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Impacts of Salinity Stress on Plants and Their Tolerance Strategies: A Review

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ABSTRACT

The environmental stress is a major area of scientific concern because it constraints plant as well as crop productivity. This situation has been further worsened by anthropogenic activities. Salinity is a major abiotic stress limiting growth and productivity of plants in many areas of the world due to increasing use of poor quality of water for irrigation and soil salinization. Plant adaptation or tolerance to salinity stress involves complex physiological traits, metabolic pathways, and molecular or gene networks. A comprehensive understanding on how plants respond to salinity stress at different levels and an integrated approach of combining molecular tools with physiological and biochemical techniques are imperative for the development of salt-tolerant varieties of plants in salt-affected areas. Salt stress causes decrease in plant growth and productivity by disrupting physiological processes, especially photosynthesis. The accumulation of intracellular sodium ions at salt stress changes the ratio of K: Na, which seems to affect the bio energetic processes of photosynthesis. Here, we review recent discoveries on regulatory systems that link sensing and signaling of these environmental cues focusing on the integrative function of transcription activators. Key components that control and modulate stress adaptive pathways include transcription factors (TFs) ranging from bZIP, AP2/ERF, and MYB proteins to general TFs. Recent studies indicate that molecular dynamics as specific homodimerizations and eterodimerizations as well as modular flexibility and posttranslational modifications determine the functional specificity of TFs in environmental adaptation. Function of central regulators as NAC, WRKY, and zinc finger proteins may be modulated by mechanisms as small RNA (miRNA)-mediated posttranscriptional silencing and reactive oxygen species signaling. In addition to the key function of hub factors of stress tolerance within hierarchical regulatory networks, epigenetic processes as DNA methylation and posttranslational modifications of histones highly influence the efficiency of stress-induced gene expression. Comprehensive elucidation of dynamic coordination of drought and salt responsive TFs in interacting pathways and their specific integration in the cellular network of stress adaptation will provide new opportunities for the engineering of plant tolerance to these environmental stressors.

Keywords: genomics, metabolomics, plant productivity, proteomics, salinity stress, salinity tolerance, transcriptomics

1. Introduction

Stress is defined as any external abiotic (salinity, heat, water, etc.) or biotic (herbivore) constraint that limits the rate of photosynthesis and reduces a plant's ability to convert energy to biomass Grime, (1977). A major challenge towards world agriculture involves production of 70% more food crop for an additional 2.3 billion people by 2050 worldwide FAO, (2009). Salinity is a major stress limiting the increase in the demand for food crops. More than 20% of cultivated land worldwide (~ about 45 hectares) is affected by salt stress and the amount is increasing day by day. Plants because of adaptive evolution can be classified roughly into two major types: the halophytes (that can withstand salinity) and the glycophytes (that cannot withstand salinity and eventually die). Majority of major crop species belong to this second category. Thus salinity is one of the most brutal environmental stresses that

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hamper crop productivity worldwide Flowers, (2004); Munns and Tester, (2008). Salinity stress involves changes in various physiological and metabolic processes, depending on severity and duration of the stress, and ultimately inhibits crop production James *et al.,* (2011); Rozema and Flowers, (2008). Soil salinity is known to represses plant growth in the form of osmotic stress that is then followed by ion toxicity James *et al.,* (2011); Rahnama *et al.,* (2010). During the initial phases of salinity stress, water absorption capacity of root systems decreases and water loss from leaves is accelerated due to osmotic stress of high salt, accumulation in soil and plants, and therefore salinity stress is also considered as hyperosmotic stress Munns, (2005) Fig. (1) .

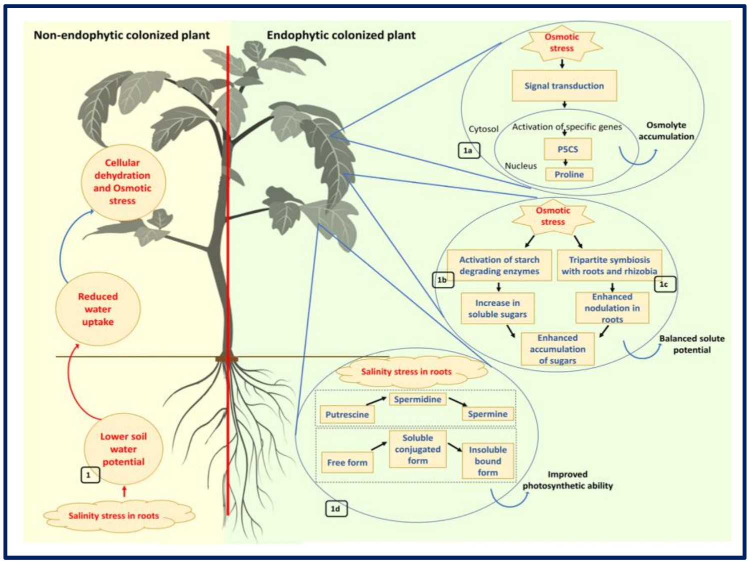

Fig. 1: Salinity stress induced osmotic stress tolerance mechanisms in plants. Increase in salt in soil lowers the soil water potential of plant cells. This reduces water uptake by plants and consequently causes cellular dehydration (1) (left). To combat this issue, plants accumulate osmolytes, such as proline, sugars and polyamines in higher concentration. Osmolyte accumulation results in lowering of cellular water potential and maintains a favorable gradient for water uptake from soil to roots. Endophytic fungi alleviate osmotic stress by influencing the expression of specific genes, P5CS, pyroline-5-carboxylate synthase (1a) (right), involved in the biosynthesis of the osmolyte proline, activation of starch degrading enzyme, glucan-water dikinase (1b) (right) and forming tripartite symbiosis with roots and rhizobia (1c) (right) to elevate the accumulation of sugars and by increasing the biosynthesis of polyamines such as spermidine and spermine (1D) (right). See text for relevant references and further details

Osmotic stress in the initial stage of salinity stress causes various physiological changes, such as interruption of membranes, nutrient imbalance, impairs the ability to detoxify reactive oxygen species (ROS), differences in the antioxidant enzymes and decreased photosynthetic activity, and decrease in stomatal aperture Munns and Tester, (2008), Rahnama *et al.,* (2010) Fig. (2). Salinity stress is also considered as a hyperionic stress. One of the most detrimental effects of salinity stress is the accumulation of Na^+ and Cl^- ions in tissues of plants exposed to soils with high NaCl concentrations. Entry of both Na^+ and Cl^- into the cells causes severe ion imbalance and excess uptake might cause significant physiological disorder(s). High Na^+ concentration inhibits uptake of K^+ ions which is an essential element for growth and development that results into lower productivity and may even lead to death James *et al.,* (2011)

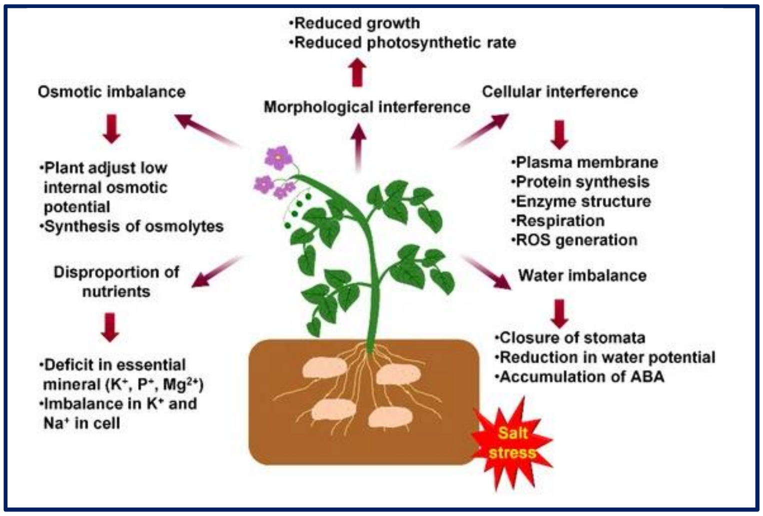

Fig. 2: Schematic model showing the effects of salinity in potato. Salt stress causes visible morphological changes such as leaf aging, premature, senescence and decline in root growth. It interferes with the osmotic balance due to the accumulation of toxic ions. Toxic ions lead to cellular interference and ROS generation that causes plasma membrane disruption, hindrance to respiration and damage to enzyme structure. These ions cause deficiency of essential nutrients and their imbalance. Salt stress also causes osmotic stress that leads to water imbalance and due to which closure of stomata and reduction of water potential occurs. After Kumar *et al.,* (2021)

In response to salinity stress, the production of ROS, such as singlet oxygen, superoxide, hydroxyl radical, and hydrogen peroxide, is enhanced Apel and Hirt, (2004), Ahmad and Umar, (2011). Salinity-induced ROS formation can lead to oxidative damages in various cellular components such as proteins, lipids, and DNA, interrupting vital cellular functions of plants. Genetic variations in salt tolerance exist, and the degree of salt tolerance varies with plant species and varieties within a species. Amongmajor crops, barley (*Hordeumvulgare*) shows a greater degree of salt tolerance than rice (*Oryza sativa*) and wheat (*Triticum aestivum*). The degree of variation is even more pronounced in the case of dicotyledons ranging from *Arabidopsis thaliana*, which is very sensitive towards salinity, to halophytes such as *Mesembryanthemum crystallinum*, *Atriplex sp.*, *Thellungiella salsuginea* (previously known as *T. halophila*) Munns and Tester, (2008), Pang *et al.,* (2010), Abrah´am *et al.,* (2011). In the last two decades, sumptuous amount of research has been done in order to understand the mechanism of salt tolerance in model plant *Arabidopsis* Zhang and Shi, (2013). Genetic variations and differential responses to salinity stress in plants differing in stress tolerance enable plant biologists to identify physiological mechanisms, sets of genes, and gene products that are involved in increasing stress tolerance and to incorporate them in suitable species to yield salt tolerant varieties.

2. Causes of salinity

2.1. Natural cause

Most of the saline Sodic soils are developed due to natural geological, hydrological and Pedological processes. Some of the parent materials of those soils include intermediate igneous rocks such as phenolytes, basic igneous rocks such as basalt, undifferentiated volcanic rocks, sandstones, alluvium and lagoonal deposits Wanjogu *et al.,* (2001). Climatic factors and water management may accelerate salinization. In arid and semi-arid lands, evapo-transpiration plays a very important role in the pedogenesis of saline and sodic soils Fig. (3).

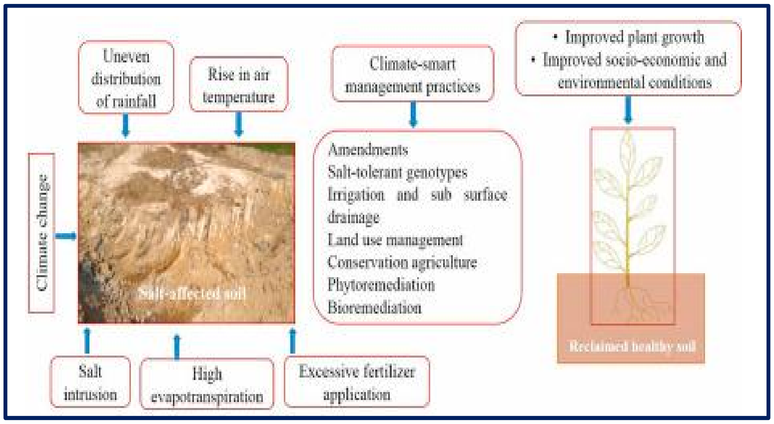

Fig. 3: Soil salinity under climate change: Challenges for sustainable agriculture and food security

Another type of salinity occurs in coastal areas subjected to tides and the main cause is intrusion of saline water into rivers Cyrus *et al.,* (1997) or aquifers Howard and Mullings, (1996). Coastal rice crops in Asia, for instance, are frequently affected by exposure to seawater brought in by cyclones around the Indian Ocean Sultana *et al.,* (2001). Cyclic salts are ocean salts carried inland by wind and deposited by rainfall, and are mainly sodium chloride Fig. (4).

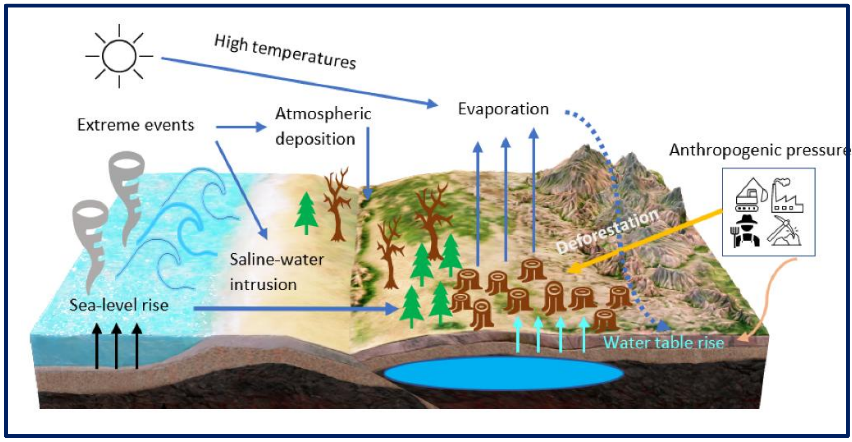

Fig. 4: Current processes leading to salinization. Sea-level rise and extreme events promote seawater flooding and intrusion into coastal land that leads to deforestation. Deforestation can result in increased rates of evaporation that brings salt to the surface layers of the soil and catalyse deforestation and soil fertility reduction. Human practices can induce salinization through deforestation, effluent discharge and water-table rise that may bring salts to the top layers of the soil. High temperatures lead to increased evaporation and other extreme events can cause atmospheric deposition of salts. After Rocha *et al.,* (2020)

Depending on prevailing winds and distance from the seacoast, the rainwater composition greatly varies. The composition of seawater is expressed as g kg-1 or ppt (parts per thousands) and is almost uniform around the globe. The electrical conductivity of seawater is 55 dS m^{-1} while that of rainwater is about 0.01 dS m^{-1}.

2.2. Anthropogenically induced salinity

Secondary salt affected soils are those that have been salinized by human caused factors, mainly because of improper methods of irrigation. Poor quality water is often used for irrigation, so that eventually salt builds up in the soil unless the management of the irrigation system is such that salts are leached from the soil profile. Szaboles, (1992); Garg and Manchanda, (2008) estimated that 50% of all irrigated schemes are salt affected. Too few attempts have been made recently to access the degree of human-induced secondary salinization and, according to Flowers and Yeo, (1995); this makes it difficult to evaluate the importance of salinity to future agricultural productivity. Nevertheless, Ponnamperuma, (1984) has reported increasing salinization with increasing irrigation since 1950's and in the Shansa Province in China, more than one third of the total area of irrigated land is salinized Qiao, (1995). Anthropic salinization occurs in arid and semi-arid areas due to waterlogging brought about by improper irrigation Ponnamperuma, (1984). Secondary salt affected soils can also be caused by human activities other than irrigation and include, but are not limited to the following:

2.2.1. Deforestation

It is recognized as a major cause of salinization and alkalization of soils because of the effects of salt migration in both the upper and lower layers. Deforestation leads to the reduction in average rainfall and increased surface temperature Hastenrath, (1991); Shukla, (1990). Top thin soil rapidly is eroded in the absence of soil green cover. Without the trees there to act as a buffer between the soil and the rain, erosion is practically inevitable. Soil erosion then leads to greater amounts of run-off and increased sedimentation in the rivers and streams. The combination of these factors leads to flooding and increased salinity of the soil Domries, (1991); Hastenrath, (1991). The Indian plains formed by the rivers of north India increasingly getting salt affected as coastal areas of Ganges particularly lower Ganges plains and Sundarban estuarine areas. In southeast India, for example, vast areas of farmer forestland became increasingly saline and alkaline within a few years after the felling of the woods Szaboles, (1994). In Australia, a country where one-third of the soils are Sodic and 5% saline Fitzpatrick, (1994), there is serious risk of salinization if land with shallow unconfined aquifers containing water with more than 0.25% total soluble salt is decreased of trees Bui *et al.,* (1996).

2.2.2. Accumulation of air-borne or water-borne salts in soils

Szaboles, (1994) has reported that chemicals from industrial emissions may accumulate in the soil, and if the concentration is high enough, can result in salt accumulation in the upper layer of soil. Similarly, water with considerable salt concentration such as wastewater from municipalities and sludge may contaminate the upper soil later causing salinization and/or alkalization Bond, (1998)

2.2.3. Contamination with chemicals

It often occurs in modern intensive agricultural systems, particularly in green houses and intensive farming systems.

2.2.4. Overgrazing

This process occurs mainly in arid and semi-arid regions, where the natural soil cover is poor and scarcely satisfies the fodder requirement of intensive animal husbandry Szaboles, (1994). The natural vegetation becomes sparse and progressive salinization develops, and sometimes the process ends up in desertification as the pasture diminishes due to overgrazing. Factors modifying the salinity: The severity of secondary salinity arises when salt stored in the soil profile or groundwater is mobilized and enters the root zone. It happens often when extra water reaches the system due to irrigation or other human activities, viz. deforestation and land clearing. Extra water raises water tables or increases pressures in areas confined or affected by primary salinity particularly in arid and semiarid regions. Their condition varies in severity from slight salinity with little effect on plant growth to severe salinity where semi-confined aquifers causing the upward movement of water to the soil surface. Saline water from deep aquifers or salt deposits from deep soil horizons can move upwards with the rising water. When the water table comes near or reaches the soil surface, appreciable upward movement of water occurs due to evaporation from the soil surface and salts accumulate in the root zone Abrol, (1986). Beyond the threshold level of the water table, the rate of evaporation and associated salinization increase rapidly. The high temperature conditions often exaggerate these conditions. Different soil types have different threshold levels, but these are commonly reached in irrigated situations. Secondary salinization can also occur due to the use of inadequate quantities of irrigation water to leach salts that accumulate in the root zone due to evaporation Umali, (1993). It was realized that the reaction of crops to saline irrigation water was affected not only by the salinity level but also by soil characteristics, irrigation practices such as the type of system and timing and the amount of irrigation applications. Moreover, different crop varieties react differently. Whether to use irrigation water of marginal quality would also depend on the level of yield reduction one is prepared to accept Rhoades and Loveday, (1990). For conventional surface irrigation, and a leaching fraction of 0.1 (i.e. 10% more water than is needed to satisfy the crop evaporative demand), water salinity should not exceed 1dS m^{-1} for sensitive crops. For moderately sensitive, the threshold is 1.8 dS m^{-1}; for moderately tolerant, 3.3 dS m^{-1}; and for tolerant crops, 5.8 dS m^{-1}. In each of these categories, water of higher salinity would lead to yield decline. Higher leaching fractions move the threshold value up, but by how much, depends on the circumstances Rhoades and Loveday, (1990).

3. Factors modifying the salinity

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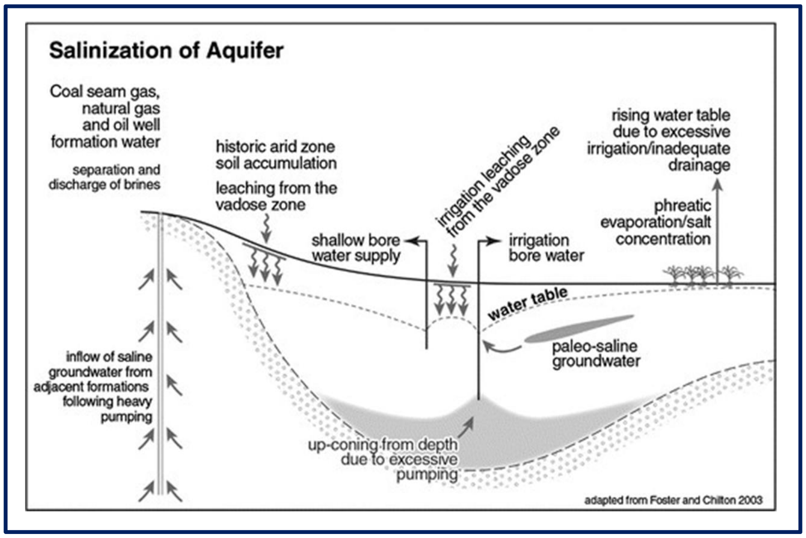


Fig. 5: Processes leading to salinization of aquifers in inland areas. After Foster and Chilton, (2003) and Rocha *et al.,* (2020)

The main causes of water salinization are the accelerated groundwater seepage to surface systems and discharge of irrigation return flows. However, domestic and industrial discharges of wastewater also contribute to surface water salinization. Intrusion of seawater into coastal aquifers also adds salinization of groundwater resources. The over-extraction of groundwater on the one hand result into decline of water tables and depletion of aquifers, on the other hand it results into increased salinity of the water that remains.

3.1. Effects of salinity on plants

Soil salinity is a major factor that limits the yield of agricultural crops, jeopardizing the capacity of agriculture to sustain the burgeoning human population increase Flowers, (2004); Munns and Tester, (2008); Parida and Das, (2005). At low salt concentrations, yields are mildly affected or not affected at all Maggio *et al.,* (2001). As the concentrations increase, the yields move towards zero, since most plants, glycophytes, including most crop plants, will not grow in high concentrations of salt and are severely inhibited or even killed by 100-200 mM NaCl. The reason is that they have evolved under conditions of low soil salinity and do not display salt tolerance Munns and Termaat, (1986). On the contrary, halophytes can survive salinity in excess of 300-400 mM. Halophytes are known to have a capability of growth on salinized soils of coastal and arid regions due to specific mechanisms of salt tolerance developed during their phylogenetic adaptation. Depending on their salt-tolerating capacity, these plants can be either obligate and characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50% sea water or facultative and found in less saline habitats along the border between saline and non-saline upland and characterized by broader physiological diversity which enables them to cope with saline and non-saline conditions Parida and Das, (2005). Measurements of ion contents in plants under salt stress revealed that halophytes accumulate salts whereas glycophytes tend to exclude the salts Zhu, (2007).

Halophyte-glycophytes associations, in many arid and semi-arid regions are saline and are not thus proper for the cultivation of traditional crops. In these soils, two major vegetation types can coexist (i) a halophytic vegetation, naturally salt-tolerant and (ii) a glycophytic vegetation, generally salt sensitive, but capable of growing in association with halophytes Fig. (6). The coexistence of both types of vegetation (halophytes and glycophytes) can be explained by the stratification of root systems of perennial halophytes, to exploit only the deepest and salty horizons, and root systems of annuals, which thrive in the less saline surface areas Abdelly *et al.,* (2006). Several hypotheses can explain the low salinity of the higher horizon. The upper layer can be washed away by a lateral flow of water lightly loaded to the center of the depression. Halophytes, by exploiting the saline deep horizons, may limit the rise of saline groundwater to the surface allowing rainwater to penetrate the upper horizon of the profile. Finally, the halophytes, through their shallow roots, can help maintaining low levels of salt in surface horizon. These factors favor the rapid development of a carpet of annuals less resistant to salt stress but very efficient in the acquisition of mineral resources as soon as the water resources permit Abdelly *et al.* (2006). These data clearly show that some halophytes are capable of desalinizing and fertilizing soils, thus creating micro- habitats favorable for the development of several salt-sensitive annual plants. The latter are represented mainly by Medicago species that are highly preferred by livestock Abdelly *et al.,* (2011). Other halophytes are well grazed and contribute directly to the pastoral value of marginal zones. Many of these species are capable of maintaining high growth potentials, under a wide range of salinities, and in the case of the Poaceae to produce plant biomass with low salt concentrations Abdelly *et al.,* (2011). Such highly interesting findings, when properly and explicitly explained to farmers, may encourage using saline soils and plants in agricultural systems. Farmers will also need to know more about the different kinds of halophytes, their requirement, the mechanisms of their salt tolerance and especially their potential interests.

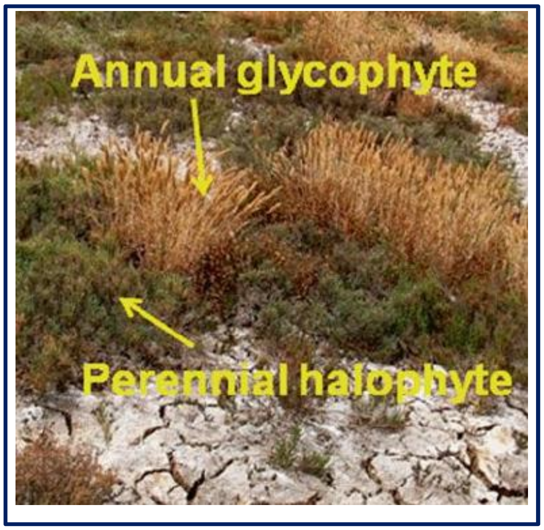


Fig. 6: Perennial halophytes in Sabkhas favouring the growth of annuals (Leguminous, Poaceae) through efficient salt removal from the soil, N and P fertilization. After Abdelly *et al.,* (2006) & (2011) and Ben Hamed *et al.,* (2014)

High salinity affects plants in two main ways, high concentrations of salts in the soil disturb the capacity of roots to extract water, and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many physiological and biochemical processes such as nutrient uptake and assimilation Hasegawa *et al.,* (2000), Munns, (2002); Munns *et al.,* (1995); Munns and Tester, (2008). Excessive amounts of salt enter the plant in the transpiration stream, there will be injury to cells in the transpiring leaves and this may cause further reductions in growth. This is called the salt specific or ion-excess effect of salinity Greenway and Munns, (1980). These salinity effects has threefold effects viz. it reduces water potential and causes ion imbalance or disturbances in ion homeostasis and toxicity; this altered water status leads to initial growth reduction and limitation of plant productivity. Together, these effects reduce plant growth, development and survival. A two-phase model describing the osmotic and ionic effects of salt stress was proposed by Munns *et al.,* (1995) Fig (7), (8).

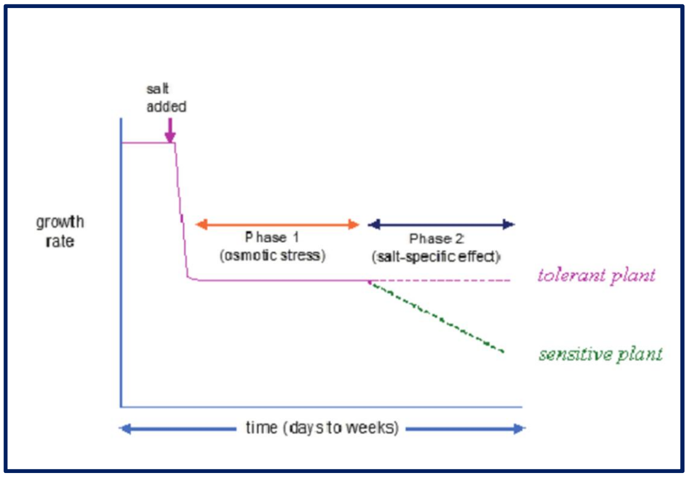


Fig. 7: Scheme of the two-phase growth response to salinity. After Munns, (1995).

Plants sensitive or tolerant to salinity differ in the rate at which salt reaches toxic levels in leaves. Timescale is days, weeks, or months, depending on the species and the salinity level. During phase 1, growth of both type of plants is reduced because of the osmotic effect of the saline solution outside the roots. During phase 2, old leaves in the sensitive plant die and reduce the photosynthetic capacity of the plant. This exerts an additional effect on growth. In the first, osmotic phase, which starts immediately after the salt concentration around the roots increases to a threshold level making it harder for the roots to extract water, the rate of shoot growth falls significantly. An immediate response to this effect, which also mitigates ion flux to the shoot, is stomatal closure. However, because of the water potential difference between the atmosphere and leaf cells and the need for carbon fixation, this is an untenable long-term strategy of tolerance Hasegawa *et al.,* (2000). Shoot growth is more sensitive than root growth to salt- induced osmotic stress probably because a reduction in the leaf area development relative to root growth would decrease the water use by the plant, thus allowing it to conserve soil moisture and prevent salt concentration in the soil Munns and Tester, 2008). A reduced leaf area and stunted shoots Läuchli and Epstein, (1990) commonly express reduction in shoot growth due to salinity. The growth inhibition of leaves sensitive to salt stress appears to be also a consequence of inhibition by salt of symplastic xylem loading of Ca^{2+} in the root Läuchli and Grattan, (2007) Fig. (8).

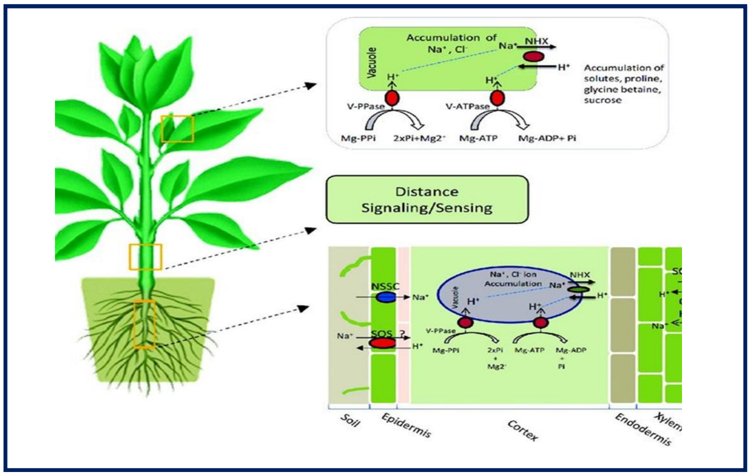


Fig. 8: The three main mechanisms of Salinity tolerance in a crop plants. Tissue tolerance where high salt concentrations are found in leaves but are compartmentalized at the cellular and intracellular level (especially in the vacuole), a process involving ion transporters, proton pumps and synthesis of compatible solutes. Osmotic tolerance, which is related to minimizing the effects on the reduction of shoot growth and may be related to as yet un known sensing and signaling mechanisms. Ion exclusion, where Na+ and Cl transport processes, predominantly in roots, prevent the accumulation of toxic

concentrations of Na+ and Cl within leaves. Mechanisms may include retrieval of Na+ from the xylem, compartmentation of ions in vacuoles of cortical cells and/or efflux of ions back to the soil. After Pravin *et al.,* (2018)

Final leaf size depends on both cell division and cell elongation. Leaf initiation, which is governed by cell division, was shown to be unaffected by salt stress in sugar beet, but leaf extension was found to be a salt-sensitive process Papp *et al.,* (1983), depending on Ca^{2+} status. Moreover, the salt-induced inhibition of the uptake of important mineral nutrients, such as K^+ and Ca^{2+}, further reduces root cell growth Larcher, (1980) and, in particular, compromises root tips expansion. Apical region of roots grown under salinity show extensive vacuolization and lack of typical organization of apical tissue. A slight plasmolysis due to a lack of continuity and adherence between cells is present with a tendency to the arrest of growth and differentiation. Otherwise, control plants root tips characterizing by densely packed tissues with only small intercellular spaces. The second phase, ion specific, corresponds to the accumulation of ions, in particular Na^+, in the leaf blade, where Na^+ accumulates after being deposited in the transpiration stream, rather than in the roots Munns, (2002). Accumulation of Na^+ turns out to be toxic especially in old leaves, which are no longer expanding and so no longer diluting the salt arriving in them as young growing leaves do. If the rate at which they die is greater than the rate at which new leaves are produced, the photosynthetic capacity of the plant will no longer be able to supply the carbohydrate requirement of the young leaves, which further reduces their growth rate Munns and Tester, (2008). Abiotic stresses including salinity have been widely shown to severely impact all the phases of photosynthesis, the most fundamental and intricate physiological process in plants Jahan *et al.,* (2020); Sehar *et al.,* (2021);Ghanem *et al.,* (2021). In fact, the overall status of photosynthesis can be due to stress-induced change in its various components including photosynthetic pigments and photosystems, the electron transport system, and CO2 reduction pathways. Chlorophyll (Chl) is among the sensitive indicators of cellular metabolic state Ghanem *et al.,* (2021). The content of Chl (a) and Chl (b) was significantly reduced under salinity in cucumber seedlings Fatma *et al.,* (2021). The photosynthetic pigments as Chl (a) and Chl (b), carotenoids and net photosynthesis rate along with stomatal conductance were highly affected by the salt concentration in watermelon plants Li *et al.,* (2017). In another study, 100 mM NaCl-mediated reduction of Chl (a) and Chl (b) and carotenoids contents was shown in rice Mahdieh *et al.,* (2015). In salinity exposed *T. aestivum*, a greater decline in the photosynthetic rate and electron transport rate and saturating photosynthetically active photo flux density was noted Sehar *et al.,* (2021). Moreover, there were reductions in the number of photosynthetic pigments such as Chl and carotenoids with the net photosynthesis, stomatal conductance, intercellular CO_2 concentration, and transpiration rate under stress in tomato plants Jiang *et al.,* (2017). The photosystem II (PS II) is the prime site affected by any change in electron transport chain activity due to stress such as salinity Jiang *et al.,* (2017) Fig (9).

