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On

Role of Exogenous Trehalose in Regulation of Plants Antioxidants in Salt Stress

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Role of Exogenous Trehalose in Regulation of Plants Antioxidants in Salt Stress [1]

By

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ABSTRACT

Salt stress is one of the most threated abiotic stressor that impairs plant growth, development, and crop yields. Therefore, addressing the adverse effects of salt in all plant species has a significant impact on sustainable food production. In salt stress overproduction of reactive oxygen species (ROS) is one of the serious consequences, which results in oxidative stress. Although, plants exhibits self-antioxidant defense mechanism but it is not sufficient for plants to combat against salt induced oxidative stress .Use of exogenous osmoprotactants have been in the limelight now a days. Trehalose, a disaccharide, has been getting importance over time as an osmoprotectant against stress triggering the antioxidant molecules both enzymatic and non-enzymatic. This review aims to screen out the functions of exogenous trehalose in different plants under saline stress conditions and also elucidate the role of trehalose in mitigating salt-induced stress by regulating antioxidant activities (both enzymatic, and non-enzymatic).As most of the plants are sensitive to salt stress, but in many studies showed that exogenous trehalose (Tre) at different concentrations (like10 mM,15 m,25 mM, 30mM,50mM) and also trehalose in combination of salt elevated both enzymatic and non-enzymatic antioxidants, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione peroxidase (GPX), glutathione S-transferase (GST), and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants, such as glutathione (GSH), ascorbate (AsA), and carotenoid contents in variety of plant species. Therefore, this paper reviewed the research work done on trehalose promoting antioxidant activities against salinity stress to understand its mechanism and also tried to identify the knowledge and research gaps of trehalose. This information may complement breeders to understanding of the importance of the exogenous application of trehalose or to develop cultivars with improved trehalose biosynthesis ensuring improved plant tolerance against salt stress.

Key words: Abiotic stress; salt stress; crop improvement; oxidative stresses; osmoprotactants; antioxidant enzymes

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CHAPTER 1

INTRODUCTION

Population all across the world has been increasing day by day. It is estimated that we will need about 70% of more food than we consumed today to feed 9.7 billion people in 2050 (Cole *et al.*, 2018). But different environmental stresses may be the major constraints to plant growth and yield, causing low crop productivity and affecting global food security (Asghari *et al*., 2020). Among different stress conditions, salinity is one of the major abiotic stresses in arid and semi-arid regions that reduced crop production significantly, resulting the average yield loss of major crops (Bray *et al*., 2000). The world's most productive regions for sustainable agriculture are now being affected by soil salinization in numerous countries, including Bangladesh (Clarke *et al*., 2015). It has detrimental effects on seed germination, plant growth, and development for both local plant populations and many crops throughout the world (Munns and Tester, 2008; Minhas and Dagar, 2016; Hossen *et al.,* 2022). In order to ensure sustained agricultural productivity, effective strategies should be established in both local and global aspects (Pereira *et al*., 2020).

Soil salinity has negative effects, manifested by osmotic stress, ion imbalance, nutritional imbalance, oxidative damage through reactive oxygen species (ROS), metabolic disturbances, and reduction in cell division (Parida and Das, 2005; Arif *et al*., 2018 ; Hafez *et al.,* 2021a). Plants exposed to soil salinity result in sodium-ion itself causes direct cellular damage to plants, and additionally, a higher concentration of Na^+ in the root zone reduces K^+ absorption due to their antagonistic effects (Kheir *et al*., 2019; Hafez *et al*., 2021b) interfering with source-sink connection, cellular metabolisms such as protein synthesis and enzyme activity (Ahmad and Prasad, 2011; Chourasia *et al*., 2021). Various cellular components, including proteins, lipids, and DNA, can lead to oxidative damage due to salinity-induced ROS production, interfering with vital processes in plants (Gupta and Huang , 2014; Kumar *et al.*, 2017; Khedia *et al.*, 2019).

A typical response observed in several plant systems is the formation of osmoprotectants such as, proline (Pro), glycine-betaine (GB), sugar like trehalose (Tre) (Chen *et al.,* 2010; Suprasanna *et al.*, 2016; Fardas *et al.*, 2021) play a crucial for reducing oxidative stress through scavenging of ROS.Interestingly, trehalose exhibit an amazing mechanism to improve plant resistant against salinity stress in several plant species has been grabbed a considerable attention.

Trehalose, reducing sugar is the basic cellular biosynthetic product found in many higher plants which has unique properties to act as a potential osmoprotectant against stress triggers the antioxidant molecules both enzymatic and non-enzymatic that act as an activator of stress tolerance in plants (Garg *et al.,* 2002; Abdallah *et al.*, 2016; Luo *et al.*, 2021; Rohman *et al.*, 2021). Its mechanisms as a protectant by regulating antioxidant activities have recently got more attention from researchers to conduct experiments for stress mitigation. Moreover, the protective roles of antioxidants have been studied in different plant species but the depth studies on the variations of antioxidant activities in regards of trehalose application in salinity mitigation have not yet been elucidated demanding further studies. Therefore, this paper reviewed the research work done on trehalose promoting antioxidant activities against salinity stress to understand its mechanism and also tried to identify the knowledge and research gaps of trehalose. This information may complement breeders to understanding of the importance of the exogenous application of trehalose or to develop cultivars with improved trehalose biosynthesis ensuring improved plant tolerance against salt stress.

Therefore the current study is generalized with two objectives-

1. To screen out the functions of trehalose in different plants under saline stress conditions.
2. To elucidate the role of trehalose in mitigating salt-induced stress by regulating antioxidant activities (both enzymatic, and non-enzymatic).

CHAPTER 2

MATERIALS AND METHODS

This seminar paper is genuinely a review paper. Hence, the data assembled for writing this paper are secondary data collected exclusively from different published reports, articles, conference papers in various journals and websites, and other books available on the internet. Moreover, I improved this paper with valuable suggestions from my respected major professor and course instructors. After gathering all relevant information, it was compiled and rationally presented in its current form.

