



Trehalose: a promising osmo-protectant against salinity stress—physiological and molecular mechanisms and future prospective

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Abstract

Salt stress is one of the leading threats to crop growth and productivity across the globe. Salt stress induces serious alterations in plant physiological, metabolic, biochemical functioning and it also disturbs antioxidant activities, cellular membranes, photosynthetic performance, nutrient uptake and plant water uptake and resulting in a significant reduction in growth and production. The application of osmoprotectants is considered as an important strategy to induce salt tolerance in plants. Trehalose (Tre) has emerged an excellent osmolyte to induce salinity tolerance and it got considerable attention in recent times. Under salinity stress, Tre helps to maintain the membrane integrity, and improves plant water relations, nutrient uptake and reduces the electrolyte leakage and lipid per-oxidation. Tre also improves gas exchange characteristics, protects the photosynthetic apparatus from salinity induced oxidative damages and brings ultra-structure changes in the plant body to induce salinity tolerance. Moreover, Tre also improves antioxidant activities and expression of stress responsive proteins and genes and confers salt tolerance in plants. Additionally, Tre is also involved in signaling association with signaling molecules and phytohormones and resultantly improved the plant performance under salt stress. Thus, it is interesting to understand the role of Tre in mediating the salinity tolerance in plants. Therefore, in this review we have summarized the different physiological and molecular roles of Tre to induce salt tolerance in plants. Moreover, we have also provided the information on Tre cross-talk with various osmolytes and hormones, and its role in stress responsive genes and antioxidant activities. Lastly, we also shed light on research gaps that need to be addressed in future studies. Therefore, this review will help the scientists to learn more about the Tre in changing climate conditions and it will also provide new insights to insights that could be used to develop salinity tolerance in plants.

Keywords Anti-oxidant · Genes expression · Hormones · Membrane stability · Photosynthetic performance · Trehalose

Abbreviations

SS Salinity stress
ROS Reactive oxygen species
Na⁺ Sodium
K⁺ Potassium
MDA Malondialdehyde

H₂O₂ Hydrogen peroxide
Tre Trehalose
Cl⁻ Chloride
CO₂ Carbon dioxide
RWC Relative water contents
PS-II Photo system-II
APX Ascorbate peroxidase
GXP Glutathione peroxidase
GR Glutathione reductase
SOD Superoxide dismutase
POD Peroxides
CAT Catalase
ABA Abscisic acid
GA Gibberellic acid
JA Jasmonic acid

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SA	Salicylic acid
EL	Electrolyte leakage
LOX	Lipoxygenases
MG	Methylglyoxal

Introduction

Soil salinization is a major problem across the globe which is negatively affecting crop production and putting global food security at great risk [1]. It has been reported that more than 20% of arable lands are salt affected which causes huge yield losses every year [2, 3]. Soil salinity (SS) adversely affects all phases of plant development, including germination, seedling, vegetative and mature stages [4]. However, the effects of SS largely depend on the severity and duration of stress, plant species and stage of plant growth [5, 6]. Seed germination is the first phase of plant life that is negatively affected by SS. The higher concentration of salts in growing medium reduced the germination by decreasing water uptake, disrupting enzymatic activities and imposing salt induced oxidative damage [7–11]. Salinity stress also disturbs hormones crosstalk, antioxidant activities, ionic homeostasis and induced production of reactive oxygen species (ROS) that reduce the growth and biomass production and cause damage to cellular membranes, proteins and DNA [7, 12–16]. Further, SS also inhibits soil microbial and enzymatic activities which negatively affect soil fertility and overall crop production [18].

Salinity stress is considered to be complex abiotic stress which involves ionic, osmotic and oxidative stresses [19–21]. Osmotic stress occurs shortly after exposure of salts and it reduces the plant's ability to uptake nutrients and water [3, 22]. Likewise, excessive sodium (Na^+) accumulation in plant cytoplasm causes potassium (K^+) deficiency and disrupts photosynthetic processes, enzymatic activities and biosynthesis of proteins [3, 23]. Moreover, salinity induces oxidative stress that produce ROS which are highly cyto-toxic and cause huge damage to lipids, proteins and nucleic acid and resulting in DNA mutation, lipid peroxidation and denaturation of proteins [19]. Additionally, SS also reduces the synthesis of chlorophyll contents, soluble proteins and free amino acids and increases the membrane damage, malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) accumulation which in turn causes a huge reduction in growth and productivity [24].

Plant use different defense mechanisms to ensure their survival and maintain growth under different abiotic stresses [25–28], especially SS [29]. One of the most important protective mechanisms is an anti-oxidant system which comprises of different enzymatic and non-enzymatic anti-oxidant which counter the salinity induced oxidative damage by increasing the scavenging of ROS [30–33]. Indeed,

higher anti-oxidant activities provide resistance to plants and reduce the salinity induced oxidative damages [33]. The second most important defense mechanism is an osmotic adjustment which is vital process that induce stress tolerance in the plant by synthesis of different organic solutes [34]. Plants accumulate different solutes including proline, glycine-betaine, amino acids and different sugars that maintain ionic balance of vacuole and protect plant organelles by scavenging ROS [31, 35]. Moreover, osmolytes also improve the photosynthetic efficiency and improve the anti-oxidant activities resulting in appreciable improvement in growth and production under stress conditions [36, 37].

Trehalose (Tre) is non-reducing sugar that synthesized in plants and it plays a protector role under different stresses [38]. This sugar has white color with no odor and it 45% times sweeter as compared to sucrose [39]. Tre play a significant role in plant functioning and it is considered to be potential osmo-protectant [31, 40]. Trehalose stabilized cellular membranes, enzymes, proteins and protects the biological system from damaging impacts of SS [31, 40]. It also works as an elicitor of genes involved in stress responses and detoxification ROS [41–43]. Tre protects the biological structures from SS by working as signaling molecule and increasing anti-oxidant activities [44]. The application of Tre has been found to increase the plant growth and yield by overcoming adverse of SS [45]. However, production of Tre is not sufficient to mitigate the adverse of different stresses. Therefore, exogenous application of Tre increased endogenous Tre and it is considered as an alternate strategy to improve stress tolerance [41, 46]. Therefore, in this review we discussed the physiological and biochemical roles of Tre under SS. We have also presented the Tre mediated improvement in anti-oxidant activities, its cross talk with different osmo-regulating compounds and success stories of engineering Tre to induce salinity tolerance in plants. Additionally, we also highlighted the research gaps where future research must be conducted to explore the role of this important osmo-protectant under SS.