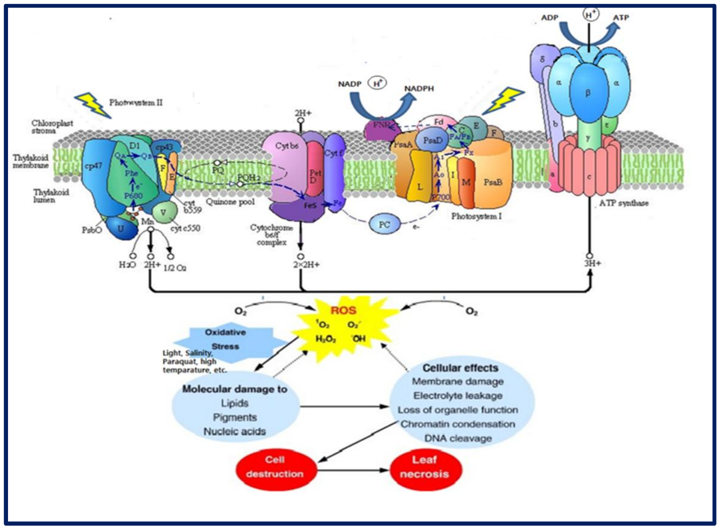


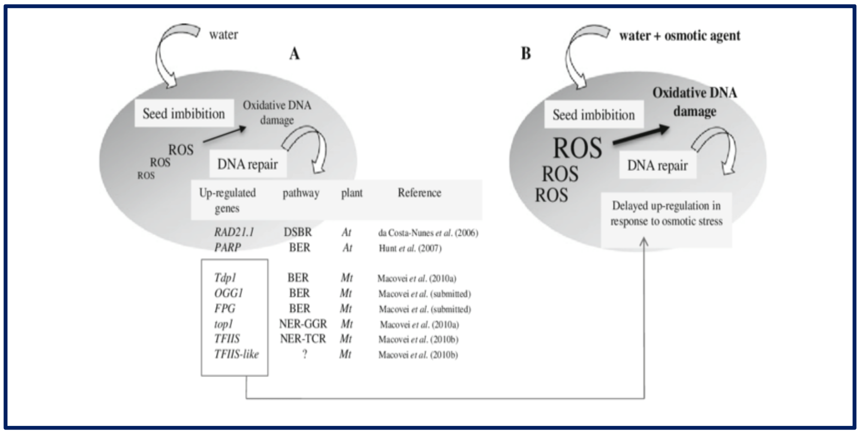
Fig. 9: Illustrates the photosystem II (PS II) affected by abiotic stresses including salinity have been severely impact all the phases of photosynthesis

Severe reduction in the efficiency of PS II, the electron transport system, and the CO_2 assimilation rate under salinity stress has been reported Sehar *et al.,* (2021). Decreased growth was obtained in barley plants due to salt-accrued damaged Chl fluorescence and oxygen evolving complex Kalaji *et al.,* (2011). It has been observed that growth becomes reduced in plants due to damage of PS II and electron transport rates under stress Fatma *et al.,* (2021). In B. juncea, the increased concentration of salt significantly affected net photosynthetic rate, stomatal conductance, intercellular CO_2, quantum yield of PS II, Rubisco activity, and PNUE Jahan *et al.,* (2021). The study of Singh et al. Singh *et al.,* (2016) showed the response towards variable concentration of salt, which hampered the photosynthetic apparatus and the water splitting efficiency complex. The photosynthetic pigment content and plant growth were greatly reduced under salinity stress in salt-sensitive Sorghum plants Nxele *et al.,* (2017). Salt stress was also reported to cause reductions in leaf area, pigment content, Hill reaction, $^{14}CO_2$ fixation, and morphology of chloroplasts, number of reaction centers, net CO_2 assimilation rate, and Rubisco activity in wheat Aldesuquy *et al.,* (2014). Salinity-mediated down regulation of photosynthetic gas exchange rate, water utilization efficiency was reported to lead to reductions in quantum yield of PS II, photochemistry, and photochemical quenching Wu *et al.,* (2012). Hussain *et al.,* (2019) showed that salt stress reduced net photosynthetic rate, and intercellular CO_2 concentration in rice. In photosynthetic tissues, in fact, Na^+ accumulation affects photosynthetic components such as enzymes, chlorophylls, and carotenoids Davenport, *et al.,* (2005); El-Sebai *et al.,* (2016). In addition, Abdallah *et al.,* (2016) noticed that, the rice varieties Giza 178 showed a more pronounced increased in photosynthetic pigments as compared with Giza 177 from the previous observations Giza 177 was considered less tolerant to salinity than Giza 178. The inhibitory effect of salinity stress on the photosynthetic pigments may be due to the effect of salinity on the activities of photosynthetic enzymes and this may be a secondary effect mediated by the reduced CO_2 partial pressure in the leaves caused by stomatal closure. The derived reduction in photosynthetic rate in the salt sensitive plants can increase also the production of reactive oxygen species (ROS). Dolatabadian and Saleh Jouneghani, (2009) found that, salinity stress leads to an increase in free radicals in chloroplasts and destruction of chlorophyll molecules by ROS, which results in reduction of photosynthesis and growth of common bean.

Normally, antioxidative mechanisms, but salt stress Allan and Fluhr, (1997) rapidly remove ROS; Foyer and Noctor, (2003), can impair this removal. ROS signalling has been shown to be an integral part of acclimation response to salinity. ROS play, in fact, a dual role in the response of plants to abiotic stresses functioning as toxic by-products of stress metabolism, as well as important signal transduction molecules integrated in the networks of stress response pathway mediated by calcium, hormone and protein phosphorylation Miller *et al.,* (2010). ABA plays an important role in the response of plants to salinity and ABA-deficient mutants perform poorly under salinity stress Xiong *et al.,* (2001). Salt stress signalling through Ca^{2+} and ABA mediate the expression of the late embryogenesis–abundant (LEA)-type genes including the dehydration-responsive element (DRE)/C-repeat (CRT) class of stress-responsive genes Cor. The activation of LEA-type genes may actually represent damage repair pathways Xiong *et al.,* (2002). Both ABA dependent and independent signalling pathways mediate salt and osmotic stress regulation of Lea gene expression. Both the pathways use Ca^{2+} signalling to induce LEA- gene expression during salinity. It has been shown that ABA-dependent and - independent transcription factors may cross talk to each other in a synergistic way to amplify the response and improve stress tolerance Shinozaki and Yamaguchi-Shinozaki, (2000)

3.2. Germination

The abiotic stress is known as salinity all over the world and especially in arid and semi-arid areas harms plant growth and yields Abbasi *et al.,* (2016); Rani *et al.,* (2019). According to Okorogbona *et al.,* (2018), these elements mark nearly one-third of the world's irrigated land. When a plant is exposed to a salt stress condition, this factor disturbs the normal metabolism of the plant; as a result, the plant's growth and its productivity are reduced (Abbasi *et al.,* 2014). When seeds are sown in a saline environment, these seeds with low osmotic-potential don't absorb water in a saline medium, accumulation process of different toxic ions (such as Na^+ and Cl^-) increases, finally, the process of seed-germination first delayed, reduced, and disrupted. This feature also triggered a negative impression on the germination process, its percentage, and seedling-growth Agnihotri *et al.,* (2006). Seed germination is one of the most fundamental and vital phases in the growth cycle of a plant that determines the yield. However, it has been established that salinity adversely affects the process of germination in various plants like Posidonia Fernández-Torquemada and Sánchez-Lizaso, (2013), Oryza sativa (Xu *et al.,* 2011), Triticum aestivum Akbarimoghaddam et al. (2011), Zea mays Carpıcı et al. (2009); Khodarahmpour *et al.,* (2012), and Brassica spp. Ibrar *et al.,* (2003); Ulfat *et al.,* (2007). Salinity affects the germination process many-folds. It alters the imbibition's of water by seeds due to lower osmotic potential of germination media Khan and Weber, (2008) causes toxicity which changes the activities of enzymes of nucleic acid metabolism Gomes-Filho et al. (2008), alters protein metabolism Dantas *et al.,* (2007), disturbs hormonal balance Khan and Rizvi, (1994) and reduces the utilization of seed reserves Othman *et al.,* (2006). The germination rates and percentage of germinated seeds at a particular time vary considerably among species and cultivars Fig. (10). Lauchli and Grattan, (2007) proposed a generalized relationship between percent germination and time after adding water at different salt levels. Kaveh *et al.,* (2011) found a significant negative correlation between salinity and the rate and percentage of germination that resulted in delayed germination and reduced germination percentage in Solanum lycopersicum.



Up-regulated genes	pathway	plant	Reference
RAD21.1	DSBR	*At*	da Costa-Nunes *et al.* (2006)
PARP	BER	*At*	Hunt *et al.* (2007)
Tdp1	BER	*Mt*	Macovei *et al.* (2010a)
OGG1	BER	*Mt*	Macovei *et al.* (submitted)
FPG	BER	*Mt*	Macovei *et al.* (submitted)
top1	NER-GGR	*Mt*	Macovei *et al.* (2010a)
TFIIS	NER-TCR	*Mt*	Macovei *et al.* (2010b)
TFIIS-like	?	*Mt*	Macovei *et al.* (2010b)

Fig. 10: Schematic representation of the seed imbibition process occurring under physiological conditions (water) and in the presence of osmotic stress (water? osmotic agent). A Reactive oxygen species (ROS) accumulation, which is concomitant with water intake, causes oxidative DNA damage within embryo cells and the consequent activation of DNA repair mechanisms. The gene functions and the related DNA repair pathways, already demonstrated to be upregulated during seed imbibition, are listed. B When seed imbibition is carried out in the presence of an osmotic agent, the rate of water uptake is reduced and the level of oxidative DNA damage strongly increases. In this case, changes are observed in the expression profiles of DNA repair genes, since their up-regulation is temporally delayed. At Arabidopsis thaliana, Mt Medicago truncatula, DSBR double strand break repair, BER base excision repair, NER–GGR nucleotide excision repair–global genome repair, NER–TCR nucleotide excision repair–transcription coupled repair, PARP poly(ADP-ribose)polymerase, Tdp tyrosyl-DNA phosphodiesterase, TFIIS transcription elongation factor II-S, Top1 DNA topoisomerase I. After Balestrazzi *et al.,* (2011)

Bordi, (2010) reported that the germination percentage in Brassica napus significantly reduced at 150 and 200 mM NaCl. Germination rate also decreased on increasing concentration of salinity levels. Compared with control, germination percentage, and germination speed were decreased by 38 and 33, respectively, at 200 mM NaCl. In a recent study, Khodarahmpour et al. (2012) observed drastic reduction in germination rate (32 %), length of radicle (80 %) and plumule (78 %), seedling length (78), and seed vigor (95 %) in *Z. mays* seeds exposed to 240 mM NaCl Fig.(11).

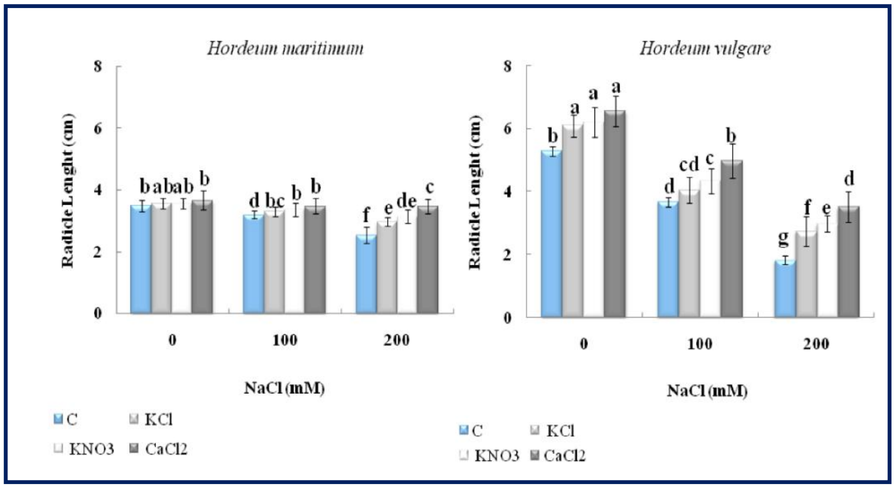


Fig. 11: Illustrates the effect of KCl, KNO_3, and CaCl2 seed priming on the final germination rate (FG%) of two b barley species, *Hordeum maritimum* and *Hordeum vulgare* (L. Manel), subjected to various salt concentrations species, Hordeum maritimum and Hordeum vulgare (L. Manel), subjected to various salt concentrations (0, 100, and 200 mM NaCl) for 7 days at the germination stage. Values are means of 20 replicates _ standard error. Data with the same letter are not significantly different at $p < 0.05$ (Duncan's test). Ben Youssef *et al.,* (2021).

3.3. Growth

One of the initial effects of salt stress is the reduction of growth rate. Salt in soil water inhibits plant growth for two reasons. First, it reduces the plant's ability to take up water and this leads to slower growth. This is the osmotic or water deficit effect of salinity. Second, it may enter the transpiration stream and eventually injure cells in the transpiring leaves, further reducing growth Fig. (12). Zorb *et al.,* (2019) stated that Na^+ and Cl^- at high amounts are toxic to plants, especially if they increase in the cytosol. Despite this relevance, not much is known about cytosolic processes that are impaired by excessive concentrations of salt ions. For instance, toxicity effects of chloride in the cytosol remain to be elucidated Geilfus, (2018a). Plants that are exposed to excessive concentrations of salt ions are poisoned and eventually die. The ion-toxicities have diverse consequences resulting in ionic imbalance i.e. in terms of uptake competition of Na^+ with K^+ , Ca^{2+} and Mg^{2+} and may accelerate senescence of transpiring leaves, not only because of toxic concentrations of deleterious ions in photosynthetic active tissues but also reduced availability of the beneficial nutrients. The energy gain of a crop under salinity stress is schematized in Fig. 12. At any given time, a finite amount of energy and resources that can be harvested by the plant through photosynthesis or metabolically utilized Munns and Gilliham, (2015). Under non-stressed conditions, plants use the majority of the energy in processes necessary for maintenance and vegetative and generative growth. However, resource allocation changes with increasing levels of salinity as increasing resources are invested in the mitigation of stress Fig. (12). the majority of vegetable crops have a very low salinity threshold that is 2.5 dS m^{-1} Snapp *et al.,* (1991). Thus, the area of soils with restrictions for vegetable crop production is therefore greater than the area that is defined as 'salinized'. Since a saline soil is generally defined as showing an EC value of the saturation extract (ECe) in the root zone that exceeds 4 dS m^{-1} (approximately 40 mM NaCl) at 25 °C and having an exchangeable Na^+ level of 15% Shrivastava and Kumar, (2014). The performance of sensitive and tolerant crops in dependence of soil salinity can be summarized in a simplified scheme as shown in Fig. (12 B).

This is the salt-specific or ion-excess effect of salinity. The two effects give rise to a two-phase growth response to salinity given by Munns, (1993&2005); reported that the first phase of the growth response results from the effect of salt outside the plant. The salt in the soil solution reduces leaf growth and to a lesser extent root growth Munns, (1993). The cellular and metabolic processes involved are in common to drought-affected plants. Neither Na^+ nor Cl^- builds up in growing tissues at concentrations that inhibit growth: meristematic tissues are fed largely in the phloem from which salt is effectively excluded, and rapidly elongating cells can accommodate the salt that arrives in the xylem within their expanding vacuoles. Phase 2: The second phase of the growth response results from the toxic effect of salt inside the plant. The salt taken up by the plant concentrates in old leaves: continued transport into transpiring leaves over a long period eventually results in very high Na$^+$ and Cl$^-$concentrations, and the leaves die. The cause of injury is probably the salt load exceeding the ability of cells to compartmentalize salts in the vacuole. Salts would then build up rapidly in the cytoplasm and inhibit enzyme activity. Alternatively, they might build up in the cell walls and dehydrate the cell.

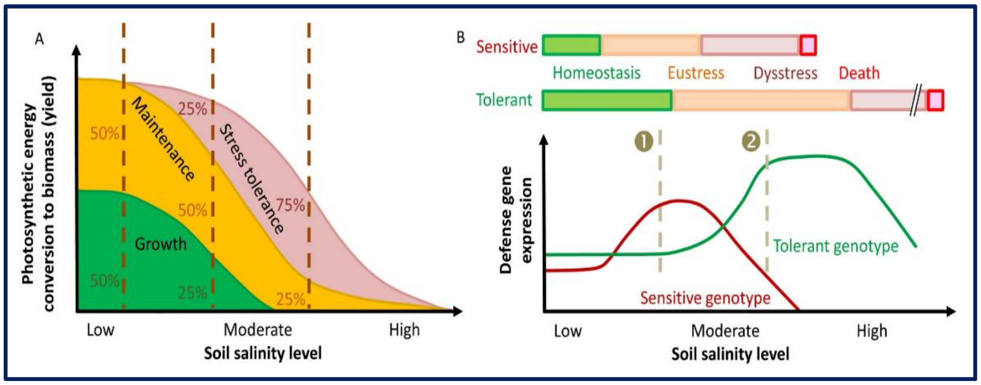


Fig. 12: Schematic of energy gain and energy use by a crop plant and performance of crops under salinity stress. (A) The proportion of energy used for maintenance, growth and stress defense is portrayed. The relative proportions will change depending on the developmental stage of the plant and exposure to salt stress–maintenance costs will be greater when plants are larger. Total energy gain will decrease with greater salinity by decreasing photosynthetic rate following induced closure of stomata and damage to cellular and photosynthetic machinery. Stress tolerance mechanisms represent additional costs to the plant required to deal with the salt load in the soil (for example, but not limited to, greater costs in ion exclusion or compartmentation, maintaining ion homeostasis and reactive oxygen species (ROS) detoxification). At high salinity, there will be zero growth, as the total costs to the plant equal energy gain; when costs exceed energy gained, then tissue will senesce. Source; adapted from a concept by A. H. Millar and H. Lambers, based on data and reasoning of Van der Werf*et al.,* (1988); Munns and Gilliham, (2015). (B) Response of a sensitive and a tolerant crop to soil salinity. Both crop types display response to salinity that can be grouped in phases: homeostasis maintains high growth rate, eustress elicits defense gene expression and dysstress causes stagnation and death. The salinity range is narrow in sensitive crops and broad in tolerant ones. The induction of defense in sensitive crops occurs early, with less magnitude. After Zorb *et al.,* (2019)

The excessive salt concentration correspondingly increases the osmotic potential of the soil that restricts the water uptake by plants. The Na$^+$ and Cl$^-$ ions are the major ions that produce many physiological disorders and detrimental effects on plants. However, Na+ is the primary ion as it interferes with the uptake of potassium (K$^+$) ion and disturbs stomatal regulation that ultimately causes water loss while the Cl$^-$ ion disturbs the chlorophyll production and causes chlorotic toxicity. Cl$^-$ is more dangerous than Na+ Tavakkoli *et al.,* (2011). Moreover, the need of Cl$^-$ in plant is essential as well and is required for the regulation of turgor pressure and pH and enzyme activities in the cytoplasm. Dang *et al.,* (2008). Colmenero-Flores *et al.,* (2019), stated that a recently reported and unexpected effect of Cl$^-$ nutrition on the physiology (Photosynthesis, and Water-Use Efficiency (WUE) of tobacco plants is the reduction of leaf transpiration because of a lower stomatal conductance (gs; Franco-Navarro *et al.,* 2016). This effect was not a consequence of a lower stomatal opening, but resulted from the reduction of the stomatal density associated to the higher enlargement of leaf cells in Cl$^-$-treated plants Franco-Navarro *et al.,* (2019). Therefore, Cl$^-$ simultaneously stimulates growth and reduces water consumption, which results in a clear improvement of water-use efficiency (WUE), Franco-Navarro *et al.,* (2016), Franco-Navarro *et al.,* (2019). Interestingly, the reason why a lower gs does not result in lower photosynthetic capacity (as expected for C$_3$ plants) is that Cl$^-$ specifically increases the mesophyll diffusion conductance to CO$_2$ (gm), Franco-Navarro *et al.,* (2019). This phenomenon is associated, at least in part, with a higher surface area of chloroplasts exposed to the intercellular airspace of mesophyll cells, pointing to a role of Cl^- nutrition on chloroplast performance. The higher gm compensates for the reduction in gs, resulting in overall higher WUE Fig. (13). Increasing crop yields, while also improving WUE has become a major focus of plant research. The beneficial effect of macronutrient Cl^- levels in maintaining high photosynthesis rates while improving WUE is particularly challenging in C_3 plants, in which water loss through transpiration is inherent to the process of fixing atmospheric CO_2. Based on number of field trials, concluded that Cl^- concentration in the soil was more important to growth and yield reduction than Na+ and the critical level (defined as the concentration that reduces the growth or yield by 10 %) of subsoil Cl^- concentration was estimated to be 490 mg. Cl^- .kg^{-1} soil. The Cl^- concentration in the youngest mature leaf of bread wheat, durum wheat, and chickpea showed greater variability with increasing levels of subsoil constraints than Na^+ concentration Dang et al. (2006). However, it is toxic to plants at high concentrations with critical levels for toxicity reported to be 4–7 mg. g^{-1} Cl^-- sensitive species and 15–50 mg. g^{-1} Cl^-, tolerant species, Xu *et al.,* (2000); White and Broadley, (2001).

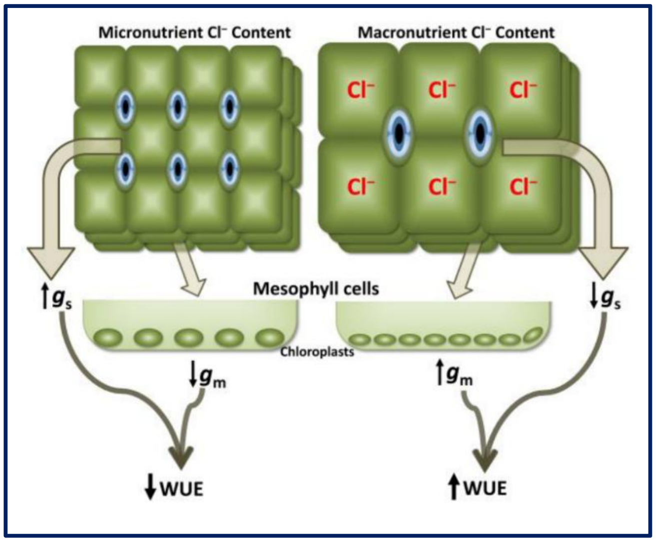


Fig. 13: Chloride (Cl^-) nutrition at macronutrient levels significantly increases the size of leaf cells, resulting in a reduction in stomatal density and, therefore, conductance (gs). At the same time, C^{l-} improves mesophyll diffusion conductance to CO_2 (gm), due, at least in part, to increased surface area of chloroplasts exposed to the intercellular airspace. The higher mesophyll diffusion conductance compensates for the reduction in stomatal conductance, resulting in overall higher WUE Franco-Navarro *et al.,* (2019). Upward arrows indicate higher values, and downwards indicate lower values. Maron, 2019. After Colmenero-Flores *et al.,* (2019).

3.4. Yield

Effects of salt stress on plants ultimately lead to reduction of yield production that is the most countable effect of salt stress in agriculture. Different yield components of Vigna radiate were significantly affected by salinity stress as reported by Nahar and Hasanuzzaman, (2009) Fig. (14). Nahar and Hasanuzzaman, (2009) reported that numbers of pods per plant, seeds per pod, and seed weight were negatively correlated with salinity levels. The reproductive growth of V. radiata was also affected by salinity as the number of pods per plant substantially decreased with increasing salinity levels. Application of 250 mM NaCl gradually reduced the yield production by about 77, 73, and 66 % V. radiata cv. BARI mung-2, BARI mung-5, and BARI mung-6, respectively as compared to the untreated one. The reduction of yield production may be attributed to low production, expansion, senescence, and physiologically less active green foliage under salt stress Wahid *et al.,* (1997), and thus, reduced photosynthetic rate might be a supplementary effect Seemann and Critchley, (1985); Sadak *et al.,* (2012).

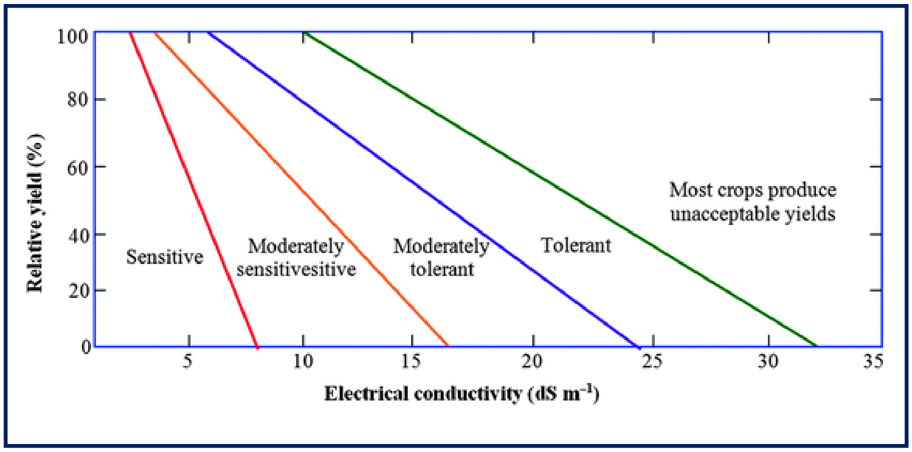


Fig. 14: Relative yield in response to different salinity levels and varying degree of salt tolerance. After Mass, (1986) and Hasanuzzaman *et al.,* (2013)

Hasanuzzaman *et al.,* (2009) stated that in *O. sativa* varieties, grain yield, which is the ultimate product of yield components, is greatly influenced by salinity levels. The loss of grain yield due to 150mM salinity was 50, 38, 44, and 36% over control for the cultivars BR11, BRRI dhan41, BRRI dhan44, and BRRIdhan46, respectively. The severe inhibitory effects of salts on fertility may be due to differential competition in carbohydrate supply between vegetative growth and constrained supply of these to the developing panicles (Murty and Murty, (1982). In addition, reduced viability of pollen under stress condition could result in failure of seed set Abdullah *et al.,* (2001). Linghe and Shannon, (2000) and Gain *et al.,* (2004) also report grain yield reduction of rice varieties due to salt stress earlier. Greenway and Munns, (1980) reported that, application of 200 mM NaCl, a salt-tolerant species such as sugar beet might have a reduction of only 20 % in dry weight, a moderately tolerant species such as cotton might have a 60 % reduction, and a sensitive species such as soybean might be dead. On the other hand, a halophyte such as Suaeda maritima might be growing at its optimum rate Flowers *et al.,* (1986). Semiz *et al.,* (2 012) stated that increasing irrigation with saline water particularly in F. vulgare, gradually decrease the yields and plant growth parameters such as plant height, fresh weight yield, and biomass.

3.5. Salinity and ionic toxicity

The presence of excessive soluble salts in the soil competes with the uptake and metabolism of mineral nutrient that are essential to plants. The appropriate ion ratios provide a tool to the physiological response of a plant in relation to its growth and development Wang *et al.,* (2003). However, increased salt uptake induces specific ion toxicities like that of high Na^+, Cl^-, or sulfate ($SO4^{2-}$) that decrease the uptake of essential nutrients like phosphorus (P), potassium (K^+), nitrogen (N), and calcium (Ca^{++}; Zhu, (2001); El-Sebai, *et al.,* (2016) Fig. (15).

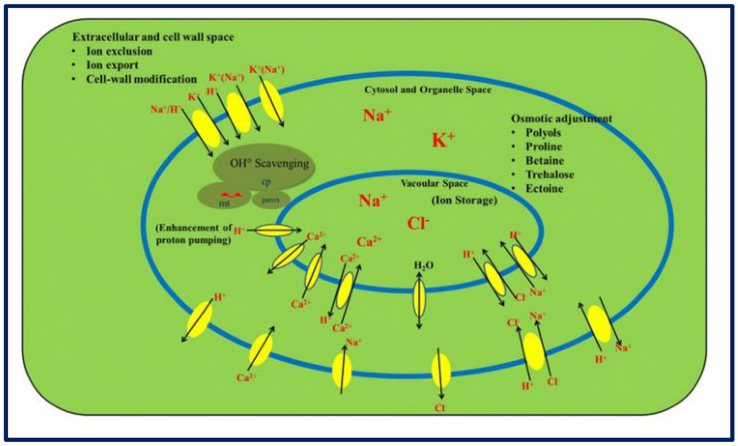


Fig. 15: The schematic presentation of a plant cell includes three compartments that are defined by the extracellular space; cytosolic space and vacoula rspace. Indicated are the osmolytes and ions compartmentalized in the cytoplasm and vacuole, and transport proteins responsible for Na+ and Cl– homeostasis across the plasma membrane and tonoplast. Included are organelles (chloroplast (chlcp), mitochondrion (mitmt), and peroxisome (perox) for which the importance of ROS-scavenging is implicated. After Parihar *et al.,* (2015)

Salinity enhances the Na^+ content in Vicia faba while the Na^+/K^+ ratio was decreased Gadallah, (1999) thus suggesting a negative relationship between Na^+ and K^+. In addition, many of the deleterious effects of Na^+ seem to be related to the structural and functional integrity of membranes Kurth *et al.,* (1986). Salinity stress causes an increase in the levels of Na^+ and Cl^- in Atriplex griffithii in root, stem, as well as in leaves, and the highest ion accumulation was found in leaves followed by stem and root suggesting a positive relationship between Na^+ and Cl^- concentration. The Ca^{2+} content was reduced in shoots and leaves of A. griffithii plants grown at high salinity; however, being stable in roots and the K^+ content was reduced with increased levels of salinity, particularly in leaves. On the other hand, Mg^{2+} concentration was not much affected in stems and roots but the decrease in leaf was more prominent Khan *et al.,* (2000). Decrease in Ca^{2+} and Mg^{2+} content of leaves upon salinity stress suggests increased membrane stability and decreased chlorophyll content, respectively Parida et al. (2004). Despite the fact that most plants accumulate both Na^+ and Cl^- ions in high concentrations in their shoot tissues when grown in saline soils, Cl^- toxicity is also an important cause of growth reduction. Tavakkoli *et al.,* (2011) studied the extent to which specific ion toxicity of Na^+ and Cl^- reduces the growth of four barley genotypes grown in saline soils under varying salinity treatments. High Na^+, Cl^-, and NaCl separately reduced the growth of barley; however, the reductions in growth and photosynthesis were greatest under NaCl stress and were mainly additives of the effects of Na^+ and Cl^- stress. They also reported that Na^+ and Cl^- exclusion among barley genotypes are independent mechanisms and different genotypes expressed different combinations of the two mechanisms. High concentrations of Na^+ reduced K^+ and Ca^{2+} uptake and reduced photosynthesis mainly by reducing stomatal conductance, while high Cl^- concentration reduced the photosynthetic capacity due to non-stomatal effects and chlorophyll degradation Tavakkoli *et al.,* (2011). There is abundant literature indicating that plants are particularly susceptible to salinity during the seedling and early vegetative growth stage. One of the studies in O. sativa showed a remarkable reduction in plant height and tiller number and leaf area index in plants grown in saline soil Hasanuzzaman *et al.,* (2009). In Suaeda salsa, plant height, number of branches, length of branches, and diameter of shoot were significantly affected by salt stress that was due to the increased content of Na^+ and Cl^- Guan *et al.,* (2011). While studying with Glycine max, Dolatabadian *et al.,* (2011) observed that salinity stress significantly decreased shoot and root weight, total biomass, plant height, and leaf number. In one of the recent studies on Foeniculum vulgare, it has been shown that yields and plant growth parameters including plant height, fresh weight, yield, and biomass were affected significantly by irrigation water salinities at 0.01 probability levels Semiz *et al.,* (2012). However, there are many mechanisms that plants employ to combat the salt stress, retain homoeostasis, and overcome ion toxicity Zhu, (2001); Parida *et al.,* (2005). Some of these mechanisms include restriction of the mechanisms involved in salt uptake, control of long distance transport of salt, compartmentalization of salt, extrusion of salt from the plant, and prioritization of the maintenance of K^+/Na^+ ratio in the cytosol.

3.6. Photosynthetic pigments and photosynthesis

Photosynthesis is one of the most important biochemical pathways by which plants convert solar energy into chemical energy and grow. The reduction in photosynthetic rates in plants under salt stress is mainly due to the reduction in water potential. Photosynthesis is also inhibited when high concentrations of Na+ and/or Cl^- are accumulated in the chloroplasts and chlorophyll being important content of photosynthesis directly correlates to the healthiness of plant Zhang *et al.,* (2005) Fig. (16).

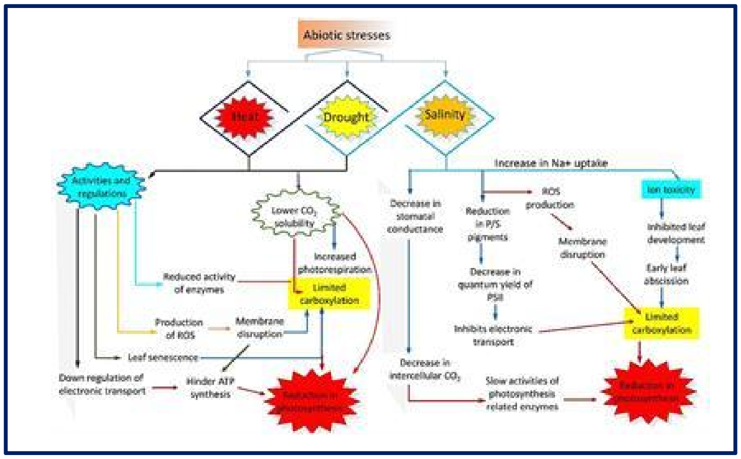


Fig. 16: Schematic representation of the photosynthesis performance under abiotic stresses (heat, drought, and salinity). Drought and heat stress down-regulate enzymatic activity and electron transport chain (ETC) and cause membrane rupture, low CO_2 solubility, leaf senescence, and reactive oxygen species (ROS) production. On the other hand, salinity causes ion toxicity, membrane disruption, reduced stomatal conductance, lower quantum yield of PSII, slow electron transport, and reduced activity of photosynthesis related enzymes. After Muhammad *et al.,* (2021)

Muhammad *et al.,* (2021), stated that Salt Stress Markedly Affects Photosynthesis. Excess of salt or saline soil substantially alters biochemical and physiological processes, especially during photosynthesis, causing stunted plant growth, and poor productivity. Gururani *et al.,* (2015); Ahmad *et al.,* (2018); Sharma *et al.,* (2020) reported that Salt stress decrease the crop productivity by about 50%. Moreover, salinity-induced osmotic stress reduces photosynthesis via the ionic effect on the structure of subcellular organelles and the inhibition of metabolic processes Lawlor, (2009); Sade *et al.,* (2010); Ahmad *et al.,* (2020). The cellular membranes exhibit stress responses Ashraf and Ali, (2008); Tayefi-Nasrabadi *et al.,* (2011), high concentration of ions, such as sodium (Na+) and chloride (Cl−) ions, in chloroplasts causes significant damage to the thylakoid membrane Wu and Zou, (2009); Omoto *et al.,* (2010). Furthermore, inorganic salts at high concentrations can cause irrecoverable inactivation of photophosphorylation and obstruction of electron transport in the thylakoid membrane Veiga *et al.,* (2007), Mittal *et al.,* (2012). Previously, several studies showed that severe salt stress breaks down Chl, and the excess sodium ions Na+ effect electron transport and destabilize photosynthetic activity Pinheiro *et al.,* (2008); Li *et al.,* (2010). A reduction in photosynthetic pigments under salt stress was reported in several plant species such as wheat (Arfan *et al.,* (2007); Perveen *et al.,* (2010), alfalfa (*Medicago sativa*) Winicov and Seemann, (1990), castor bean (*Ricinus communis*) (Pinheiro *et al.,* (2008), and sunflower (*Helianthus annuus*) Ashraf and Sultana, (2000); Akram and Ashraf, (2011). Najafpour et al. (2015) reported that the high Na+ ion concentration in cells alters the potassium ion (K^+): Na^+ ratio, which instantaneously affects the bioenergetics processes of photosynthesis (degradation of photosynthetic pigments) in cyanobacteria as well as in plants Najafpour *et al.,* (2015). Similarly, Eckardt, (2009) showed that salt-induced alterations impair the biosynthesis and accelerate the degradation of photosynthetic pigments Eckardt, (2009). Other studies further summarized the reduction of Chl a and Chl b contents under salt stress in field crops, such as Paspalum vaginatum Ivanov and Velitchkova, (2014), Centaurium erythraea Sundby and Andersson, (1985), common bean (*Phaseolus vulgaris*) Sundby and Andersson, (1985), *Catharanthus roseus*, cowpea (*Vigna unguiculata*) Taffouo *et al.,* (2010), and *Vigna subterranean* Muranaka *et al.,* (2002). Additionally, under salt stress, the Chl precursors, glutamate, and 5-aminolaevulinic acid (ALA), remarkably affect the biosynthesis of Chl in sunflower callus and plants Vieira Santos *et al.,* (2001); Santos, (2004). Salt tolerance plant species show an increase in Chl content, when grown under saline conditions Khan *et al.,* (2009); Akram and Ashraf, (2011), This lead to the concept that salt tolerant plant species with high Chl content exhibit greater membrane stability and higher Chl pigment content. So far, several salt tolerant plant species such as pea (*Pisum sativum*) Noreen *et al.,* (2010), melon (*Cucumis melo*) Romero *et al.,* (1997), sunflower Akram and Ashraf, (2011), wheat Raza *et al.,* (2006); Arfan *et al.,* (2007), alfalfa Monirifar and Barghi, (2009), and proso millet (*Panicum miliaceum*) Sabir *et al.,* (2009) have been screened for their salt tolerance capacity. In contradiction to the aforementioned salt screening strategy, Juan et al. (2005) observed weak linkage between leaf Na^+ level and photosynthetic pigment content in tomato (*Solanum lycopersicum*) plants, indicating that chlorophyll content assimilation is not always associated with salt tolerance, but is an indicator of saline conditions, depending on the plant species Juan *et al.,* (2005). A recent study revealed that salt stress (7–8 dS. m^{-1}) is also responsible for the reduction in the amount of carotenoids and Chl in sugarcane (*Saccharum officinarum* L.) plants at different growth stages Gomathi and Rakkiyapan, (2011). Another study in hot pepper (*Capsicum annuum* L.) showed a significant increase in Chl and carotenoid contents in the presence of 60 mM salt Ziaf *et al.,* (2009). Therefore, we speculate that the carotenoid content of plants under salt stress could be a useful selection criterion. Additionally, salt tolerance at gene level has great potential; for example, the rice (*Oryza sativa* L.) OsSUV3 gene, which encodes the Ski2 family of DExH/D-box helicases, functions under salt stress to facilitate photosynthetic processes and assist the antioxidant machinery Tutej *et al.,* (2014). Together, the studies described above prove that Chl content, photosynthetic pigments, membrane damage, and biochemical changes are of the primary targets under salt stress, where membrane instability and pigment degradation severely affect the growth, development, and physiological parameters of plants.