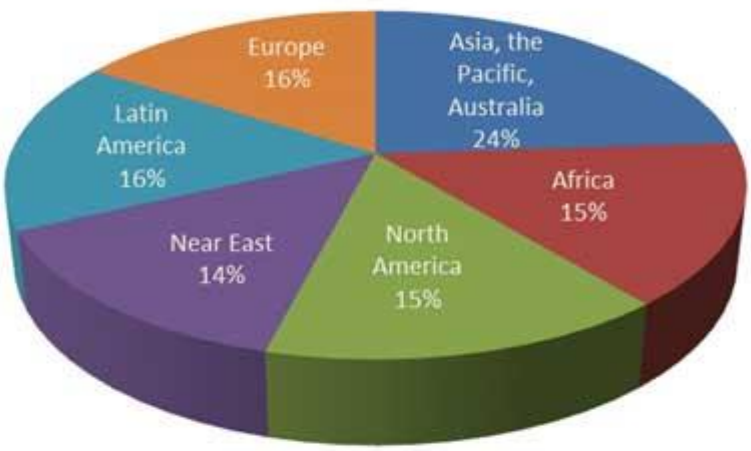
CHAPTER 3

REIEW OF FINDINGS

3.1 Salinity

Salinity is the term used to describe a soil's high soluble salt content. A large area of the world's productive land for sustainable agriculture, including Bangladesh, is currently being affected by soil salinization (Clarke *et a*l., 2015). Increased soil salinity will be a glaring barrier for many crops around the world as well as native plant communities. When salt is deposited on soils, it happens naturally (primary) or as a result of human activity (secondary). Three primary processes are atmospheric deposition, seawater deposition, and weathering of parent rocks. Inadequate drainage systems, irrigation with brackish groundwater, long periods of continuous irrigation, poor water management practices, and cultural irrigation techniques are examples of secondary processes (FAO, 2015).

Around 20 percent of the world's cultivable land is currently thought to be under saline stress and by 2050, that percentage is expected to rise to 30 percent (Otlewska *et al*., 2020).Based on Srivastava *et al.,* (2019), figure 1 shows the distribution of saline soils around the world.



(Source: Srivastava *et al.*, 2019)

Figure 1. Distribution of salt affected soils in the world (Mha).

The amount of coastal land in Bangladesh that has already been impacted by salinity ranges from 0.87 Mha to 2.85 Mha (Lutts *et al.,* 1995).One-third of the world's irrigated land area and about 6% of the planet's total land area are both impacted by salinity, either directly or by secondary salinity. 20% of irrigated land and 2% of dry land in the cultivable area are affected by salinity either directly or by secondary salinity (Munns and Tester, 2008; Hossen *et al.,* 2022).

3.2 Impact of salinity on plants

Plant productivity and survival can be impacted by biotic and abiotic stresses including herbivory, inadequate nutrient availability, salinity, drought, and diseases (Pandey *et al*., 2017). Soil salinity is one of the main stresses that inhibit plant growth and development. Many of the morphological, physiological, and biochemical processes that are disrupted by salt stress are visible at the cellular level in plants (Maslenkova *et al*., 1992; Kordrostam *et al.*,2017; Polash *et al.*,2019).

Excessive salinity can cause a number of detrimental effects in plant cells, including ionic stress due to the buildup of Na^+ and Cl^-, osmotic stress caused water deficit, and oxidative stress involved the excessive production of reactive oxygen species (ROS) (Munns and Tester, 2008; Gupta and Huang, 2014). Salinity can also lead to nutritional imbalance, particularly K^+ deficiency, by preventing K^+ uptake and causing K^+ leakage from cells (Cuin *et al*., 2008; Parihar *et al*., 2015). In response to salt stress, there is an increase in the production of ROS, including singlet oxygen ($^1O_{2)}$, superoxide, hydroxyl radicals ($O_2^{\bullet-}$) and hydrogen peroxide ($OH^{\bullet}$). Salinity-induced cytotoxic ROS causing oxidative damage to a variety of cellular constituents, including proteins, lipids, and DNA, interfering with crucial cellular processes in plants (Apel and Hirt, 2004; Ahmad, 2010; Ahmad and Prasad, 2011; Ahmad and Umar, 2011). The most frequent method of detoxifying ROS produced during the stress response is the induction of ROS-scavenging enzymes, which includes both enzymatic and non-enzymatic antioxidants, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione peroxidase (GPX), glutathione S-transferase (GST), and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants, such as glutathione (GSH), ascorbate (AsA), tocopherols, total phenolic, total flavonoids, and carotenoids (Tanveer and Shabala, 2018; Tewari *et al.*, 2021; Mostofa *et al.*, 2020; Bhat *et al*., 2022). But plants are compelled intensively while overcoming salinity stress causing decreased production. It is clear that global agricultural sustainability and food security are severely threatened by salinity. Therefore, it is critical to construct efficient and practical ways to reduce salt stress detrimental effects on plant growth and development (Phang *et al*., 2008).

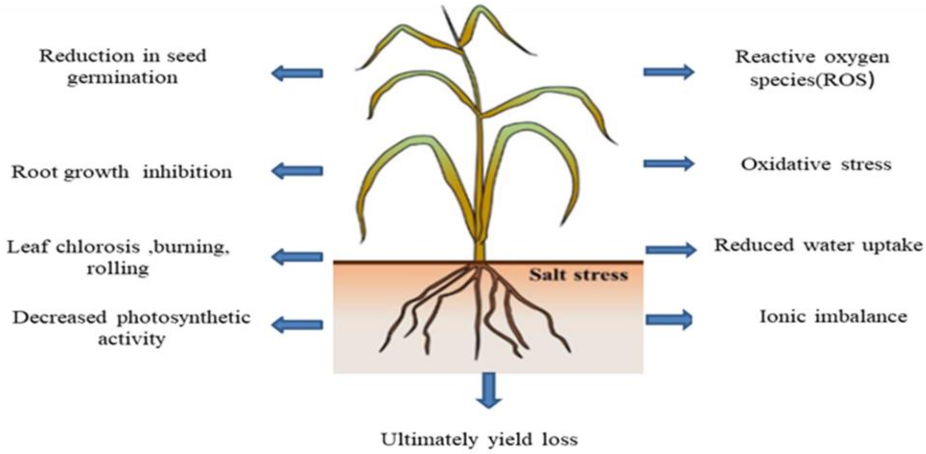


Figure 2. Impact of salinity on plant.