Plant responses to salinity stress

Seed germination is most critical stage of plant life [47]. Generally, SS delays or decrease the seed germination [48] by reducing water uptake and decreasing soil osmotic potential [48, 49]. Excessive Na^+ and chloride (Cl^-) concentration in growing medium also cause toxicity to seed embryo, alter protein synthesis, energy production, hormonal and nutrient balance which in turn delay the seed germination [47, 50]. Reducing enzymatic activities (α -amylase) during germination reduce the translocation of sugar to growing embryo which reduce and delay in germination [51, 52]. SS also negatively affect growth and development of plants however,

response of plants can differ due to plant growth stage, plant species, duration and intensity of SS [53]. Generally, SS decrease the plant growth in two phases. In first phase plant growth is reduced within a few minutes where higher concentration of salts reduces growth rate and water uptake owing to osmotic stress [54]. SS reduces the expansion of both root and shoot cells [55], induce stomata closure, and reduce the CO₂ assimilation which resultantly cause reduction in growth [56, 57].

Further, plants are grown under SS also face changes in plant physiological and metabolic processes, enzymatic activities, plant water relations, carbon dioxide (CO₂) assimilation, synthesis of proteins and efficiency of PS-II which also contribute toward a reduction in growth [53, 58]. In second phase growth is reduced due to the accumulation of salts in plant leaves which reach to threshold levels and cause toxicity. This phase is a long phase and it can take a few days to weeks or months to complete [53]. During this phase higher Na⁺ accumulation in plant body inhibit enzymatic activities. For instance, the activities of different enzymes involved in the synthesis of starch, glycolysis, polyamine, phenylpropanoid pathway and Calvin cycle are disturbed under SS which causes a reduction in growth [59, 60].

Plants also show chlorosis, necrosis, senescence and reduced leaf area owing to a reduction in photosynthetic activities which also contributed to a reduction in growth in the second phase [53]. The threshold levels of ionic toxicity vary from among plant species, cultivars and genotypes. For instance magnitude of reduction in grain yield was maximum (67%) in sensitive cultivars as compared to adapted wheat cultivar (41%) at a salinity level of 120 mM [54]. The availability of moisture significantly affects physiological

and metabolic processes taking place within the plant body. During, SS plants undergo osmotic stress that decreases cell water potential and reduces the water uptake [54]. Relative water contents (RWC) are considered to be important criteria to select plants for salinity tolerance [61]. For instance, Nassar et al. [62] noted a reduction of 3.5% in RWC of salt tolerant wheat cultivar, whereas these authors noted a reduction of 6.7% in RWC of salt sensitive wheat cultivar. Salinity stress also reduced membrane stability and increases the loss of important substances [63] (Table 1).

SS induced the production of ROS that cause membrane damage and increase the production of MDA and lipid peroxidation [24]. The ability of a plant to maintain a normal transpiration rate under SS reflects their stress however, SS reduced the transpiration rate [72]. Chlorophyll plays a significant role in processes of photosynthesis however, SS causes significant reduction in chlorophyll contents [73]. Salinity stress reduced the chlorophyll contents by the disintegration of chlorophyll structure and excessive ROS production that denature enzymes needed for the synthesis of chlorophyll [74]. SS also reduced the photosynthetic rate which is associated with reduced stomatal conductance, rubisco activities and efficiency of PS-II [75]. A higher concentration of salts also induces early leaf senescence which reduced the leaf area and consequently reduced the rate of photosynthesis and leads to a reduction in biomass production [76].

SS also disturbs nutrient homeostasis, and plant metabolic processes and increases the production of ROS that damage DNA, lipids and membranes and cause leakage of cell solutes [54]. However, plants possess an excellent defense system comprising enzymatic and non-enzymatic

Table 1 Effect of different salinity on growth, physio-biochemical process and antioxidant activities of various crops

Crop species	Salinity stress (mM)	Effects	References
Wheat	200	Salinity stress reduced root and shoot growth, relative growth rate of root and shoot, chlorophyll contents, stomata conductance, and increased accumulation of Na ⁺	[64]
Maize	100	Salinity stress reduced chlorophyll contents, germination%, and leaf area in maize genotypes	[65]
Rice	100	Salt stress reduced RWC, K contents, and shoot dry matter and photosynthetic pigments	[45]
Cotton	360	Salinity stress reduced root volume, seed germination rate, root and crown ration, and root length	[66]
Soybean	100	Salinity stress reduced growth and biomass, chlorophyll contents, intercellular carbon dioxide concentration and yield of soybean plants	[67]
Faba bean	100	Salinity stress reduced enzymatic activities, proline content, protein contents, biomass, RWC, chlorophyll and carotenoids contents and increased the MDA and H ₂ O ₂ accumulation	[68]
Pistachios	150	Salinity decreased growth, RWC, photosynthetic pigments, K ⁺ uptake and increased the Na ⁺ accumulation	[69]
Wheat	200	Salt stress induced ROS lipid peroxidation and reduced the RWC and yield of wheat	[70]
Barley	150	Salt stress reduced gas exchange parameters, ions uptake, biomass production and induce ROS production	[71]

mM millimolar, RWC relative water contents, K potassium, H₂O₂ hydrogen peroxide, Na sodium

antioxidant enzymes to scavenge ROS [77]. The increase in anti-oxidant activities is considered to be vital process to improve salinity tolerance. For instance, the activities of ascorbate peroxidase (APX), glutathione peroxidase (GPX), glutathione reductase (GR) and superoxide dismutase (SOD) were significantly increased under a SS of 100 mM [78]. SS also cause osmotic stress which induces a reduction in plant growth. However, plants minimize the deleterious impacts of osmotic stress by a mechanism known as osmoregulation [54]. In this mechanism plants accumulate various osmolytes (proline, glycine-betaine, amino acids and different sugars) which regulate plant water relations and antioxidant activities to improve salinity tolerance [79].

Ionic homeostasis is considered as an essential mechanism to mitigate toxic effects of SS. Keeping a higher ration of K^+/Na^+ in cytosol prevent the cellular damages and increase the salinity tolerance in plants [80, 81]. However, SS significantly increased the accumulation Na^+ and cause reduction in calcium (Ca), magnesium (Mg) and K uptake and accumulation [24]. Plants also accumulate various hormones that regulate the plant responses under stress conditions. For instance, in water stress different hormones including abscisic acid (ABA), gibberellic acid (GA), jasmonic acid (JS) and salicylic acid (SA) acted together to regulate the plant responses in *A. thaliana* [82]. Moreover, ABA and JA showed synergistic impacts in signaling pathways to regulate each other responses against salinity stress [83].