Decreasing in chlorophyll content under salt stress is a commonly reported phenomenon, and in various studies, chlorophyll concentration has been used as a sensitive indicator of the cellular metabolic state Chutipaijit *et al.,* (2011). In *O. sativa* leaves, the reduction of chlorophyll a and b contents of leaves was observed after NaCl treatment (200 mM NaCl, 14 days) where chlorophyll b content of leaves (41 %) was affected more than the chlorophyll a content (33 %) Amirjani, (2011). In another study, *O. sativa* exposed to 100 mM NaCl showed 30, 45, and 36 % reduction in chlorophyll a, chlorophyll b, and carotenoids contents as compared to the control Chutipaijit et al. (2011). Saha *et al.,* (2010) observed a linear decrease in the levels of total chlorophyll, chlorophyll a, chlorophyll b, carotenoids, and xanthophylls as well as the intensity of chlorophyll fluorescence in *Vigna radiata* under increasing concentrations of NaCl treatments. Compared to control, the pigment contents decreased on an average by 31 % for total chlorophyll, 22 % for chlorophyll a, 45 % for chlorophyll b, 14 % for carotene, and 19 % for xanthophylls Saha *et al.,* (2010). In one of the studies in cucumber, it has been shown that total leaf chlorophyll contents significantly decreased with an increasing NaCl levels. The decrease in total chlorophyll contents was 12, 21, and 30%at 2 and 3, and 5 dS m^{-1} of salt stress, respectively, compared to non-treated plants Khan *et al.,* (2013). Associated with the decline in pigment levels, there was an average 16% loss of the intensity of chlorophyll fluorescence as well. Usually, there is dominance of chlorophyll “a” over chlorophyll “b” in plants but their values become closer with increasing salinity Mane *et al.,* (2010). The decrease in chlorophyll content under stress is a commonly reported phenomenon, and in various studies, this may be due to different reasons, one of them is related to membrane deterioration Mane *et al.,* (2010). Photosystem II (PS II) is a relatively sensitive component of the photosynthetic system with respect to salt stress Allakhverdiev *et al.,* (2000). A considerable decrease in the efficiency of PS II, electron transport chain (ETC), and assimilation rate of CO_2 under the influence of salinity has been noticed Piotr and Grazyna, (2005). Demetriou *et al.,* (2007) noticed alterations in photosynthetic characteristics of Scenedesmus oblique’s that result into declined biomass accumulation. In citrus, salinity stress decreased growth by reducing of net photosynthetic rate, stomatal conductance, performance of PSII, and photosynthetic efficiency Lòpez-

Climent *et al.,* (2008). Kalaji *et al.,* (2011) reported that salinity stress affects growth of barley by altering chlorophyll fluorescence (PS II) and function of oxygen evolving complex. Furthermore, Mittal *et al.,* (2012) observed that salt stress affects growth of *Brassica juncea* by affecting photosynthetic (PS II) and electron transport rates, and D1 protein. There are some other factors that reduce photosynthetic rates under salt stress: dehydration of cell membranes that reduce their permeability to carbon dioxide, salt toxicity, enhanced senescence, changes in enzyme activity induced by alterations in cytoplasmic structure, and negative feedback by reduced sink activity Iyengar and Reddy, (1996). Desingh and Kanagaraj, (2007) also, presume that salinity stress might affect the biochemistry of photosynthesis by causing disorientation of the lamellar system of chloroplasts and loss of chloroplast integrity leading to a decrease in the activities of photosystems. The decrease in chlorophyll content may be due to the formation of proteolytic enzymes such as chlorophyllase that is responsible for chlorophyll degradation Dolatabadian, and Jouneghani, (2009). They also added that, an increase in ROS generation due to abiotic stress such as salt stress would result in further damage to PSII and/or cause serious damage to organelles such as chloroplast, mitochondria and plasma membrane.

3.7. Water relation

Water potential is an important physiological parameter for determining the water status of the plants Parida and Das, (2005). According to Romero-Aranda *et al.,* (2001) an increase of salt in the root medium can lead to a decrease in leaf water potential and, hence, may affect many plant processes. At very low soil water potentials, this condition interferes with plant's ability to extract water from the soil and maintain turgor. However, at low or moderate salt concentration (higher soil water potential), plants adjust osmotically (accumulate solutes) and maintain a potential gradient for the influx of water. In one of the experiments in *Cucumis sativa*, it has been shown that the water potential decreases linearly with increasing salinity levels Khan *et al.,* (2013) Fig. (17).

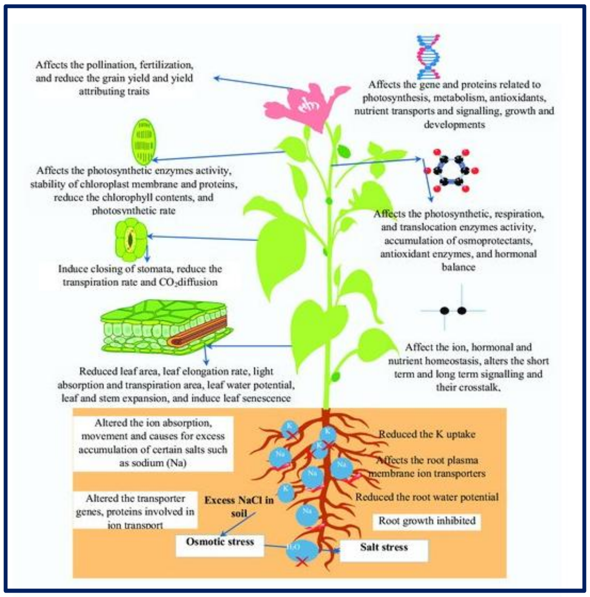


Fig. 17: Illustrates the effect of salinity stress on root growth, ionic homeostasis, physiological, biochemical, and molecular processes. After Singha *et al.,* (2021).

3.8. Nutrient imbalance

Crop performance may be adversely affected by salinity-induced nutritional disorders. However, the relations between salinity and mineral nutrition of crops are very complex Grattan and Grieve ,(1999). The nutritional disorders may result from the effect of salinity on nutrient availability, competitive uptake, transport, or distribution within the plant Fig. (18). Numerous reports indicated that salinity reduces nutrient uptake and accumulation of nutrients into the plants Rogers *et al.,* (2003), Hu and Schmidhalter, (2005). The availability of micronutrients in saline soils is dependent on the solubility of micronutrients, the pH of soil solution, redox potential of the soil solution, and the nature of binding sites on the organic and inorganic particle surfaces.

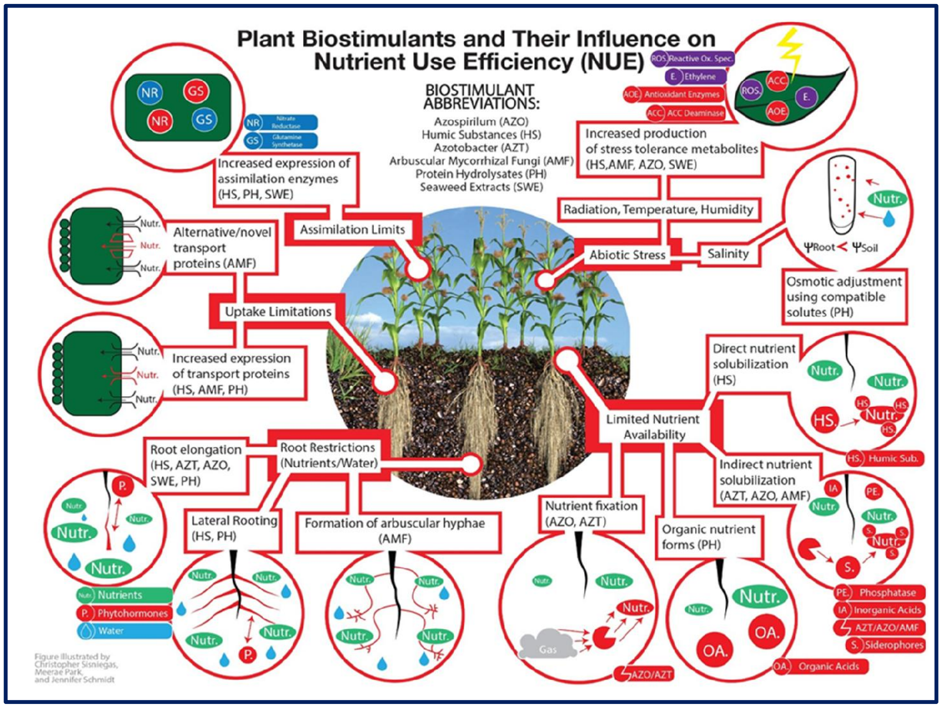


Fig. 18: Diagram represents the mode of actions of biostimulants that induce the natural processes in crops for enhancing nutrient uptake, nutrient use efficiency (NUE), resistance to abiotic stress (salinity stress) and quality traits, as well as increasing the presence of nutrients in t soil rhizosphere.

In addition, salinity can differently affect the micronutrient concentrations in plants depending upon crop species and salinity levels Oertli, (1991).Micronutrient deficiencies are very common under salt stress because of high pH Zhu *et al.,* (2004). Numerous plant studies have demonstrated that salinity could reduce nitrogen accumulation in plants. Decreased N uptake under saline conditions occurs due to interaction between Na^+ and NH_4^+ and /or between Cl^- and $NO3^-$ that ultimately reduce the growth and yield of the crop Rozeff, (1995). This reduction in $NO3^-$ uptake is associated with Cl^- antagonism Bar *et al.,* (1997) or reduced water uptake under saline conditions Lea-Cox and Syvertsen, (1993). The availability of phosphorous is also reduced in saline soil due to (**a**) ionic strength effects that reduced the activity of PO_4^{3-}, (**b**) phosphate concentrations in soil solution was tightly controlled by sorption processes, and (**c**) low solubility of Ca-P minerals. Hence, it is noteworthy that phosphate concentration in agronomic crops decreases as salinity increases Qadir and Schubert, (2002). Sodium concentration in plant tissues increases in the high NaCl treatment and Leaf Ca^{2+}, K^+, and N decreases Tuna *et al.,* (2007). Elevated sodium chloride (NaCl) levels in the root medium reduce the nutrient assimilation, especially of K and Ca, resulting in ion imbalances of K, Ca, and Mg Keutgen and Pawelzik, (2009). In a recent study, it has been reported that Ca^{2+} and Mg^{2+} concentrations of all plant organs transiently declined in response to external NaCl salinity Hussin et al. (2013). The reduction in Ca^{2+} and Mg^{2+} uptake under salt stress conditions might be due to the suppressive effect of Na^+ and K^+ on these cations or due to reduced transport of Ca^{2+} and Mg^{2+} ions. In addition, salinity has an antagonistic effect on the uptake of Ca and Mg which caused by displacing Ca in membranes of root cells Asik *et al.,* (2009) on wheat.

3.9. Salinity and oxidative stress

Besides direct impact of salinity on plants, a common consequence of salinity is induction of excessive accumulation of reactive oxygen species (ROS) which can cause peroxidation of lipids, oxidation of protein, inactivation of enzymes, DNA damage, and/or interact with other vital constituents of plant cells. Salt stress can lead to stomatal closure, which reduces carbon dioxide availability in the leaves and inhibits carbon fixation, exposing chloroplasts to excessive excitation energy which in turn increase the generation of ROS such as superoxide (O2 •–), hydrogen peroxide (H_2O_2), hydroxyl radical (OH•), and singlet oxygen (1O2; Parida and Das, (2005); Ahmad and Sharma, (2008); Ahmad *et al.,* (2010a&2011) Fig. (19). On the other hand, as salt stress is complex and imposes a water deficit because of osmotic effects on a wide variety of metabolic activities Greenway and Munns, (1980); Cheeseman, (1988). This water deficit leads to the formation of ROS Sairam, Tyagi, (2004). ROS are highly reactive and may cause cellular damage through oxidation of lipids, proteins, and nucleic acids Apel and Hirt, (2004); Ahmad *et al.,* (2010a, b). In many plant studies, it was observed that production of ROS is increased under saline conditions and ROS-mediated membrane damage has been demonstrated to be a major cause of the cellular toxicity by salinity in different crop plants such as rice, tomato, citrus, pea, and mustard Gueta-Dahan *et al.,* (1997); Dionisio-Sese and Tobita, (1998); Mittova *et al.,* (2004); Ahmad *et al.,* (2009), (2010b).

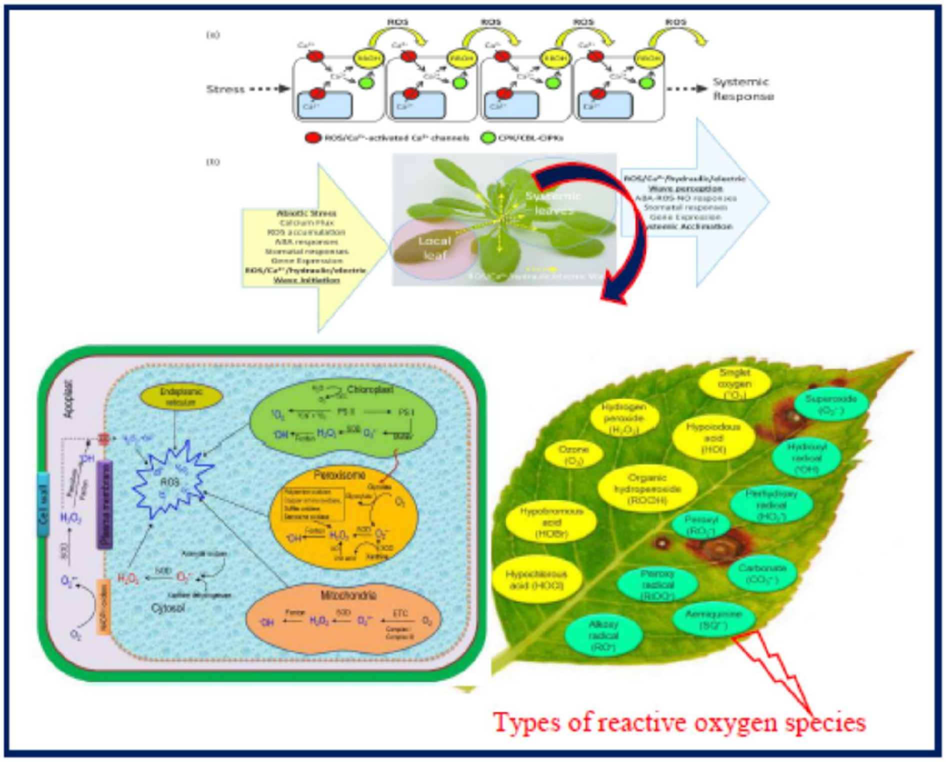


Fig. 19: Reactive oxygen species (ROS) generation process and localization in plant cells. In different cell organelles, ROS are produced through metabolic reactions where different enzymatic and non-enzymatic pathways are involved. ROS—reactive oxygen species; H_2O_2-hydrogen peroxide; $1O_2$-singlet oxygen; ETC-electron transport chain; •OH—hydroxyl radical; 3Chl -triplet chlorophyll; PS I-photosystem I; PS II-photosystem II; O_2 •−superoxide anion; XOD-xanthine oxidase; SOD- superoxide dismutase; NADPH-Nicotinamide adenine dinucleotide phosphate; UO-urate oxidase. After Hasanuzzaman *et al.,* (2021)

Hasanuzzaman *et al.,* (2021) reported that sthe generation of oxygen radicals and their derivatives, known as reactive oxygen species, (ROS) is a part of the signaling process in higher plants at lower concentrations, but at higher concentrations, those ROS cause oxidative stress. Salinity-induced osmotic stress and ionic stress trigger the overproduction of ROS and, ultimately, result in oxidative damage to cell organelles and membrane components, and at severe levels, they cause cell and plant death. The antioxidant defense system protects the plant from salt-induced oxidative damage by detoxifying the ROS and by maintaining the balance of ROS generation under salt stress. Different plant hormones and genes are also associated with the signaling and antioxidant defense system to protect plants when they are exposed to salt stress. Salt-induced ROS overgeneration is one of the major reasons for hampering the morpho-physiological and biochemical activities of plants that can be largely restored through enhancing the antioxidant defense system that detoxifies ROS.

In one of the studies, it has been shown that long-term salinity treatments (EC 5.4 and 10.6 dS. m^{-1}, 60 days) causes significant increase in H_2O_2 and lipid peroxidation in wheat seedlings, which was higher in salt-sensitive cultivar than salt tolerant cultivar Sairam *et al.,* (2002). In a recent study, increased lipid peroxidation and levels of H_2O_2 were observed with increased salinity in Brassica napus Hasanuzzaman and Fujita, (2011a) and Triticum aestivum Hasanuzzaman and Fujita, (2011b). It has been shown that the production of ROS during environmental stresses such as salinity is one of the main causes for decreases in crop productivity Halliwell and Gutteridge, (1989); Asada, (1994). Therefore, regulation of ROS is a crucial process to avoid unwanted cellular cytotoxicity and oxidative damage Halliwell and Gutteridge (1989).

4. Salt tolerance strategies in plants

Salt tolerance is the ability of plants to grow and complete their life cycle on a substrate that contains high concentrations of soluble salt. Plants that can survive on high concentrations of salt in the rhizosphere and grow well are called halophytes. Depending on their salt-tolerating capacity, halophytes are either obligate or characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50 % seawater or facultative and found in less saline habitats along the border between saline and non-saline upland and characterized by broader physiological diversity that enables them to cope with saline and non-saline conditions. Salt tolerance is a complex trait involving several interacting properties. There has been increasing interest in studying the omics tools, i.e., genomics, transcriptomics, proteomics, metabolomics, etc. to identify and understand salt tolerance components and mechanisms at molecular level Inan *et al.,* (2004) Fig.(20).

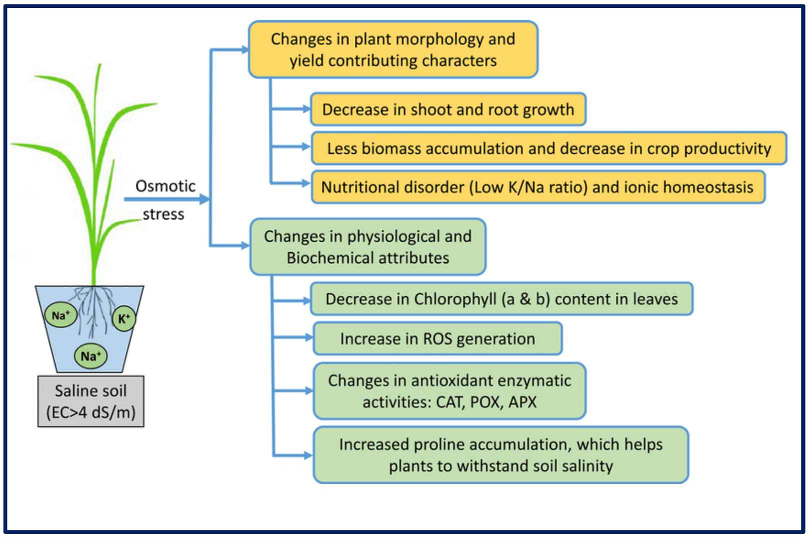


Fig. 20: Plant responses subjected to salt stress. Decreasing rates of new cell production may cause the inhibition of growth as reported by Shabala *et al.,* (2000). The reduction in dry weight accumulation could be attributed to increasing stiffness of the cell wall due to altered cell wall structure induced by salinity. Salt stress in the root zone causes the development of osmotic stress, which disrupts cell ion homeostasis by inducing both the inhibition in uptake of essential nutrients such as K^+ and increased accumulation of Na^+ and Cl^- Paranychianakis and Chartzoulakis, (2005). Higher uptake of Na^+ competes with the uptake of other nutrient ions, especially $K^+$and causes K^+ deficiency which leads to lower K^+/Na^+ ratio in plants under salt stress Kibria *et al.,* (2017). Salt-stressed plants also show significant changes in physiological and biochemical parameters of plants such as lower level of leaf chlorophyll content, decrease in protein synthesis, increased ROS accumulation, enhanced accumulation of compatible solutes such as proline, changes in antioxidant enzymatic activities. Thus, all the morphological, physiological and biochemical changes of plants exposed to salt stress are combinedly responsible for overall changes in plant growth and productivity. After Kibria and Anamul Hoque, (2019)

We will briefly review the roles of genomics, transcriptomics, proteomics, and metabolomics in salt stress tolerance and their possible use in enhancing salinity tolerance in plants.

4.1. Physiological and Biochemical Mechanisms of Salt Tolerance

Plants develop various physiological and biochemical mechanisms in order to survive in soils with high salt concentration. Several mechanisms such as, (**a**) ion homeostasis and compartmentalization, (**b**) ion transport and uptake, (**c**) biosynthesis of osmoprotectants and compatible solutes, (**d**) activation of antioxidant enzyme and synthesis of antioxidant compounds, (**e**) synthesis of polyamines, (**f**) generation of nitric oxide (NO), and (**g**) hormone modulation.

4.2. Ion Homeostasis and Salt Tolerance.

Niu *et al.,* (1995), Hasegawa, (2013) stated that maintaining ion homeostasis through ion uptake and compartmentalization is not only crucial for normal plant growth but is also an essential process for growth during salt stress. Irrespective of their nature, both glycophytes and halophytes cannot tolerate high salt concentration in their cytoplasm. Reddy *et al.,* (1992);Zhu, (2003) reported that excess of salt either transported to the vacuole or sequestered in older tissues that eventually are sacrificed, thereby protecting the plant from salinity stress. Major form of salt present in the soil is NaCl, so the focus of research is the study about the transport mechanism of Na^+ ion and its compartmentalization. The Na+ ion that enters the cytoplasm is then transported to the vacuole via Na^+/H^+ antiporter. Two types' of H^+ pumps are present in the vacuolar membrane: vacuolar type H^+-ATPase (V-ATPase) and the vacuolar pyrophosphatase (V-PPase) Dietz *et al.,* (2001), Wang *et al.,* (2001). Of these, V-ATPase is the most dominant H+ pump present within the plant cell. During nonstress conditions, it plays an important role in maintaining solute homeostasis, energizing secondary transport and facilitating vesicle fusion. Under stressed condition, the survivability of the plant depends upon the activity of V-ATPase Dietz *et al.,* (2001). In a study performed by De Lourdes Oliveira Otoch *et al.,* (2001) in hypocotyls of *Vigna unguiculata* seedlings, it was observed that the activity of VATPase pump increased when exposed to salinity stress but under similar conditions, activity of V-PPase was inhibited, whereas in the case of halophyte *Suaeda salsa,* V-ATPase activity was upregulated and V-PPase played a minor role Wang *et al.,* (2001). Increasing evidence demonstrates the roles of a Salt Overly Sensitive (SOS) stress-signalling pathway in ion homeostasis and salt tolerance Hasegawa *et al.,* (2000); Sanders, (2000). The SOS signalling pathway consists of three major proteins, SOS1, SOS2, and SOS3. *SOS1,* which encodes a plasma membrane Na^+/H^+ antiporter, is essential in regulating Na^+ efflux at cellular level. It also facilitates long distance transport of Na^+ from root to shoot. Overexpression of this protein confers salt tolerance in plants Shi *et al.,* (2000); Shi *et al.,* (2002). *SOS2* gene, which encodes a serine/threonine kinase, is activated by salt stress elicited Ca^+ signals. This protein consists of a well-developed N-terminal catalytic domain and a C-terminal regulatory domain Liu *et al.,* (2000). The third type of protein involved in the SOS stress-signalling pathway is the SOS3 protein that is a myristoylated Ca^+ binding protein and contains a myristoylation site at its N-terminus. This site plays an essential role in conferring salt tolerance Ishitani *et al.,* (2000). C-terminal regulatory domain of SOS2 protein contains a FISL motif (also known as NAF domain), which is about 21 amino acid long sequence, and serves as a site of interaction for Ca^{2+} binding SOS3 protein. This interaction between SOS2 and SOS3 protein results in the activation of the kinase Guo *et al.,* (2004). The activated kinase then phosphorylates SOS1 protein thereby increasing its transport activity which was initially identified in yeast Quintero *et al.,* (2002). SOS1 protein is characterised by a long cytosolic C-terminal tail, about 700 amino acids long, comprising a putative nucleotide-binding motif and an auto inhibitory domain. This auto inhibitory domain is the target site for SOS2 phosphorylation. Besides conferring salt tolerance, it also regulates pH homeostasis, membrane vesicle trafficking, and vacuole functions Quintero *et al.,* (2002), Oh *et al.,* (2010). Thus with the increase in the concentration of Na^+ there is a sharp increase in the intracellular Ca^{2+} level which in turn facilitates its binding with SOS3 protein. Ca^{2+} modulates intracellular Na^+ homeostasis along with SOS proteins. The SOS3 protein then interacts and activates SOS2 protein by releasing its self-inhibition. The SOS3-SOS2 complex is then loaded onto plasma membrane where it phosphorylates SOS1. The phosphorylated SOS1 results in the increased Na^+ efflux, reducing Na^+ toxicity Mart´ınez-Atienza *et al.,* (2007). Many plants have developed an efficient method to keep the ion concentration in the cytoplasm in a low level. Membranes along with their associated components play an integral role in maintaining ion concentration within the cytosol during the period of stress by regulating ion uptake and transport Sairam and Tyagi, (2004) Fig. (21). Different carrier proteins, channel proteins, antiporters, carry out the transport phenomenon and symporters. Maintaining cellular Na$^+$/K$^+$ homeostasis is pivotal for plant survival in saline environments. Ma *et al.,* (2012) have reported that Arabidopsis NADPH oxidases *AtrbohD* and *AtrbohF* function in ROS-dependent regulation of Na$^+$/K$^+$ homeostasis in Arabidopsis under salt stress.

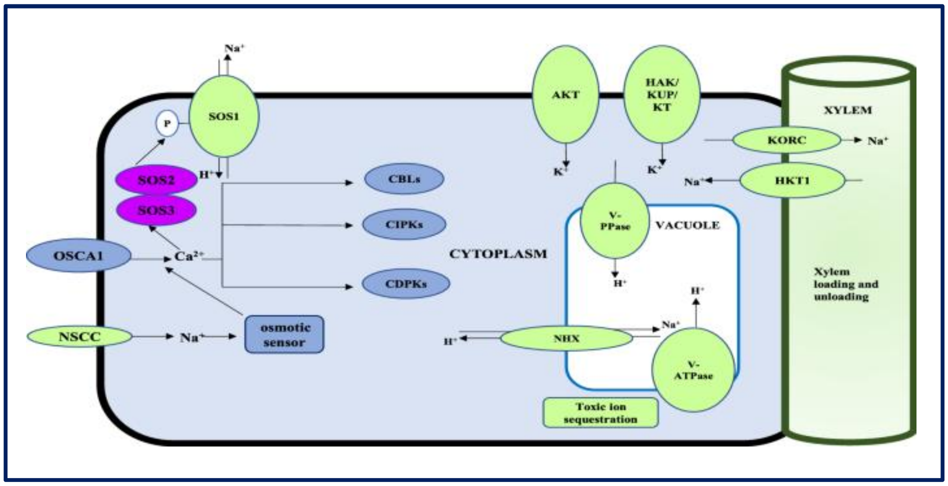


Fig. 21: Schematic overview of ion transport mechanism in salt stress signalling pathway. Na ions enter the cell through NSCCs under salt stress followed by increased cytosolic Ca2 concentration that activates SOS pathway. The proteins involved in SOS pathway are CBL and CIPK. Calcium signalling activates CDPKs also. NHX, V-ATPase and V-PPase are involved in Na sequestration in vacuole. K uptake in root is occurred by mainly AKT and HAK. The candidate proteins for loading Na to the xylem are KORC and retrieval of Na from xylem are occurred by HKT. Abbreviations: nonselective cation channels (NSCCs), SALT OVERLY SENSITIVE (SOS), Calcineurin B-like protein (CBL), CBL-interacting protein kinase (CIPK), Na /H exchangers (NHX), vacuolar H-ATPase (VATPase) and vacuolar H?-PPase (V-PPase), Inward-rectifying K Channel (AKT) and High-affinity K transporter (HAK), Outward rectifying K channels (KORC), High affinity K transporters (HKT). After Malakar and Chattopadhyay, (2021).

Plants maintain a high level of K$^+$ within the cytosol of about 100mM ideal for cytoplasmic enzyme activities. Within the vacuole K$^+$ concentration ranges between 10mM and 200mM. The vacuole serves as the largest pool of K$^+$ within the plant cell. K$^+$ plays a major role in maintaining the turgor within the cell. It is transported into the plant cell against the concentration gradient via K$^+$ transporter and membrane channels. K$^+$ transporters mediate high affinity K$^+$ uptake mechanisms when the extracellular K$^+$ concentration is low, whereas K$^+$ channels carry out low affinity uptake when the extracellular K$^+$ concentration is high. Thus, uptake mechanism is primarily determined by the concentration of K$^+$ available in the soil. On the other hand, a very low concentration of Na$^+$ ion (about 1mMor less) is maintained in the cytosol. During salinity stress, due to increased concentration of Na$^+$ in the soil, Na$^+$ ion competes with K+ for the transporter as they both share the same transport mechanism, thereby decreasing the uptake of K$^+$ Munns and Testerm (2008); Sairam and Tyagi, (2004). A large number of genes and proteins, such as HKT and NHX, encoding K$^+$ transporters and channels have been identified and cloned in various plant species. During salt stress, expression of some low abundance transcripts is enhanced that are found to be involved in K$^+$ uptake. This was observed in the halophyte *Mesembryanthemum crystallinum* Yen *et al.,* (2000). Transporters located on the plasma membrane; belonging to the HKT (histidine kinase transporter) family, also play an essential role in salt tolerance by regulating transportation of Na$^+$ and K$^+$. Class 1 HKT transporters that have been identified in Arabidopsis protect the plant from the adverse effects of salinity by preventing excess accumulation Na+ in leaves. Similar results were observed in the experiment that was carried out with rice where class 1 HKT transporter removes excess Na$^+$ from xylem, thus protecting the photosynthetic leaf tissues from the toxic effect of Na$^+$ Schroeder *et al.,* (2013). Intracellular NHX proteins are Na$^+$,

K^+/H^+ antiporters involved in K^+ homeostasis, endosomal pH regulation, and salt tolerance. Barrag´an *et al.,* (2012) showed that tonoplast localized NHX proteins (NHX1 and NHX2: the two major tonoplast-localized NHX isoforms) are essential for active K^+ uptake at the tonoplast, for turgor regulation, and for stomatal function. In fact more such NHX isoforms have been identified and their roles I en ion (Na^+, K^+, H^+) homeostasis established from different plant species (e.g., LeNHX3 and LeNHX4 from tomato) ´alvez *et al.,* (2012).

4.3. Compatible Solute Accumulation and Osmotic Protections

Compatible solutes, also known as compatible osmolytes, are a group of chemically diverse organic compounds that are uncharged, polar, and soluble in nature and do not interfere with the cellular metabolism even at high concentration. They mainly include proline Hoque *et al.,* (2007), Tahir *et al.,* (2012), glycine betaine Khan *et al.,* (2000), Wang and Nii, (2000), sugar Kerepesi and Galiba, (2000), Bohnert *et al.,* (1995), and polyols Ford; (1984), Saxena *et al.,* (2013). Organic osmolytes are synthesized and accumulated in varying amounts amongst different plant species. For example, quaternary ammonium compound beta alanine betaine's accumulation is restricted among few members of Plumbaginaceae Hanson *et al.,* (1994), whereas accumulation of amino acid proline occurs in taxonomically diverse sets of plants Saxena *et al.,* (2013) Fig. (22).

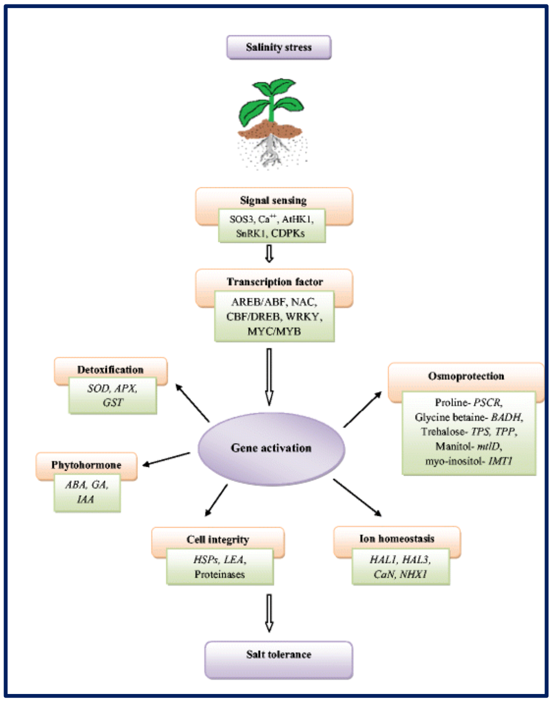


Fig. 22: A generalized schematic presentation of salinity stress responses of plant after **-** Chen *et al.,* (2014), Agarwal *et al.,* (2013). Adaptation to salt stress starts from stress perception of complex stimuli. The sensor proteins perceive signal, these stress signals triggers the downstream signaling processes and gene activation through transcription factors. The mechanisms include cell integrity, phytohormones, antioxidants, synthesis of osmolytes and ion homeostasis. The coordinated action leads to re-establish the cellular homeostasis, protection of functional and structural proteins and membranes, and ultimately the tolerance to salinity stress. After Muchate *et al.,*

The concentration of compatible solutes within the cell is maintained either by irreversible synthesis of the compounds or by a combination of synthesis and degradation. The biochemical pathways and genes involved in these processes have been thoroughly studied. As their accumulation is proportional to the external osmolarity, the major functions of these osmolytes are to protect the structure and to maintain osmotic balance within the cell via continuous water influx Hasegawa *et al.,* (2000). Amino acids such as cysteine, arginine, and methionine, which constitute about 55% of total free amino acids, decrease when exposed to salinity stress, whereas proline concentration rises in response to salinity stress El-Shintinawy and. El-Shourbagy, (2001). Proline accumulation is a well-known measure adopted for alleviation of salinity stress Saxena *et al.,* (2013), Matysik *et al.,* (2002), and Ben Ahmed *et al.,* (2010). Intracellular proline that is accumulated during salinity stress not only provides tolerance towards stress but also serves as an organic nitrogen reserve during stress recovery. Proline is synthesized from either glutamate or ornithine. In osmotically stressed cell, glutamate functions as the primary precursor. The biosynthetic pathway comprises two major enzymes, pyrroline carboxylic acid synthetase and pyrroline carboxylic acid reductase Fig. (23).