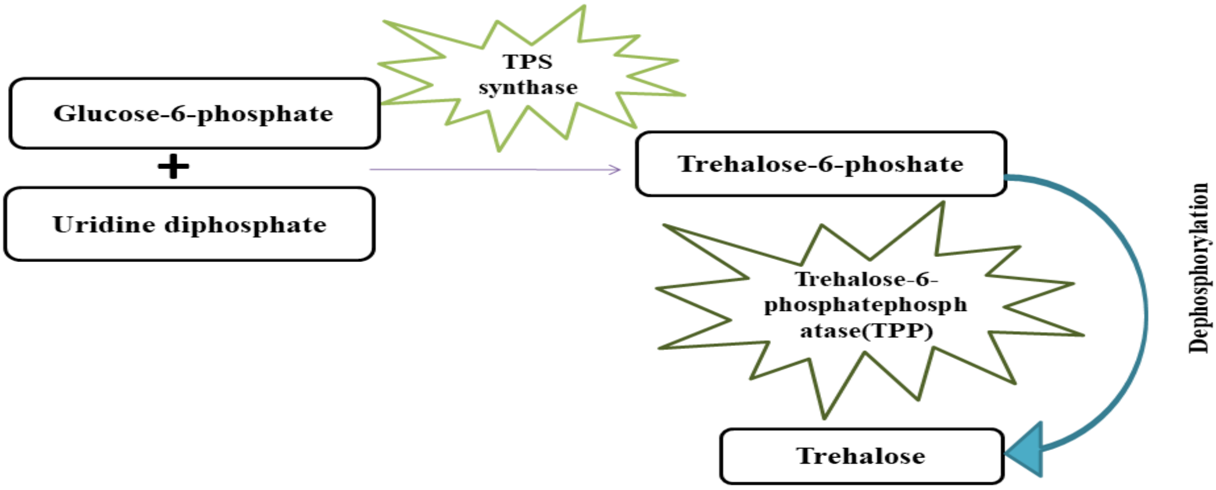
3.3 Osmoprotectants/Exogenous chemicals, its importance in salt stress mitigation

Salt stress a multigenic trait controlled by adapting certain mechanisms, like synthesis of low molecular weight compatible osmoprotectants (proline, salicylic acid,ascorbic acid, glycine-betaine, trehalose etc.) at their cellular level (Chen *et al.,* 2010; Mahboob *et al.,* 2016; Suprasanna *et al.,* 2016; Fardas *et al.,* 2021). These osmoprotectants have the capacity to adjust osmotic balance by scavenging ROS at cellular level during stressful conditions (Gill and Tuteja, 2010). The external application of osmoprotectants, like ascorbic acid, proline, salicylic acid, and trehalose evolved dynamic mechanisms that the plants can withstand salt stress even in growth and development stages (Sing *et al.,* 2015; Noreen *et al.,* 2018).

3.4 Trehalose, its structure and biosynthesis in plants

Trehalose (Tre) is a non-reducing disaccharide, composed of two glucose subunits linked by α , α-1, 1 glycosidic bond that make them unique from the other disaccharides (Teramoto *et al.*, 2008).

In many plants including *Selaginella lepidophylla, Myrothamnus fabellifolius*, tobacco and rice Tre is naturally present (Gechev *et al.,* 2014; Schwarz *et al.,* 2017; Kosar *et al.,*2019). In plants Tre biosynthesis related to 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) (Ponu *et al*.,2011) (figure 3).But unfortunately the synthesis of trehalose in plants is not sufficient to protect against abiotic stress.



(Source: Wingler, 2002)

Figure 3. Biosynthesis of trehalose in plants.

3.5 Trehalose induce salt stress tolerance by regulating antioxidants

Interestingly, trehalose exhibit an amazing mechanism to improve plant resistant against salinity stress in several plant species has been grabbed a considerable attention (Bae *et al.*, 2005; Phang *et al.*, 2008). Trehalose stabilizes the biological molecules like dehydrated enzymes, proteins and membranes, DNA, RNA etc. from the devastating impacts of abiotic stresses (Luo *et al.*, 2021; Rohman *et al.*, 2021). In many previous studies, revealed that exogenous trehalose has no impact on CAT activity however, it significantly increased the activities of POD and SOD to protect the negative effects of salt stress (Luo *et al.*, 2010; Nounjan *et al.*, 2014; Abdallah *et al.*, 2011).In other studies, documented that trehalose application alleviated adverse effects of salt stress by decreasing H_2O_2 production through enhanced antioxidant activities (APX, CAT, POD and SOD) (Theerakulpisut *et al.*, 2013; Shahbaz *et al.*, 2017).Also, Feng *et al.*, (2019) proposed that exogenous supply of trehalose reduced osmotic and oxidative injuries by increasing the activities of CAT, POD and SOD during salinity stress. Trehalose application was effective to stabilize different biological molecules like protein, DNA, RNA, membranes and activate the antioxidant defense system (Abdallah *et al*,. 2016; Rohman *et al.*, 2019),which in turn reduced ion leakage and lipid peroxidation, resulting in substantial plant homeostasis under salt stress (Zeid, 2009). Trehalose also provokes the accumulation antioxidant activities like,ascorbic peroxidase(APX); catalase (CAT); peroxidase (POD); superoxide dismutase (SOD), which protected the plants from salt-induced oxidative stress and improved growth (Abdallah*et al.*, 2020).

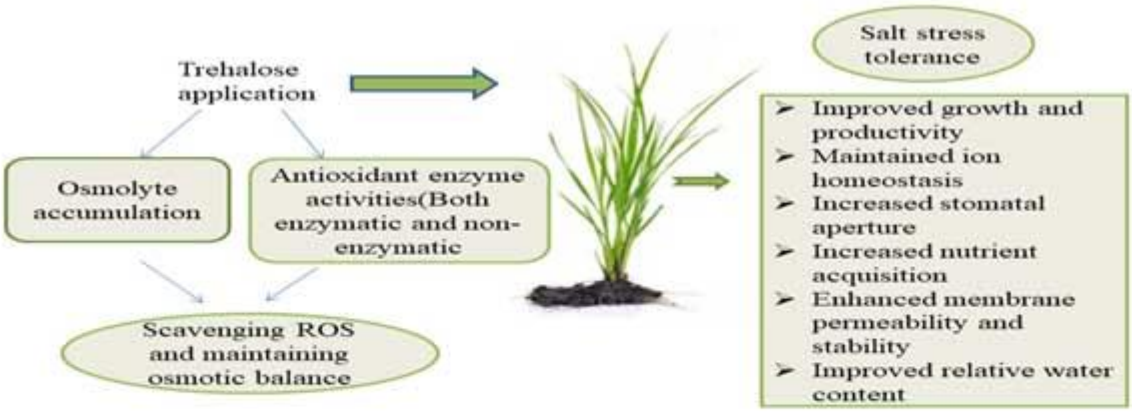


Figure 4. Trehalose induced salt tolerance by activating antioxidants defense mechanism

Exogenously applied trehalose upregulated the osmolytes accumulation that scavenge the rising level of toxic ion ROS and elevated the antioxidant activity as a result plant showed tolarancy (figure 4)

3.6 Antioxidant defense mechanisms in plants

The accumulation of reacting oxygen species (ROS) is the signaling molecule that exhibit that plants were in stress (Ferreira *et al.*, 2007).Then the antioxidant defense system was activated to protect the plant from oxidative damage under stress conditions(Singh *et al.,* 2008).Some major ROS scavenging antioxidant enzymes (table 1) had been seen.