Salinity stress also negatively reduced the yield and final quality of crops. For example, SS (4 dSm^{-1}) reduced the grain weight, number of grains and grain yield of rice [84]. SS also causes flower abortion, reduce the growth of pollen tube grain filling duration and cause significant yield losses [79]. The concentration of salts reduces the concentration of starch and amylase and modulates the texture of grains [85, 86]. Moreover, in the maize crop SS increased the carbohydrate concentration while SS decreased the grain protein contents [85]. In another study it was noted that SS decreased the rice yield by 36% however, it did not affect the texture of grain as compared to the control [87]. Additionally, in barley crop SS reduced grain size and grain carbohydrate concentration but increase the protein contents [88], conversely, in wheat crop, SS significantly reduced the grain protein content [89].

Trehalose biosynthesis, metabolism and structural properties

Tre biosynthesis in plants involves the production of trehalose-6-phosphate (T6P) from glucose-6-phosphate and UDP-glucose by trehalose-6-phosphate synthase (TPS), and the subsequent dephosphorylation of T6P to Tre by

trehalose-6-phosphate phosphatase (TPP) [90]. Two molecules of uridine-diphospho-glucose (UDP-Glc) and glucose-6-phosphate (Glc-6-P) are used for biosynthesis of Tre in plants. The enzyme TSP catalyzed UDP-Glc and Glc-6-P into T6P [91, 92], whereas enzyme trehalose-6-phosphate phosphatase (TPP) catalyzed the T6P into Tre as the final product [93]. The presence of Tre has been reported in many plants including *Selaginella lepidophylla* and *Myrothamnus flabellifolius*, tobacco and rice [41, 94, 95].

A lower concentration of Tre is not solely due to the action of Tre but also owing to tight regulation of TPS and TPP genes expression and enzymatic activities [96]. For instance addition of validamycin A to the growing medium increased Tre accumulation by inhibiting Tre however, it did not stimulate Tre biosynthesis [97]. The regulation of Tre genes increased the Tre biosynthesis which in turn conferred the stress tolerance [96]. For instance expression of yeast and *E. coli* derived Tre genes made plants tolerant against, cold, salinity and drought stress [98]. In rice plants higher expression of TSP genes increased the plant acclimation against, cold, drought and salt stress [99]. Similarly, up-regulation of AtTPS1 in Arabidopsis plants caused an increase in Tre biosynthesis which in turn increased the cold [100]. Moreover, in *A. thaliana* high temperature increased the Tre levels by two folds whereas the levels of Tre were increased by eight folds under cold stress (4°C) [101]. The expression of Tre transgenes also activates biosynthetic pathways in plant organs exposed to stress conditions. For example, in cotton crop TPS1 genes were expressed only in leaves and roots whereas in the maize crop TPS1 genes were expression occurred in ears under water deficiency [102]. Sometimes, Tre degradation regulates its levels in different plant tissues. For instance in *Medicago* expression of the Tre gene MtTRE1 was blocked under SS and Tre concentration was increased in plant nodules [103]. Moreover, a microarray showed that in *A. thaliana* the instance of abiotic stress caused a marked increase in the expression of genes involved in Tre metabolism [98]. Tre is effectively involved in stress tolerance and transgenic plants with improved Tre biosynthesis and stress tolerance support this logic [41, 104].

Tre is a non-reducing disaccharide sugar comprising two glucose subunits linked by an alpha, alpha-1,1 glycosidic bond. Tre has special characteristics as compared to other disaccharides owing to the fact both reducing subunits in Tre are used in making the glycosidic bond [39]. Tre has a substantiated resistance against hydrolysis and remains durable insoluble at a very temperature [105]. The α - α linkage of Tre is very stable and it possesses higher hydrophilicity owing to its inability for internal hydrogen bonding [106]. All these properties make Tre a useful molecule for the protection of membranes and proteins [107]. Moreover, Tre also has excellent dehydrating and vitrification ability [41] and in case of dehydration, Tre forms hydrogen bonding

with molecules and membranes by replacing the water molecules [108]. It also crystallized into glassy appearance under dehydration which preserves molecules from de-naturation [109, 110]. Tre is an inert sugar and it has low bond energy (1 kcal mol^{-1}) as compared to sucrose (27 kcal mol^{-1}) [95]. Lastly, Tre does not break down into reducing monosaccharide until it is exposed to extreme hydrolytic conditions or Tre action [107].

Trehalose a potential osmolyte to improve plant performance under salinity stress

Salinity stress is serious abiotic stress negatively affecting crop growth and productivity across the globe. Salt stress induces serious alterations in plant physiological, biochemical and metabolic functioning and causes serious growth and yield losses. Tre has emerged as an excellent osmo-protectant that substantially improved plant growth and subsequent performance under salinity stress [40, 111, 112]. Moreover, Tre also strengthens the antioxidant defense system and protects the plants from salinity induced oxidative damage [41, 46]. Here we systematically presented the different roles of Tre in inducing the salinity stress in plants.

Trehalose maintains membrane stability and plant water relationships under salinity stress

Generally, SS causes the production of ROS that damages cell membranes and increased lipid per-oxidation, and leading to an increase electrolyte leakage (EL) and loss of membrane permeability [24, 29]. Salinity induced increase in lipoxygenases (LOX) activity increased the oxidation of polyunsaturated fatty acids and thus increases lipid per-oxidation under stress conditions [113, 114]. However, Tre appreciably protects the membranes and improve the plant performance under SS. The application of Tre reduced the H_2O_2 production by activating antioxidant defense system which protects the membranes and reduces the MDA accumulation and membranes damage and EL [44, 115]. Tre application decreases H_2O_2 productions by increasing the anti-oxidant activities APX, catalase (CAT), peroxidases (POD) and SOD that alleviate salinity induced damage to the membrane and improve membrane stability [116]. Moreover, Tre application also increased the accumulation of phenolic compounds which activate anti-oxidant defense system for ROS scavenging therefore, improve membrane stability and reducing the EL and lipid peroxidation [29, 116].

The increased activity of LOX causes lipid peroxidation and increased in MDA contents. However, Tre pretreatment reduced the LOX activities and MDA accumulation by scavenging ROS, stabilizing membranes and modulating the antioxidant activities [117, 118]. Tre application

also improved the plant water accumulation under SS. The application of Tre improved the root growth and reduce the salinity inducing, osmotic stress by improving water uptake, therefore, maintain higher RWC under SS [118]. Tre reduced the inhibitory effects of SS on plant growth by improving the water status of plant tissues by stomata closing and osmoregulation [44, 119]. In another study, it was reported that SS decreased the leaf RWC by 25%, however, Tre foliar spray appreciably increase the leaf RWC by 34% as compared to the control [117]. Therefore, all aforementioned findings suggested that Tre improves the membrane stability by increasing antioxidant activities, and reducing LOX activity, therefore, reduce the MDA accumulation and maintain higher RWC under salinity stress.