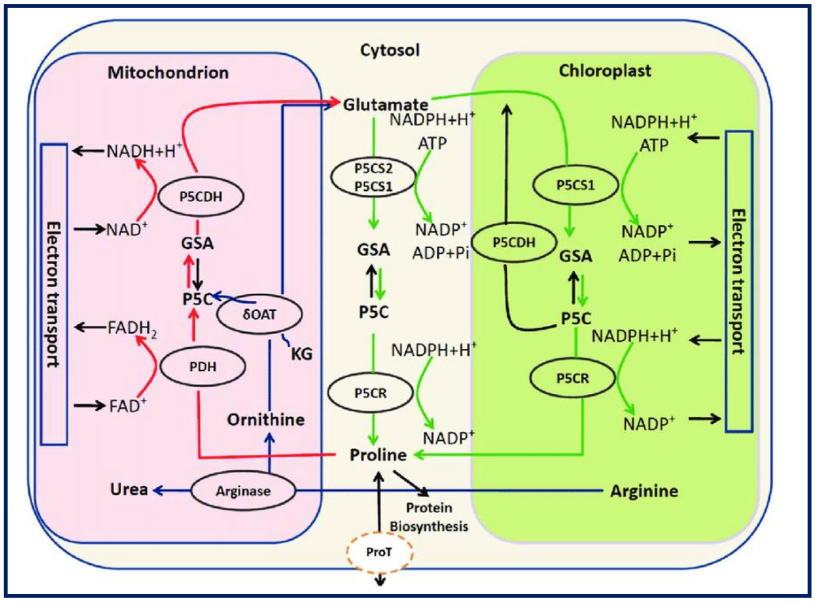


Fig. 23: Proline metabolism in plants: Proline synthesis occurs in the cytosol and chloroplast. Proline degradation occurs in mitochondria. P5C - δ-pyrroline-5-carboxylate, P5CR - pyrroline-5-carboxylate reductase, P5CS - pyrroline-5- carboxylate synthase, GSA - glutamic semialdehyde, PDH - Proline dehydrogenase, OAT - Ornithine aminotransferase, KG - Ketoglutarate, ProT-Proline transporter. After Khanna-Chopra *etal.,* (2019)

Khanna-Chopra *et al.,* (2019) reported that proline is an important compatible solute that exhibits numerous roles during plant growth and development and under abiotic stresses including drought and salinity. Proline protects plants against these stresses mainly by maintaining osmotic adjustment, ROS scavenging, and modulating major enzymatic components of the antioxidant defense system. Proline also stabilizes proteins and protein complexes in the chloroplast and cytosol and protects the photosynthetic apparatus and the enzymes involved in detoxification of ROS during stress. The enhanced rate of Pro biosynthesis in chloroplasts can contribute to the stabilization of redox balance and maintenance of cellular homeostasis by dissipating the excess of reducing potential when electron transport is saturated during adverse conditions. Proline catabolism in the mitochondria is connected to oxidative respiration and provides energy for resumed growth after stress. Moreover, Pro oxidation can regulate mitochondrial ROS levels and influence programmed cell death. Proline appears to function as a metabolic signal that regulates metabolite pools and redox balance controls the expression of numerous genes and influences plant growth and development.

Both these regulatory steps are used to overproduce proline in plants Oh *et al.,* (2010). It functions as an O_2 quencher thereby revealing its antioxidant capability. This was observed in a study carried out by Matysik *et al.,* (2002); Ben Ahmed *et al.,* (2010), they observed that proline supplements enhanced salt tolerance in olive (*Olea europaea*) by amelioration of some antioxidative enzyme activities, photosynthetic activity, and plant growth and the preservation of a suitable plant water status under salinity conditions. It has been reported that proline improves salt tolerance in *Nicotiana tabacum* by increasing the activity of enzymes involved in antioxidant defence system Hoque *et al.,* (2008). Deivanai et al. Deivanai *et al.,* (2011) also demonstrated that rice seedlings from seeds pretreated with 1mM proline exhibited improvement in growth during salt stress. Glycine betaine is an amphoteric quaternary ammonium compound ubiquitously found in microorganisms, higher plants and animals, and is electrically neutral over a wide range of pH. It is highly soluble in water but also contains nonpolar moiety constituting 3-methyl groups. Because of its unique structural features it interacts both with hydrophobic and hydrophilic domains of the macromolecules, such as enzymes and protein complexes. Glycine betaine is a nontoxic cellular osmolyte that raises the osmolarity of the cell during stress period; thus, it plays an important function in stress mitigation. Glycine betaine also protects the cell by osmotic adjustment Gadallah, (1999) stabilizes proteins Makela *et al.,* (2000) and protects the photosynthetic apparatus from stress damages Cha-Um and Kirdmanee, (2010)] and reduction of ROS Ashraf and Foolad, (2007), Saxena *et al.,* (2013). Accumulation of glycine betaine is found in a wide variety of plants belonging to different taxonomical background. Glycine betaine is synthesized within the cell from either choline or glycine. Synthesis of glycine betaine from choline is a 2-step reaction involving two or more enzymes. In the first step, choline is oxidised to betaine aldehyde that is then again oxidized in the next step to form glycine betaine. In higher plants, the first conversion is carried out by the enzyme choline monooxygenase (CMO), whereas the next step is catalyzed by betaine aldehyde dehydrogenase (BADH) Ahmad *et al.,* (2013), another pathway that is observed in some plants, mainly halophytic, demonstrated the synthesis of glycine betaine from glycine. Here glycine betaine is synthesized by three successive N-methylation and the reactions are catalyzed by two S-adenosyl methionine dependent methyl transferases, glycine sarcosine N-methyl transferase (GSMT), and sarcosine dimethyl glycine N-methyl transferase (SDMT). These two enzymes have overlapping functions as GSMT catalyzes the first and the second step while SDMT catalyzes the second and third step Ahmad *et al.,* (2013). Rahman *et al.,* (2002) reported the positive effect of glycine betaine on the ultrastructure of *Oryza sativa* seedlings when exposed to salt stress. Under stressed condition (150 mM NaCl), the ultrastructure of the seedling shows several damages such as swelling of thylakoids, disintegration of grana and intergranal lamellae, and disruption of mitochondria. However, these damages were largely prevented when seedlings were pretreated with glycine betaine. When glycine betaine is applied as a foliar spray in a plant subjected to stress, it led to pigment stabilization and increase in photosynthetic rate and growth Cha-Um and Kirdmanee, (2010); Ahmad *et al.,* (2013). Polyols are compounds with multiple hydroxyl functional groups available for organic reactions. Sugar alcohols are a class of polyols functioning as compatible solutes, as low molecular weight chaperones, and as ROS scavenging compounds Ashraf and Foolad, (2007). They can be classified into two major types, cyclic (e.g., pinitol) and acyclic (e.g., mannitol). Mannitol synthesis is induced in plants during stressed period via action of NADPH dependent mannose-6-phosphate reductase. These compatible solutes function as a protector or stabilizer of enzymes or membrane structures that are sensitive to dehydration or ionically induced damage. It was found that the transformation with bacterial *mltd* gene that encodes formannitol-1-phosphate dehydrogenase in both *Arabidopsis* and tobacco (*Nicotiana tabacum*) plants confer salt tolerance, thereby maintaining normal growth and development when subjected to high level of salt stress Binzel *et al.,* (1988), Thomas *et al.,* (1995). Pinitol is accumulated within the plant cell when the plant is subjected to salinity stress. The biosynthetic pathway consists of two major steps, methylation of myo-inositol that results in formation of an intermediate compound, ononitol, which undergoes epimerization to form pinitol. Inositol methyl transferase enzyme encoded by *imt* gene plays major role in the synthesis of pinitol. Transformation of *imt* gene in plants shows a result similar to that observed in the case of *mltd* gene. Thus, Pinitol plays a significant role in stress alleviation. Accumulation of polyols, either straight chain metabolites such as mannitol and sorbitol or cyclic polyols such as myo-inositol and its methylated derivatives, is correlated with tolerance to drought and/or salinity, based on polyol distribution in many species, including microbes, plants, and animals Bohnert *et al.,* (1995) Fig. (24).

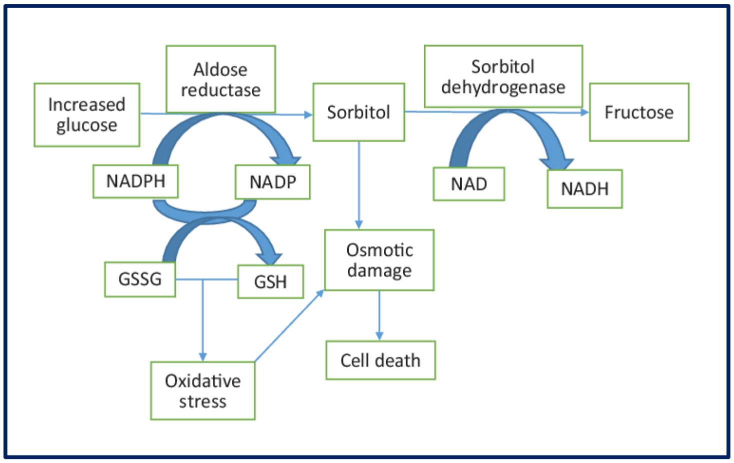


Fig. 24: Illustrates polyol pathway. Hyperglycaemia increases flux through the polyol pathway that metabolises excess glucose. The consumption of nicotinamide adenine dinucleotide phosphate (NADPH) in the initial conversion of glucose to sorbitol results in less NADPH availability for the generation activity of glutathione reductase that maintains the adequate levels of reduced glutathione (GSH), which is an important cellular antioxidant. The depletion of GSH may lead to increased levels of reactive oxygen species, leading to oxidative stress. (NADPH, Nicotinamide adenine dinucleotide phosphate (reduced form); NADP, nicotinamide adenine dinucleotide phosphate; NAD, nicotinamide adenine dinucleotide; NADH, nicotinamide adenine dinucleotide (reduced form); GSSG, oxidized glutathione; GSH, reduced glutathione). After Solani David Mathebula, (2018)

Solani David Mathebula, (2018) reported that in cellular glucose metabolism, a small fraction of glucose is normally metabolized through the polyol pathway , Nishikawa *et al.,* (2000); Gabbay, (1973); Oates, (2002) ; Gabbay, (1975); Kinoshita, (1990); Coucha *et al.,* (2015) and Mathebula, (2015). In diabetes, there is an increase in the flux of glucose, and the excess glucose is metabolized in this pathway. Two enzymes control the polyol pathway. Aldose reductase, the first enzyme, reduces glucose into sorbitol using nicotinamide adenine dinucleotide phosphate (NADNP) as a cofactor. Sorbitol is then oxidised or converted to fructose by sorbitol dehydrogenase, the second enzyme, with nicotinamide adenine dinucleotide (NAD) as a cofactor Fig. (24). Under euglycaemic conditions, sorbitol level is low, while during Hyperglycaemia, sorbitol level increases owing to the flux of glucose through the polyol pathway. Since sorbitol is impermeable and cannot easily diffuse through cell or plasma membranes, and there is a slow metabolism of sorbitol to fructose, it accumulates within the retinal cells and causes osmotic damage to the retinal vascular cells, leading to DR

Accumulations of carbohydrates such as sugars (e.g., glucose, fructose, fructans, and trehalose) and starch occur under salt stress Parida *et al.,* (2004). The major role played by these carbohydrates in stress mitigation involves osmoprotection, carbon storage, and scavenging of reactive oxygen species. It was observed that salt stress increases the level of reducing sugars (sucrose and fructans) within the cell in a number of plants belonging to different species Kerepesi and Galiba, (2000). Besides being a carbohydrate reserve, trehalose accumulation protects organisms against several physical and chemical stresses including salinity stress. They play an osmoprotective role in physiological responses Ahmad *et al.,* (2013). Sucrose content was found to increase in tomato (*Solanum lycopersicum*) under salinity due to increased activity of sucrose phosphate synthase Gao *et al.,* (1998). Sugar content, during salinity stress, has been reported to both increase and decrease in various rice genotype Alamgir and Yousuf Ali, (1999). In rice roots, it has been observed that starch content decreased in response to salinity while it remained unchanged in the shoot. Decrease in starch content and increase in reducing and nonreducing sugar content were noted in leaves of *Bruguiera parviflora* Parida *et al.,* (2004).

4.4. Antioxidant Regulation of Salinity Tolerance.

Abiotic and biotic stress in living organisms, including plants, can cause overflow, deregulation, or even disruption of electron transport chains (ETC) in chloroplasts and mitochondria. Under these conditions molecular oxygen (O_2) acts as an electron acceptor, giving rise to the accumulation of ROS. Singlet oxygen ($^1O_2$), the hydroxyl radical (OH^-), the superoxide radical ($O^-{}_2$), and hydrogen peroxide (H_2O_2) are all strongly oxidizing compounds and therefore potentially harmful for cell integrity Gro *et al.,* (2013). Antioxidant metabolism, including antioxidant enzymes and nonenzymatic compounds, play critical parts in detoxifying ROS induced by salinity stress. Salinity tolerance is positively correlated with the activity of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR) and with the accumulation of nonenzymatic antioxidant compounds Asada, (1999); Gupta *et al.,* (2005) ;Gill *et al.,* (2013) and Tuteja *et al.,* (2013) have recently reported a couple of helicase proteins (e.g., DESD-box helicase and OsSUV3 dual helicase) functioning in plant salinity tolerance by improving/maintaining photosynthesis and antioxidant machinery Fig.(25).

Kim *et al.,* (2013) showed that silicon (Si) application to rice root zone influenced the hormonal and antioxidant responses under salinity stress. The results showed that Si treatments significantly increased rice plant growth compared to controls under salinity stress. Si treatments reduced the sodium accumulation resulting in low electrolytic leakage and lipid peroxidation compared to control plants under salinity stress. Enzymatic antioxidant (catalase, peroxidase, and polyphenol oxidase) responses were more pronounced in control plants than in Si-treated plants under salinity stress. Anthocyanin is a flavonoid whose accumulation in plant exposed to salt stress has been largely documented.

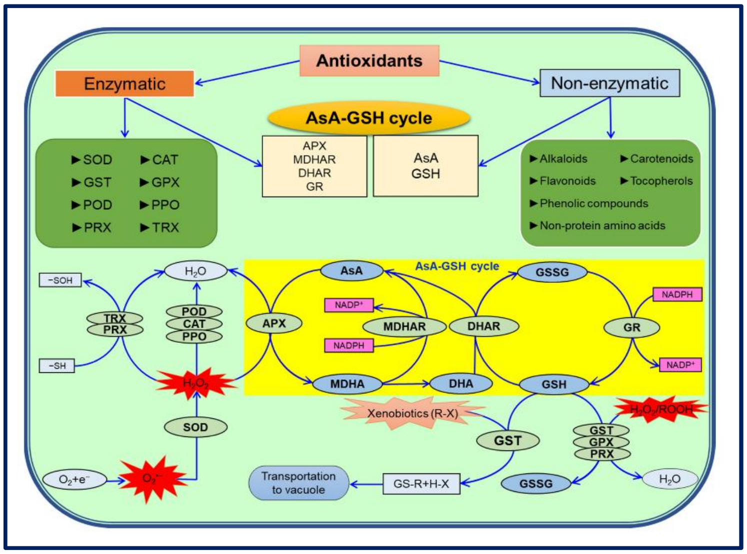


Fig. 25: Represents different types of antioxidants and their combined mechanisms Hasanuzzaman *et al.,* (2020). Such as (SOD)-superoxide dismutase; (CAT)-catalase; (POX)-peroxidases; (AsA)-ascorbate; (DHA)-Dehydroascorbate; (GSSG)-oxidized glutathione; (GSH)-reduced glutathione; (APX)-ascorbate peroxidase; (MDHA)-monodehydroascorbate; (MDHAR)-monodehydroascorbate reductase; (DHAR)-dehydroascorbate reductase; (GR)-glutathione reductase; (GST)- glutathione S-transferase; (GPX)-glutathione peroxidase; (PPO)-polyphenol oxidase; (PRX)-peroxiredoxins; (TRX)-thioredoxin; (NADPH)-nicotinamide adenine dinucleotide phosphate; (O_2)-oxygen; e^--electrons; (H_2O_2)-hydrogen peroxide; (O_2) •–-superoxide anion; R-aliphatic, aromatic or heterocyclic group; X-sulfate, nitrite or halide group; ROOH-hydro peroxides; -(SH)-thiolate; -(SOH)-sulfenic acid. After Mirza Hasanuzzaman *et al.,* (2021).

Van Oosten *et al.,* (2013) isolated the *anthocyanin-impairedresponse- 1* (*air1*) mutant that is unable to accumulate anthocyanins under salt stress. The *air1* mutant showed a defect in anthocyanin production in response to salt stress but not to other stresses such as high light, low phosphorous, high temperature, or drought stress. This specificity indicated that *air1* mutation did not affect anthocyanin biosynthesis but rather its regulation in response to salt stress. The discovery and characterization of AIR1 opens avenues to dissect the connections between abiotic stress and accumulation of antioxidants in the form of flavonoids and anthocyanins. Ascorbate is one of the major antioxidants present within the cell. Pea plants grown under saline (150mM NaCl) stress showed an enhancement of both APX activity and Snitrosylated APX, as well as an increase of H_2O_2, NO, and S-nitrosothiol (SNO) content that can justify the induction of the APX activity. Proteomic data have shown that APX is one of the potential targets of PTMs mediated byNO-derived molecules Begara-Morales *et al.,* (2014) Using recombinant pea cytosolic APX, the impact of peroxynitrite ($ONOO^-$) and S-nitrosoglutathione (GSNO), which are known to mediate protein nitration and S-nitrosylation processes, respectively, was analysed. While peroxynitrite inhibits APX activity, GSNO enhances its enzymatic activity. The results provide new insight into the molecular mechanism of the regulation of APX, which can be both inactivated by irreversible nitration and activated by reversible S-nitrosylation Begara-Morales *et al.,* (2014). Exogenous application of ascorbate mitigates the adverse effects of salinity stress in various plant species and promotes plant recovery from the stress Agarwal and Shaheen, (2007); Munir and Aftab, (2011) and El-Sebai, *et al.,* (2015) Fig.(26).

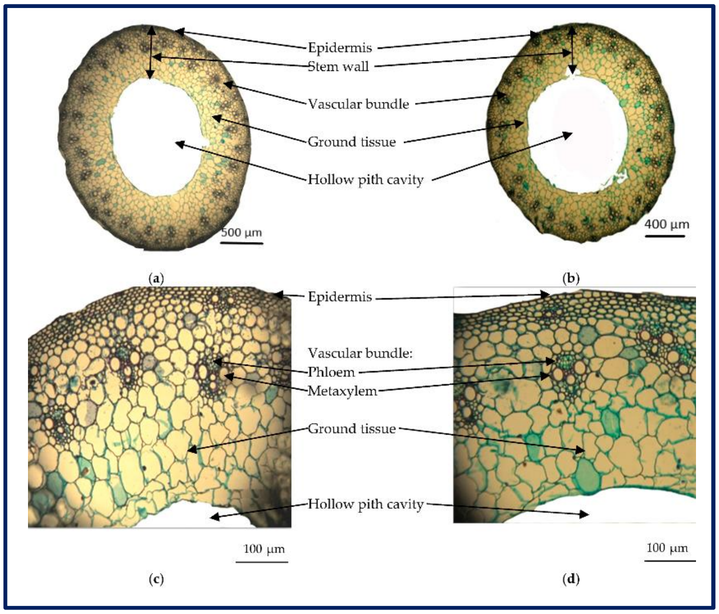


Fig. 26: Transverse sections through the median portion of the main stems of wheat plants grown for 56 days at 0.23 and 6.0 dS m^{-1} salt stress (×68) (a) 0.23 dS m^{-1} ; (b) 6.0 dS m^{-1} , and magnified portionfrom transverse sections shown in (a,b) (×330); (c) 0.23 dS m^{-1} ; (d) 6.0 dS.m^{-1} After Rania *et al.,* (2020)

Rania *et al.,* (2020) stated that examination of ^{14}C fixation and its distribution in biochemical leaf components, as well as the physiological and anatomical were conducted, using wheat plants (*Triticum aestivum* L.) grown in diluted seawater at 0.2, 3.0, 6.0, and 12.0 dS m^{-1}. Results revealed that application of diluted seawater significantly reduced the chlorophyll content, ^{14}C fixation (photosynthesis), plant height, main stem diameter, total leaf area per plant, and total dry weight at particularly at 3.0, 6.0, and 12.0 dS m^{-1} seawater salt stress. The ^{14}C loss was very high at 12.0 ds m^{-1} after 120 h. ^{14}C in lipids (ether extract), significant changes at 12.0 dS m^{-1} at 96 and 120 h. The findings indicated the leaf and stem anatomical feature change of wheat plants resulting from adaptation to salinity stress. A reduction in the anatomical traits of stem and leaf diameter, wall thickness, diameter of the hollow pith cavity, total number of vascular bundles, number of large and small vascular bundles, bundle length and width, thickness of phloem tissue, and diameter of the metaxylem vessel of wheat plants was observed. They also concluded salt stress induces both anatomical and physiological changes in the stem and leaf cells of wheat, as well as the tissues and organs, and these changes in turn make it possible for the plants to adapt successfully to a saline environment. They also stated that most plant physiological processes associated with salinity are linked to anatomical structure adaptation, which allows plants to grow under abiotic stress Hameed *et al.,* (2009). For instance, salt stress resulted in physiological and morpho-anatomic changes in Lotus tenuis Paz *et al.,* (2014). The obtained results on wheat plants grown under salt stress in terms of the anatomical structures of the main stems and leaves are supported by previous reports on wheat Akram *et al.,* (2002), kallar grass Abd-Elbar *et al.,* (2012), and faba beans Semida *et al.,* (2014). Moderate and high salinity concentrations (3000 and 6000 mg.kg^{-1} NaCl) reduced xylem and phloem tissue and metaxylem vessel diameter, as well as the primary sorghum bundle size Arafa *et al.,* (2009). In the present study, seawater salt stress decreased the cross-sectional area of the vascular bundle throughout the stems and leaflets, resulting in a significantly diminished conductive potential of the phloem and xylem Fig. (26). Moreover, seawater application reduced the vascular bundle area and the vessel diameter. Salt stress increased the flowing resistance of water from roots to leaves, reduced vascular tissue transportation efficiency, and restricted the transportation of water due to dissolved salt ions absorbed by the roots Akram *et al.,* (2002). However, seawater salt stress had a more visible effect on phloem than on xylem, in which translocation of water dissolved salt ions was severely restricted to the ground parts, and the transportation of photosynthetic materials was decreased to the plant apex and young roots.

Another antioxidant in stress mitigation is glutathione, which can react with superoxide radical, hydroxyl radical, and hydrogen peroxide, thereby functioning as a free radical scavenger. It can also participate in the regeneration of ascorbate via ascorbate-glutathione cycle Foyer *et al.,* (1997). When applied exogenously glutathione helped to maintain plasma membrane permeability and cell viability during salinity stress in *Allium cepa* Aly-Salama and Al-Mutawa, (2009). Application of glutathione and ascorbate was found to be effective in increasing the height of the plant, branch number, fresh and dry weight of herbs and flowers, and the content of carbohydrates, phenols, xanthophylls pigment, and mineral ion content when subjected to saline condition Rawia Eid *et al.,* (2011). Many studies have found differences in levels of expression or activity of antioxidant enzymes; these differences are sometimes associated with the more tolerant genotype and sometimes with the more sensitive genotype. Munns and Tester, (2008), suggested that differences in antioxidant activity between genotypes may be due to genotypic differences in degrees of stomatal closure or in other responses that alter the rate of CO_2 fixation and differences that bring into play the processes that avoid photo inhibition and for which the plant has abundant capacity Munns and Tester, (2008),. Roy *et al.,* (2014) in their recent review have argued that there are three main traits in plants, which help them in their adaptation to salinity stress: ion exclusion, tissue tolerance, and salinity tolerance. It seems that antioxidants have some role in tissue and salinity tolerance mechanism.

4.5. Roles of Polyamines in Salinity Tolerance.

Polyamines (PA) are small, low molecular weight, ubiquitous, polycationic aliphatic molecules widely distributed throughout the plant kingdom. Polyamines play a variety of roles in normal growth and development such as regulation of cell proliferation, somatic embryogenesis, differentiation and morphogenesis, dormancy breaking of tubers and seed germination, development of flowers and fruit, and senescence Knott *et al.,* (2007); Galston et al. (1997). It also plays a crucial role in abiotic stress tolerance including salinity and increases in the level of polyamines are correlated with stress tolerance in plants Gupta *et al.,* (2013); Kov´acs *et al.,* (2010) Fig. (27).

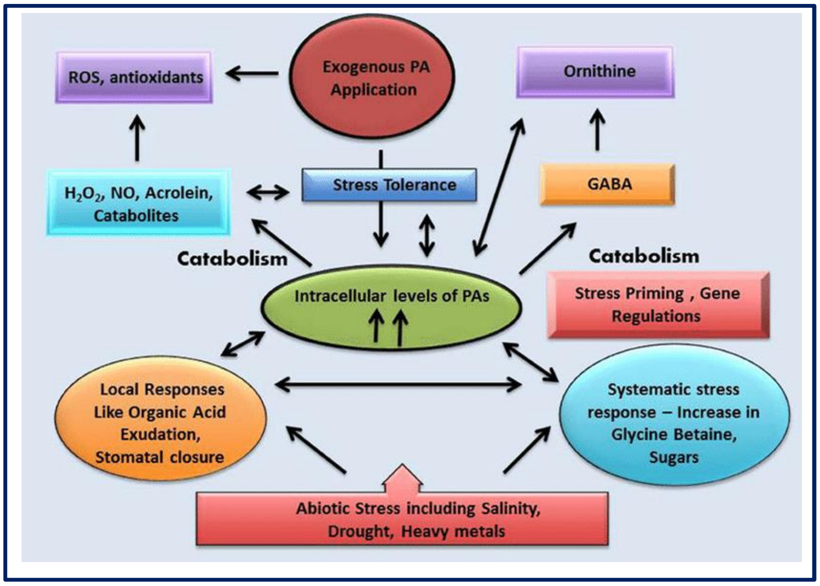


Fig. 27: Illustrates the role of polyamine (PA) in plant abiotic stress tolerance.

The most common polyamines that are found within the plant system are diamine putrescine (PUT), triamine spermidine (SPD), and tetra-amine spermine (SPM) Alc´azar *et al.,* (2011), Shu *et al.,* (2012). The PA biosynthetic pathway has been thoroughly investigated in many organisms including plants and has been reviewed in details Alet *et al.,* (2012); Rambla *et al.,* (2010) PUT is the smallest polyamine and is synthesized from either ornithine or arginine by the action of enzyme ornithine decarboxylase (ODC) and arginine decarboxylase (ADC), respectively Gupta *et al.,* (2013), Hasanuzzaman *et al.,* (2014). N-carbamoyl-putrescine is converted to PUT by the enzyme N-carbamoyl-putrescine amino hydrolase Alc´azar *et al.,* (2010); Bouchereau *et al.,* (1999). The PUT thus formed functions as a primary substrate for higher polyamines such as SPD and SPM biosynthesis. The triamine SPD and tetramine SPM are synthesized by successive addition of amino propyl group to PUT and SPD, respectively, by the enzymes spermidine synthase (SPDS) and spermine synthase (SPMS) Alc´azar *et al.,* (2006); Fluhr and Mattoo, (1996). ODC pathway is the most common pathway for synthesis of polyamine found in plants. Most of the genes involved in the ODC pathway have been identified and cloned. However, there are some plants where ODC pathway is absent; for instance in *Arabidopsis* polyamines are synthesized via ADC pathway Kusano *et al.,* (2007); Hanfrey *et al.,* (2001). All the genes involved in polyamine biosynthesis pathways have been identified from different plant species including *Arabidopsis* Urano *et al.,* (2003); Janowitz *et al.,* (2003). Polyamine biosynthesis pathway in *Arabidopsis* involves six major enzymes: DC encoding genes (*ADC1* and *ADC2*); SPDS (*SPDS1* and *SPDS2*) and SAMDC (*SAMDC1, SAMDC2, SAMDC3, and SAMDC4*) Janowitz *et al.,* (2003); Hashimoto *et al.,* (1998). On the contrary, single genes represent SPM synthase, thermospermine synthase, agmatine iminohydrolase and N-carbamoyl putrescine amidohydrolase only Urano *et al.,* (2004); Hanzawa *et al.,* (2002). Increase in endogenous polyamine level has been reported when the plant is exposed to salinity stress. Intracellular polyamine level is regulated by polyamine catabolism. Polyamines are oxidatively catabolized by amine oxidases that include copper binding diamine oxidases and FAD binding polyamine oxidases. These enzymes play a significant role in stress tolerance Takahashi and Kakehi, (2010); Cona *et al.,* (2006) Fig. (28).

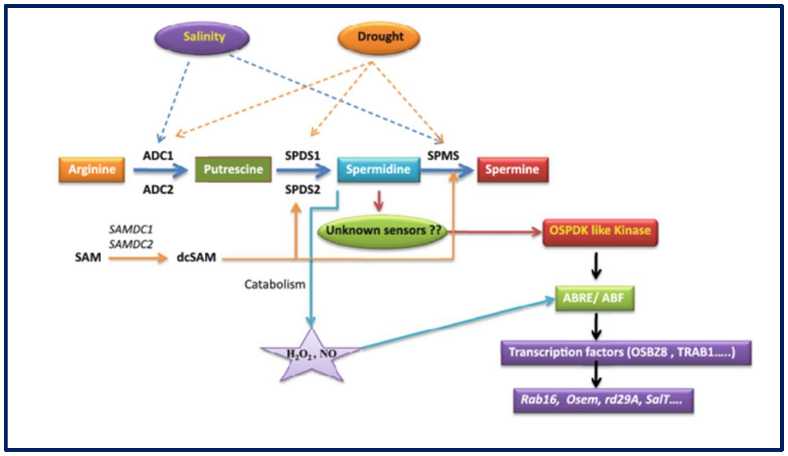


Fig. 28: Metabolism of polyamines in plants. ADC arginine decarboxylase, ODC ornithine decarboxylase, dcSAM decarboxylated S-adenosylmethionine, SAM S-adenosylmethionine, SAMDC S-adenosylmethionine decarboxylase, SPDS spermidine synthase, SPMS spermine synthase, PAO polyamine oxidase, PMT putrescine N-methyltransferase, CuAO copper-dependent amine (diamine) oxidase. Biosynthesis is indicated by blue arrow and degradation pathway by orange arrow. After Kamala Gupta *et al.,* (2013)

Kamala Gupta *et al.,* (2013), reported that significance of naturally occurring intracellular polyamines (PAs), such as spermine, spermidine, and putrescine, in relation to the mechanism and adaptation to combat abiotic stress has been well established in plants. Because of their polycationic nature at physiological pH, PAs bind strongly to negative charges in cellular components such as nucleic acids, proteins, and phospholipids. Accumulation of the three main PAs occurs under many types of abiotic stress, and modulation of their biosynthetic pathway confers tolerance to drought or salt stress. Maintaining crop yield under adverse environmental conditions is probably the major challenge faced by modern agriculture, where PAs can play important role. Over the last two decades, genetic, transcriptomic, proteomic, metabolomic, and phenomics approaches have unraveled many significant functions of different PAs in the regulation of plant abiotic stress tolerance. In recent years, much attention has also been devoted to the involvement of PAs in ameliorating different environmental stresses such as osmotic stress, drought, heat, chilling, high light intensity, heavy metals, mineral nutrient deficiency, pH variation, and UV irradiation

The changes in cellular polyamine level due to stress provide possible implications in stress but do not provide evidence of their role in counteracting stress. Hence, to understand whether polyamines actually protect cells from stress-induced damages, exogenous application of polyamines, which is expected to increase endogenous polyamine, has been investigated before or during stress Tisi *et al.,* (2008); Navakoudis *et al.,* (2003). Application of exogenous polyamine has been found to increases the level of endogenous polyamine during stress. Positive effects of polyamines have been associated with the maintenance of membrane integrity, regulation of gene expression for the synthesis of osmotically active solutes, reduction in ROS production, and controlling accumulation of Na^+ and Cl^- ion in different organs Tisi *et al.,* (2008); Yiu, *et al.,* (2009). It was observed that plant deficient in *ADC1* and *ADC2* is hypersensitive to stress Hussain *et al.,* (2011). In *Arabidopsis*, expression of *ADC* and *SPMS* increases when exposed to salinity stress. Whereas mutants of polyamine biosynthetic genes show sensitivity to salinity Yamaguchi *et al.,* (2006). Overproduction of PUT, SPD, and SPM in rice, tobacco, and *Arabidopsis* enhances salt tolerance Roy and Wu, (2002). Salt stress regulates polyamine biosynthesis and catabolism by acting as a cellular signal in hormonal pathways thereby regulating abscisic acid (ABA) in response to stress Shevyakova *et al.,* (2013). Additionally, SPM and SPD are regarded as potent inducers of NO that is another important signalling molecule Moschou *et al.,* (2008) and its involvement in salinity tolerance is discussed below. It has been reported that exogenous application of polyamines could alleviate salt-induced reduction in photosynthetic efficiency, but this effect depends on polyamine concentration, types, and level of stress Duan *et al.,* (2008). When the seedling of *Sorghum bicolor* treated with 0.25mM SPM is subjected to salt stress it shows improvement in growth and partial increase in the activity of peroxidase and glutathione reductase enzyme with a concomitant decrease in the level of membrane lipid peroxidation Chai *et al.,* (2010); Li *et al.,* (2013) performed 2-DE gel electrophoresis and MALDITOF/ TOFMS with cytosolic proteins to understand the effect of exogenous SPD on proteomic changes under normal and NaCl stress of 3 days old cucumber seedling leaves. Many changes were observed in the levels of proteins involved in energy and metabolic pathways, protein metabolic, stress defense, and other functional proteins. They observed that increased salt tolerance by exogenous SPD would contribute to higher expressions of proteins involved in the SAMs metabolism, protein biosynthesis, and defense mechanisms on antioxidant and detoxification. Li *et al.,* (2013) also argued that the regulation of Calvin cycle, protein-folding assembly, and the inhibition of protein proteolysis by SPD might play important roles in salt tolerance.

4.6. Roles of Nitric Oxide in Salinity Tolerance.

Nitric oxide (NO) is a small volatile gaseous molecule, which is involved in the regulation of various plant growth and developmental processes, such as root growth, respiration, stomata closure, flowering, cell death, seed germination and stress responses, as well as a stress-signalling molecule Delledonne *et al.* (1998), Crawford (2006). NO directly or indirectly triggers expression of many redox-regulated genes. NO reacts with lipid radicals thus preventing lipid oxidation, exerting a protective effect by scavenging superoxide radical and formation of peroxynitrite that can be neutralized by other cellular processes. It also helps in the activation of antioxidant enzymes (SOD, CAT, GPX, APX, and GR) Bajgu (2014) Fig. (29).