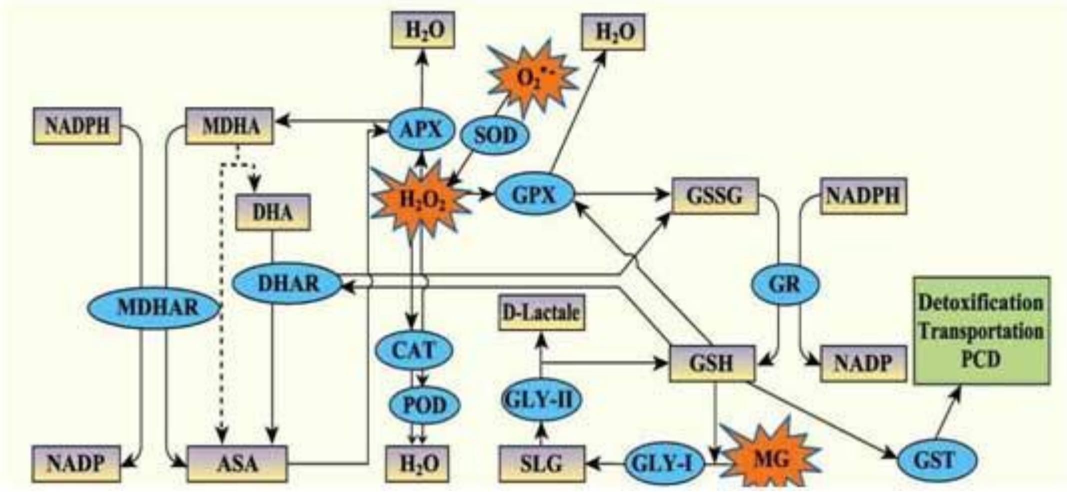
Table 1. Major reacting oxygen species (ROS) scavenging antioxidant enzymes

Enzymatic antioxidants	Enzyme code	Reactions catalyzed
Superoxide dismutase(SOD)	EC 1.15.1.1	$O_2^{\bullet-}+O_2^{\bullet-}+2H^+ \rightarrow 2H_2O_2+O_2$
Catalase(CAT)	EC 1.11.1.6	$H_2O_2 \rightarrow H_2O + 1/2O_2$
Ascorbate peroxidase (APX)	EC 1.11.1.11	$H_2O_2 + AA \rightarrow 2H_2O + DHA$
Glutathione peroxidase (GPX)	EC 1.11.1.7	$H_2O_2 + GSH \rightarrow H_2O + GSSH$
Monohydroascorbate reductase(MDHAR)	EC 1.6.5.4	$MDHA + NDA(P)H \rightarrow AA + NDA(P)^+$
Dehydroascorbate reductase (DHAR)	EC 1.8.5.1	$DHA + 2GSH \rightarrow AA + GSSG$
Glutathione reductase(GR)	EC 1.6.4.2	$GSSG + NAD(P)H \rightarrow 2GSH + NAD(P)^+$

(Source: Monsur *et al.*, 2022)

Antioxidants are two types.

1. Enzymatic antioxidants: SOD, POD, CAT, APX, MDHAR, DHAR, GR, GPX, GST.
2. Non-enzymatic antioxidants: AsA, GSH, Phenolic compounds, Alkaloids, Carotenoids etc.



(Source: Hossain *et al.*, 2011)

Figure 5. Mechanism of antioxidants to detoxify reactive oxygen species (ROS) [SOD-Superoxide dismutase; POD- Peroxidase; CAT-Catalase; GPX-Glutathione peroxidase; GST-Glutathione S-transferase; APX-Ascorbate peroxidase; MDHAR-Monodehydroascorbate reductase; DHAR- Dehydroascorbate reductase; GR-Glutathione reductase; ASA-Ascorbic acid; DHA-Dehydroascorbate; GSH-Reduced glutathione; GSSG- Oxidized glutathione; MG-Methylglyoxal; Gly-I- Glyoxalase-I;Gly-II- Glyoxalase-II].

During salt stress,in antioxidant defense network the singlet oxygen species $O_2^{\bullet-}$ was converted to $H_2O_2$was detoxified by SOD. Then CAT, POD, APX rapidly decomposes H_2O_2 and produced H_2O and O_2.But in absence of APX all enzyme function was stopped. In the AsA-GSH cycle,APX detoxify H_2O_2 and oxides AsA to produce monohydroascorbate(MDHA) and ascorbate dehydroascorbate(DHA) that recycle the AsA.GSSG is from the oxidation of GSH,GR reduces GSSG to GSH.GPX reduces H_2O_2 and protect the cell from oxidative stress. GST accelerated the activity of GPX and significantly reduced the reactive oxygen species (ROS) (figure 5)

3.7 Role of Exogenous Trehalose in regulation of antioxidant activities during salt stress in different plant species

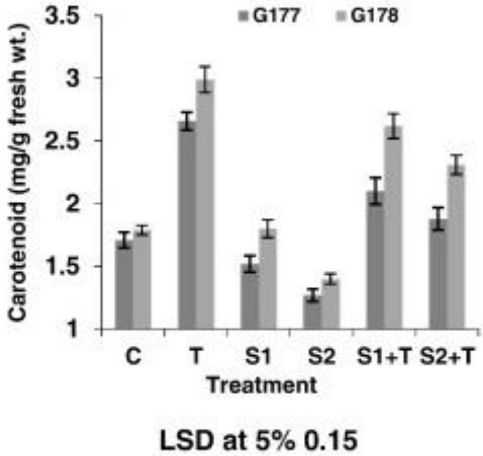
Improvement of plant resistance against salinity stress by different concentrations of trehalose application in several plant species in (table 2) had been seen.