Trehalose improves nutrient uptake under salinity stress

Nutrients play an important role in plant growth and development however, SS significantly disrupts the nutrient uptake and causes a reduction in growth and yield [24, 120, 121]. Tre appreciably improves nutrient uptake and cause significantly improved growth and productivity under SS. For instance, Tre supplementation significantly improves the nitrogen (N), phosphorus (P) and potassium (K) uptake under SS and cause marked improvement in the growth and yield of cowpea plants [122]. In another study, Shahbaz et al. [123] reported that Tre supplementation reduced the adverse impacts of SS by increasing the uptake of calcium in rice plants [123]. Tre works as a source of energy and the exogenous application of Tre significantly improved the Ca and K accumulation while reduced the Na^+ accumulation in rice plants grown under SS [123]. Moreover, Zeid [119] reported Tre supply increase the K^+ uptake and maintains the optimum K^+/Na^+ ratio to confer salinity tolerance in maize plants. In another study, it was recorded that Tre supplementation (10 and 30 mM) increased the K contents by three folds as compared to control plants [124]. Tre plays a beneficial role in nutrient uptake and it reduces the P deficiency by increasing P uptake in maize plants grown under SS and P deficiency [111]. Additionally, Tre also retains higher K^+ in plant stem and leaves that improves the salinity tolerance and plant responses against SS [125]. These are the limited information available in the literature about the role of Tre on nutrient uptake. Moreover, studies are needed to explore the role of Tre on nutrient uptake under SS.

Trehalose protects the photosynthetic apparatus and improves photosynthesis under salinity stress

Salinity stress causes a significant reduction in plant photosynthetic efficiency mainly due to the closing of stomata, limited CO_2 assimilation and reduction in chlorophyll

synthesis. Nonetheless, Tre supplementation significantly improves plant photosynthetic efficiency under SS. SS negatively affects gas exchange characteristics including CO₂ assimilation rate (Ci), transpiration rate (Tr) and stomatal conductance [123]. However, Tre application improved all these gas exchange characteristics by improving anti-oxidant activities and leads to an appreciable increase in photosynthetic performance [123]. Moreover, the exogenous supply of Tre also decreased the activity of NPQ and increased the electron transport, photochemical quenching (qP) thereby appreciably improves plant photosynthetic efficiency [119].

Tre pre-soaking (25 mM) significantly increased the chlorophyll and carotenoid contents which are also major reasons of Tre induced increase in photosynthetic efficiency under SS [45]. Moreover, the Tre supply also increased the Rubisco activity owing to an increase in the amount of Rubisco protein, chlorophyll synthesis and protection of photosynthetic apparatus [45]. Likewise, Ali, Ashraf [126] also noted the same results and they concluded that Tre induced increase in biomass production is linked with an increase in Rubisco activity and an increase in anti-oxidant activities. Maintenance of chlorophyll contents and plant water status play a crucial role in salinity tolerance [90]. Tre preserves the stability of chloroplast and maintains chloroplast, osmotic potential, therefore, improve the chlorophyll synthesis and subsequent plant growth under SS [44]. Similarly, different authors also noted a substantial increase in chlorophyll synthesis and photosynthetic efficiency with Tre under SS [5, 118].

Because of the protective impact of carotenoid in energy dissipation with PS-II and its function as a non-enzymatic anti-oxidant during stress conditions [135, 136], this higher concentration of carotenoid is considered to be protective mechanism [131]. Tre application (30 mM) significantly improved the leaf carotenoid contents under SS and lead to a significant increase in salinity tolerance [131]. Tre supplementation improves the performance of PS-II, electron transport and increases the synthesis of chlorophyll contents which contribute to improvement in photosynthetic efficiency in strawberry plants under SS [131]. The foliar application of regulates plant photosynthetic efficiency by improving chlorophyll synthesis and bringing favorable anatomical changes in plant body under SS [41, 122]. In conclusion, Tre protects the photosynthetic apparatus by increasing antioxidant activities and improves chlorophyll synthesis, Rubisco activity, and efficiency of PS-II resulting in a significant increase in photosynthesis under salt stress.

Trehalose maintains osmolytes accumulation and hormones crosstalk under salinity stress

Osmo-regulation is an important practice used by plant to counter the effects of SS. Plant accumulates different

osmotic substances that protect macromolecules and stabilize the protein structure by scavenging ROS. Proline is an important osmolyte accumulated by plants under SS that stabilize cellular structure and proteins and improve plant performance under SS [137]. The controversial reports are available in literature about the effect of Tre on proline accumulation under SS. Likewise, Tre application reduced the accumulation of proline in salt stresses plants indicating low demand for proline or a compensating mechanism for Tre since both Tre and proline works as osmo-protectant [115]. However, some authors also noted significant increase in proline accumulation with Tre application under SS. The application of Tre significantly improved the accumulation of proline which indicates that Tre being a sugar stimulated proline synthesis [138]. Similarly, Feng et al. [132] reported that Tre supply increased the photosynthetic pigments and proline synthesis in plants grown under SS [132]. Moreover, Sadak [44] also suggested that Tre increased the biosynthesis of proline that prevented the wheat plants from adverse impacts of SS [44].

Tre application significantly improved the level of glycine betaine (GB) and total soluble proteins (TSP) under SS which markedly improved the plant tolerance against SS [123]. There is also interplay between Tre and amino acids accumulation under SS. The exogenous supply of Tre also significantly increased the total essential amino acids (valine, leucine, lysine, arginine, isoleucine, phenylalanine, histidine, and methionine) and non essential amino acids (proline, tyrosine, serine, glycine, cysteine, alanine, glutamic acid) which improved the plant stress tolerance [130]. Moreover, the exogenous supplementation of Tre also markedly improved the accumulation of different sugars (glucose, fructose, galactose and xylose, sucrose and total soluble sugars) in wheat and contributes significantly towards improvement in salinity tolerance [124, 130]. Tre application reduced the accumulation of starch, and promotes the conversion of starch into soluble sugars, therefore improved concentration of total soluble sugars under SS [132]. Tre being a non-reducing sugar regulate sugar accumulation and distribution by affecting the activities of sugar transporters and regulating sugar metabolism and ABA metabolism therefore, significantly improved SS tolerance [132]. The interplay between Tre and ABA plays a significant role under SS. Tre application increased ABA accumulation to induced salinity responses by regulating the genes linked with ABA synthesis and metabolism [132]. In crux, Tre application improves osmolytes accumulation and maintains hormonal crosstalk which in turn improves the plant performance under salinity stress.