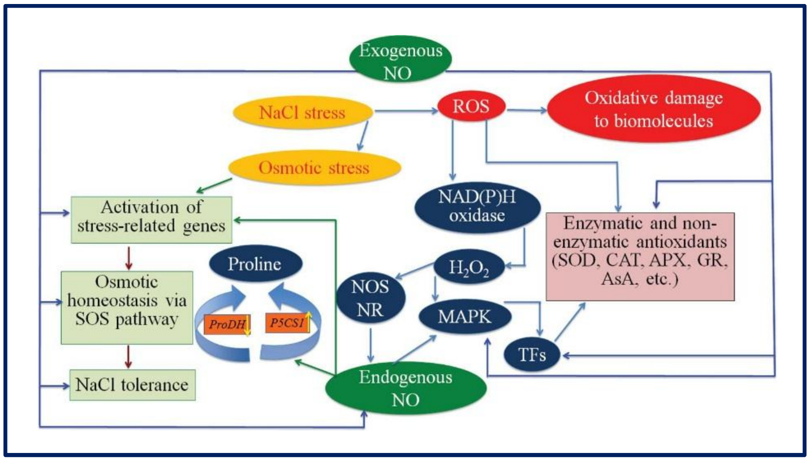


Fig. 29: Potential mechanisms of NaCl stress mitigation by application of exogenous NO. Excessive NaCl causes osmotic and oxidative stresses in plants. Salt stress induces ABA accumulation, which promotes H_2O_2 generation through NAD (P) H oxidase. Stress-induced H_2O_2 triggers generation of endogenous NO by activating NR (nitrate reductase) and NOS (nitric oxide synthase)-like enzymes. Exogenous application of NO to plants may enhance the biosynthesis of endogenous NO, as well as that of antioxidant enzymes through MAPK (mitogen-activated protein kinase) and other unknown signaling pathways. Exogenous NO supplementation to plants can also up-regulate genes involved in proline synthesis, such as P5CS1, and other stress-related genes responsible for NaCl tolerance, whereas it might down-regulate ProDH that is involved in proline catabolism. Exogenous NO treatment may also help balance osmotic homeostasis in plants under salt stress via the SOS (salt overly sensitive) pathway, by increasing plasma membrane H+-ATPase activity. APX, ascorbate peroxidase; AsA, ascorbic acid; CAT, catalase; GR, glutathione reductase; H_2O_2, hydrogen peroxide; P5CS1, δ1-pyrroline-5-carboxylate synthetase; ProDH, proline dehydrogenase; ROS, reactive oxygen species; SOD, superoxide dismutase; TFs, transcription factors. After Ahmad *et al.* (2016)

Ahmad *et al.* (2016) reprted that External application of nitric oxide (NO) in the form of its donor S-nitroso-N-acetylpenicillamine (SNAP) could mitigate the deleterious effects of NaCl stress on chickpea (*Cicer arietinum* L.) plants. SNAP (50 µM) was applied to chickpea plants grown under non-saline and saline conditions (50 and 100 mM NaCl). Salt stress inhibited growth and biomass yield, leaf relative water content (LRWC) and chlorophyll content of chickpea plants. High salinity increased electrolyte leakage, carotenoid content and the levels of osmolytes (proline, glycine betaine, soluble proteins and soluble sugars), hydrogen peroxide (H_2O_2) and malondialdehyde (MDA), as well as the activities of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase in chickpea plants. Expression of the representative SOD, CAT and APX genes examined was also up regulated in chickpea plants by salt stress. On the other hand, exogenous application of NO to salinized plants enhanced the growth parameters, LRWC, photosynthetic pigment production and levels of osmolytes, as well as the activities of examined antioxidant enzymes that is correlated with up-regulation of the examined SOD, CAT and APX genes, in comparison with plants treated with NaCl only. Furthermore, electrolyte leakage, H_2O_2 and MDA contents showed decline in salt-stressed plants supplemented with NO as compared with those in NaCl-treated plants alone. Thus, the exogenous application of NO protected chickpea plants against salt stress-induced oxidative damage by enhancing the biosynthesis of antioxidant enzymes, thereby improving plant growth under saline stress. Taken together, our results demonstrate that NO has capability to mitigate the adverse effects of high salinity on chickpea plants by improving LRWC, photosynthetic pigment biosynthesis, osmolyte accumulation and antioxidative defense system.

Exogenous NO application has been found to play roles in stress mitigation Sung and Hong (2010), Xiong *et al.* (2010), but the effects depend on NO concentration Fig. (30).

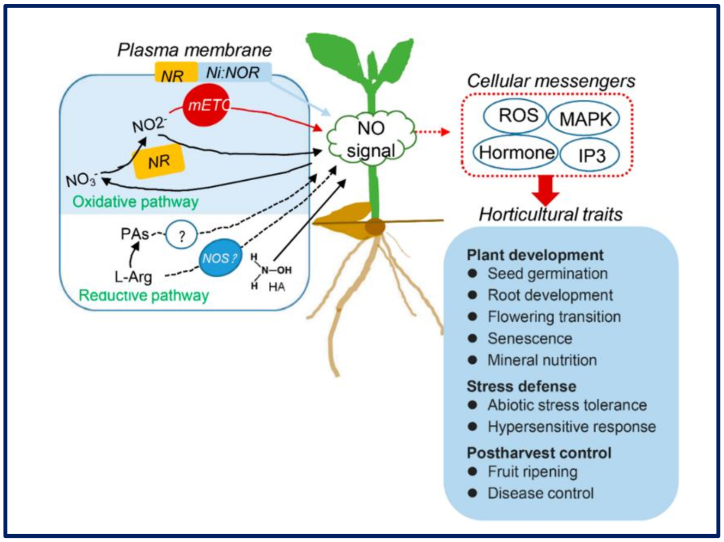


Fig. 30: Sources of NO production and NO functions in regulating plant growth, development, and adaptive processes. The reductive pathway is based on the reduction of nitrite to NO, whereas the oxidative route relies on the oxidation of aminated molecules, such as L-Arg. The produced NO can be used to transduce external and internal signals to regulate plant development and stress responses by interacting with other cellular messengers. NR, nitrate reductase; Ni: NOR, NO-forming nitrite reductase; mETC, mitochondrial nitrite reduction; NOS, nitric oxide synthase; L-Arg, L-arginine; PA, polyamine; HA, hydroxylamine. After Sun et al. (2021)

Sun *et al.* (2021) stated that nitric oxide (NO) regulates plant growth, enhances nutrient uptake, and activates disease and stress tolerance mechanisms in most plants, making NO a potential tool for use in improving the yield and quality of horticultural crop species. Although the use of NO in horticulture is still in its infancy, research on NO in model plant species has provided an abundance of valuable information on horticultural crop species. Emerging evidence implies that the bioactivity of NO can occur through many potential mechanisms but occurs mainly through S-nitrosation, the covalent and reversible attachment of NO to cysteine thiol. In this context, NO signaling specifically affects crop development, immunity, and environmental interactions. Moreover, NO can act as a fumigant against a wide range of postharvest diseases and pests. However, for effective use of NO in horticulture, both understanding and exploring the biological significance and potential mechanisms of

NO in horticultural crop species are critical. This review provides a picture of our current understanding of how NO is synthesized and transduced in plants, and particular attention is given to the significance of NO in breaking seed dormancy, balancing root growth and development, enhancing nutrient acquisition, mediating stress responses, and guaranteeing food safety for horticultural production

Exogenous application of sodium nitroprusside (SNP), a NO donor, on *Lupinus luteus* seedlings subjected to salt stress enhanced seed germination and root growth Kopyra and Gw´o´zd´z (2003) .Seed germination was promoted at concentrations between 0.1 and 800 μM SNP in a dose-dependent manner. Stimulation was most pronounced effects after 18 and 24 h and ceased after 48 h of imbibition. The promoting effect of NO on seed germination persisted even in the presence of heavy metals (Pb and Cd) and NaCl. Kopyra and Gw´o´zd´z (2003) further showed that the pretreatment of *L. luteus* seedlings for 24 h with 10 μM SNP resulted in efficient reduction of the detrimental effect of the abiotic stressors on root growth and morphology. Pretreatment of maize seedlings with 100 μMSNP increases dry matter of roots and shoots under salinity stress; however, when the concentration of SNP was increased to 1000 μM shoot and root dry weight decreased Zhang *et al.* (2006). Thus, this experiment highlighted both the protective effects of low NO concentration and the toxic effect of high NO concentration on plants. The positive effects of NO on salinity tolerance attributed to antioxidant activities and modulation of ROS detoxification system Mishra *et al.* (2011). Improved plant growth under salinity stress by exogenous application of NO was associated with increases in antioxidant enzymes such as SOD, CAT, GPX, APX, and GR Zhao *et al.* (2004), and suppression of malondialdehyde (MDA) production or lipid peroxidation Nalousi *et al.* (2012). Effects of NO on salinity tolerance are related to its regulation of plasma membrane H^+-ATPase and Na^+/K^+ ratio Crawford (2006). NO stimulates H^+-ATPase (H^+-PPase), thereby producing a H^+ gradient and offering the force for Na^+/H^+ exchange. Such an increase of Na^+/H^+ exchange may contribute to K+ and Na+ homeostasis Zhang *et al.* (2006). Although NO acts as a signal molecule under salt stress and induces salt resistance by increasing PM H^+-ATPase activity, research results from Zhang *et al.* (2007) with calluses from *Populus euphratica* also indicated NO cannot activate purified PM H^+-ATPase activity, at least in vitro. They initially hypothesized ABA or H_2O_2 might be downstream signal molecules to regulate the activity of PM H^+-ATPase. Further results indicated H_2O_2 content increased greatly under salt stress. Since H_2O_2 might be the candidate downstream, signal molecule, Zhang *et al.* (2007) tested PM H^+-ATPase activity and K to Na ratio in calluses by adding H_2O_2. The results suggested that H_2O_2 inducing an increased PM H+-ATPase activity resulted in an increased K to Na ratio leading to NaCl stress adaptation.

4.7. Hormone Regulation of Salinity Tolerance.

Abscisic acid (ABA) is important phytohormones whose application to plant ameliorates the effect of stress condition(s). Salinity stress causes osmotic stress and water deficit, increasing the production of ABA in shoots and roots He and. Cramer (1996), Popova *et al.* (1995). Accumulation of ABA can mitigate the inhibitory effect of salinity on photosynthesis, growth, and translocation of assimilates Popova *et al.* (1995), Jeschke *et al.* (1997) Fig. (31). The positive relationship between ABA accumulation and salinity tolerance has been at least partially attributed to the accumulation of K^+, Ca^{2+} and compatible solutes, such as proline and sugars, in vacuoles of roots, which counteract with the uptake of Na^+ and Cl^- Chen *et al.* (2001), Gurmani *et al.* (2011).

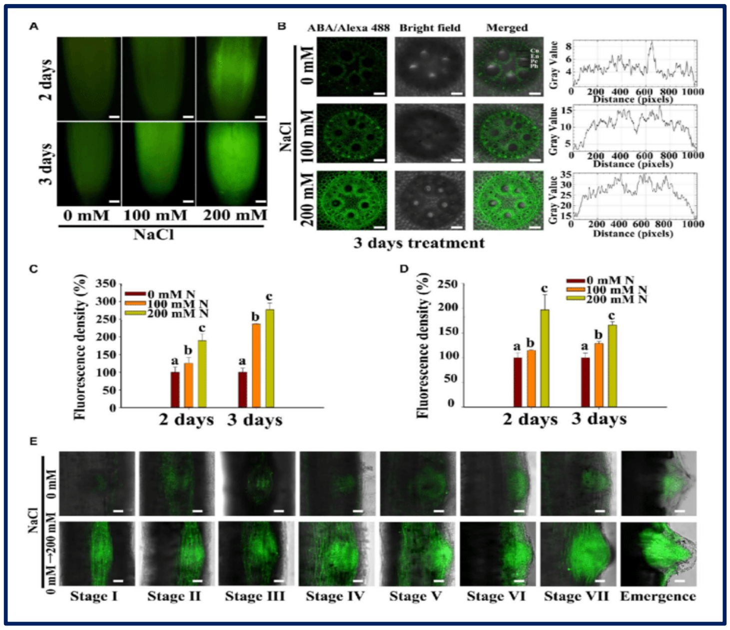


Fig. 31: Illustrates salt stress stimulated the accumulation of endogenous ABA in the root tips and LRs. (A) Observations of the distribution of ABA accumulation by immunofluorescence in PRs subjected to 0, 100, and 200 mM NaCl via confocal microscopy. Bars = 100 µm. (B) Observations of ABA localization by immunofluorescence in transverse root sections in the presence of 0, 100, and 200 mM NaCl under confocal microscopy. The curve on the right of the picture shows the ABA/Alexa Fluor 555 fluorescence intensity. En, endodermis; Pc, pericycle; Ph, Phloem. Bars = 50 µm. (C) Fluorescence intensity (%) of fluorescence portion in picture (A). The data represent the means ± SEs of five replicates, with 10 seedlings each. N, NaCl. (D) Fluorescence intensity (%) of the fluorescence part in picture (B). The data represent the means ± SEs of five replicates, with 10 seedlings each. N, NaCl. (E) Observations via confocal microscopy of the ABA distribution and concentration at different developmental stages of LRs subjected to 0 mM or 200 mM NaCl treatment for 8 h. Bars = 50 µm. The figures were selected from five replicates, with 10 seedlings per replicate. The different letters represent significant differences ($P < 0.05$, based on Student's t-test). After Lu *et al.* (2019)

Lu *et al.* (2019) reported that root architectures are important organs in plant. Lateral root (LR) initiation (LRI) and development play a central role in environmental adaptation. The mechanism of LR development has been well investigated in Arabidopsis. When we evaluated the distribution of auxin and abscisic acid (ABA) in maize, we found that the mechanism differed from that in Arabidopsis. The distribution of ABA and auxin within the primary roots (PRs) and LRs was independent of each other. Auxin localization was observed below the quiescent center of the root tips, while ABA localized at the top of the quiescent center. Furthermore, NaCl inhibited LRI by increasing ABA accumulation, which mainly regulates auxin distribution, while auxin biosynthesis was inhibited by ABA in Arabidopsis. NaCl and exogenous ABA disrupted the polar localization of ZmPIN1 in maize. An inhibitor of ABA biosynthesis, fluridone (FLU), and the ABA biosynthesis mutant vp14 rescued the phenotype under NaCl treatment. Together, all the evidence suggested that NaCl promoted ABA accumulation in LRs and that ABA altered the polar localization of ZmPIN1, disrupted the distribution of auxin and inhibited LRI and development Fig. (31).

ABA is a vital cellular signal that modulates the expression of a number of salt and water deficit-responsive genes. Fukuda and Tanaka (2006) demonstrated the effects of ABA on the expression of two genes, *HVP1* and *HVP10*, for vacuolar H+-inorganic pyrophosphatase, and of *HvVHA-A,* for the catalytic subunit (subunit A) of vacuolar H^+-ATPase in *Hordeum vulgare* under salinity stress. ABA treatment in wheat induced the expression of MAPK4-like, TIP 1, and GLP 1 genes under salinity stress

Keskin *et al.* (2010). Some other compounds having hormonal properties, such as salicylic acid (SA) and brassinosteroids (BR), also participate in plant abiotic stress responses Fragnire *et al.* (2011), Clause and Sasse (1998). Under salinity stress, endogenous level of SA increased along with the increase in the activity of salicylic acid biosynthetic enzyme in rice seedling Sawada *et al.* (2006). Jayakannan *et al.* (2013) have recently shown that SA improves salinity tolerance in *Arabidopsis* by restoring membrane potential and preventing salt-induced K^+ loss via a guard cell outward rectifying K^+ (GORK) channel. *Arabidopsis* seedling pretreated with SA showed upregulation of H^+-ATPase activity, thereby improving K^+ retention during salt stress; SA pretreatment did not prevent accumulation of Na^+ in roots but somehow helped to reduce the concentration of accumulated Na^+ in the shoot Jayakannan, et al. (2013) .The application of SA also promoted salinity tolerance in barley, as manifested by increases in the content of chlorophyll and carotenoid and maintaining membrane integrity, which was associated with more K^+ and soluble sugar accumulation in the root under saline condition El-Tayeb (2005), Nazar, et al. (2011) have argued that SA alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in mung bean cultivars. BR El-Mashad and. Mohamed (2012), Ashraf *et al.* (2010) may also mitigate the negative effects of salinity. Application of BR enhanced the activity of antioxidant enzymes (SOD, POX, APX, and GPX) and the accumulation of nonenzymatic antioxidant compounds (tocopherol, ascorbate, and reduced glutathione) El-Mashad and. Mohamed (2012). Both BRs and SA are ubiquitous in the plant kingdom, affecting plant growth and development in many different ways, and are known to improve plant stress tolerance. Ashraf, *et al.,* (2010), have reviewed and discussed the current knowledge and possible applications of BRs and SA that could be used to mitigate the harmful effects of salt stress in plants. They have also discussed the roles of exogenous applications of BRs and SA in the regulation of various biochemical and physiological processes leading to improved salt tolerance in plants.

5. Role of Silicon in Salinity Tolerance

5.1. Mechanisms of Silicon in Alleviating Salinity Stress

Salinity stress is one of the most common environmental stresses that pose threats to the agriculture industry worldwide. The effects of salinity stress on plants are mainly manifested in the following areas. (**a**) Osmotic stress caused by excessive soluble salt in the soil decreases the osmotic potential of soil solutions and decreases the ability of plant root systems to absorb water, resulting in physiological drought. (**b**) Ion toxicity results from the toxic effect of salt ions like Na^+ and Cl^- inside plant cells. Excessive accumulation of intracellular salt ions results in ion imbalance and metabolic disorders. (**c**) Secondary stresses causing by osmotic and ionic stresses, including the accumulation of toxic compounds like ROS and disruption of nutrient balances in plants. For example, under high salinity conditions, Na^+ competes with Ca^{2+} and K^+ in the cell membrane, resulting in reproductive disorders Zhu (2016). In recent years, there have been a large number of reports about the roles of Si in alleviating salinity-induced ion stress and oxidative damage Wu *et al.* (2015), Debona *et al.,* (2017), Luyckx *et al.,* (2017) Fig. (32).

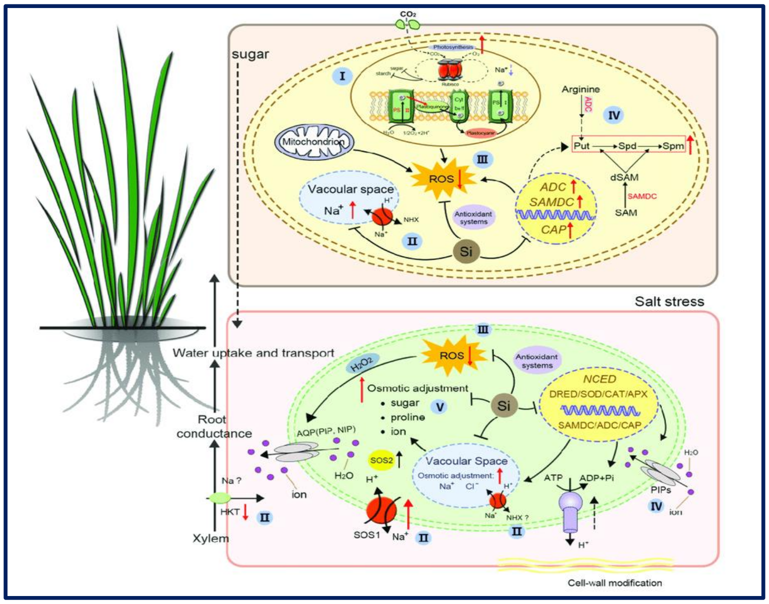


Fig. 32: Presents a schematic model for the beneficial impact of silicon on plant under salt stress. Six main strategies are involved in Si's alleviation of salt stress: For strategy I, Si could enhance photosynthesis by maintaining the integrity of photosynthetic organs, increasing the CO_2 utilization rate in plants and increasing the openness and activity of the PSII reaction center. For strategy II, Si regulates ion homeostasis through mediating Na + uptake, transport, and compartmentalization, and corresponding gene expression (e.g., NHX and HKT). For strategy III, Si can regulate the activity/concentration of enzymatic and/or nonenzymatic antioxidants and endogenous polyamine accumulation to alleviate oxidative damage caused by salinity stress. For strategy IV and V, Si enhances the root hydraulic conductance through regulating aquaporin activities and improving osmoregulatory capacities, which contributes to an increase in water uptake and transport. For strategy VI, Si may mediate ion homeostasis and decrease oxidative damage through regulating polyamine metabolism. Single solid black line ended with bar: process of mediating. Single dash black line: speculated mechanisms that need to be experimentally proved. Red arrow: increase (up) or decrease (down). '?' represents mechanisms that are different between species. Chloroplast and mitochondrion component in this schematic model are modified from Yamori (2016). After Zhu *et al* (2019)

Recently, progresses have been made in elucidating the alleviative effects of Si in salt-induced osmotic stress Zhu *et al.,* (2015), oxidative damage Yin *et al.,* (2019), and Na^+ accumulation Flam-Shepherd *et al.,* (2018). Thus, this review covered the latest research. In addition, because of the available published results, a model describing how Si is involved in alleviating salt stress damage was proposed. We also proposed further studies that are required to address these mechanisms.

5.2. Modulation of Seed Germination, Plant Growth, and Photosynthesis

5.2.1. Seed Germination

Seed is a crucial organ in higher plants. Seed germination and early seedling growth signify a key stage in the plant life cycle Karunakaran, etal. (2013). Si significantly increases germination characteristics (e.g., germination percentage, germination rate and shoot length) under both normal and stress (e.g., salt/drought) conditions Shi, etal. (2014), Karunakaran, etal. (2013). The mechanisms for Si-mediated salt tolerance in seed germination stage still remain obscure, but have been proposed to be associated with the alleviated oxidative stress Shi, etal. (2014), Karunakaran, etal. (2013). In mung bean under salt stress, application of Si and salicylic acid (SA) was reported to improve seed physiological quality through increasing K^+ and decreasing Na+ accumulation in seeds Lotfi, etal. (2015). Till now, the interaction between Si and hormones (e.g., abscisic acid and gibberellins), which play a role in controlling seed development and germination, are still not fully understood Sah, etal. (2016). Thus, to further reveal the mechanisms of Si-mediated salt tolerance during seed germination, studies are needed to elucidate changes in hormones and hormone-responsive genes in response to salt stress and Si treatment. The use of Si-uptake mutants can aid researchers to better understand the biochemical function of Si in plant growth and development, in which physical barrier induced by Si deposition on seed surface could be partly excluded. Under salinity stress, Zhang, et al. (2009) studied the effects of Si on the germination of Si-mutant rice seeds that accumulate less Si in the shoot Ma (2002). Their results showed that the application of exogenous Si increased the bud length, bud weight, and germination rate more obvious in mutant rice than the wild type rice. This might be due to the changes in the mutant seed embryo and seed coat, which enables it to utilize Si more efficiently. The study of Isa, etal. (2002) found that even though the Si-mutant rice forms relatively less SiO_2 bodies in the leaves, Si application could still significantly promote the growth of these mutants, suggesting that Si participates in the physiological and biochemical processes of rice. Actually, Laane (2017), (2018) proposed that foliar SA and nano-SiO_2 could be classified as biostimulants ('plant growth promoter') that enhance nutritional efficacy and decrease abiotic and biotic stresses. The Si-uptake mutants should be investigated further to better understand the alleviating mechanisms of Si, including its potential biostimulants functions, in seed germination under salinity stress.

5.2.2. Plant Growth and Photosynthesis

The enhancement of plant shoot and/or root growth by Si under salt stress have been reported in many plant species, such as rice, maize, wheat, cucumber, tomato, and so on Wu etal (2015) Fig. (33),(34).

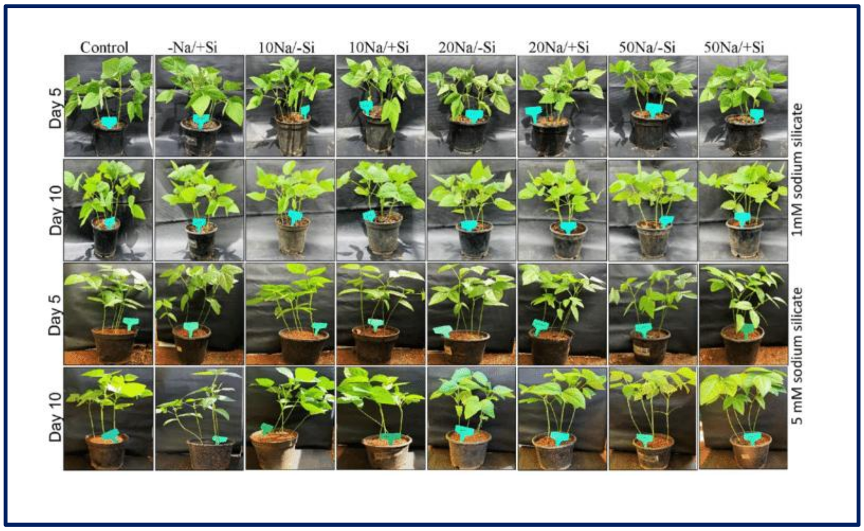


Fig. 33: Experimental setup of mung bean (Vigna radiata) under 1mM (Si1) and 5mM (Si2) Si supply and salinity stress after eight treatments: (i) control (T1), (ii) −NaCl+Si (1mM/5mM) (T2), (iii) 10mM NaCl/−Si (T3), (iv) 10mM NaCl/+Si (1mM/5mM) (T4), (v) 20mM NaCl/−Si (T5), (vi) 20mM NaCl/+Si (1mM/5mM) (T6), (vii) 50mM NaCl/−Si (T7), and (viii) 50mM NaCl/+Si (1mM/5mM) (T8) for a period of 10days. After Musa Al Murad and Sowbiya Muneer, (2021).

Roots play a key role in plant development and are the first tissue to perceive salt stress. Si has been reported to regulate root growth and architecture of salt-stressed plants Zhu, etal. (2015), Kim, etal. (2014), in cucumber, Si was found to increase the root–shoot ratio of salt-stressed plants and improve root hydraulic conductance, likely accounting for improved plant water balance Wang, etal. (2015) Fig. (34).

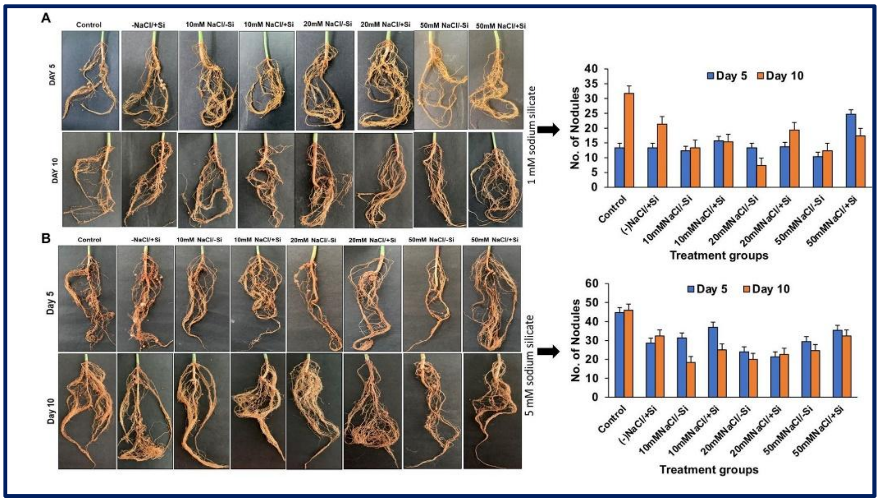


Fig. 34: Changes in the formation of root nodules of mung bean (Vigna radiata) under (A) 1mM (Si1) and (B) 5mM (Si2) Si supply and salinity stress after eight treatments: (i) control (T1), (ii) −NaCl+Si (1mM/5mM) (T2), (iii) 10mM NaCl/−Si (T3), (iv) 10mM NaCl/+ Si (1mM/5mM) (T4), (v) 20mM NaCl/−Si (T5), (vi) 20mM NaCl/+Si (1mM/5mM) (T6), (vii) 50mM NaCl/−Si (T7), and (viii) 50mM NaCl/+Si (1mM/5mM) (T8) for a period of 5 and 10days. Vertical bars indicate Mean±SE of the means for n=4. Means denoted by the different letters are significantly different at $p \leq 0.05$ according to the Tukey's studentized range test. Musa Al Murad and Sowbiya Muneer, (2021).

In rice and sorghum, Si might improve root growth by promoting Casparian band formation and stimulating suberin and lignin biosynthesis or by increasing cell wall extensibility in the growth region Hattori, etal. (2003) Fleck, etal. (2015). Plant growth and yield depend largely on photosynthesis Chaves, etal. (2008). the salinity stress-induced growth inhibition in plants can be attributed to stress-induced reduction in photosynthesis. From the large amount of data available on the improvement effect of Si on shoot growth and net photosynthetic rate, it is reasonable to speculate that Si might function to maintain a high photosynthetic rate in salt-stressed plants Zargar, etal. (2019), Coskun, etal. (2019), Yin, etal. (2013). the reason why salinity stress results in reduced photosynthetic rate in plants includes the following aspects. (**a**) Modification of the structure and function of organelles that are responsible for photosynthesis; (**b**) ion toxicity and oxidative stress to thylakoid membranes and other cellular components; (**c**) osmotic stress-induced reduction in CO_2 assimilation rate, which enhances stomatal closure and CO_2 availability; and (**d**) inhibition of the transfer of assimilation products Chaves, etal. (2008), Yamori (2016). Accordingly, the mechanisms by which Si improves plant photosynthesis under salinity stress can be summarized as follows. (**A**) The addition of Si under salinity stress can decrease ion toxicity and ROS accumulation to maintain the structure and function of organelles that are responsible for photosynthesis Liang (1999), Liang, etal. (2003), (**B**) The decreased photosynthetic rate is also due to the reduction in stomatal conductance and nonstomatal inhibition, resulting in restricted availability of CO_2 for carboxylation reactions. Abbas, et al. (2015) found that Si supplementation in two okra (Abelmoschus esculentus) cultivars with different salt tolerance could increase stomatal conductance, transpiration rate, and number and size of stomata, leading to efficient photosynthetic activity under salinity stress. These results showed that Si supplication under salinity stress could improve photosynthesis by maintaining the integrity of photosynthetic organs and photosynthetic pigment levels and by increasing the CO_2 utilization rate in plants Fig. (35)

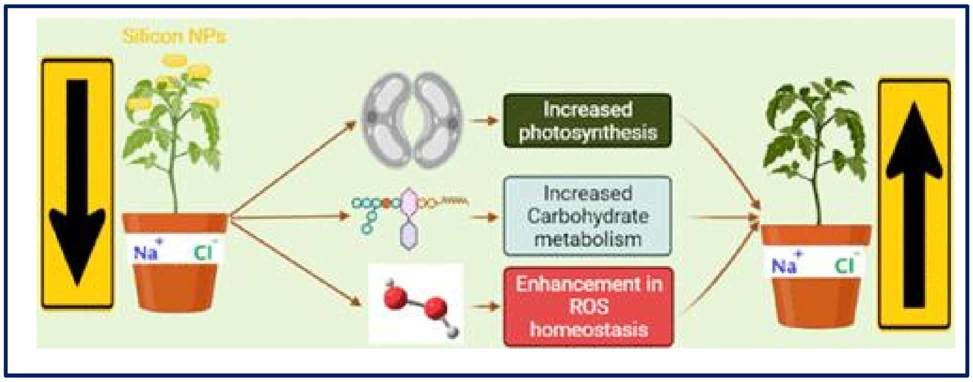


Fig. 35: Illustrates nanoparticle-induced regulation of carbohydrate metabolism, photosynthesis, and ROS homeostasis in solanum lycopersicum Subjected to Salinity Stress, Alam *et al.,* (2022)

(**D**) Salinity stress affects the transport and allocation of photosynthetic products. This results in the accumulation of photosynthetic products such as sucrose and starch, causing feedback inhibition of photosynthesis and decreasing plant growth. Currently, relatively few systematic studies have been conducted on the effects of Si on carbohydrate metabolism. In cucumber, Zhu, *et al.,* (2016) demonstrated that Si application decreased the soluble sugar and starch content in leaves, but increased the starch content in roots through mediating the activities of carbohydrate metabolism enzymes, and thus alleviated photosynthetic feedback repression in leaves and provided more energy storage for root growth. However, experimental evidence is still lacking in this study. Thus, molecular biology approaches should be used to further reveal the mechanisms by which Si affects carbohydrate metabolism, antioxidants system, polyamine accumulation, and water relationship. However, whether Si regulates these metabolisms directly. In recent years, chlorophyll fluorescence parameters have been widely used to study various photosynthetic reactions under stress conditions Gorbe, (2012). Photosystem II (PS II) appears to be a salt stress-sensitive component of the photosynthetic system Parihar *et al.,* (2015). In cucumber, salinity stress significantly decreased the Fv'/Fm' (PSII effective photochemical efficiency), Fv/Fm (PSII maximum photochemical efficiency), qP (photochemical quenching coefficient), and FPSII (PSII actual photochemical efficiency), whereas it significantly increased the NPQ (non-photochemical quenching coefficient). However, Si application could increase Fv/Fm, Fv'/Fm', FPSII, and qP, and decrease NPQ during salinity stress Zhu *et al.,* (2015). Similarly, in salt-stressed aloe, Si application was reported to decrease minimum fluorescence (FO), and increase variable fluorescence (Fv) and the potential activity of photosystem II (PSII), thus improving photosynthetic efficiency in aloe Munns and Tester, (2008). These results showed that the addition of Si helps to increase the openness and activity of the PSII reaction center, facilitating the use of more energy in PSII electron transfer and increasing the efficiency of converting light energy into chemical energy Zhu *et al.,* (2015). In conclusion, Si enhances photosynthesis in salt-stressed plants by decreasing salt-ion accumulation, scavenging ROS, and regulating carbohydrate metabolism. However, further in-depth research is needed to understand the molecular mechanisms of how Si regulates ROS and carbohydrate metabolism, such as its regulatory effects on the gene expression levels of related enzymes.

5.2.3. Silicon and Ion Homeostasis Regulation

High concentrations of salt ions, particularly Na^+ and Cl^- ions generally affect the absorption of other nutrients (such as potassium and calcium) by plants and cause increased cell membrane permeability, resulting in metabolism disorders and dysregulation Xu *et al.,* (2015). To cope with salt stress, the plant can reduce Na^+ uptake, increase Na^+ efflux, and compartmentalization of Na^+ in the vacuole to reduce cytoplasmic ion toxicity Parida and Das, (2005) Fig. (36).