Table 2. List of some plant species that are trehalose mediated and effects on regulation of antioxidant defense system under different concentrations of salt stress

Plant species	Stress conditions	Trehalose application	Impact on antioxidant defense	References
Rice	200 mM NaCl	10mM	Increased SOD,CAT,APX and POD activity	Nounjan *et al*.,2012
	250 mM NaCl	10mM	Reduced LOX,ROS,MDA and increased SOD,APX,GPX,GR and decreased CAT and GST	Mostafa *et al*.,2015
	170 mm NaCl	10mM	Reduced $H_2O_2$and MDA	Theerakulpisuland Gunnula, 2012
	100 mM NaCl	10mM	Increased APX,CAT and proline content	Nounjan *et al*.,2014
Maize	150 mM NaCl	15mM	Increased CAT,APX,GPA,GR,DHAR and MDHAR	Rohman *et al*.,2019
Wheat	200 mM NaCl imposed after 20 days after sowing	10mM	Trehalose improves soluble protein,proline	Mohamed *et al*.,2018
Cotton	17 ds/m	50mMI	Increased SOD,POD andAPX	Shahzad *et al*.,2020
Tomato	200 mM	10mM	Increased RWC ,sugar accumulation,ABA content and decreased MDA content	Feng *et al*., 2019
Cowpea	6.30 ds/m	1mM	Improved total phenolic contents	Eisa and Ibrahim,2016

3.7.1 Role of Tre on Rice

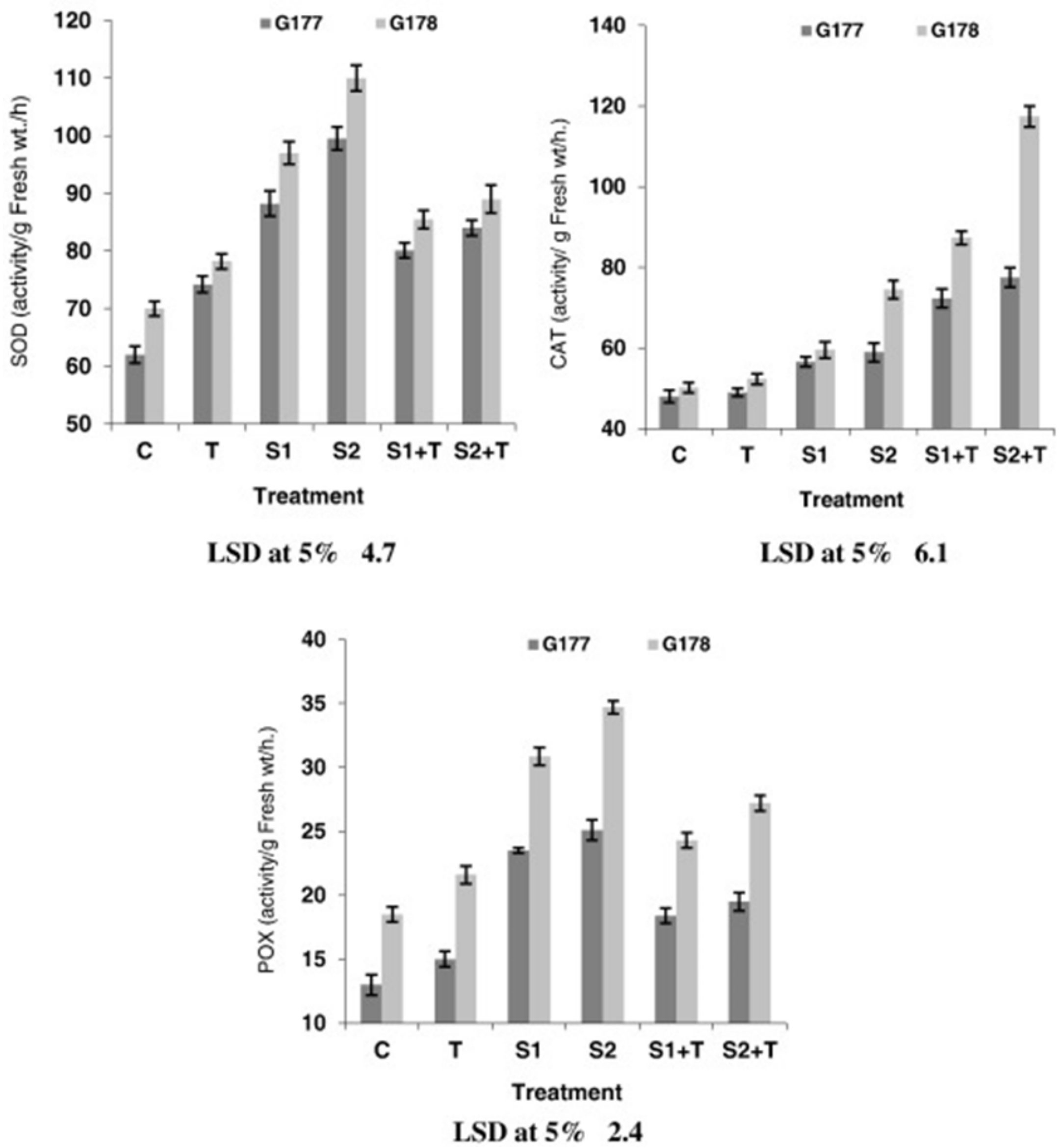
Several studies were conducted to find out the effects of trehalose regulate the antioxidant activities in rice plant that’s why the rice plant showed the better performance even in salinity stress. Results suggested that exogenous trehalose at different concentrations or foliar spray enhanced antioxidant enzymes activity that can scavenge the toxic effects of salt induce stress (figure 6,7,8 and table 3).



(Source: Abdallah*et al.*, 2016)

Figure 6. Effects of salinity (S), Trehalose (T) and their interaction on carotenoid content as (mg/g fresh weight) of rice plants grown under salinity stress (at 35 days after sowing) [Each value represents the mean ± standard error (n = 3)].

