides and starch content	Muthuchelian et al. (1996)

RBN-3060 cultivar of *Brassica napus* L. receiving sprays of 0.5 and 1.0 mg/L TRIA improved chlorophyll contents, water use efficiency and net CO₂ assimilation rate (Zulfiqar and Shahbaz 2013). *Mentha piperita* L. being provided with two sprays of 1 μ M TRIA reduced the inhibitory effects of salinity by improving the chlorophyll content and gas exchange parameters (Khanam and Mohammad 2018). Such TRIA-mediated improvements in plant growth could be due to the improvement in size and number of the chloroplast, which might be responsible for an increase in chlorophyll and carotenoids contents leading to an increase in photosynthetic CO₂ assimilation in plants (Ivanov and Angelov 1997; Naeem et al. 2009; Khan et al. 2014). Also, TRIA causes up-regulation of antioxidant enzymes, photosynthetic genes and activation of secondary messengers or metabolites that elicits vital enzymes (proteins) involved in proper regulation of various metabolic processes in plants (Aziz and Shahbaz 2015).

Mineral Nutrient Acquisition

Salinity stress causes nutrient imbalance or deficiencies due to sodium (Na⁺) ion accumulation in plant tissues exposed to higher NaCl concentrations. High Na⁺ level competed with potassium (K⁺) ion uptake and disturbed stomatal regulation and consequently photosynthesis (Gupta and Huang 2014). Application of TRIA minimised the effects of Na⁺ ion in plants by reducing its uptake, while enhanced the K⁺ and calcium (Ca²⁺) ion uptake in salt-stressed plants (Krishnan and Kumari 2008). Further, Shahbaz et al. (2013) reported that pre-treated canola seeds with 0.5 mg/L TRIA improved

root and shoot K⁺ content under 150 mM salt stress. However, in contrary to this, pre-sowing treatment of wheat seeds with TRIA showed a non-significant effect on uptake and use efficiency of K⁺ and Ca²⁺ ion contents (Perveen et al. 2012a). In another study, spray treatments of 10 and 20 μ M TRIA at three growth stages reduced shoot Na⁺ content, increased shoot K⁺ content and root and shoot Ca²⁺ contents in wheat (Perveen et al. 2014). In a subsequent study, Perveen et al. (2017) reported that triacontanol maintains the ionic homeostasis in maize by reducing the uptake of Na⁺, while increased shoot K⁺ contents in maize. Furthermore, Khanam and Mohammad (2018) noticed that spray of 1 μ M TRIA twice reduced the inhibitory of salinity in *Mentha piperita* L. by improving leaf N, P, K contents. The increased K⁺ ion concentration under salt conditions might be playing a role in normal stomatal functioning as the stress-related proteins and genes of ABA are down-regulated by TRIA (Chen et al. 2002; Perveen et al. 2014).

Oxidative Stress and Antioxidant Enzyme Activities

In plants, the generation of ROS such as hydroxyl radicals (OH⁻), hydrogen peroxide (H₂O₂), superoxide radicals (O₂⁻) and singlet oxygen (¹O₂) under salt stress is an indispensable consequence of the disruption, de-regulation or over reduction of electron transport chains (ETC) in chloroplasts and mitochondria (Abogadallah 2010). Molecular oxygen acts an electron acceptor during the functioning of ETC giving rise to ROS accumulation. Higher concentration of ROS accumulation becomes toxic for cell integrity by way of causing

oxidative stress-induced damages such as lipid peroxidation resulted from the production of malondialdehyde (MDA) and thiobarbituric-acid-reactive substances (Wani et al. 2018; Farooq et al. 2019) and denaturation of DNA, proteins, lipids and other constituents in the cell (Foyer and Noctor 2009; Groß et al. 2013). Under salt stress conditions, PGRs produce various ROS-related divergent signals to maintain normal metabolisms in plants (Fahad et al. 2015; Ryu and Cho 2015; Khan et al. 2019). Under these circumstances, TRIA acts an antioxidant agent, as it increases activities of antioxidant enzymes on one hand and decreases lipid production on the other. For example, spray treatments of 10 and 20 μM TRIA reduced the oxidative stress-induced membrane damage in wheat cultivars (MH-97 and S-24) by causing markedly increased peroxidase (POD) activity and a consequent reduction in the H_2O_2 and MDA levels (Perveen et al. 2014). Further, three foliar sprays each of 50 and 100 μM TRIA ameliorated the harmful effects of salinity by up-regulating the activities of POD, superoxide dismutase (SOD) and glutathione reductase (GR) enzymes in sunflower (Aziz and Shahbaz 2015). Nevertheless, Karam and Karamat (2017) reported that foliar sprays of 10 and 20 μM TRIA proved effective in reducing the toxic effects of salinity stress on *Coriandrum sativum* L. through modulating the MDA, H_2O_2 , CAT, ascorbate peroxidase (APX), SOD and POD enzyme activities. In addition, Perveen et al. (2017) further noticed that four sprays each of 2 and 5 μM TRIA improved salinity tolerance by significantly decreasing relative membrane permeability, H_2O_2 and MDA contents in maize seedlings. Moreover, in a recent study, Khanam and Mohammad (2018) examined the effect of TRIA on the antioxidant systems of *Mentha piperita* L. under different salinity levels. Foliar sprays of 1 μM TRIA reduced the salinity effects by markedly increasing CAT, POD and SOD activity. The alleviation of salt stress effect by TRIA has been ascribed to increased antioxidant enzyme activity, which took part in the detoxification of ROS, thereby leading to balance between the ROS generation and scavenging that resulted in alleviating the toxic effects of salinity on plants and hence influenced the overall growth of plants (Perveen et al. 2014; Karam and Keramat 2017). Therefore, from the above discussion it can be suggested that the TRIA application can nullify the salt-induced damages in tested plants by modulating antioxidant defense system which provide clues to unravel the underlying mechanisms, which confer salt stress tolerance in not only tested plants but in other plants too.