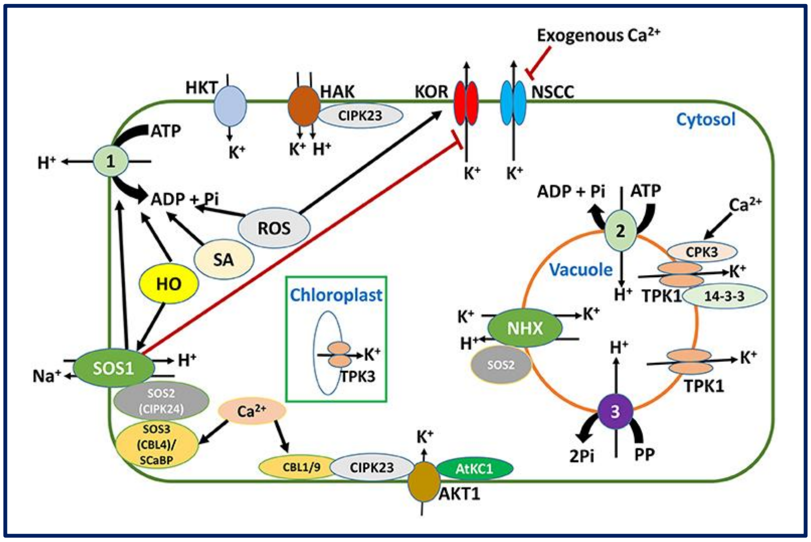


Fig. 36: Intracellular Na+ homeostasis mediated by Na^+ transporters, channels, and their regulatory elements. In this figure, 1 stands for plasma membrane (PM) H^+-ATPase, 2 stands for tonoplast (TP) H^+-ATPase and 3 stands for TP H^+-pyrophosphatase. Some new components in these transport mechanisms have recently been added, i.e., the regulation of stelar-localized SOS1 activity by Nax1 and Nax2 Na^+ exclusion loci in rice. This regulation improves salt stress tolerance by enhancing the retrieval of Na^+ from xylem back into stellar cells. Another component is the potential involvement of plant aquaporins (AQP, AtPIP2;1 in particular) in Na+ uptake. Equally important is the role of FV (fast vacuolar) and SV (slow vacuolar) channels that mediate vacuolar Na^+ leakage to the cytosol, deemed a salt-sensitive trait. Worthy of note also is the role of PM and TP H^+ pumps that generate a pmf to energize Na+ transport via the two Na^+/H^+ exchangers (SOS1 and NHXs), as well as the importance of Na^+ efflux from chloroplasts mediated by the chloroplastic sodium hydrogen antiporter (NHD1). The NADPH dehydrogenase (NDH)-dependent cyclic electron flow (CEF) constitutes an important source of ATP required to fuel Na+ sequestration into vacuoles. Red line indicates inhibition, while black arrows indicate activation. After Assaha *et al.,* (2017)

Accordingly, the possible mechanisms by which Si regulates ion homeostasis under salt stress can be classified into three main categories as follows.

5.2.4. Silicon Restricts Na^+ Uptake and Transport

Studies on the mechanisms by which Si alleviates salinity stress in plants are mostly focused on decreasing Na^+ in the root and/or shoot. For example, the addition of Si to salt-stressed barley could significantly decrease the levels of Na^+ and Cl^- in the root system, with Na^+ and K^+ being more evenly distributed throughout the entire root. This has been regarded as one of the major mechanisms by which Si alleviates salinity stress in barley Liang, (1999). In salt-stressed alfalfa (*Medicago sativa L.*), Si application significantly decreases Na^+ levels in the roots, but has no effects on Na^+ accumulation unclear whether Na^+ decrease along with Si addition is due to the changes in the root structure and/or a reduction in the transpiration stream in the xylem, which need to be studied in more species, in the shoot Wang *et al.,* (2007). In wheat, Tuna *et al.,* (2008) reported that the addition of Si could simultaneously decrease Na^+ accumulation in both shoot and root. Garg and Bhandari, (2016) found that the addition of Si decreases Na^+ absorption in the root system and translocation toward the leaves, as well as increases the K^+/Na^+ ratio, in chickpeas (*Cicer arietinum L.*). However, the mechanisms for these reductions are still largely unknown in most species except in rice. In rice, Si application showed an increased formation of Casparian bands in the exodermis and endodermis Fleck *et al.,* (2015), Fleck and Nye, (2011) which might partly hinder the penetration of Na^+ ions into the symplast and/or transpiration stream Wu *et al.,* (2015); Guerriero *et al.,* (2016). Accordingly, Gong *et al.,* (2006) showed that in rice ('IR36'), the addition of Si did not change Na^+ levels in the root but decreased the upward transport of Na^+ through apoplastic pathway Fig. (37).

Pannaga Krishnamurthy *et al.,* (2009) reported that increasing soil salinity reduces crop yields worldwide, with rice being particularly affected. We have examined the correlation between apoplastic barrier formation in roots, Na^+ uptake into shoots and plant survival for three rice (*Oryza sativa* L.) cultivars of varying salt sensitivity: the salt-tolerant Pokkali, moderately tolerant Jaya and sensitive IR20. Rice plants grown hydroponically or in soil for 1 month were subjected to both severe and moderate salinity stress. Apoplastic barriers in roots were visualized using fluorescence microscopy and their chemical composition determined by gas chromatography and mass spectrometry. Na^+ content was estimated by flame photometry. Suberization of apoplastic barriers in roots of Pokkali was the most extensive of the three cultivars, while Na^+ accumulation in the shoots was the least. Saline stress induced the strengthening of these barriers in both sensitive and tolerant cultivars, with increase in mRNAs encoding suberin biosynthetic enzymes being detectable within 30 min of stress. Enhanced barriers were detected after several days of moderate stress. Overall, more extensive apoplastic barriers in roots correlated with reduced Na^+ uptake and enhanced survival when challenged with high salinity.

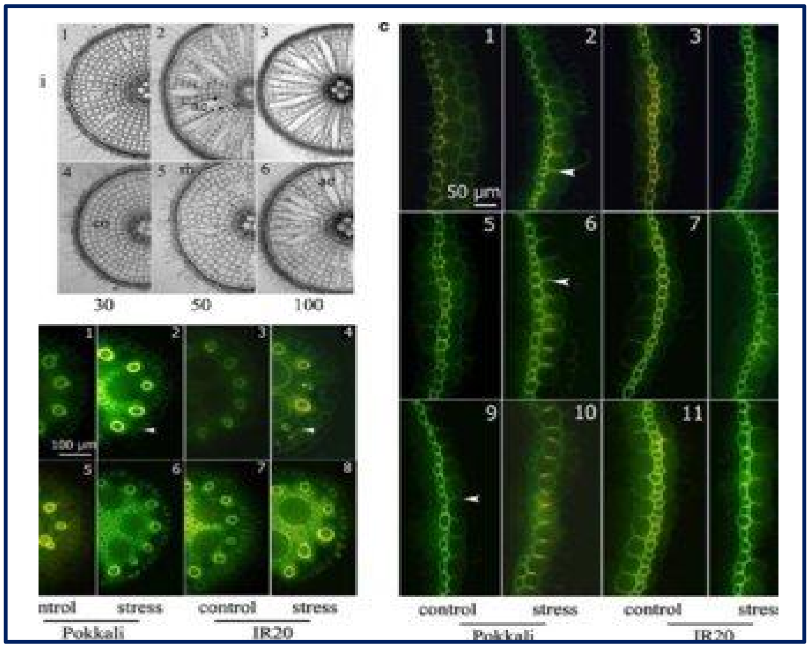


Fig. 37: Development of aerenchyma and Casparian bands in rice roots. a Aerenchyma development (1–6). Cross-sections were made from 1-month-old rice roots grown in hydroponic culture. Images of sections made at 30 mm (1, 4), 50 mm (2, 5) and 100 mm (3, 6) from the root tip in Pokkali and IR20 under control conditions. b Casparian bands in the endodermis (1–8). Freehand cross-sections were stained with berberine-aniline blue and viewed using blue light. Arrowheads show Casparian bands in the endodermis. Control (1, 5) and stressed Pokkali (2, 6) at 20 mm and 30 mm. Control (3, 7) and stressed IR20 (4, 8) at 20 mm and 30 mm. c Casparian bands in the exodermis (1–12) stained with berberine-aniline blue. Freehand cross-sections taken at 10 mm (1, 2), 20 mm (5, 6) and 30 mm (9, 10) of control and stressed Pokkali, respectively. Sections at 10 mm (3, 4), 20 mm (7, 8), and 30 mm (11, 12) from root tip of control and stressed IR20, respectively. Arrowheads show Casparian bands in the exodermis. Numbers indicate the distance from the root tip. ae aerenchyma, co cortical cells, rh rhizodermis. Bars 100 µm (b), 50 µm (c). After Pannaga Krishnamurthy *et al.,* (2009)

However, most recently, Flam-Shepherd *et al.,* (2018) measured the radiotracer fluxes of 24 Na^+ and proposed that Si does not affect Na^+ transport across cell membranes and within the bulk root apoplast. Moreover, their study revealed that Si reduced Na^+ translocation via bypass flow only in the salt-tolerant ('Pokkali') rice cultivars, but not in the salt-sensitive ('IR29') ones, in which the bypass flow was small and not affected by Si. The decline in the shoot Na^+ concentration of salt-sensitive ('IR29') rice cultivars can be explained by the pronounced stimulation of leaf growth and shoot-to-root ratio. Therefore, much more remains to be explored about the effect of Si on Na^+ dynamics across membranes and through extracellular space in plants. However, many determinants have not been studied in sufficient detail in salt-stressed plants with or without silicon addition, such as the Na^+ signal perception process. Moreover, it is unclear whether Na^+ decrease along with Si addition is due to the changes in the root structure and/or a reduction in the transpiration stream in the xylem.

5.2.5. The Regulatory Mechanisms Mediating Na+ Compartmentalization

Excessive Na exclusion, or its compartmentation into vacuoles, is an important adaptive strategy for plants in response to salt stress Farooq *et al.,* (2015). Na^+/H^+ antiporter protein plays an extremely important role in Na+ flux and vacuole partitioning Zhao *et al.,* (2017). In higher plants, the H^+-ATPases located on the cell membrane utilize the energy generated from ATP hydrolysis to pump H+ out of the cells to generate a transmembrane proton gradient. This provides a driving force for the Na^+/H^+ antiporter protein on the plasma membrane. The Na^+ is expelled out of the cells against an electrochemical gradient when H+ is transported into the cells along an electrochemical gradient Blumwald, (2000); Liang *et al.,* (2005). Previous studies showed that compared to the salinity stress alone, Si application significantly increased the activities of H+-ATPases on the plasma membrane, as well as the activities of H+-ATPase and H+-PPase on vacuolar membranes in the roots of barely Liang, et al. (2005). The Si-mediated elevation of the H+-ATPase activity was conducive for the expulsion of Na+ out of the cell, while the elevation in the activities of H+-ATPase and H+-PPase in vacuolar membranes facilitates the distribution of Na^+ into vacuoles, thereby decreasing the Na+ toxicity in the root Liang et al. (2005), (2006). However, further studies are required to determine whether Si can directly regulate the activity of the Na+/H+ antiporter and H+-ATPase on the plasma membrane and vacuolar membranes. Fig. (38), (39).

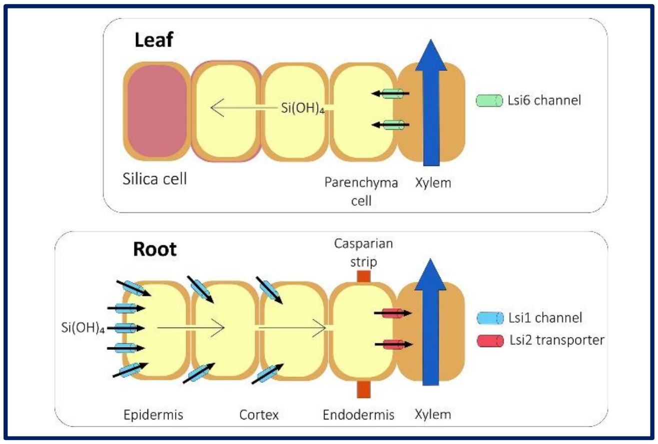


Fig. 38: Presents the Si transport in a typical grass species. Silicic acid from the soil is transported into the root symplast by the action of aquaporins such as Lsi1 channels. The silicic acid then diffuses across the root into the endodermis. At the endodermis, Lsi2 transports silicic acid into the stelar apoplast from where it diffuses into the xylem and is transported to the shoot in the transpiration stream. In rice, the presence of aerenchyma means that Lsi2 is localized at both the exodermis and endodermis. In the shoot, silicic acid is unloaded from the xylem by further aquaporins such as Lsi6 and deposited in the cell walls and in specific silica cells. Based on Ma and Yamaji, (2015). After Thorne *et al.,* (2020)

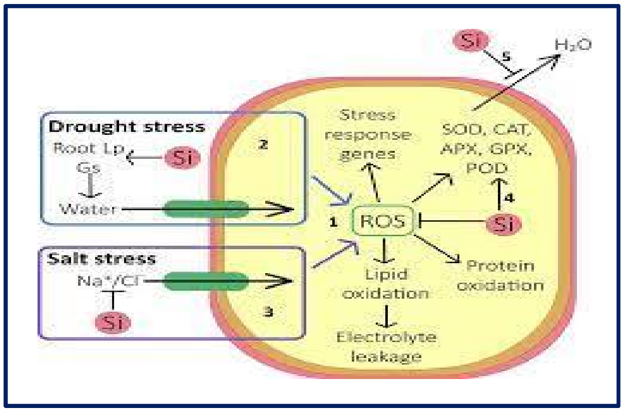


Fig. 39: Illustrates the effect of Si on oxidative stress. (1) Under abiotic stress conditions, accumulation of reactive oxygen species (ROS) inside the cell causes protein oxidation, lipid oxidation (resulting in increased electrolyte leakage out of the cell), and activation of stress response genes. (2) During drought stress, Si increases the root hydraulic conductance and stomatal conductance, but reduces cuticular transpiration (5). On balance, this can allow more water to enter the cell and thus reduce the accumulation of ROS. (3) During salt stress, as well as improving the plant water status, Si reduces Na+ and Cl- accumulation in shoot by forming endodermal barriers in the root. This reduces the accumulation of ROS and limits ion toxicity. (4) Antioxidative enzymes are activated by increased cellular ROS, and Si may further increase their activity. These enzymes scavenge ROS within the cell, thus protecting it against oxidative damage. (5) Si deposited outside the cell reduces evapotranspiration, protecting the plant against water stress. After Thorne *et al.,* (2020)

Thorne *et al.,* (2020) stated that salinity affects around 20% of all arable land while an even larger area suffers from recurrent drought. Together these stresses suppress global crop production by as much as 50% and their impacts are predicted to be exacerbated by climate change. Infrastructure and management practices can mitigate these detrimental impacts, but are costly. Crop breeding for improved tolerance has had some success but is progressing slowly and is not keeping pace with climate change. In contrast, Silicon (Si) is known to improve plant tolerance to a range of stresses and could provide a sustainable, rapid and cost-effective mitigation method. The exact mechanisms are still under debate but it appears Si can relieve salt stress via accumulation in the root apoplast where it reduces “bypass flow of ions to the shoot. Si-dependent drought relief has been linked to lowered root hydraulic conductance and reduction of water loss through transpiration. However, many alternative mechanisms may play a role such as altered gene expression and increased accumulation of compatible solutes. Si can reduce oxidative damage that occurs under stress conditions through increased antioxidative enzymes while Si-improved photosynthesis has also been reported. Si fertilizer can be produced relatively cheaply and to assess its economic viability to improve crop stress tolerance we present a cost-benefit analysis. It suggests that Si fertilization may be beneficial in many agronomic settings but may be beyond the means of smallholder farmers in developing countries. Si application may also have disadvantages, such as increased soil pH, less efficient conversion of crops into biofuel and reduced digestibility of animal fodder. These issues may hamper uptake of Si fertilization as a routine agronomic practice. Here, we critically evaluate recent literature, quantifying the most significant physiological changes associated with Si in plants under drought and salinity stress. Analyses show that metrics associated with photosynthesis, water balance and oxidative stress all improve when Si is present during plant exposure to salinity and drought. We further conclude that most of these changes can be explained by apoplastic roles of Si while there is yet little evidence to support biochemical roles of this element.

In addition, an excessively high concentration of salt ions in the soil will affect the absorption of other elements (such as nitrogen and calcium) by plants, resulting in ion imbalance, whereas Si has been found to increase the concentration of macroelements, such as Ca, P, and Mg, and microelements, such as B, Fe, Zn, and Mn, in many kinds of plants Zhu *et al.,* (2014). Aquaporin has been reported to play important roles in nutrient homeostasis and recent researches suggested that Si could improve plant water content through regulating the activities of root aquaporins.

5.2.6. Potential Interaction between Silicon and Ionic Stress Signaling Pathways

Under salt stress conditions, rapidly sensing excess Na^+ signal is a prerequisite for initiating the reestablishment of cellular ionic homeostasis Yang and Guo (2018). Generally, salt treatment activates the salt overly sensitive (SOS) signaling pathway within a short time period, which is crucial for the regulation of plant ionic homeostasis through extruding Na+ into the apoplast Yang and Guo (2018) Fig. (40).

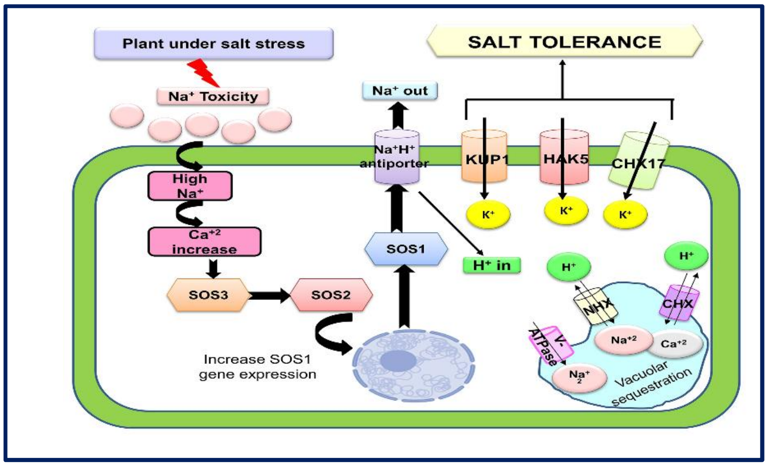


Fig. 40: Illustrates ion homeostasis in response to salt stress. In response to salinity stress, SOS pathway (enabling Na^+ efflux), vacuolar sequestration of Na^+ and K^+ inclusion play an important role in inducing salt tolerance in the cells under stress. The SOS pathway isa cascade that involves SOS 1, 2 and3. SOS3 is itself a Na^+H^+ antiporter that helps in Na^+ exclusion from cells under stress. High extracellular Na^+ ion concentration leads to calcium-dependent activation of SOS3. SOS2 increases the nuclear translation ofSOS1genes and extrudes Na^+ from the cells. Tonoplast-associated transporters such as NHX, CHX and VATP-ases are required for vacuolar sequestration of Na^+ ions. Plasma membrane-associated transporters KUP1, HAK5and CHX17 cause an increase in intracellular concentration of K^+ that is required for tolerance induction during increased cytosolic Na+ concentrations. After Amina *et al.,* (2021).

Amina *et al.,* (2021) stated that, sodium chloride is the most important salt responsible for inducing salt stress by disrupting the osmotic potential. Due to various innate mechanisms, plants adapt to the sodic niche around them. Genes and transcription factors regulating ion transport and exclusion such as salt overly sensitive (SOS), Na+/H+ exchangers (NHXs), high sodium affinity trans-porter (HKT) and plasma membrane protein (PMP) are activated during salinity stress and help in alleviating cells of ion toxicity. For salt tolerance in plants, signal transduction and gene expression is regulated via transcription factors such as NAM (no apical meristem), ATAF (Arabidopsis transcription activation factor), CUC (cup-shaped cotyledon), Apetala2/ethylene responsive factor (AP2/ERF), W-box binding factor (WRKY) and basic Leucine zipper domain (bZIP). Cross talk between all these transcription factors and genes aid in developing the tolerance mechanisms adopted by plants against salt stress. These genes and transcription factors regulate the movement of ions out of the cells by opening various membrane ion channels. Mutants or knockouts of all these genes are known to be less salt-tolerant compared to wild types. Using novel molecular techniques such as analysis of genome, transcriptome, ionome and meta bolome of a plant, can help in expanding the understanding of salt tolerance mechanism in plants. In this review, we discuss the genes responsible for imparting salt tolerance under salinity stress through trans-port dynamics of ion balance and need to integrate high-through put molecular biology techniques to delineate the issue.

High-affinity K+ channel (HKT1) is a key determinant of plant salinity tolerance that may function to mediate Na+ influx across the plasma membrane and decrease Na+ accumulation in the shoot, thus protecting leaves from Na+ toxicity and improving salt tolerance Yang and Guo, (2018). Until now, little is known about the effect of Si on putatively SOS1-mediated NaCl efflux. More recently, Bosnic *et al.,* (2018) proposed that Si decreased Na accumulation in both root apex and cortex of maize. Meanwhile, Si addition allocated more Na^+ to the leaves via the xylem through upregulating ZmSOS1 and ZmSOS2 in the root cortex, but down regulating ZmHKT1. Furthermore, Si enhanced sequestration of Na^+ into the vacuoles by upregulating ZmNHX, and thus decreased Na+ accumulation in the chloroplasts. This study firstly experimentally demonstrated the direct effect of Si on the expression of SOS and HTK genes. However, the deeper mechanism, such as the detailed regulation mechanisms of Si on SOS signaling pathways, remains obscure. Moreover, it would be interesting to dissect the interaction between Si and other salt stress sensors (e.g., Mitogen-activated protein kinase (MAPK)) involved in salt-induced stress signaling in plants.

5.2.7. Participation of Polyamine in Silicon-Mediated Ion Homeostasis

Recent studies suggested that the effects of Si on the levels of ions, particularly Na+ and K+, during salinity stress might be associated with the regulation of polyamine metabolism. Polyamines are small aliphatic polycations that are widely distributed in prokaryotic and eukaryotic cells. In higher plants, putrescine, spermidine, and spermine are the most abundant polyamines, they can be present in different forms, including free, insoluble-bound, and soluble conjugated Yin *et al.,* (2019). During salinity stress, polyamines can regulate the transport of Na^+ and K^+ in plants through nonselective ion channels Zhao *et al.,* (2007), recently, the regulatory effects of Si on polyamine metabolism under salt stress have been reported in cucumber and sorghum. In sorghum, Yin *et al.,* (2016) found that the addition of Si could increase free and total polyamine levels and decrease Na^+ accumulation. Moreover, Si application balanced the metabolism of polyamines and ethylene through inhibiting the level of 1-aminocyclopropane-1-1-carboxylic acid (ACC), an important ethylene precursor, to mitigate salt stress. Wang *et al.,* (2015) also found that Si had some regulatory effects on polyamine levels (increasing the concentrations of free and conjugated putrescine and free spermidine, but decreasing the concentration of conjugated spermidine), as well as alleviating K^+/Na^+ homeostasis in salt-stressed cucumber, suggesting the involvement of polyamine in Si's reduction of ion toxicity. However, it is still hard to draw the conclusion that Si could mediate the K^+/Na^+ homeostasis through regulating polyamines content according to these studies, because under certain conditions, polyamines will not decrease, but promote K^+ efflux under salinity stress Yin *et al.,* (2016). Therefore, more evidence is required to prove how Si regulates polyamine metabolism and determine under which conditions (e.g., NaCl concentration, stress duration, and seedling age) that Si could regulate polyamine metabolism to balance the K^+/Na^+ homeostasis. Taken together, these studies show that the Si addition can decrease Na^+ absorption in the root and/or transport to shoot to alleviate the damage caused by salinity stress. However, this mechanism varies between species and varieties and the influence of Si on Na partitioning at the cell, tissue, and organelle levels is still unclear. Moreover, the exact mechanisms of how Si regulates transcription of various mineral transporter genes remain unclear. One may speculate that the regulation of Na+ absorption by Si in different species might be affected by the Si absorption ability of roots. In addition, the relationship of SiO_2 – plant cell wall has been well documented in Si accumulators, including monocots and pteridophytes Guerriero, *et al.,* (2016). Coskun *et al.,* (2019) proposed an apoplastic obstruction model to explain beneficial effects of Si in plants, which proved guidance for further study. Nevertheless, the role of Si-induced modifications in the mechanical properties and composition of the cell wall in decreasing Na^+ uptake and/or transport is largely unknown. On the other hand, some recent studies have shown that interfering with Na^+ uptake and assimilation is not the only mechanism by which Si alleviates salinity stress damage in plants. For example, in tomato, Romero-Aranda *et al.,* (2006) found that addition of Si did not decrease Na^+ and Cl^- concentrations in leaves, but increased the tissue water content to dilute the salt ions that were absorbed. Chen *et al.,* (2014) carried out a study in wheat, and found that Si application could alleviate both ion toxicity and osmotic stress caused by salinity stress, with the alleviative effect of the latter being more significant. Zhu *et al.,* (2015) reported that the decrease in Na^+ levels in two cucumber cultivars was not the main mechanism by which Si alleviated salinity stress damage. Apart from ionic stress upon long-term salinity exposure, osmotic effect upon short-term salinity exposure reduces the ability of the plant to take up water and inhibit growth rate Yang and Guo, (2018). However, current studies on Si's alleviation of osmotic stress caused by salinity stress are limited; this is not conducive to further explore the alleviation mechanisms of Si under salt stress.

5. 2.8. Silicon and plant water balance under salinity stress

The presence of salt in the external soil environment reduces the ability of plants to extract water and these results in physiological drought, which is the major stress affecting plant growth during short-term salinity stress. However, previous studies on Si's alleviation of salinity stress have mostly focused on the alleviation of ionic stress, and there are relatively few integrated studies on the regulatory effect of Si on water absorption and transport.

5.2.9. Water Relation

Earlier studies showed that Si could decrease the transpiration rate through its deposition on the surface of leaves, thereby decreasing water loss through transpiration and maintaining relative higher water content in plants Matoh *et al.,* (1986). However, Si application does not always result in decreased plant transpiration. For example, Gong *et al.,* (2006) and Zhu *et al.,* (2015) found that Si addition increased the leaf transpiration rate of salt-stressed rice and cucumber seedlings, suggesting a possible role of Si in regulating water uptake in plants. The root system is the first tissue that perceives salt stress and salinity affects the root architecture Yang and Guo, (2018). Recent studies have revealed that Si addition under salinity stress can increase water content in plants through increasing root water absorption Yin *et al.,* (2019), Wang *et al.,* (2015). In tomato, Li *et al.,* (2015) found that Si promoted root growth and root hydraulic conductance, thereby increasing root water uptake and further improving leaf water content. In sorghum, Liu *et al.,* (2015) reported that Si could increase root hydraulic conductance and water absorption by regulating the activity of aquaporins under salt stress Fig. (41).

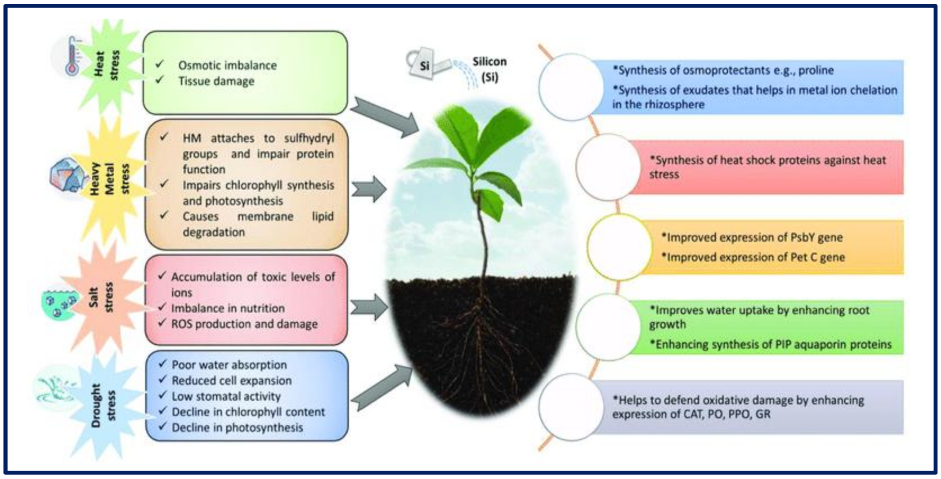


Fig. 41: Illustrates impact of abiotic stress on various aspects of plant growth and defense mechanisms evoked by application of Si. After Mir etal (2022)

After Mir *et al.,* (2022) reported that crop plants might grow well in the absence of Si, although in a few plants, such as rice and horsetail, the absence of Si may make them vulnerable to fungal infections Law and Exley, (2011). Si has been reported to play numerous roles in mitigating abiotic stress conditions Alamri *et al.,* (2020), Salim *et al.,* (2021). For instance, Si mediates diverse strategies to sequester the metal ions by modulating soil pH, metal speciation, precipitation, and compartmentalization Debona *et al.,* (2017). Recent trends have proved the evolution of Si-based fertilizers to impart growth and developmental effects of crop plants, such as enhancing photosynthesis and regulating electrolytic leakage under stress conditions Chen *et al.,* (2011). For example, Si enhances photosynthesis in mango trees and increases water and nutrient uptake under abiotic stress conditions Santos *et al.,* (2014). Si is found in almost all the plants in variable amounts, imparting varying physiological effects Cooke and Leishman, (2011). Apart from its critical role in stress tolerance imposed by excess salt and drought, uptake of Si results in enhanced mechanical support to shoots and leaf blades Zhu *et al.,* (2019a). Numerous reports reveal the application of Si in mitigating abiotic and biotic stresses in various plant species Zargar *et al.,* (2019); Gou *et al.,* (2020). Moreover, Si plays a vital role in ameliorating metal toxicity in several crop plants Singh *et al.,* (2019); Wu *et al.,* (2019). Moreover, Si helps to mitigate metal ion stresses like that of aluminum (Al) and manganese (Mn) stress in crop plants Tripathi *et al.,* (2016). Water uptake through aquaporins and root hydraulic conductance is upregulated by administering exogenous Si Liu *et al.,* (2015).

In these studies, an elevation in leaf water status facilitated the maintenance of stomata in an open state, thereby increasing CO_2 uptake and thus photosynthetic rate. Zhu *et al.,* (2015) proposed that Si increased the expression of the main plasma membrane aquaporins in two-cucumber cultivars 'JinYou 1' and 'JinChun 5', thus increasing the root hydraulic conductance under salt stress. This, together with an increased stem hydraulic conductance with Si addition, allows for an increase in leaf water content and finally dilutes the absorbed salt ions. However, it is still unclear whether the increase in hydraulic conductance is due to an improvement in the root system structure. Moreover, the effect of silicon on the capacity of the main plasma membrane aquaporins still needs to be confirmed using a molecular biology approach. Wang *et al.,* (2015) reported similar results in another cucumber cultivar, 'JinChun 10'. Nevertheless, Si application not only improved the water content in the leaves of 'JinChun 10', it also significantly decreased the Na^+ content and increased the K^+ content in leaves, while it was less likely that Si was actively involved in reducing Na^+ accumulation in 'JinYou 1' and 'JinChun 5'. These differences might be related to different cucumber cultivars (salt stress-tolerant or -sensitive), salinity stress duration, and salt concentrations used in the two studies. Previous studies found that Si deposition on cell walls increases the affinity of xylem vessels for water, thereby affecting water transport capabilities in the xylem Gao *et al.,* (2005). However, Liu, et al. (2014), pointed out that stem water transport is not the major limiting factor affecting water transport during water-deficit stress in sorghum. Therefore, further studies are required to determine the effects of Si on different transport vessel structures in plants. In addition, the aquaporin inhibitor, mercury chloride ($HgCl_2$) has been used in some studies to prove that Si increases root hydraulic conductance through regulating expression of root AQPs Zhu *et al.,* (2015);Yang and Guo, (2018) and Liu *et al.,* (2014). In salt-stressed sorghum, Si treatment could significantly increase the transpiration rate, whereas the $HgCl_2$ treatment incensing the effect of Si in transpiration rate; after recovery induced by dithiothreitol (DTT); however the transpiration rate was higher in $Na+Na_2SiO_3$-$9H_2O$ treated seedlings than Na- treated seedlings Liu *et al.,* (2014), However, it is worth noting that Hg^{2+} can act as an inhibitor of both aquaporin and K+ channels. K^+ is an important compatible solute that can regulate water absorption and transport in the root system Coskun *et al.,* (2012); Dolan and Davies, (2004). Besides, not all plant aquaporins are sensitive to Hg, and Hg could have other secondary effects as well Aroca *et al.,* (2011). The mechanism by which Si increases root water uptake requires more evidence.

5.2.10. Osmotic Regulation

Osmoregulation is a primary adaptive strategy of plants at the cellular level to derogate the effects of salinity-induced osmotic stress. Salinity stress activates the salt-mediated osmotic stress pathways that induce the synthesis and accumulation of compatible osmolytes (e.g., proline, betaine, and soluble sugars) to increase the osmoregulatory functions of plants Parida, and Das, (2005), Gupta and Huang (2014). Some studies have shown that Si participates in regulating the accumulation of osmoregulatory substances in plants. Examples of this include sorghum and wheat, where researchers found that the addition of Si could significantly alter the soluble sugar and proline content in plants Yin, etal (2013). Sattar, etal. (2017). In cucumber, $Na^+Na_2SiO3.9H_2O$ treatment could increase the accumulation of soluble sugars (mainly sucrose and glucose) and decrease the osmotic potential of xylem sap in the root system compared with Na treatment, thus contributing to the promotion of root water uptake Zhu, et al. (2016). However, this regulatory effect of Si exhibits intercultivar differences, and whether Si participates in enhancing assimilate transport to provide more energy storage in the roots needs to be experimentally proved. Moreover, carbohydrates such as sugars (e.g., glucose, fructose, and fructans) are involved not only in osmoprotection, but also in carbon storage and scavenging of ROS Zhu et al. (2016).

5.2.11 Silicon and Reactive Oxygen Species in Responses to Salt Stress

During salinity stress, one of the immediate responses of plants is overproduction of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), superoxide (O_2^-), and hydroxyl radicals

(OH.). The increase of ROS will cause oxidative damage to membranes and organelles Liu, etal. (2015). The antioxidant systems include enzymatic and nonenzymatic antioxidants. In plants, enzymatic antioxidants mainly include catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), and ascorbate peroxidase (APX). Nonenzymatic antioxidants mainly include vitamin E, ascorbic acid, and glutathione reductase (GR) Choudhury, et al. (2017). Previous studies have shown that Si could improve ROS scavenging ability by regulating the activities/contents of enzymatic/nonenzymatic antioxidants in plants, and the regulatory effect is different depending on plant species. For example, in barley, Si could increase the activity of CAT, SOD, and GR, but had no effect on the APX activity Liang, et al. (2003). In cucumber, the addition of exogenous Si could increase the activities of APX, SOD, GPX, and GR, but had no effects on the CAT activity Zhu, et al. (2004). In sorghum, Si application has been proposed to reduce the accumulation of H_2O_2, which plays a negative role in regulating the activity of aquaporin to enhance aquaporin activity, and thus increase water uptake Liu, et al. (2015). Similar results were also found in okra (Abelmoschus esculentus) Abbas et al. (2015), grapes (Vitis vinifera L.) Soylemezoglu, et al. (2009), wheat Tuna, *et al.,* (2008), tomato Li *et al.,* (2015), and rice Abdel-Haliem et al. (2017). Moreover, the regulatory pattern is different depending upon plant species and Si intensity. Application of Si gradually enhanced AsA-GSH particularly in two rice cultivars differing in salt tolerance. Such effect were more pronounced upon Si administration in the sensitive cultivar Das, et al. (2018). One study on Glycyrrhiza uralensis showed that the exogenous addition of 1, 2, 4, and 6 mM Si could significantly increase POD activity and reduce malondialdehyde (MDA) concentrations compared to salinity stress alone. However, the SOD activity significantly increased when 4 mM Si was used Li, et al. (2016). These results showed that even though the regulatory effects of Si on antioxidant defense systems under salinity stress can vary with plant species, treatment duration, treatment concentration, and growth conditions, overall, Si can decrease the accumulation of ROS through regulating both enzymatic and nonenzymatic antioxidants.