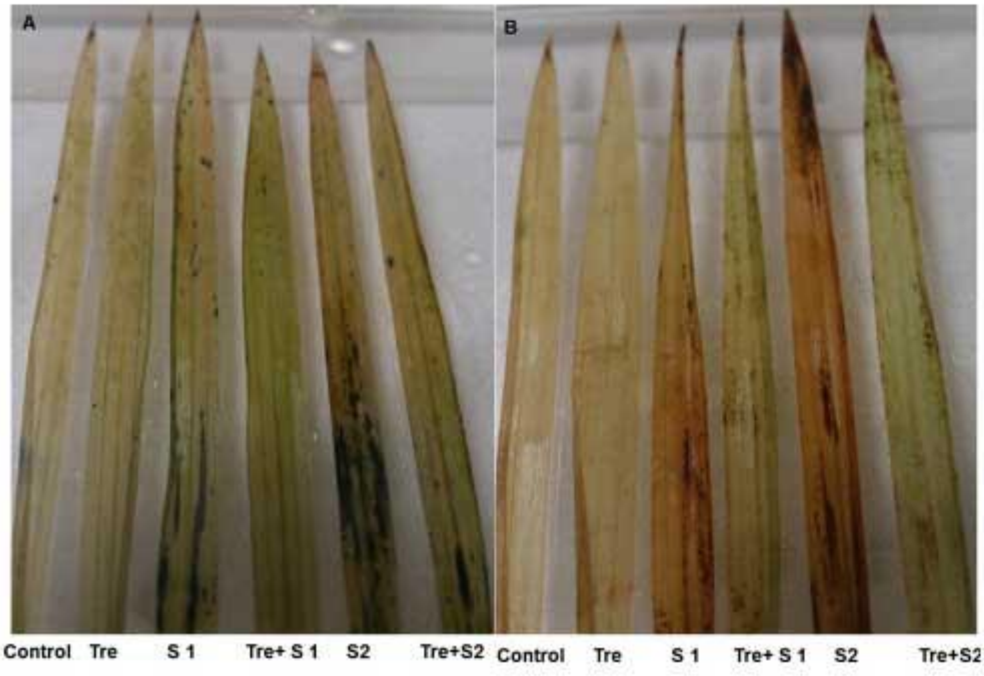
Abdallah *et al.,*(2016), in his study, pre-soaked rice seeds were treated with trehalose at concentration of 25mM that significantly increased carotenoid content when compared with the control plants and saline treatment plants of both varieties (figure 6). Trehalose with the combination of different concentrations of salt (S1+T; S2+T), progressively increased chlorophyll content in rice seedlings of both varieties (G 177, G178). Carotenoids have the capacity to scavenge free radical, then increasing of carotenoid content in both varieties when treated with trehalose enhance their capacity to turn increased chlorophyll content of rice seedlings during salt stresses.



(Source: Abdallah*et al.,* 2016)

Figure 7. Effects of salinity (S), Trehalose (T) and their interactions on superoxide dismutase (SOD), catalase (CAT) and peroxidase (POX) enzymes (activity/g fresh weight/hours) of rice plants (at 35 days after sowing) [Each value represents the mean ± standard error (n = 3)].

In the same study, we observed that the pre-soaked rice seeds when treated with trehalose at concentration of 25mM and trehalose with the combination of different concentrations of salt (S1+T; S2+T), rice variety Giza 178 had higher activities of SOD, CAT and POX than Giza 177 when compared the both varieties with normal and stressed plants(figure 7). These increased antioxidant enzymes superoxide dismutase (SOD), catalase (CAT) have the positive effects to scavenge superoxide radicals and H_2O_2 scavenge by mitigating salt-induced oxidative stress (Dolatabadian and Saleh Jouneghani, 2009).



(Source: Mostofa *et al.*, 2015)

Figure 8: Effect of exogenous trehalose on $O_2^{\bullet-}$(A) and H_2O_2 (B) production in rice seedlings with and without NaCl stress (Control, Tre, S1, Tre+S1, S2, and Tre+S2 correspond to control, 10 mM trehalose, 150 mM NaCl, 10 mM trehalose+150 mM NaCl, 250 mM NaCl, and 10 mM trehalose+250 mM NaCl, respectively).

Exogenously application of trehalose, increased the SOD antioxidant enzyme that has the potent ability to reduce the contents of $O_2^{\bullet-}$ and H_2O_2 in Tre and combined application of trehalose (Tre+S1 and Tre+ S2) and diminished at varying degrees of staining was lighter (figure 8).

Table 3.Effect of exogenous trehalose on the levels of non-enzymatic antioxidants (AsA and GSH) in rice seedlings with and without NaCl stress (Data are represented as means ± SD from three independent experiments. Different letters within the same column indicate significant differences between treatments at $p<0.05$, according to DMRT)

Treatment	Total AsA content(nmol/g FW)	AsA/DHA ratio	GSH content(nmol/g FW)	GSH/GSSG ratio
Control	5,180.83±226.66e	5.27±1.26d	501.98±18.76a	21.75±2.55de
Tre	6,189.33±149.56f	5.79±1.03d	507.53±27.25a	20.36±2.57d
S1	4,505.83±156.97c	2.43±0.28b	676.27±48.40b	12.65±1.68b
Tre+S1	4,837.50±397.81d	4.39±0.89c	706.72±62.86b	22.25±3.13e

S2	1,882.60±152.67a	1.49±0.27a	970.13±64.87c	9.98±1.58a
Tre+S2	3,437.50±352.75b	2.08±0.15b	1,047.05±66.29d	15.43±0.77c

(Source: Mostofa *et al.*, 2015)

Mostofa *et al.*, (2015), in his study we observed that in, the dark blue staining indicate that rice leaves which was exposed to salt compared to control plants, which indicates the formation of $O_2^{\bullet -}$,but application of trehalose (Tre) and combination of trehalose with NaCl (Tre+S1, Tre+S2) significantly able to reduce staining intensity, which can be achieved through tre-mediated increased SOD activity (figure 8).But exogenous application of trehalose (Tre) and also the combined activity of trehalose (Tre+S1, Tre+S2) were able to fold up the level of CAT, GPX,GST, APX, MDHAR, DHAR and GR of these antioxidants. Same trend happened on the levels of non-enzymatic antioxidants (table 3).

3.7.2 Role of Tre on Wheat

Sadak *et al.*, (2019), in his study reported that exogenous application of trehalose at different concentrations (0mM, 10mM and 50mM) increased both the enzymatic and non-enzymatic antioxidant activities during salt stress.