Trehalose improves accumulation of secondary metabolites under salinity stress

Phenolic compounds possess an excellent anti-oxidant activity and they play a significant role in stress tolerance [45, 139]. The exogenous supplementation of Tre significantly increased phenolic compounds in cowpea leaves [122]. Similarly, a medical alkaloid (vinblastine) and its two precursors vindoline and catharanthine also showed a significant increase in Tre treated plants as compared to control plants [140, 141]. The exogenous supply of Tre (10 and 30 mM) significantly increased the alkaloid content under SS by its ability to control C/N metabolism pathway [124]. Tre supplementation significantly improved the phenolic contents under SS which appreciably reduced the deleterious impacts of salinity stress on quinoa in plants [142]. The beneficial effects of Tre in increasing the phenolic contents are results from its signaling function through the induction of diverse metabolic pathways [114]. Additionally, Tre foliar supply also causes an increase in flavonoids and anthocyanins content under SS. Since phenolics substances provide photo-protection therefore Tre mediated increase in these substances can lead to the preservation of photosystem under SS [131]. Anthocyanin regulates ROS accumulation and maintains photosynthetic efficiency [143, 144], therefore, Tre mediated increase in anthocyanin content decreases damage to the photosynthetic apparatus and improves the plant's photosynthetic efficiency and overall productivity [131]. Trehalose mediated increase in secondary metabolites improves antioxidant activities and protects the photosynthetic apparatus which therefore improves the plant growth under salinity stress.

Trehalose strengthens anti-oxidant activities under salinity stress

The major effect of SS is the production of ROS that damage cellular structures, proteins, lipids and DNA. Nonetheless, Tre appreciably scavenges the ROS by improving anti-oxidant activities to reduce salinity induced damages. Tre signaling contributes to plant adaption under SS by modulating anti-oxidant activities. For instance, exogenous Tre has no impact on CAT activity however, it significantly increased the activities of POD and SOD to counter the negative effects of SS [45, 115, 126]. Luo et al. [145] also documented that Tre plays a major role in scavenging O_2^{2-} by modulating the SOD activity. CAT has a low affinity for H_2O_2 and it is considered a bulk removal of excessive H_2O_2 produced under SS [146]. The exogenous supply of Tre significantly enhanced the CAT activity in rice plants which indicates an efficient mechanism of Tre to scavenge ROS under SS [45] (Figs 1, 2, 3).

The exogenous application of Tre (2.5 and 5 mM) significantly reduced the salt induced oxidative injuries in quinoa plants by increasing the activities of APX, CAT, POD and SOD [134]. In other studies, conducted on rice and wheat crop it was noted that Tre application alleviated adverse effects of SS by decreasing H_2O_2 production through enhanced anti-oxidant activities (APX, CAT, POD and SOD) [118, 123, 145]. According to Feng et al. [132] exogenous supply of Tre (2 mM) reduced the salinity induced osmotic and oxidative injuries by increasing the activities of CAT, POD and SOD under SS. In another study conducted on rice it was recorded that Tre application reduced the MDA and H_2O_2 accumulation by increasing activities of potential anti-oxidant including APX, CAT and POD [115]. Conversely,

Fig. 1 Salinity stress reduced the osmotic potential, water uptake, and it induced leaf rolling, chlorosis, necrosis, disturbs the membrane integrity, DNA, proteins, inhibits nutrient and water uptake, cause ionic and oxidative stress, therefore, cause significant reduction in growth and yield

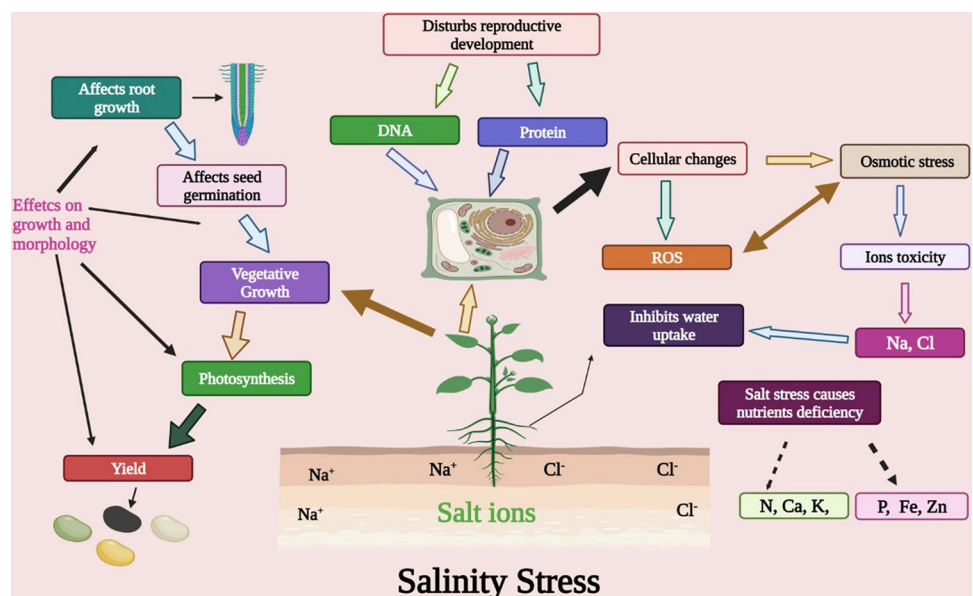


Fig. 2 Role of Tre under salinity stress. Tre application maintains optimum K^+/Na^+ , diverts excessive Na^+ , improves electron transport, efficiency of PS-11, osmolytes accumulation, genes expression, anti-oxidant activities, and reduces the MDA accumulation, ROS production and LOX therefore improve plant growth under salinity stress