5.2.12. The regulatory effect of silicon on genes expression in responses to salt stress

Owing to the advancement of molecular genetics and genome wide technologies, significant research advances have been made to enhance our understanding of the involvement of Si in increasing stress tolerance. Kim, et al. (2014) reported that Si application significantly upregulated the expression of genes associated with ABA synthesis (zeaxanthin epoxidase (ZEP) and 9-cis-epoxycarotenoid dioxygenase (NCED1 and NCED4)) in rice after 6 and 12 h of the NaCl treatment, but decreased the expression of these genes after 24 h of treatment. In sorghum and cucumber, Si application increased the plasma membrane aquaporin expression in the roots to increase the hydraulic conductance and water uptake ability Yang and Guo (2018), Liu, et al. (2014),. In tobacco, Liang, et al. (2015) discovered the cooperation between Si and ethylene signaling pathway. They found that Si application rapidly upregulated the expression of crucial ethylene biosynthesis genes, 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) and 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS), which increased ethylene levels and regulated plant responses to salinity stress. However, when ethylene was absent, Si did not increase the tolerance of cells to salinity stress, but promoted the production of hydrogen peroxide, leading to cell death. Competition is considered to exist between ethylene and polyamines since they share a common precursor, S-adenosyl-L-methionine (SAM).

5.2.13. Impacts of Si in Alleviating Salt-Induced Oxidative Damage

Salinity is one of the most important environmental factors limiting crop production in arid and semi-arid regions. Salinization of land and water resources is a threat for sustainability of irrigated agriculture Qureshi, *et al.,* (2007). They reported that half of the irrigated area of Iran falls under different types of salt affected soils and average yield losses may be as high as approximately 50%. Following primary effects of salt stress, secondary stresses such as oxidative damage may occur. Oxidative damage occurs by accumulation of reactive oxygen species (ROS) that cause lipid and protein oxidation and eventually leads to cell death Molassiotis *et al.,* (2006). The antioxidant defence system in the plant cell includes both enzymatic antioxidants such as APX (EC1.11.1.11), CAT (EC1.11.1.6), SOD (EC1.15.1.1), POX (EC 1.11.1.7), and GR (EC 1.6.4.2) and some non-enzymatic antioxidants such as ascorbate, glutathione and αtocopherol Ashraf and Harris (2004); Gunes, *et al.,* (2007); Ashraf, (2009).

Salinity is a major abiotic stress that limits the growth and yield of agricultural and horticultural crops worldwide. Primarily, salinity hampers the osmotic balance in plants by affecting the electrochemical gradients and vascular transportation of solutes Marschner (1995). In higher plants, salt stress leads to several physiological and metabolic modulations such as retardation of photosynthesis, ion toxicity, oxidative burst, and nutrient imbalance Allakhverdiev, etal. (2000), Kosova, etal. (2011). In addition, higher accumulation of Na+ and Cl− ions during saline conditions hinders the uptake of essential nutrients Agarie, etal. (1998).Furthermore, salinity accelerates the production of harmful reactive oxygen species (ROS) that cause oxidative damage to proteins, lipids, and nucleic acids by affecting normal cellular metabolism Zhu,etal.(2004). Hence, an alternative strategy of silicon (Si) supplementation to overcome the negative effects of salinity in plants can be considered as a valuable approach. Silicon is the second most abundant element in the Earth's crust, covering 27.70% of the lithosphere. Numerous plant biologists have extensively studied the essential roles of Si in plant systems for several years, but by definition, Si is considered as a "quasi-essential" or nonessential element for plants, because most plant species can complete their life cycle without it Arnon and Stout (1939). However, there are several hypotheses concerning the physiological functions of Si in monocots and dicots. Under abiotic stress like salinity, Si application resulted in the alleviation of stress and enhancement of plant growth Soundararajan, etal. (2014), Li, et al. (2015). During salt stress, the apoplastic transport of Na+ and Cl− ions was decreased by Si deposition Shi, et al. (2013), Gong, et al. (2005). According to Zhu .and Gong (2014), the mechanisms behind silicon-mediated alleviation of salt stress include the following aspects: (a) maintenance of optimal water content; (b) enhancement of photosynthesis and curbing transpiration rate; (c) limiting oxidative stress by alleviating ion toxicity; and (d) biosynthetic regulation of solutes and plant hormones. In line with other researchers, Al-aghabary, et al. (2005) observed increased activities of antioxidant enzymes and enhanced photochemical efficiency of PSII under salt stress. Although the beneficial effects of Si against abiotic stresses are evident from previous reports, to date there is a lack of understanding of the molecular regulation of Si mediated stress tolerance. In order to gain a deeper insight into Si induced salt tolerance in pepper plants, proteomic analysis based on two-dimensional gel electrophoresis- (2DE-) mass spectrometry (MS) has been employed in the present study. Moreover, proteomic strategies are considered the best molecular approach to study the dynamics of proteins, particularly the response of Si in a stressed environment Rahman, et al. (2015), Campos, et al. (2003). Therefore, to our knowledge, for the first time, the current study has attempted to investigate the effect of Si on the growth, physiology, antioxidant enzyme activities, nutrient content, and protein expression in C. annuum under salinity stress.

Application of Si suggested as an alternative approach to alleviate salinity stress in crops (Liang *et al.,* 2007). However, Si content of the plant varies greatly with the plant species, ranging from 0.1 to 10.0% of dry weight Takahashi *et al.,* (1990). Si, increases root activity, K uptake, reduction of Na uptake, improvement of membrane permeability and anti-oxidative activity (Liang *et al.,* 2007). Sorghum is one of the most important crops of arid and semi-arid regions. It is moderately tolerant to salinity and can grow well in saline soils Maas *et al.,* (1986). However, at higher levels of salinity, considerable reduction in its growth takes place; therefore, improvement of its salinity tolerance by any means is a great challenge for plant scientists. Although a variety of strategies are currently in vogue to counteract the salinity problem, application of Si considered as one of the convenient and cost-effective approaches of overcoming the salinity menace.

Most recently, studies suggested that Si might participate in regulating the antioxidant defense system and relieving oxidative stress through enhanced endogenous polyamine accumulation (mainly spermidine and spermine) Yin *et al.,* (2019). The interactive effects between Si and exogenous substances including mineral element and plant hormone have been reported in several species. In chickpea, Garg and Bhandari, (2016) evaluated the individual and cumulative effect of Si and arbuscular mycorrhiza (AM) under salinity stress conditions. The results showed that mycorrhiza significant improved Si uptake and Si addition, alone or combined with mycorrhizal inoculation, increased the activities of antioxidant enzymes, such as SOD, CAT, and GPOX, and decreased ROS accumulation under salinity stress. Study of the combination effect of exogenous application of Si and/or other substances like beneficial soil microorganisms and elements in alleviating biotic/abiotic stresses may facilitate the use of Si in more plant species, especially for Si excluders. Potassium (K) is a macro-element that has been reported to ameliorate adverse effects of salt stress in many species Bybordi, (2014). A great interactive effect between Si and K were reported in improving antioxidant enzyme activity, photosynthetic rate, K uptake, and yield Lotfi, (2015). Selenium (Se), an important micronutrient in animals and humans, functions as a beneficial element in some crops. Studies proved that the combined application of Si and Se was more effective than Si alone in alleviating the toxic effects of salt stress on wheat seedlings through increasing antioxidant enzyme activity and accumulation of osmoprotectants like proline and soluble sugar Liu *et al.,* (2015). Salicylic acid (SA), a plant hormone, is an important signal molecule for modulating plant responses to environmental stresses. Application of salicylic acid and Si has been reported to improve seed quality of mung bean under salinity Lotfi and Ghassemi-Golezani, (2015). Future work is needed to investigate the interactions between silicon and other substance and their coupled response/functionality under salt stress conditions. Although studies have unraveled the regulatory effect of Si in ROS scavenging, many questions related to its mode of regulation remain unanswered. First and most important, whether this was a primary or a secondary effect of Si on ROS detoxifying proteins (e.g., SOD, APX, CAT, and GPX), and antioxidants such as ascorbic acid and glutathione (GSH) remains unclear from these studies. In the review of Coskun *et al.,* (2019) proposed that there are no biochemical roles for Si $(OH)_4$, an uncharged and unreactive molecule, in terms of interactions with enzymes or other intracellular constituents. Therefore, more studies are needed to examine the possible promotion effects of Si on the activities of antioxidant enzymes of plants under stress conditions. Second, metabolic and signaling ROS are shown to accumulate in the different compartments of the cells, mainly chloroplast, mitochondria, peroxisome, and apoplast. Moreover, each set of different biotic and abiotic stress conditions will result in abiotic stress-specific ROS signaling AO *et al.,* (2005), Sewelam *et al.,* (2016). If Si plays an active role in regulating ROS scavenging, it should be further specified when, where, and how (through regulating stress acclimation proteins and enzymes or expressions of genes involved in managing the level of ROS?). Third, it is worth noting that ROS is not always damaging. If cells maintain high enough energy reserves to detoxify ROS, they primarily function as signal transduction molecules that regulate different pathways during plant growth as well as the acclimation of plants to stress Sah *et al.,* (2016); Choudhury *et al.,* (2017). How this conflict of ROS production (metabolically or for signaling purposes) and ROS scavenging is resolved in plants is largely unknown, but it is mainly controlled by the ROS gene network Mittler *et al.,* (2004). Taking the complex nature of the ROS gene network and its function in plant signal transduction pathways into consideration, the cellular/molecular mechanisms controlling Si-induced/eliminated ROS signaling need to be elucidated.

6. Toxicity Symptoms related to Ionic and Nutritional Balance in Plants

Saline solutions impose ionic and osmotic stress in plants. The effects of this stress can be observed at different levels. In sensitive plants, the growth of aerial parts and roots is rapidly reduced. Reduction phenomenon appears to be independent of the tissue Na^+ concentration but would rather be a response to the osmolarity of the culture medium Munns, (2002). The specific toxicity of Na^+ ions is related to the accumulation of these ions in the leaf tissues and leads to necrosis of the aged leaves. Generally, this necrosis begins with the tip and the edges to finally invade the entire leaf. The reduction in growth is due to a reduction in leaf life, and thus there will be a reduction in growth and productivity Munns, (1993) & (2002). In saline soils, Na^+ ions induce deficiency in other elements Silberbush *et al.,* (2005). The effects of Na^+ are also the result of deficiency in other nutrients and interactions with other environmental factors, such as drought, which increase the problems of Na^+ toxicity. The excess of Na^+ ions inhibits the uptake of other nutrients either by competition at the sites of the root cell plasma membrane transporters or by inhibition of root growth by an osmotic effect. Thus, the absorption of water and the limitation of the nutrients essential for the growth and the development of the microorganisms of the soil can be inhibited. Leaves are more sensitive to Na^+ ions than roots because these ions accumulate more in the aerial parts than in the roots. These can regulate the concentration of Na^+ ions by their export either to the aerial parts or to the ground. The metabolic toxicity of Na^+ is mainly related to its competition with K^+ at sites essential for cell function. Thus, more than 50 enzymes are activated by K^+ ions; Na^+ ions cannot replace K^+ in these functions Bhandal and Malik, (1988); Tang *et al.,* (2015); Gu *et al.,* (2016). For that, a high concentration of Na+ can affect the functioning or the synthesis of several enzymes. In addition, protein synthesis requires high K+ concentrations for tRNA binding on ribosomes Blaha *et al.,* (2000) and probably for other ribosome functions Wyn Jones *et al.,* (1979). The disruption of protein synthesis by the high concentration of Na^+ represents the major toxic effect of Na^+ ions. Osmotic stress could occur following an increase in Na^+ concentration at leaf apoplasm Oertli, (1968). This result was verified by microanalyses (R-X) of Na^+ concentration in apoplasm of rice leaves Flowers *et al.,* (1991). The presence of high concentrations of Na^+ in the cells allows the plant to maintain its water potential lower than that of the soil to maintain its turgor and water absorption capacity. This leads to an increase in osmotic concentration by absorption of solutes either from the soil or by synthesis of compatible solutes. The former, usually Na^+ and Cl^- , are toxic, while the latter are compatible but energetically expensive for the plant.

6.1. Effects of NPs on plant under salinity stress

Nanoparticles enter the plant system by several routes, mainly through roots and leaves NPs interact with plants at cellular and subcellular levels after entry, promoting changes in morphological, biochemical and physiological and molecular states Khan *et al.,* (2019b). These interactions may be positive or negative, depending on the nature of the NPs and the plant species Fig. (42).

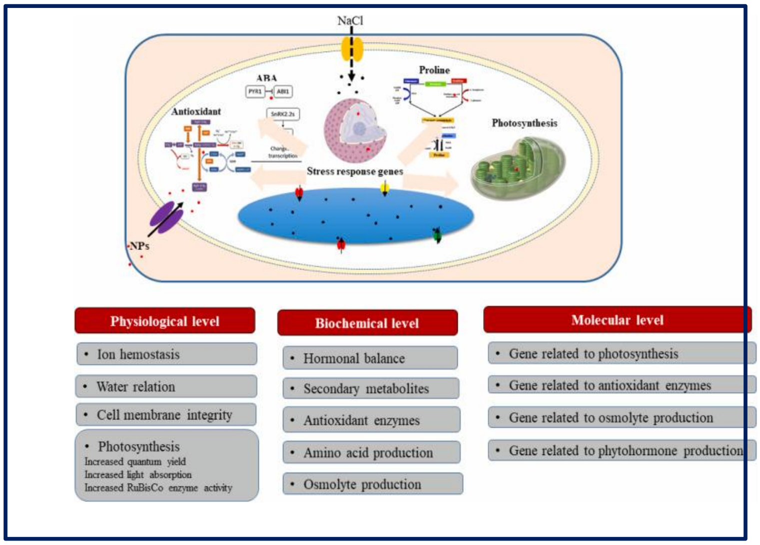


Fig. 42: Illustrates the interactions of NPs on plant under salinity stress at physiological, biochemical and molecular levels. After Etesami *et al.,* (2021)

The chemical nature, reactivity, size, and specifically concentration of NPs in or on the plant could determine NPs' effects on plant systems Ma *et al.,* (2010), Paramo *et al.,* (2020); Tripathi *et al.,* (2017a); Zulfiqar and Ashraf, (2021). Available evidence has shown that different NPs can promote salinity-stressed plant growth and development Ali *et al.,* (2021); Aslani *et al.,* (2014); Zulfiqar and Ashraf (2021) at concentrations below certain limits by various known mechanisms. These studies were mostly performed under artificial treatment conditions such as plate growth medium and hydrophobic or pot conditions. To understand the impact of NPs on plant growth, we discuss the positive effects of NPs to improve plant salinity stress tolerance.

6.2. Trace Elements and Nanoparticles

During the last few years, rapid advances of nanotechnology are associated with release of different types of nanoparticles. Some of them may be accumulated in soil or natural environment with negative effects on biota Alharby *et al.,* (2016), Yassen *et al.,* (2017). The authors have reported the detrimental effects of nanoparticles (usually at relatively high concentration) on plant health. However, there is evidence about the positive effects of nanoparticles, which is achieved at relatively low concentrations. This provides the scope for possible agricultural applications of nanoparticles Siddiqui *et al.,* (2014), Siddiqui and Al-Whaibi, (2014); Askary *et al.,* (2016). One of the promising ways is the use of nanofertilizers. Applying the nutrients in the form of nanoparticles improves the nutrient use efficiency, with low risk of toxicity for soil microbiota and roots Fig. (43).

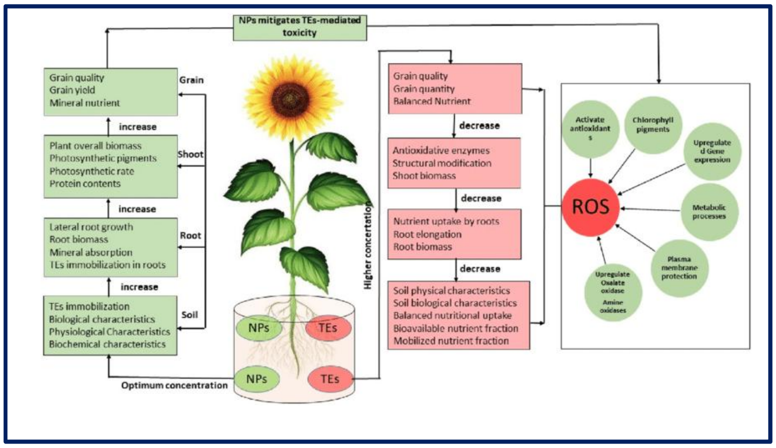


Fig. 43: Schematic diagram illustrating the potential role of nanoparticles (NPs) in alleviating the toxic effects of trace elements in plants through several potential mechanisms. After Rahman *et al.,* (2022)

Rahman *et al.,* (2022) reported that using of nanoparticles (NPs) as nano-fertilizers or nano-pesticides is gaining popularity worldwide. The NPs-mediated fertilizers encourage the balanced availability of essential nutrients to plants compared to traditional fertilizers, especially in the presence of excessive amounts of TEs. Moreover, NPs could reduce and/or restrict the bioavailability of TEs to plants due to their high sorption ability. They stated that the potential influence of NPs on plant physiological attributes, mineral absorption, and TEs sorption, accumulation, and translocation. It also unveils the NPs-mediated TE scavenging-mechanisms at plant and soil interface. NPs immobilized TEs in soil solution effectively by altering the speciation of TEs and modifying the physiological, biochemical, and biological properties of soil. In plants, NPs inhibit the transfer of TEs from roots to shoots by inducing structural modifications, altering gene transcription, and strengthening antioxidant defense mechanisms. On the other hand, the mechanisms underpinning NPs-mediated TEs absorption and cytotoxicity mitigation differ depending on the NPs type, distribution strategy, duration of NP exposure, and plants (e.g., types, varieties, and growth rate), NPs may bring new possibilities for resolving the issue of TE cytotoxicity in crops, which may also assist in reducing the threats to the human dietary system. Moreover, such a way of application reduces the frequency of the application and prevents the risk of over dosage. Hence, the potential of nanotechnology to support the sustainable farming is high, including developing countries Naderi and Danesh-Shahraki, (2013); Yassen *et al.,* (2017). The second way of application relates to exogenous use of trace elements and nanoparticles to mitigate stress effects by influencing some specific plant processes Zhao, et al. (2012); Rico, et al. (2013); Rossi, et al. (2016). For example, the zinc treatment led to lower MDA and H_2O_2 concentration in tissues in the experimental plants under salt stress, which was associated with upregulation of total APX, CAT, POD, and PPO activities under salt stress Weisany *et al.,* (2012); El-Bassiouny *et al.,* (2020). Decreasing of lipid peroxidation and proline contents under salinity by applying Fe_2O_3NPs has been found in the peppermint plants. The appropriate concentration of iron nanoparticles can be used for stress resistance of the peppermint Askary *et al.,* (2017). Fathi *et al.,* (2017) and Soliman *et al.,* (2015) haves demonstrated the positive influence of Zn and Fe and their NPs in stress conditions. Nanoparticles were more efficient than other tested forms of these micronutrients Fig. (44).

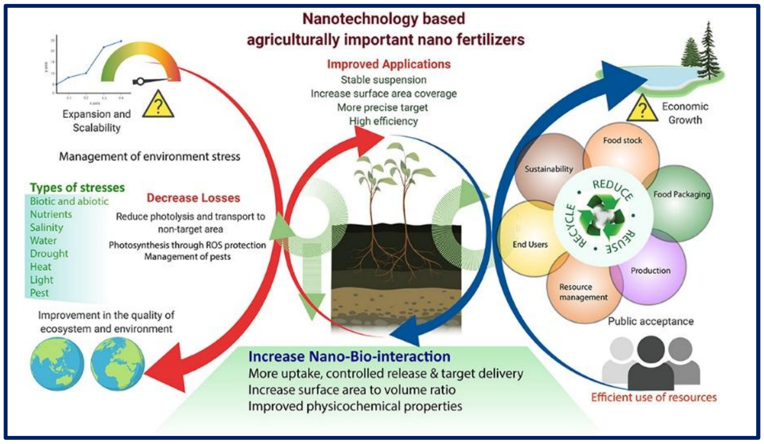


Fig. 44: Illustrates nanotechnology-based agriculturally important nano fertilizers increase agronomic productivity, efficiency, and reduce environmental stress. Efficient utilization of nanotechnology in agriculture for future sustainability. After Mittal *et al.,* (2020)

Mittal *et al.,* (2020) stated that it is an urgent requirement to satisfy the nutritional demands of the rapidly growing global population. Using conventional farming, nearly one third of crops is damaged, mainly due to pest infestation, microbial attacks, natural disasters, poor soil quality, and lesser nutrient availability. More innovative technologies are immediately required to overcome these issues. In this regard, nanotechnology has contributed to the agro technological revolution that has imminent potential to reform the resilient agricultural system while promising food security. Therefore, nanoparticles are becoming a new-age material to transform modern agricultural practices. The varieties of nanoparticle-based formulations, including nano-sized pesticides, herbicides, fungicides, fertilizers, and sensors, have been widely investigated for plant health management and soil improvement. In-depth understanding of plant and nanomaterial interactions opens new avenues toward improving crop practices through increased properties such as disease resistance, crop yield, and nutrient utilization, could benefit productivity and food security in future

It can be caused by their size, shape, distribution, and other physical characteristics. Latef *et al.,* (2017) reported that priming of seeds with ZNPs is a useful strategy to increase the salt tolerance of lupine plants. The most efficient was concentration of ZnO NPs 60 mg L^{-1}. El-Bassiouny *et al.,* (2020) reported that, seed-priming with ZnO-NPs or ZnO-bulk in the presence and absent of *Arbuscular mycorrhiza* (AM) fungi increased the levels of organic solutes (TSS, proline and FAA) in two wheat cultivars under salinity stress. Nano-ZnO (10mg/l) in the presence of AM was the most effective treatments on both wheat cultivars. Moreover, application of ZnO-NPs is the main defense mechanism, as a possible initiator of oxidative stress of the plant via enhanced the secondary metabolism is mainly due to the increase in phenolic compounds and antioxidant enzyme activities Fig.(45). It has been also shown that exogenous nanoparticles such as cerium oxide nanoparticles (CeO2-NPs) positively influence plant growth and production under normal growth conditions. Depending on soil moisture content, CeO_2-NPs supported photosynthesis, which led to increase of water use efficiency (WUE), especially in water-restricted conditions Cao *et al.,* (2017). Under salinity, it was found that CeO_2-NPs application led to improved plant growth and physiological responses of canola, improving the salt stress responses. However, the stress effects were not fully alleviated by CeO_2-NPs Rossi *et al.,* (2016).

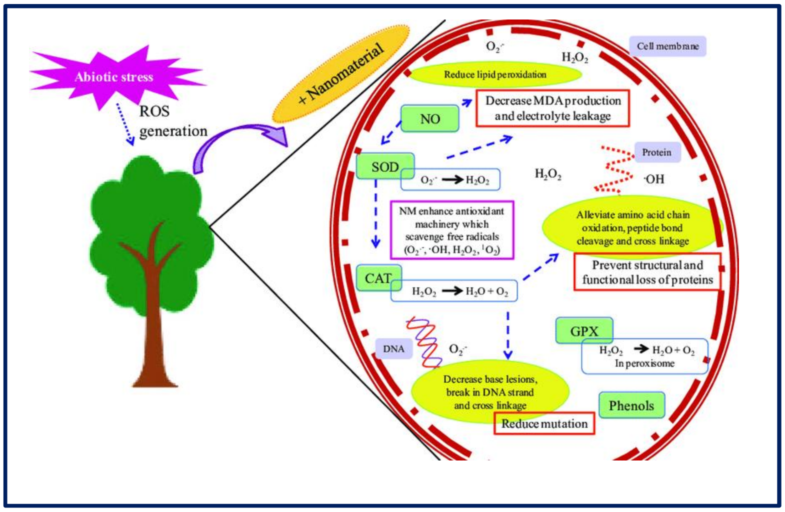


Fig. 45: Mechanism of alleviation of oxidative stress in plant by nanomaterials. Amendment of Nanomaterials induces Nitric oxide (NO) production that initiate signal and trigger generation of enzymatic and non-enzymatic antioxidant superoxide dismutase (SOD), guaiacol peroxidase (GPX), catalase (CAT) and phenols that scavenge ROS (O_2 −·, H_2O_2, OH−) generated in different cell organelles due to abiotic stress. SOD dismutate superoxide radical (O_2 −·) into hydrogen peroxide (H_2O_2), which on action of CAT and GPX converted into water molecule (H_2O) and molecular oxygen (O_2), thereby reducing ROS concentration and oxidative damage to proteins, lipids and nucleic acid After Sachdev and Ahmad, (2021).

Adding SiO_2 nanoparticles was found to be able to improve germination and seedling early growth under salinity stress, Sabaghnia and Janmohammadi, (2014), Siddiqui and Al-Whaibi, (2014). In similar, nano-silicon (N-Si) was shown to improve seed germination, plant growth, and photosynthesis under environmental stresses in tomato Almutairi, (2016 a & b). Also in the case of application of AgNPs, the alleviative effects in conditions of salt stress were found, including positive influence on seed germination, growth of roots, and thus the overall growth and dry mass increase in tomato seedlings under NaCl stress Almutairi, (2016a) Fig.(46),(47).

Pereira *et al.,* (2021) reported that new agriculture revolution is needed in order to increase the production of crops and ensure the quality and safety of food, in a sustainable way. Nanotechnology can contribute to the sustainability of agriculture. Seed nano-priming is an efficient process that can change seed metabolism and signaling pathways, affecting not only germination and seedling establishment but also the entire plant lifecycle. Studies have shown various benefits of using seed nano-priming, such as improved plant growth and development, increased productivity, and a better nutritional quality of food. Nano-priming modulates biochemical pathways and the balance between reactive oxygen species and plant growth hormones, resulting in the promotion of stress and diseases resistance out coming in the reduction of pesticides and fertilizers. The present research provides showing the challenges and possibilities concerning the use of nanotechnology in seed nano-priming, as a contribution to sustainable agricultural practices.

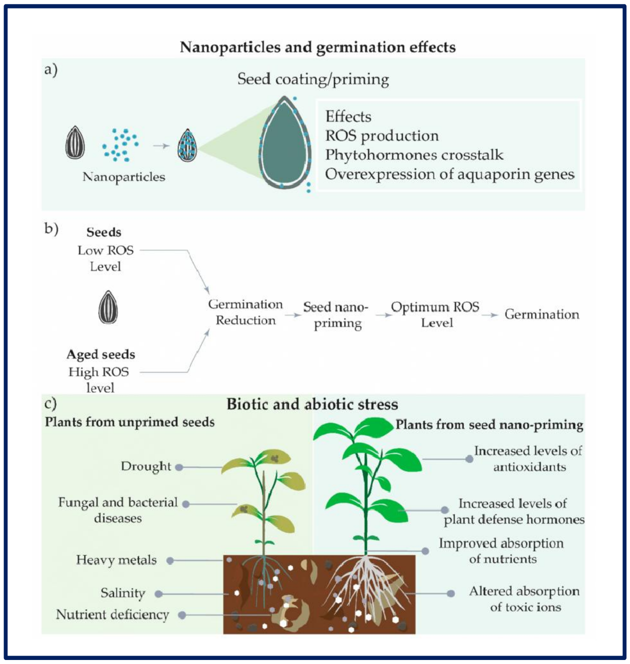


Fig. 46: Illustrates Seed nano-priming topics covered in this review and its potential benefits for sustainable agriculture. In addition to providing protection for seeds during storage, the use of seed nano-priming can result in improved establishment of plants in the soil with a reduced need for fertilizers. By growing faster, plants have an increased ability to compete with weeds for resources, consequently increasing productivity and food quality. The plants may also become more resistant to abiotic and biotic stresses, resulting in reduced use of pesticides. After Pereira *et al.,* (2021)

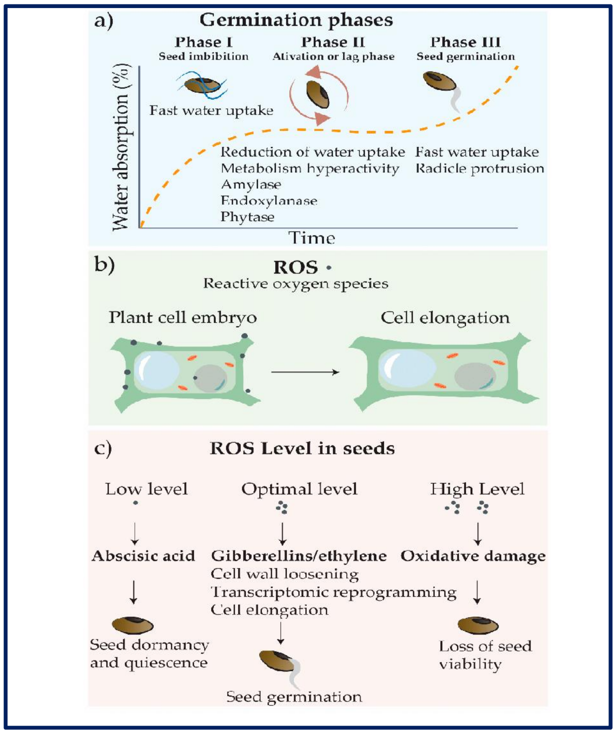


Fig. 47: Illustrates germination phases and reactive oxygen species (ROS) effects. (a) The germination process is subdivided into three phases: phase I (water uptake), phase II (metabolic activity, with initiation of degradation of starch reserves and preparation for embryo development), and phase III (embryo development and emergence

of the radicle). (b) The ROS act by destabilizing cell wall, allowing water uptake and cell elongation; (c) ROS level in seeds and hormones production. After Pereira *et al.,* (2021)

The combined application of AgNPs and salinity increased the soluble sugars and proline contents. On the other hand, it decreased catalase activity and increased peroxidase activity compared to the respective AgNP treatments alone. AgNPs enhanced the salt tolerance in wheat, but the long-term response of AgNPs under salt stress needs further investigation. El-Sharkawy *et al.,* (2017) have demonstrated that application of K nanoparticles in alfalfa may be more efficient than the use of conventional fertilizers, as the nutrition can be more adequate and this way of application may prevent the negative effects of salt stress in some specific conditions. The abovementioned results suggest that the application of different nanoparticles is a promising strategy to stimulate the plant tolerance to salt stress. According to the many researchers, engineered nanoparticles have a great chance of getting into agricultural lands Delfani *et al.,* (2014); Benzone *et al.,* (2015); Liu *et al.,* (2015); Liu and Lai, (2015); Mastronardi *et al.,* (2015); Rastogi *et al.,* (2017). We report that a common industrial nanoparticle could in fact have a positive impact on crops. Modern nanofertilizers are expected to contribute to the improvement of crop growth, photosynthesis, and tolerance to environmental stress, which will result to better nutrient and water use efficiency and yield increase.

6.3. Effects of NPs on molecular aspects of plants

The plant's biological functions depend on the events that occur at the molecular level. However, little progress has been made at the molecular level influenced by NPs, which is an important step in evaluating potential mechanisms and plants' effects Ali *et al.,* (2021). Certainly, NPs cannot be so effective without interfering with cellular mechanisms and gene expression because salinity stress affects the expression of genes and as a result influences the plant growth through changes in the expression of many genes involved in the different parts of cells and their products Fig. (48).

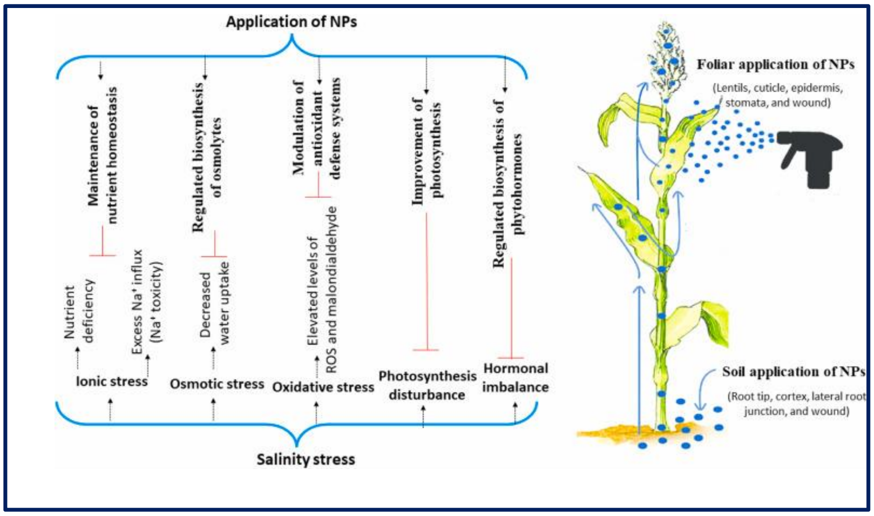


Fig. 48: Illustrates the interaction of nanoparticles and soil salinity at physiological and biochemical and molecular Levels in plants

Research in this area was performed by analyzing the expression of microRNA in NPs-treated cells Kumar *et al.,* (2019). According to the results of these researchers, the NPs affected the expression of miR398 and miR408, which are responsible for regulating seed germination, the growth of roots and seedlings, as well as antioxidants and free radical scavenger. It should also be noted that excessive expression of microRNA causes the mentioned factors to be prevented. Therefore, it is necessary to obtain complete information about the optimal amount of each NPs. NPs-mediated increase in root growth is attributed to the decrease in miR164 expression, which is involved in the signaling of auxin hormone. Increase in miR169 expression and decrease in miR167 expression can result in lateral root production and acceleration in flowering Kumar *et al.,* (2019); Tolaymat *et al.,* (2017). In a study, the simultaneous effect of Zn oxide NPs (0, 20, and 40 mg $L-1$) and plant growth-promoting bacteria (Bacillus subtilis, Lactobacillus casei, and Bacillus pumilus) on cytosine methylation in tomato plants

(Solanum lycopersicum L. 'Linda) was examined under 250 mM NaCl Hosseinpour *et al.,* (2020). While salinity stress was able to increase the polymorphism ratio, the combined use of the NPs and bacteria reduced the DNA hyper methylation caused by salinity stress. In fact, DNA methylation is one of the epigenetic changes in the cell for the expression of genes, and the cell changes the expression of genes during methylation and demethylation in salinity stress Peng and Zhang, (2009). In another study, the foliar application of Zn-NPs on rapeseed plant (Brassica napus L.) under salinity stress caused a change in the expression of genes involved in stress to reduce the expression of some genes (e.g., SKRD2, MYC and MPK4) and an increase in the expression of some other genes (e.g., ARP and MPK) associated with many physiological, hormonal and developmental responses, and MYC and SKRD2, which are related to transcription factor and increase in abiotic stress tolerance Hezaveh *et al.,* (2019). In the study of Hezaveh et al. (2019), the impact of exogenously applied ZnO-NPs on rapeseed grown under salinity stress was studied. The ZnO-NPs reduced ion leakage and improved Hill reaction thereby affecting the stress response genes (e.g., the expression of ARP increased while that of SKRD2, MYC and MPK4 decreased). According to these studies, the role of Zn NPs in ameliorating salinity stress is evident; but, due to the role of Zn in the functioning of intra- and inter-cellular signaling and DNA transcription Asha and Narain, (2020) and in ameliorating harsh environmental stresses such as salinity stress Arif *et al.,* (2020); Sofy *et al.,* (2020), future studies should be focused on molecular effects to deeply understand the mode of actions of the NPs under salinity stress conditions and determine the optical concentration of Zn NPs. According to a previous study, the low doses of Zn NPs could exert positive, while high doses caused toxicity even under non-stress conditions Molnar ´ *et al.,* (2020).