Table 4. Effect of trehalose on antioxidant activities (both enzymatic and non-enzymatic) of wheat plants in salt stress

Salinity(ds/m)	Trehalose con.(mM)	Chl a	Chl b	Carotenoids	Phenolic content	H_2O_2	MDA	LOX
						(nmol/g FW)		(U/min/g FW)
S_0(Tap water)	Tre0(0mM)	1.128	0.465	0.269	352.51	21.85	32.52	12.52
	Tre1(10mM)	1.302	0.536	0.323	392.52	16.52	29.42	11.54
	Tre2(50mM)	1.365	0.629	0.381	435.53	15.52	25.6	10.98
S_1(Sea water 6.25 ds/m)	Tre0(0mM)	0.858	0.335	214	424.52	41.84	45.87	21.87
	Tre1(10mM)	1.035	0.428	0.282	528.65	32.42	38.65	16.75
	Tre2(50mM)	1.169	0.537	0.317	575.35	26.85	34.54	13.84

(Source: Sadak*et al.*, 2019)

In this study, data showed that during salt stress in wheat plants the photosynthetic pigments (Chl a, Chl b),carotenoids, phenolic contents were decreased but application of trehalose at different concentration(Tre1,Tre2) the photosynthetic pigments, carotenoids, phenolic content was significantly increased when compared with salinity-stressed and unstressed leaves (table 4).Also the lipoxygenase activity in wheat leaves was increased under salinity stress (S_1) when compared to non-stressed control plants (S_0), but plants treated with trehalose combined with salinity treatment, LOX enzyme activity decreased gradually as compared to control plants and lessen the H_2O_2 and MDA content also(table 4).This shows the positive effects of antioxidant that provoked by the trehalose treatments and helps the wheat plant enduring against salt stress.

3.7.3 Role of Tre on Maize

Rohman *et al.,* (2019), revealed that application of trehalose (10mM) exogenously in two maize varieties significantly regulated the antioxidant activities during salt stress.

Table 5. Effect of trehalose on antioxidant activities in leaves of maize seedlings under saline stress [values within a column with different letters are significant at $p<0.05$, applying the LSD test, SOD (unit/min/mg protein), POD, CAT, APX (µmol/min/mg protein), GPX, GR, MDHAR, DHAR, GST (nmol/min/mg protein)]

Source of variation	Mean sum of square								
	SOD	POD	CAT	GPX	APX	GR	MDHAR	DHAR	GST
C_0(BHM-7)	107	0.49^{d-f}	45.3	76.2^{de}	1.27^{a}	54.9	46.1^{a}	118.9^{c-e}	107
C_1(BHM-9)	85.1	0.40^{fg}	33.2	76.6^{de}	0.83^{c-f}	42.4	32.3^{d-f}	80.9^{gh}	85.1
S_0(BHM-7)	103	0.57^{cd}	37.4	96.6^{bc}	1.09^{b}	58.4	45.3^{a}	128.2^{b-d}	103
S_1(BHM-9)	84.7	0.65^{bc}	31.3	98.9^{bc}	0.78^{d-f}	54.2	29.4^{d-g}	148.0^{ab}	84.7
S_0+Tre(BHM-7)	100	0.51^{de}	36.9	124.0^{a}	0.95^{bc}	69.1	42.4^{ab}	142.0^{bc}	100
S_1+Tre(BHM-9)	79.8	0.59^{cd}	30.5	109.0^{ab}	0.75^{e-g}	59.7	29.1^{d-g}	167.0^{a}	79.8

(Source: Rohman *et al.,* 2019)

In this study, data showed that trehalose significantly affects the antioxidant activities during salinity stress. SOD and POD activity was significantly increased with trehalose treatments. The enzyme like APX, GPX, DHAR, MDHAR, GR, and GST also enhances by trehalose application in two maize varieties (table 5).

3.7.4 Role of Tre on Strawberry plant

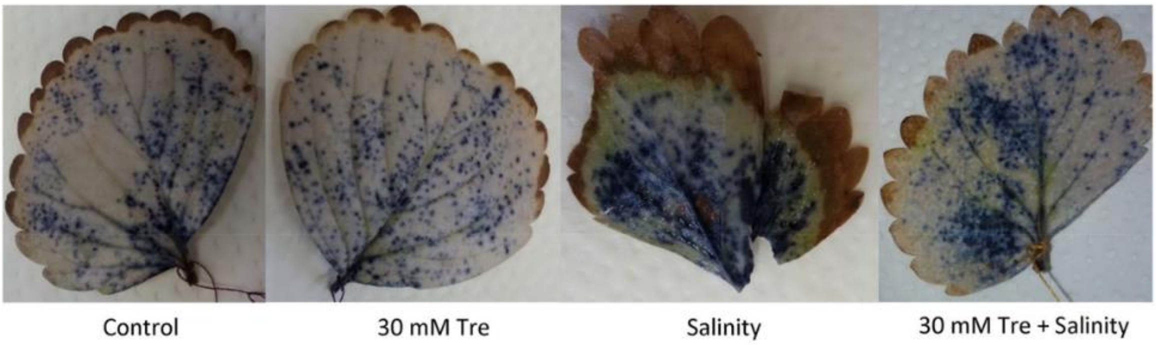
In strawberry when Trehalose applied at different concentration(0mM,10mM,30mm) in root induced antioxidant activities (Samadi *et al.*,2019)

Table 6. Effects of root-applied trehalose on the activity of superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX) of strawberry under salt stress [Measurements were performed 7 days after salt treatment, Data of each column indicated by the same letter are not significantly different (P<0.05, Tukey test). Values are the mean ± SD]

Treatments	SOD((Umg^{-1}protein)	CAT (µmol mg^{-1} protein min^{-1})	GPX(nmol mg^{-1} protein min^{-1})
−Salinity			
0 mM Tre	11.7±0.22[bc]	0.54±0.23[b]	0.76±0.45[a]
10 mM Tre	13.5±1.56[ab]	0.53±0.25[b]	0.75±0.06[a]
30 mM Tre	8.29±0.19[d]	0.55±0.20[b]	1.37±0.36[a]
+Salinity			
0 mM Tre	11.2±0.67[c]	1.49±0.27[a]	1.34±0.32[a]
10 mM Tre	12.2±1.40[bc]	1.35±0.19a	0.86±0.19[a]
30 mM Tre	14.7±0.20[a]	1.22±0.40[a]	0.82±0.13[a]

(Source: Samadi *et al.*, 2019)

Samadi *et al.,* (2019), in his study, also showed the antioxidant activities in strawberry plants treated with 30 mM trehalose enhanced SOD, CAT and GPX activity during salinity stress compared with the control plants.