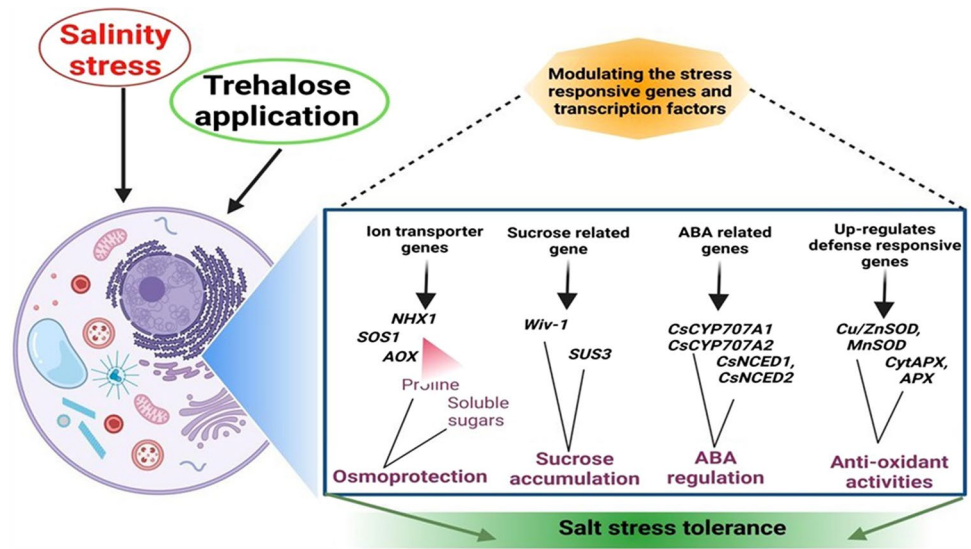
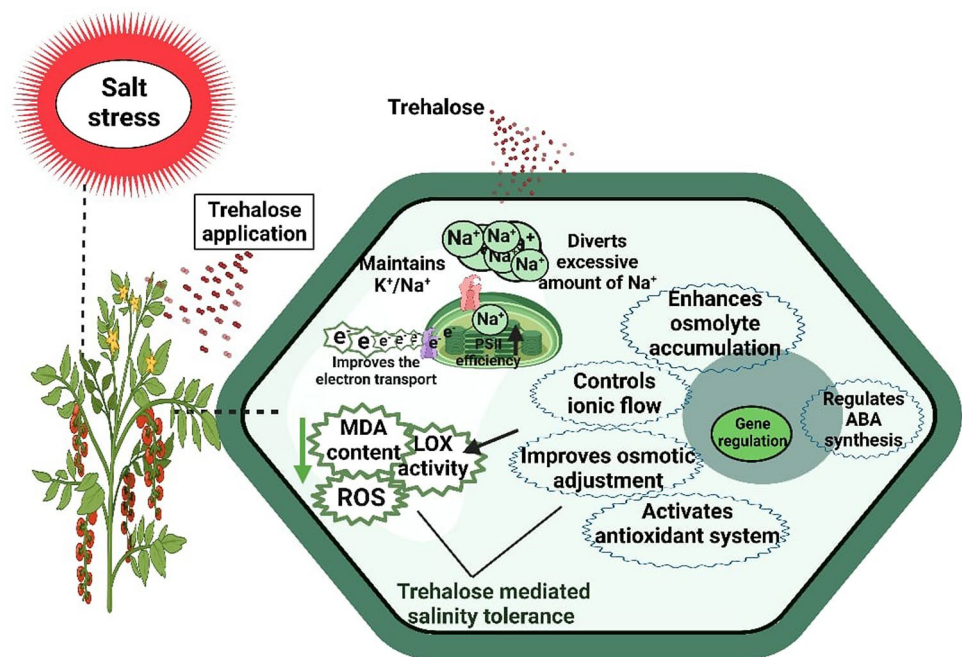


Fig. 3 Tre improves the expression of stress responsive genes and transcription factors and leading to a significant increase in salinity tolerance. Tre up-regulated the genes linked with proline and soluble sugars, and sucrose accumulation and ABA regulation and it also improved the activities of genes linked with anti-oxidant activities and leading to significant increase against salinity tolerance



Tre decreased the O_2^- accumulation and SOD activity in salt stressed rice seedlings which suggested that Tre may also take in direct scavenging of O_2^- therefore reduce the activity of SOD under SS [117].

AsA and GSH are the two major non-enzymatic antioxidants that significantly improved the stress tolerance in plants by scavenging ROS [147, 148]. Tre pre-treatment in wheat plants showed a significant ascorbic acid (AsA) and glutathione (GSH) content and their redox ratios as compared to control. Tre mediated increase in activities of AsA and GSH play a synergistic role in preventing ROS induced oxidative damage [149]. The exogenous supply

of Tre favorably modulates glycosyltransferase GTS however, it had a little impact on glutathione peroxidase (GPX) activity and confer salinity tolerance [117]. Moreover, Tre also increased activity of GSH and maintain a higher GSH/GSSG ratio in salt stress rice plants which reduced the salinity induced oxidative damages [117]. Interestingly, Tre application increased the activities of Gly-I and Gly-II which play an important role in detoxification of methylglyoxal (MG) thereby improved SS tolerance in maize plants [111]. Moreover, in maize crop Tre supplementation considerably increased the activities DHAR, MDHAR, GR and GPX and ameliorated the salinity induced oxidative damages by

scavenging ROS [111]. The strawberry plants treated with Tre also showed a marked increase in CAT, GSH and SOD activities which protected the membranes and bio-molecules by scavenging the ROS [131]. In conclusion, Tre mediated increase in antioxidant activities substantially scavenge the ROS and protect the plants from salinity induced oxidative damage.

Trehalose improves expression of stress responsive genes under salinity stress

The increase in expression of stress responsive genes improves the plant tolerance against stress conditions. The application of Tre increases the expression of AOX genes which retarded the H₂O₂ accumulation and increased the accumulation of phenolic substances to confer salinity tolerance [116]. Tre supply also up-regulated the expression of NHX1 genes and this up-regulation is linked with an increase in growth recovery and improvement in K⁺ and K⁺/Na⁺ ratio [116]. Moreover, Tre mediated increase in NHX1 also alleviated Na⁺ induced toxicity in wheat crop [116]. On the other hand, Tre also up-regulates expression of SOS1 genes which significantly decreased the Na₊ concentration and maintain a higher K⁺ and K⁺/Na⁺ ratio to confer salt tolerance [116]. The vacuolar Na⁺/H⁺ antiporter activity play a critical role in salt tolerance [150, 151]. Tre restricts the Na⁺ transportation and alleviate the salinity induced ROS production and cell death with an increase in AOX expression [116]. Additionally, an increase in expression of AOX, NHX1, and SOS1 concomitant with the regulation of proline and soluble sugars can highlight the important osmo-protective role of Tre [116].