Compatible Solutes

The accumulation of a large number of compatible solutes (proline, glycine betaine, etc.) under salinity in plants is an adaptive response to enhance their stress tolerance (Reis et al. 2012; Shahbaz et al. 2012, 2013; Per et al. 2017). It was well

documented that accumulation of proline and glycine betaine protects plants from stress by maintaining osmotic balance, stabilising structures of proteins, enzymes and membranes integrity and ROS scavenger (Ashraf and Foolad 2007; Banu et al. 2009; Hayat et al. 2010; Murmu et al. 2017; De la Torre-Gonzalez et al. 2018; Alamri et al. 2019). The leaf-applied TRIA markedly enhanced the accumulation of compatible solutes in plants under the saline regime. Pre-sowing treatment of *Brassica napus* L. seeds with (0, 0.5 and 1 mg/L) TRIA followed by salinity stress markedly enhanced the accumulation of glycine betaine (Shahbaz et al. 2013). In sunflower seedlings, sprays of (0, 50 and 100 μM) TRIA at three growth stages accumulated more glycine betaine and proline than NaCl-treated seedlings alone (Aziz and Shahbaz 2015). Similarly, Pre-treated cucumber (*Cucumis sativus* L.) seeds with (0, 25 and 50 μM) TRIA resulted in accumulation of more proline under salinity regime (Sarwar et al. 2017). However, contrary to this, Krishnan and Kumari (2008) noticed a decline in proline accumulation with TRIA treatment to soybean seedlings under NaCl conditions. Similarly, in wheat cultivars, TRIA was unable to alter the glycine betaine and free proline content under salinity conditions (Perveen et al. 2012b, 2014). Further, Perveen et al. (2017) observed that a low concentration of TRIA 5 μM increased proline accumulation in maize cultivars under salinity stress. Similarly, Khanam and Mohammad (2018) worked on peppermint found that foliar application of 1 μM TRIA improved proline content.

Yield and Quality

The TRIA not only enhances growth, physio-biochemical attributes of the plants but also improves the quality, content and yield of many crops (Naeem et al. 2009, 2010, 2011; Khan et al. 2014; Suman et al. 2017). Under salt stress, application of TRIA also proved effective for increasing the yield attributes. For example, Shahbaz et al. (2013) noticed that pre-sowing TRIA increased seed number per pod but showed a non-significant effect on yield per plant and seed weight of RBN-3060 cultivar of *Brassica napus* L. under saline conditions. Further, Perveen et al. (2014) reported that leaf-applied TRIA markedly increased seed weight, grain number and yield per plant of MH-97 and S-24 cultivars of wheat under salinity stress. Moreover, Khanam and Mohammad (2018) noticed that spray of 1 μM TRIA improved menthol and essential oil content and essential oil yield of *Mentha piperita* L. under salt stress conditions.

Conclusion

Soil salinity is a major problem for agricultural, adversely affecting physio-biochemistry of plants by creating osmotic stress, ionic imbalance, oxidative stress, membrane

disorganisation and ROS. Plants develop mechanisms to mimic the toxic effects of salinity, but at severe condition, plants fail to cope with salt stress by its own mechanism. Therefore, exogenous application of PGRs is one of the strategies used nowadays in enhancing the salinity tolerance in plants. TRIA acts as a potent plant growth regulator and has been reported to improve the overall growth and productivity of various economically essential crops under both normal and saline conditions. The exogenous application of TRIA induces the second messenger (TRIM) formation that triggers the influx of ions like Ca^{2+} , Mg^{2+} and K^{+} by opening their channels in the plasma membrane. A particular level of Ca^{2+} may be responsible for calmodulin and of Mg^{2+} and K^{+} ions may improve the cell metabolism by becoming an activator of enzymes, which may be responsible for better growth. Calmodulin may modulate transcription factors like CAMTA₃, GTL and MYB₂, which may regulate various anabolic process-related genes hence better growth of TRIA-treated plants. TRIA alleviates the ill effects of salt stress by regulating the stress mitigating genes. The superiority of foliar application of TRIA over-seed priming technique could be attributed to its prompt availability to plants. TRIA enhanced salinity tolerance in plants due to the accumulation of osmolytes, increased antioxidant enzyme activity, and osmotic adjustment, maintaining membrane integrity and limiting the lipid peroxidation and ROS generation. The lower concentration of triacontanol generally proved beneficial in enhancing the salinity tolerance in plants. There is a need for doing a lot of research on triacontanol to demonstrate its biosynthesis in plants and how triacontanol and TRIM regulate the plant metabolism and what are the transcription factors that are involved in metabolism.

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Compliance with Ethical Standards

Conflict of interest The authors declare no conflict of interest.

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