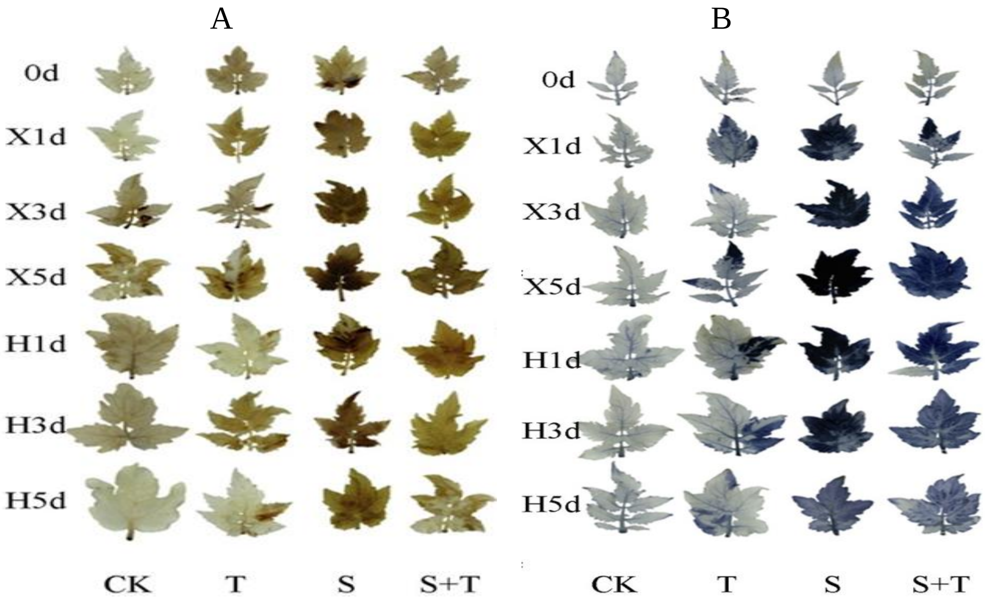
Source: Samadi *et al.*, 2019

Figure 9. Effects of root-applied trehalose on the accumulation of superoxide anion (after NBT staining) in strawberry leaves under salt stress.

We observed in, the dark blue staining indicate that leaves which was exposed to salt compared to control plants, which indicates the formation of $O_2^{\bullet-}$ but application of trehalose(30-mM) significantly able to reduce staining intensity, which can be achieved through tre-mediated increased SOD activity(figure 9).

3.7.5 Role of Tre on Tomato plant

Trehalose treatments positively regulate the antioxidant activities in tomato plant.



(Source: Yang *et al.,* 2022)

Figure 10. Effects of exogenous trehalose on the accumulation of superoxide anion in tomato leaves under salt stress [(A) Diaminobenzidine (DAB) staining. (B) Nitro blue tetrazolium (NBT) staining.CK, control; T, 10 mM Trehalose; S, 150 mM NaCl; S + T, 150 mM NaCl +10 mM Trehalose].

Yang *et al.,* (2022) in his study, showed that when salt stress was imposed in tomato plant and as a result the contents of $O^{2\bullet-}$ and H_2O_2 was increased the intensity of dark-brown and blue staining was deeper (figure 10 a and b). But the application of trehalose, increased the SOD antioxidant enzyme that has the potent ability to reduce the contents of $O_2^{\bullet-}$and H_2O_2 in S and S + T during salt stress and diminished at varying degrees of staining was lighter (figure 10).

3.7.6 Role of Tre on Quinoa plant

Different concentration of trehalose treatments positively regulates the antioxidant activities in quinoa plant (Abdhallah *et al.,* 2020).

Table 7. Antioxidant enzyme (µg/g FW) of quinoa plants treated with trehalose with (+) and without (−)compost amendment under salinity stress

Salinity (mg/L)	Trehlose conc. (mM)		SOD		CAT		POX		APX	
			-	+	-	+	-	+	-	+
0	Control		18.26	20.11	55.32	60.33	31.21	36.27	7.82	9.06
	Trehalose	2.5	20.03	21.45	60.45	61.56	38.69	40.61	12.87	12.87
	Trehalose	5.0	22.12	23.89	61.78	63.12	40.88	44.05	13.60	13.60
3000	Control		25.77	26.63	60.93	60.35	23.04	31.21	12.22	13.22
	Trehalose	2.5	28.7	30.21	61.96	6.28	28.67	36.35	14.00	14.00
	Trehalose	5.0	30.87	32.54	63.00	72.31	32.54	37.45	14.86	14.86
6000	Control		33.13	3605	62.71	62.21	15.56	23.28	14.1	14.62
	Trehalose	2.5	38.74	40.32	68.24	74.47	20.4	28.32	17.30	17.30
	Trehalose	5.0	40.01	44.14	71.30	80.46	23.58	29.14	19.33	19.33

Source: Abdhallah *et al.*, 2020

In this study, data showed the activities of the antioxidant enzymes (SOD, CAT, POX, and APX) in the shoots of quinoa plant gradually increased when treated with different concentration of trehalose (2.5mM and 5mM) but SOD, CAT, APX and POX activity gradually decreased in different saline concentration (0, 3000,600 mg/L) as compared with the control (table 7).These antioxidant enzymes helps the quinoa plant survive into salt stress by reduced the salt-induced oxidative stresses.

CHAPTER 4
CONCLUSION

According to the findings,

- In order to detoxify excess reactive oxygen species (ROS) that is created under various environmental challenges, plants are equipped with a sophisticated and very effective antioxidative defense system. The reactive oxygen species (ROS), H_2O_2 content significantly enhanced in response to salt stress, which is a clear indicator of oxidative stress in plants.Importantly,a significant reduction of ROS,such as $O_2^{\bullet-}$, H_2O_2 ,MDA content lower in exogenously treated trehalose plants with compare to control plant in different plant species during salt stress.
- The application of exogenous trehalose at different concentrations to plants under salt stresses also improves the activities of antioxidants and provides protection against oxidative stress, but the combined application of this trehalose and salt substantially upregulates the enzyme activity compared to salt alone. Several studies showed that exogenous trehalose (Tre) at concentrations of 10 mM, 15 m, 25 mM, 30 mM, 50mM gives higher SOD, POD, APX, GPX, GST, CAT, carotenoids contents and flavonoid activities compared with the control, and also the combined application of the trehalose induced salt-stressed plants by upregulating of all antioxidant activities than the salt-treated plants only.

Therefore, trehalose is a natural versatile disaccharide that not only neutralize the salt induce oxidative stress but also upregulated the antioxidant activities for different plants to combat against the salt stress.

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