The exogenous supplementation of Tre significantly enhanced the expression of SPS genes under SS and increases the accumulation of sucrose in tomato plants. Tre also increased the expression of sucrose synthase gene (SUS3) and acid invertase gene (Wiv-1) which maintained higher sucrose contents and contributed to a significant improvement in salinity tolerance [132]. Moreover, exogenous Tre increased the endogenous Tre contents in tomato plants, resulted in negative feedback regulation, inhibited the TPP expression, enhanced Tre gene expression, and promoted the conversion of excess Tre into glucose to maintain the stability of its content. Tre mediated differential expression of the aforementioned genes can directly affect the salt tolerance in plants [132]. NCED1 and NCED2 are important genes involved in ABA synthesis. The exogenous supply of Tre up-regulated the expression of these genes (NCED1 and NCED2) under salt stress and which indicates that exogenous Tre application has a positive effect on ABA synthesis. CYP707A1 and CYP707A2 are important genes involved in ABA metabolic pathway. The exogenous Tre application increased the expression of CYP707A1 and reduced the expression of CYP707A2 under SS [132].

In another study it was noted that exogenous supply of Tre up-regulated the expression of Cu/ZnSOD and MnSOD and CytAPX transcription and APX activity [152] which in turn improved anti-oxidant activities linked with genes resultantly improved the salt tolerance in rice [153]. Similarly, in another study Nounjan, Theerakulpisut [115] also found a significant increase in CytAPX and CatC expression following Tre application which resulted in significant improvement in anti-oxidant activities and SS tolerance. Tre also improves expression of different antioxidant genes (SiCu/Zn-SOD, SiFe-SOD, SiMn-SOD, SiPOD, and SiCAT) which counter the effects of SS and improve plant performance [154]. The transcription levels of Tre genes (TaTPPs and TaTPP1) also significantly increased under SS which improved the growth and development and plant tolerance against SS [155, 156]. In conclusion, Tre mediated increase in genes expression regulates proline and soluble sugars accumulation and antioxidant activities which therefore improve the plant performance under salinity stress.

Trehalose brought ultra-structure changes to induce salinity stress

Tre application also brought ultra-structural changes to induce SS tolerance in plants. For instance the exogenous application of Tre significantly increased the stem diameter (5.30%) epidermis thickness (6.91%) cortex thickness (19.62%), phloem tissue thickness (24.28%) xylem tissue thickness (45.45%) xylem rows in vascular cylinder (82.31%) and diameter of xylem vessel (21.21%) under SS. This increase in anatomical changes by Tre is linked with its ability to alleviate the deleterious impacts of SS [122]. Similarly, Akram et al. [157] also reported that Tre foliar spray and pre-treatment significantly improved thickness of leaf epidermis, vascular bundles, midrib thickness and thickness of vascular bundles in radish crop. Salt stress cause a significant reduction in thickness of leaf blades, and reduce the length and width vascular bundle and diameter of xylem vessels and mesophyll tissue in wheat plants. The reduction in aforementioned traits reduced assimilates translocation to plant parts therefore cause reduction in growth and yield [158]. However, Tre supplementation maintains vascular bundle and their thickness, diameter of xylem cells, mesophyll tissues and improved the xylem and phloem areas and ensure the better translocation of assimilates and resulting in significant improvement in growth and yield under SS stress [130].

Success stories of engineered trehalose for inducing salinity stress

The recent development in genetic engineering has provided the opportunities to build stress tolerant crops. A significant number of plants have been developed by using

engineering approaches having strong tolerance against a wide range of stresses [41]. The accumulation of different osmolytes, sugars and hormones significantly improves the salt tolerance in plants. Because of the promising characteristics of Tre, efforts are being made across the globe to develop the genotypes with increased levels of Tre to confer salt tolerance. For instance, the fusion of Tre gene from *E. coli* significantly increased the Tre biosynthesis and reduced the salinity induced toxic effects by increasing RWC, chlorophyll contents, stomatal conductance and maintaining optimum K^+/Na^+ ratio as compared to control plants [159]. Similarly, transgenic rice plants having over-expression of *OsTRE1* showed a significant increase in Tre activity. The over-expression of *OsTRE1* significantly enhanced the salt tolerance however, it did not impose any morphological alteration or any growth defect [160]. Similarly, transgenic rice plants with over-expression of *OsTPS1* showed a significant tolerance against cold, drought and SS. The over-expression of *OsTPS1* significantly improved the accumulation of Tre and proline and stress responsive genes (*WS118*, *RAB16C*, *HSP70*, and *ELI*) and contributes to improvement in salinity tolerance [99]. Another work showed that in transgenic rice plants over expression of *OsTPS8* improved SS tolerance by controlling the concentration of sugars and regulating the genes expression involved in ABA signaling via *SAPK9* regulation [161]. In another study, transgenic tomato plants were produced by introducing a gene encoding a bi-functional fusion of trehalose-6-phosphate synthase and trehalose-6-phosphate phosphatase genes from *E. coli*. The developed transgenic plants showed significantly higher

levels of Tre with higher photosynthetic rates and salt and drought tolerance [6]. Therefore, the development of salt tolerant cultivars could be a promising approach to improve SS tolerance in plants. However, engineering Tre biosynthesis pathway without creating any negative impacts is a major challenge. The genetic cascades of Tre can be investigated by comparing Tre enriched and deficient plants under both control and stressed conditions. Moreover, by figuring out the key nodes in Tre biosynthesis pathway whose modulation can be effective without any negative effect of SS. Lastly, it will depend on the degree of success to use those pathways for engineering salt tolerant crops.

Trehalose improves growth, yield and quality under salinity stress

Salinity stress causes a significant reduction in growth by inducing ionic, osmotic and oxidative stress [162]. However, Tre significantly improved the growth and salinity tolerance in plants (Table 2). Tre being non-toxic and compatible solute accumulates at higher concentration in the cytoplasm and maintains the cell turgor which contributes toward improvement in water uptake and subsequent plant growth [119]. Tre also stabilizes the membrane structure and prevent the loss the important solutes and resulting in significant improvement in growth and biomass production [134]. The exogenous supplementation of Tre improves anti-oxidant activities, and osmolytes accumulation and reduced the ROS production leading to significant improvement in

Table 2 Effect of trehalose application on growth, physiological processes and anti-oxidant activities under salinity stress

Crop species	Salinity stress	Tre application	Effects	References
Cotton	100 mM	50 mM	Tre application enhanced growth, RWC and activities of SOD, POD and CAT	[127, 128]
Rice	100 mM	30 μ M	Tre increased root and shoot growth, chlorophyll contents, proline, amino acids, carotenoids, starch and proline contents under salinity stress	[129]
Wheat	200 mM	20 mM	Tre application increased root and shoot length, photosynthetic pigments, RWC, carbohydrates, total soluble protein, amino acid concentration	[130]
Strawberry	50 mM	30 mM	Tre reduced the MDA and H_2O_2 concentration and improved carotenoid, flavonoids and anthocyanins compounds and growth and yield of strawberry	[131]
Rice	200 mM	10 mM	Tre application reduced the K^+ and Na^+ ratio and increased APX activity	[115]
Maize	150 mM	10 mM	Exogenous Tre increased plant growth, biomass production, chlorophyll contents, nutrient uptake and activity of SOD, CAT, APX, and GPT under saline stress	[111]
Tomato	200 mM	2 mM	Tre supply increased root and shoot growth, soluble sugars, and up-regulate sugar transport genes, and ABA content	[132]
Maize	150 mM	10 mM	Tre application increased growth, biomass, and SOD, POD activity and soluble protein contents	[133]
Cowpea	6.30 dSm^{-1}	2 g/L	Tre spray increased root length, nitrogen and crude protein contents, phosphorus and potassium and proline contents	
Quinoa	600 mM	5 mM	Tre supply improved the growth, biomass, chlorophyll contents, total soluble sugars, proline free amino acids, yield, oil percentage and activities of CAT, POD and SOD and uptake of N, P and K	[134]

mM millimolar, dSm^{-1} decisiemens per meter, μ M micro molar

growth and biomass production in maize, *Arabidopsis* and rice [45, 125]. In another study Tre application (10 mM) significantly increased the leaf fresh and dry weights by 30% and 42% under SS (50 mM) which was linked with improved proline and Tre accumulation and maintenance of anti-oxidant activities and photosynthetic performance [131].

Tre application improves water relations and stomata opening and leads to significant improvement in growth and biomass production under SS (250 mM) [124]. In another study, it was noted that Tre application resulted in more production of seeds/pod (6.89), pods/plant (9.33) seeds weight/plant (12.67) and 1000 seed weight (16.93 g) whereas the lowest values of seeds/pod (5.56), pods/plant (7.67) seeds weight/plant (8.56) and 1000 seed weight (15.66 g) was recorded in SS with Tre application [122]. Similarly, Shahbaz et al. [123] also found significant improvement in seeds/plant, 1000 seed weight, tillers and grain yield of rice following Tre application as compared to control. Soaking of wheat seeds in Tre (10 mM) ameliorated the adverse impacts of SS and improves the growth and biomass by increasing genes expression, osmolytes accumulation, K^+/Na^+ ratio and reducing Na^+ accumulation [116]. Moreover, Mohamed et al. [130] also reported a significant increase in wheat yield and yield contributing traits including grains/spike, grains weight, spikelet's and tillers of wheat with foliar spray of Tre (10 mM) grown under SS as compared to no Tre application. Tre mediated increase in growth and yield is linked with higher K^+ concentration, higher photosynthetic pigments, dry matter production, WUE, and reduced senescence and production of ROS, membrane damage, MDA and H_2O_2 accumulation [111]. In addition, Tre application also significantly improved the quality of crops grown under SS [130]. The exogenous application of increased the endogenous Tre contents, protein and amino acid contents of salt tolerant cultivars of wheat as compared to sensitive ones [130]. Tre being a carbon sugar significantly improved the concentration of sugars in tomatoes which contributed to a significant reduction in deleterious impacts of SS [132]. To summarize, Tre improves plant growth by increasing antioxidant activities, genes expression, osmolytes accumulation, K^+/Na^+ ratio and decreasing Na^+ , MDA and H_2O_2 accumulation.

Conclusion and future prospective

Trehalose application modulates plant growth and development under salinity stress. Salinity stress induces a serious reduction in plant growth and development by disturbing the plant's physiological, biochemical and molecular functioning. However, trehalose supplementation improves the plant performance under salinity stress by improving membrane integrity, water uptake, nutrient uptake, photosynthetic efficiency, and protecting the photosynthetic apparatus from

salinity induced oxidative damages. Trehalose supply also improves the accumulation of osmolytes and secondary metabolites and hormonal crosstalk thereby improving the plant performance under salinity stress. Besides this, trehalose also strengthens antioxidant activities, expression of stress responsive genes, and brought ultra-structural changes in the plant body for inducing salinity stress. Additionally, an increase in endogenous trehalose by engineering approaches also improve the genes expression, plant water relations, stomata conductance and photosynthetic efficiency and lead to a significant increase in salt tolerance.

Globally, efforts have been made to clarify trehalose role in plant responses under salinity stress, however, there are still many unanswered questions. The role of Tre in seed germination is not well explored, and it is interesting to explore the role of Tre in different processes and mechanisms involved in seed germination. The roles of Tre on nutrient uptake are also not well explored and limited studies are conducted on this aspect. Therefore, it is necessary to explore the role of Tre on nutrient uptake under salinity stress. Moreover, it would also be fascinating to explore the role of Tre in nutrient signaling and its effects on nutrient and ionic transporters. Moreover, anatomical changes taking place owing to Tre application also needed to be explored further for making it an important osmo-protectant. The role of Tre on stomata movements is poorly studied and it is necessary to explore the effect of Tre on stomata movements under salinity stress. The role of Tre on seed quality, composition and activities of antioxidant genes must also be explored under SS. Moreover, Tre signaling mechanisms and functions in different signal crosstalks at cell, tissue and organ levels are not fully explained and it is direly needed to acknowledge Tre role in signaling crosstalk under salinity stress at plant cell, tissue and organ levels.

There is missing information related to Tre cross talk with different hormones (abscisic acid auxins, cytokinins, ethylene, gibberellic acid and salicylic acid) and osmolytes (proline and glycine betaine) under salinity stress. Thus, it would be useful to unfold and discover the role of Tre in increasing the endogenous hormones to counter the effects of salinity stress. The complex relationship of Tre with these hormones and osmolytes must also be explored at transcriptomic level under salinity stress. It would also be fascinating to reveal the effect of Tre on genes and enzymes linked with synthesis of aforementioned hormones and osmolytes. Moreover, it is also crucial to explore the potential of modern techniques to identify the Tre related genes, metabolites and proteins for development of salt tolerant cultivars. The discovery of Tre mediated regulatory and metabolic pathways can provide new insights to understand the signaling network under salinity stress. The engineered Tre mediating metabolic pathways and signaling can open new vision into present knowledge to explore the Tre mediated salt tolerance

mechanism in plants. Additionally, the role of Tre is mostly explored in lab studies and it is direly needed to conduct field studies under different climatic conditions and cropping system to make it an important osmolyte. Lastly, it is direly needed to optimize the rates of Tre applied by different application methods for different crops keeping in mind the crop, climate and soil conditions.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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