Dubchaket *et al.,* (2010) demonstrated that, nano-particles obtained large surface to volume rate that promotes their bioavailability, bioactivity and biochemical activities. Bassiouny *et al.,* (2020) reported that, Zinc Oxide-nano or Zinc Oxide bulk raised the number of bands and density responsive proteins in wheat cultivars (Sids 13 and Sakha 94) in absence and present of AM. The protein bands at molecular weight 51 kDa and 40 kDa in both wheat cultivars can be considered as positive markers for ZnO-NPs and bulk ZnO, under salinity stress and it was noted that these bands disappearing under the control treatment. In this connection, Abedi *et al.,* (2011), found that, in wheat plant the band with Mwt 51 kDa band might be related to Rubisco activase enzyme. Moreover**,** El–Bassiouny *et al.,* (2015) reported that protein with molecular weight of 40 kDa seems to dehydrin expressed under salinity stress in flax cultivars. In addition, Merrick and Bruno, (2004) and Thomas *et al.,* (2011) found that unique gene expression patterns might help in development and validation of promising biomarkers suitable for high-through put screening methods, and for better understanding of the toxicity of nano-particles. Results show superiority of Sakha 94 cultivar in the number of protein bands and density responsive proteins than Sids 13 cultivar. In this connection, Ali *et al.,* (2007) reported that salt tolerance barley cultivar under salt treatment were recognize by a specific band and proposed that this specific bands might use as markers for the identification of tolerant cultivar under salt stress.

Ye *et al.,* (2020a) investigated the effect of manganese (III) oxide NPs (0.1, 0.5 and 1 mg. L^{-1} on pepper plants at 100 mM NaCl salinity level. The researchers found that the NPs penetrated through the seed coat, forming a corona-NPs compound. A noteworthy point in this study was key role of manganese NPs, especially at a concentration of 1 mg. L^{-1} , in increased expression of superoxide dismutase (SOD) genes, as a result production of SOD as one of the important enzymes for scavenging ROS under salinity stress. In view of the current literature, only the afore-mentioned study reporting the effect of Mn NPs on pepper can be detected, so molecular reports regarding Mn NPs induced improvement in salinity stress tolerance are rare. Thus, due to role of Mn in the reinforcement of the plant's defense system against multiple abiotic stresses Ye *et al.,* (2019), future research should focus on this domain to figure out the potential and novel roles of Mn NPs in mediating salt stress tolerance. Carbon-based NPs applications can also alleviate unfavorable environmental conditions in plants particularly salinity stress Khan *et al.,* (2017). Carbon nanotubes are one of the newest carbon-based NPs that are widely used in other industries, but much research has been done on their mechanism and effect during salinity stress Zulfiqar and Ashraf, (2021). It has been reported that multi-walled carbon nanotubes have the ability to change genes expression involved in the antioxidant and salt overly sensitive 1 (SOS1) system on rapeseed plant under salinity stress Zhao *et al.,* (2019). The application of the NPs to salt stressed rapeseed seedlings also induced intensification of nitrate reductase dependent nitric oxide biosynthesis, re-establishment of ion and redox imbalance evidenced by the decrease in ROS over generation, reduction in thiobarbituric acid production, and decrease in Na^+/K^+ ratio. The aforementioned beneficial effects were related to the NPs induced alteration in Na^+/H^+ exchanger 1 (NHX1) and K^+ transporter 1 (KT1) transcripts Zhao *et al.,* (2019). Research on carbon nanomaterials (e.g., carbon nanodots, nanofibers, nanobeads, and nano-diamonds) regarding their effects on salinity-stressed plants is rare and hence requires future studies. Further research in this domain is certainly required to elucidate how these carbon nanomaterials trigger some specific metabolic processes in salinity- stressed plants. This will help to better understand the potential of carbon nanomaterials in ameliorating salinity stress as well as to evaluate the risk related to the environment and organisms using materials containing NPs, because high doses of multi-walled carbon nanotubes showed phytotoxic effects as confirmed by biochemical and epifluorescence microscopy evidences Gohari *et al.,* (2020b). The positive effect of cerium oxide NPs also showed a significant decrease in ROS levels and an increase in calcium content in treated plants. The NPs have been shown to affect ROS and Ca^{2+} mediated signaling genes. In fact, the ROS and Ca^{2+} are important and effective in response to stress in plants. Cerium NPs were also able to affect terpene synthetase genes (CAD1 and TPS) An *et al.,* (2020). The interesting point in this study was that the NPs were found only in seed tissue and were not found in seedling tissues and claimed that the effects of the NPs are more related to their molecular effects. Research on cerium NPs in inducing salinity tolerance in plants is rare. Thus, future studies should be conducted with the major aim to evaluate the mode of actions of cerium NPs on molecular mechanisms in plants encountering the threat of climate change associated-salinity stress. In addition, the accumulation of cerium NPs in different plant organs was observed to be a dose-dependent phenomenon Singh *et al.,* (2019). Therefore, the determination of the optical concentration of Zn NPs is necessary to achieve the best yield of the plants under salinity stress. Silicon-NPs showed positive effects on Cannabis sativa L. under salinity stress conditions and led to improved growth and molecular changes in this plant Guerriero *et al.,* (2021). The results of proteomics analysis in tomato plants under salinity stress showed that silicon affected light-harvesting complexes, cytochrome b6f (Cytb6f) and ATP-synthase complex genes Muneer *et al.,* (2014). Kim *et al.,* (2014) showed that silicon treatment altered the expression of 29 genes, including genes involved in transcription factor, kinase/phosphatase, photosynthetic genes, and genes involved in stress. In addition to these effects, this element was involved in increasing the expression of OsNAC protein, which is effective in responding to stress Siddiqui *et al.,* (2020). In addition, silicon can affect the expression of genes involved in the biosynthesis of auxin and nitric oxide Tripathi *et al.,* (2020a). Moreover, another mechanism that helps to alleviate the effects of salinity stress by silicon was a change in the expression of genes such as OsZEP, OsNCED, and OsZEP, which are involved in the biosynthesis of the hormone abscisic acid (ABA) Tripathi *et al.,* (2020b). It has been reported that under salinity stress, by increasing the expression of the protein OsHMA3, silicon causes more salt transfer into the vacuole and improves plant growth, and also protects the plant against the negative effects of stress by increasing the activity of antioxidant enzymes Siddiqui *et al.,* (2020). In general, according to the published studies, which are mostly on the use of silicon in improving tolerance to salinity in plants Etesami and Jeong, (2018) and Etesami *et al.,* (2020), silicon NPs-mediated-growth improvement and salinity stress mitigation need further research. Scarcity of studies related to the use of silicon-NPs for ameliorating salinity stress demands further research in this domain. Hence, future studies should focus on the molecular mechanisms associated with increased salinity stress tolerance achieved through the supplementation of silicon-NPs. The role of Cu, as a micronutrient, in reducing harmful impacts of salinity on plants (e.g., by improving water relations, photosynthesis, and nutrition and upregulating the antioxidant defense and increased levels of osmoprotectants and amino acids) has been reported Iqbal *et al.,* (2018). In a study, Hernandez-Hern ´ ´ andez, *et al.,* (2018) also assayed the effect of Cu-NPs on tomato under salt stress and reported enhanced tomato growth by promoting the expression level of SOD and jasmonic acid (JA) genes, which resulted in alleviating ionic and oxidative stresses. The authors suggested that the application of Cu-NPs could effectively increase salinity tolerance by activating the antioxidant defense mechanism and by the octadecanoid pathway of jasmonates. Although the use of Cu-NPs for alleviating salt stress in plants is still at the infancy stage, the reports available show a considerable potential of this micronutrient in nano-forms for imparting salinity stress tolerance in plants Zulfiqar and Ashraf, (2021). Therefore, more research at molecular levels is required to find the mode of actions of Cu NPs to achieve improved salinity tolerance in plants. Due to multiple benefits related to crop improvement of Ag NPs, the use of these NPs is also making their way in agriculture. However, there are limited studies on Ag NPs as a potential solution for alleviating the negative impact of salinity on plants Zulfiqar and Ashraf, (2021). Hence, future studies should focus on deciphering their role in managing salinity stress tolerance at molecular level. Many researchers approve the use of Ag-NPs with considerable caution and care, since they can release silver ion (Ag^+) in the environment, and this ion being highly toxic in nature, can be hazardous for organisms Tortella, *et al.,* (2020). Therefore, it is important to know how Ag-NPs influence plant growth, and up to what extent they cause any prospective risk to the environment and health of the organisms Yan and Chen (2019). It is known that Fe assists plants in acquiring stress tolerance Tripathi *et al.,* (2018). Fe NPs have also great potential to ameliorate salinity stress in plants Abdoli *et al.,* (2020); Moradbeygi *et al.,* (2020), but the information on the specific metabolic pathways (at molecular level) that they regulate is not comprehensively available in the current literature Zulfiqar and Ashraf, (2021).

7. Role of Sulfur Metabolites under Salinity stress.

The mechanisms that plants operate under saline environment is essential beginning in efforts to reduce the adverse effects of salinity stress. The agricultural system is tightly linked with the fertilizer input and thus the judicious application of fertilizers is expected to lead positive effects in reversing the salinity effects. Sulfur is a macronutrient with essential roles in plant development under optimal and stressful environment. Several compounds are synthesized from sulfur metabolism useful in reversing the adverse effects of abiotic stress because of their free radicals scavenging property Fig. (49).

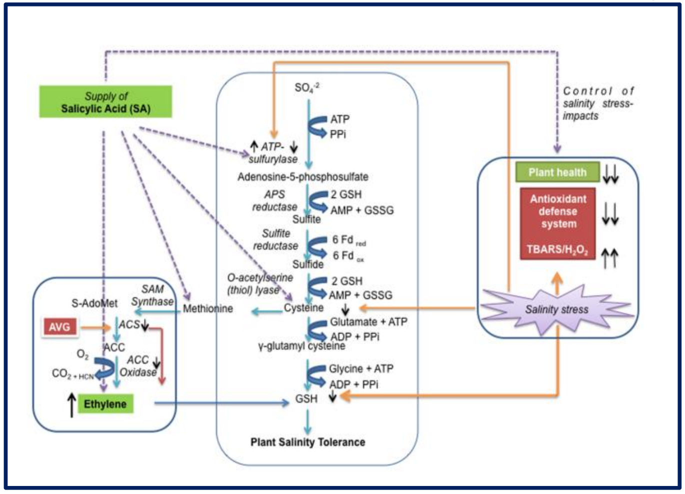


Fig. 49: Scheme representing the assimilation of sulfur (S), its involvement in the glutathione (GSH) synthesis, and GSH-mediated control of oxidants (reactive oxygen species, ROS) generated due to salinity in plants. GR, glutathione reductase; GSSH, oxidized glutathione; AsA, reduced ascorbate; MDHA, monodehydroascorbate; DHAR, Dehydroascorbate reductase; MDHAR, monodehydroascorbate reductase; APX, ascorbate peroxidase; CAT, catalase; SOD, superoxide dismutase. O2 −, superoxide; H2O2, hydrogen peroxide. After Rasheed *et al.,* (2020)

Sulfur-containing metabolites, amino acids (cysteine and methionine), vitamins (biotin and thiamine), thioredoxin system, glutathione lipoic acid and glucosinolates have potential to promote or modify physiological and molecular processes under salinity stress in plants. Thus, modulation of sulfur metabolites production could alter physiological and molecular mechanisms to provide tolerance against salinity.

7.1. Role of sulfur in Salinity Tolerance

Most of the S in higher plants is taken up in the form of sulfate through sulfate transporter from soil. Sulfate can also be taken up through leaves in the form of S gases like H_2S or SO_2. Sulfur assimilation pathway and synthesis of reduced S compounds are well documented. Once S is reduced in the cell, it either remains in cytosol or transported into the plastid or stored in the vacuole for further metabolic reactions Fig. (50).

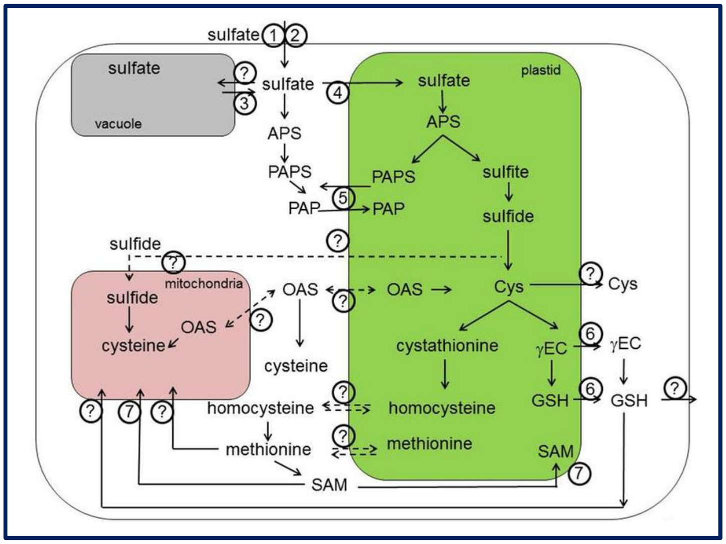


Fig. 50: Transport processes in primary sulfur assimilation. Sulfate is taken up by the root cells with the help of SULTR1;1 (1) and SULTR1;2 (2). Once crossed the plasma membrane of epidermal and cortical root cells, sulfate is transported through the series of sulfate transporters (SULTR) residing in various membranes within the plant. The SUTR4;1 and SULTR4;2 are important for the efflux from the vacuole into the cytoplasm (3). The transporter important for the sulfate influx into vacuole is still unknown. Import of sulfate into the chloroplasts is possible due to SULTR3;1 and probably other members of SULTR3 subfamily (4). PAPS is produced both in chloroplasts and in the cytoplasm and can be exchanged between these compartments by PAPST/TAAC transporter (5). The known transporter of thiols (GSH and γEC) are chloroquine-resistance transporter (CRT)-like proteins or CRLs (6). However, an alternative transport system for thiols in the plastid membrane is expected to exist. In a similar way, the GSH transporters to the mitochondria await still the discovery. S-adenosylmethionine transporter 1 (SAMT1; 7) is a chloroplastidic protein involved in the exchange of SAM with S-adenosylhomocysteine, the by-product of methylation reactions that has to be regenerated to SAM in the cytoplasm. This is also the case for the plasmalemma-localized transporters of S-methylmethionine (SMM) and GSH, which are important transport form of reduced sulfur and therefore need to be exported out of the cell. APS, adenosine 5′-phosphosulfate; Cys, cysteine; OAS, O-acetylserine; γEC, γ-glutamylcysteine; GSH, glutathione; SAM, S-adenosylmethionine; PAPS, 3′-phosphoadenosine-5′-phosphosulfate; PAP, 3′-phosphoadenosine 5′-phosphate. Dashed lines indicate theoretically possible transport pathways. After Gigolashvili, and Kopriva, (2014)

The assimilation of S is highly regulated in a demand-driven manner Lappartient and Touraine, (1996). First step in S assimilation involves the activation of sulfate to adenosine 5’-phosphosulfate (APS) catalyzed by ATP sulfurylase (ATP-S; EC 2.7.7.4). A relatively minor extension of this pathway is the phosphorylation of APS to 3’-phosphoadenosine-5’-phosphosulfate (PAPS), catalyzed by APS kinase (APK; EC: 2.7.1.25). Subsequently, APS is reduced to sulfite by APS reductase (APR; EC: 1.8.99.2) and the sulfite is further reduced to sulfide by a ferredoxin-dependent sulfite reductase (SiR; EC: 1.8.7.1) and the sulfide is incorporated into the amino acid skeleton of O-acetyl-L-Serine (OAS) by O-acetyl-L-Serine (thiol) lyase (OAS-TL), forming Cys Leustek *et al.,* (2000). Serine acetyl transferase (SAT; E.C 2.3.1.30), catalyzes the formation of OAS from L-Serine and acetyl-CoA links the serine metabolism to Cys biosynthesis Takahashi *et al.,* (2011). Subsequently, Cys is formed by the condensation of sulfide and OAS, catalyzed by cysteine synthase (CSase) Fig. (51).

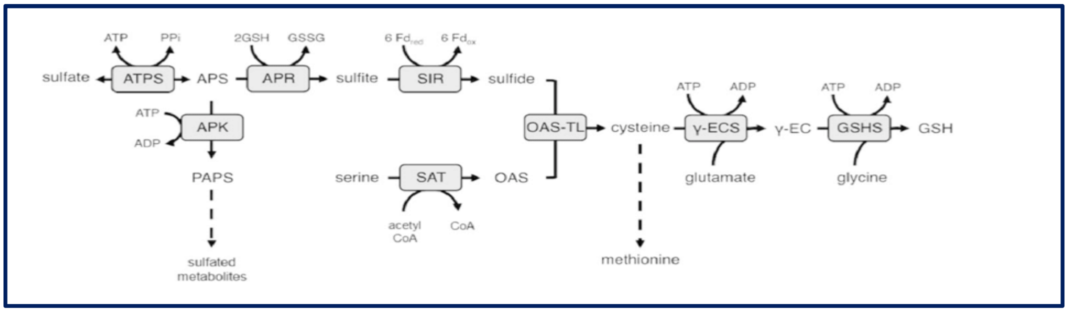


Fig. 51: Illustrates sulfate assimilation pathway in plants. ATPS, ATP sulfurylase; APS, adenosine-5′-phosphosulfate; APK, APS kinase; PAPS, 3′-phosphoadenosine-5′ phosphosulfate; APR, APS reductase; SIR, sulfite reductase; SAT, Ser acetyltransferase; OAS, O-acetyl-Ser; OAS-TL, OAS (thiol)lyase; γ-EC, γ-glutamyl-Cys; γ-ECS, γ-EC synthetase; GSH, red. Glutathione; GSHS, GSH synthetase; GSSG, ox. Glutathione; Fd, ferredoxin. After Gerlich *et al.,* (2018)

Synthesis of Cys and the activity of SAT and OAS-TL are strongly regulated by protein-protein interactions in the multi-enzyme complex of CSase Berkowitz *et al.,* (2002); Droux, (2003). Activity of SAT is strongly activated by association with OAS-TL, which is inactive and has only a regulatory role in the complex. The bound SAT exhibited higher apparent affinity for its substrate, acetyl-CoA and L-serine that might offer the possibility of regulation of synthesis of Cys in plants Droux *et al.,* (1998). Consequently, the formation of Cys is the crucial step for assimilation of reduced S into S-containing organic compounds. Plants have potential to develop several mechanisms to overcome the adverse effects of salinity stress. Among all strategies adopted by plants to cope salinity stress, availability of S along with S-containing compounds is of paramount importance. ATP-S is considered as the first rate-limiting enzyme of the S assimilation pathway and is up regulated under salinity stress Ruiz and Blumwald, (2002). It has been shown that salinity regulates key enzyme of sulfate assimilation, APR activity; mRNA levels of three APR isoforms increased by 3-folds with 150 mM NaCl treatment. Moreover, the increase in APR activity can be correlated with a higher rate of Cys synthesis to adjust the increased demand for GSH Koprivova and Kopriva, (2008). The activity of other enzymes of sulfate assimilation, SAT and salinity Ruiz and Blumwald, (2002) induce a cytosolic isoform of OAS-TL. It has been reported that salinity induces transcription and translation of OAS-TL genes probably due to higher demand of Cys or other S-containing compounds required by the plant as an adaptation/protection against higher level of salinity Romero *et al.,* (2001). Most abundant cytosolic OAS-TL isoform, OAS-A1, is known to be involved in the defense responses of Arabidopsis against salinity Barroso *et al.,* (1999), Dominguez-Solís *et al.,* (2001). The activity of OAS-TL was found increased under salinity in Typha and Phragmites contributing substantially to satisfy the higher demand of Cys for adaptation and protection. Higher Cys synthesis in both the plants supports the efficiency of the thiol-metabolism based tolerance Fediuc *et al.,* (2005). The over-expression of CSase, or SAT, key enzymes of Cys biosynthesis was related to higher tolerance to oxidative stress and the overexpression of these enzymes is considered promising tool for engineering S assimilation for higher Cys and GSH synthesis Noji and Saito, (2007) Gene expression of Atcys-3A, coding for cytosolic OAS-TL, was induced as a tolerance mechanism under salinity Barroso *et al.,* (1999). In salt-treated plants, sufficient Sulfur supply allows GSH synthesis necessary to prevent the adverse effects of ROS on photosynthesis. Plants with higher levels of thiol compounds in S-sufficient plants were more able to remove the toxic effects of salinity and were more salinity tolerant Astolfi and Zuchi, (2013). Overexpression of BrECS1 and BrECS2 in transgenic rice plants tolerated high salinity by maintaining a cellular redox state, which prevented unnecessary membrane oxidation. These rice plants also showed lower relative ion leakage and higher chlorophyll-fluorescence than wild type rice plants on exposure to salt, resulting in enhanced tolerance to abiotic stresses Bae *et al.,* (2013)

7.2. Sulfur Metabolites in Salinity Tolerance

Sulfur is a ubiquitous and essential element for all living organisms from bacteria to animals and plants. Sulfur played many important roles in plants under optimal and stressful environments, but cannot involve directly in any specific metabolic role in plants Fig. (52).

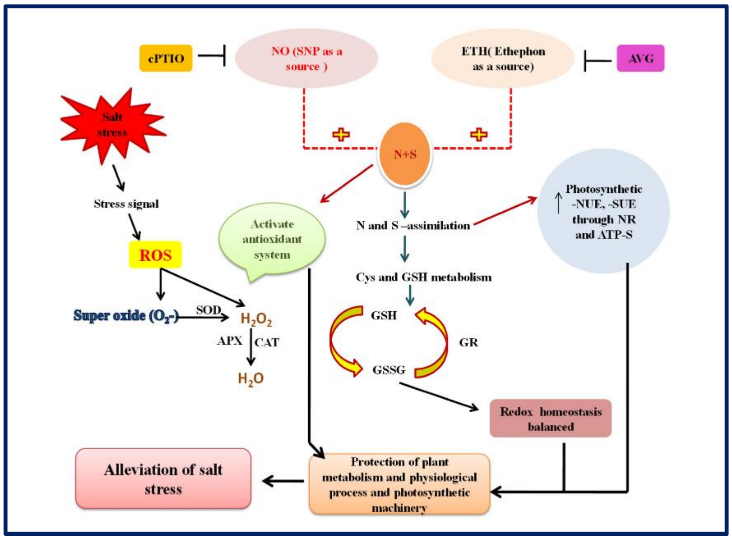


Fig. 52: Summary of the major outcomes. The involvement of NO/ETH with supplementation of N and S in eviation toxicity of salt stress. APX, ascorbate peroxidase; AVG, 1-aminoethoxy vinyl glycine; ETH, ethylene; cPTIO, 4-(carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxy-3-oxide; CAT, catalase; Cys, cysteine; GR, glutathione reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; N, nitrogen; NO, nitric oxide; NUE, nitrogen use efficiency; S, sulfur; SOD, superoxide dismutase; SUE, sulfur use efficiency. After Jahan *et al.,* (2021)

Jahan *et al.,* (2021) reported that stated that salt, stress significantly contributes to major losses in agricultural productivity worldwide. The sustainable approach for salinity-accrued toxicity has been explored. The use of plant growth regulators/phytohormones, mineral nutrients and other signaling molecules is one of the major approaches for reversing salt-induced toxicity in plants. Application of the signaling molecules such as such as nitrogen (N) and sulfur (S) play significant roles in combatting the major consequences of salt stress impacts in plants.

Maintenance of the S-status and the major biochemical and molecular studies to this end have reported to improve plant abiotic stress tolerance Per *et al.,* (2016), Fatma *et al.,* (2016). In fact, S-containing compounds (including cysteine, Cys; glutathione, GSH) significantly help in cellular redox homeostasis and thereby minimize plant protection against oxidative stress Fatma *et al.,* (2014); Kumar *et al.,* (2018). GSH acts as an important water-soluble and low molecular weight antioxidant; a major component of AsA-GSH cycle; and the main non-protein source of S to the plants Seth *et al.,* (2012), Iqbal *et al.,* (2021). Furthermore, GSH interacts with diverse stress and defense-related signaling molecules and can modulate their pathways, thereby combatting stress-impacts Kumar etal (2018). Adequate S-supply can enhance the content of GSH and improve photosynthetic and growth characteristics in salt stressed plants Fatma *et al.,* (2021), Fatma *et al.,* (2014). The imposition of salt stress significantly increased S-assimilation and the biosynthesis of Cys and GSH Jahan *et al.,* (2020). In addition, S-supplementation was also observed to improve ascorbic acid (AsA), total phenolics, tocopherol, lycopene, and antioxidant capacity, and decreased H2O2 and MDA content in Z. mays under salt conditions Riffat *et al.,* (2020). S-supply can also attenuate the inhibitory effects of salt stress on gas exchange attributes and growth of lettuce plants, decrease Na^+/K^+ ratio, and improve uptake of K and P de Souza *et al.,* (2019). Moreover, supplementation of S reduced the electrolyte leakage and Na+ accumulation while increasing K^+ and Ca^{2+} and photosynthetic rate under high salt-stressed sunflower plants Aziz *et al.,* (2019).

They also stated that the coordinated actions between N and S have emerged as an important strategy for improving plant growth and productivity under environmental stresses Jahan *et al.,* (2021), Nazar *et al.,* (2011). In fact, there occurs functional convergence and good coordination between N and S uptake, reduction assimilatory pathways Jahan *et al.,* (2020); Coleto *et al.,* (2017) and Jobe *et al.,* (2019). The status of nitrate reductase (NR; involved in N-assimilation) and ATP-sulfurylase (ATP-S; involved in S-assimilation) showed mutual interaction in terms of their coordinated role in Cys-synthesis and GSH-production Jahan *et al.,* (2020). Particularly, there exists a close relation among GSH and S and N Jahan *et al.,* (2020). The availability of its constituent amino acids, Cys, glutamine and glycine are connected with the biosynthesis of GSH which contains three moles of N per mole of S. Notably, the glutamine synthetase (GS)-glutamate synthase (GOGAT) pathway of N assimilation yields glutamic acid; whereas, S-assimilation ends with Cys synthesis Jahan *et al.,* (2020). In this way, the coordinative functions of S and N may strengthen plant capacity for stress tolerance. The literature is full on the recognition of regulatory interactions between N and S assimilation, and its significance in plant stress tolerance Jahan *et al.,* (2020), Nazar *et al.,* (2011), and Prodhan *et al.,* (2019). The synergistic relationship of N and S also contributed in enhancing plant growth, photosynthetic efficiency and proline accumulation under salt stress Rais *et al.,* (2013). The basal supplementation of S with foliarly applied salicylic acid (SA) to salt treated plants modulated enzymes involved in N assimilation, and GOGAT cycle Hussain *et al.,* (2021). During N-deficiency, hydrogen sulfide (H2S) and rhizobia synergistically regulated assimilation and remobilization of N and modulated senescence-associated genes expression Zhang *et al.,* (2020). However, the literature is scanty on N-S interactive effects in minimization of salt toxicity. The synergistic relationship of N and S also contributed to enhancement of growth and crop productivity Prodhan *et al.,* (2019). The relationship of N and S in terms of crop yield and quality has also been recognized in several studies Prodhan *et al.,* (2019). It is imperative to unveil more insights into N-S coordination, and their cumulative role in plant salt-tolerance at physiological/biochemical and molecular levels.

The smallest diatomic gas of Nitric oxide (NO), (30.006 g mol^{-1}), has emerged as a gaseous signaling molecule in plants and has also been reported to exhibit its connection with a range of phenomena from germination and senescence to photosynthesis and cellular redox balance Per *et al.,* (2017); Fatma et al.; (2016); Iqbal *et al.,* (2021); Lancaster (2015) and Fancy *et al.,* (2017). NO, can easily diffuse across the plant cells and contribute to signal transduction pathways by interacting with different cellular compounds and radicals Akram *et al.,* (2018). Even low (µM and nM) levels of NO can confer plant tolerance to a range of stresses including metal toxicity, salt, drought, high temperatures by mainly modulating the major components of antioxidant defense system and thereby limiting elevated ROS-accrued oxidative stress Jahan *et al.,* (2020); Sehar *et al.,* (2019); Jahan *et al.,* (2021); Fatma *et al.,* (2016); Per *et al.,* (2017) Ahmad *et al.,* (2018) andTian *et al.,* (2015). Both exogenous supplementation of NO-donors [e.g., sodium nitroprusside (SNP)], NO-scavengers [e.g., 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO)] and enzyme inhibitors were widely used to elucidate NO-roles in stressed plants. NO, can activate secondary messengers and/or induce transcription of genes and thereby control diverse processes in plants Gaupels *et al.,* (2011). Moreover, NO can also directly modify proteins, and react with residues of Cys (S-nitrosylation), tyrosine (nitration), or iron and zinc in metalloproteins (metal nitrosylation) Martínez-Ruiz *et al.,* (2011).

The presence of Sulfur in biomolecules is responsible for their catalytic or electro-chemical properties and thus for their involvement in specific biochemical mechanisms. In plants, S is an essential and integral part of amino acids i.e., Cys and Met, vitamins (biotin and thiamine), antioxidant (GSH), fatty acid (lipoic acid) and thioredoxin systems. These biomolecules have structural or redox control in proteins, especially Sulfur -donation in iron-S cluster and vitamin biosynthesis and detoxification of ROS and xenobiotics Leustek *et al.,* (2000); Droux, (2003); Droux, (2004) and Hell, (2003). In addition to these roles, Sulfur application improved photosynthetic efficiency and growth in two cultivars of mustard under salinity Wirtz and Droux, (2005). Cys synthesis in plants represents the final step of assimilatory sulfate reduction and the almost exclusive entry reaction of reduced S into metabolism of plants in a demand driven manner Kopriva and Rennenberg, (2004), Kopriva, (2006).

7.3. Amino Acids

Cysteine is the metabolic precursor of essential biomolecules such as vitamins, cofactors, antioxidants and many defense compounds. It is synthesized in plants in the cytosol, plastids and mitochondria by the sequential action of enzymes in S assimilationFig. (53).

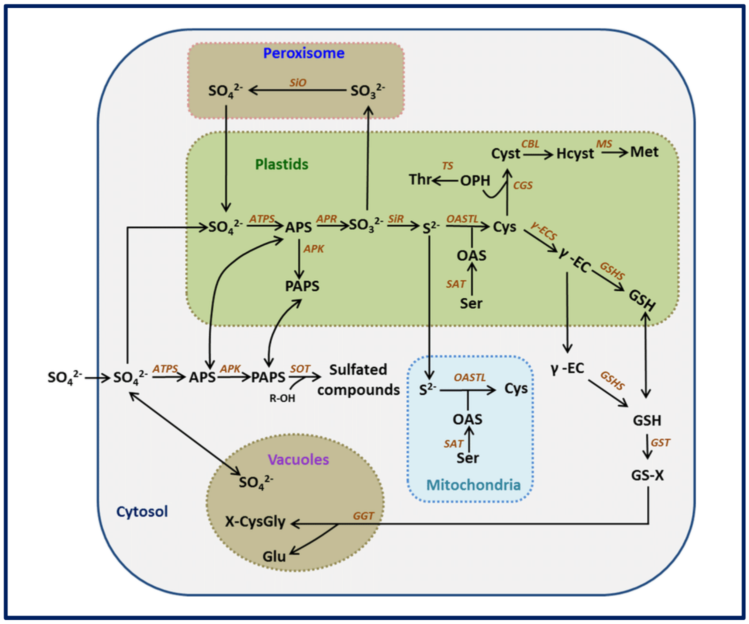


Fig. 53: Illustrates the sulfate assimilation and metabolism pathway. Enzymes are indicated in orange letters. Abbreviations of metabolites: APS, adenosine 5′-phosphosulfate; PAPS, 3′-phosphoadenosine 5′-phosphosulfate; R-OH, hydroxylated precursor; Ser, serine; OAS, O-acetylserine; Cys, cysteine; OPH, O-phosphohomoserine; Thr, threonine; Cyst, cystathionine; Hcyst, homocysteine; Met, methionine; γ-EC, γ-glutamylcysteine; GSH, glutathione; GS-X, glutathione conjugate; Glu, glutamate; X-Cys Gly, cysteinylglycine conjugate. Abbreviations of enzymes: ATPS, ATP sufurylase; APK, APS kinase; SOT, sulfotransferase; APR, APS reductase; SiO, sulphite oxidase; SiR, sulfite reductase; SAT, serine acetyltransferase; OAS-TL, OAS(thiol)lyase; CGS, cystathionine γ-synthase; TS, threonine synthase; CBL, cystathionine β-lyase; MS, methionine synthase; γ-ECS, γ-glutamylcysteine synthetase; GSHS, glutathione synthetase; GST, glutathione-S-transferase; GGT, γ-glutamyl transferase. After Li *et al.,* (2020)

SAT synthesizes the intermediary product OAS, and OAS-TL combines a sulfide with an OAS to produce Cys. Most of the Cys is formed and accumulated in the cytosol Krueger *et al.,* (2010) by the action of the major cytosolic OAS-TL, encoded by OAS-A1 Lopez-Martin, (2008a), Barroso *et al.,* (1995). It has been demonstrated that OAS-A1 is involved in the defense responses against abiotic stresses Barroso *et al.,* (1999), Dominguez-Solís *et al.,* (2001), Domínguez-Solís *et al.,* (2004) and is essential for maintaining the antioxidant capacity of the cytosol Lopez-Martin, (2008a), Lopez-Martin, (2008). In knockout oas-a1 plants, intracellular Cys and GSH levels are significantly reduced, and the GSH redox state is shifted towards its oxidized form. Moreover, oas-a1 mutant accumulates ROS in the absence of external stress, and show spontaneous cell death lesions in the leaves. Besides, Cys in conserved form has paramount importance in the function and signaling of enzymatic processes under environmental stress Meyer and Hell, (2005). Studies have shown that salinity induced higher rates of Cys synthesis with the increased expression of the cytosolic form of OASTL, and OAS-TL was related to salt tolerance Romero *et al.,* (2001), Barroso *et al.,* (1999), Fediuc *et al.,* (2005). Ruiz and Blumwald, (2002) showed that the increase in NaCl in the growth medium led to an increase in SAT in wild type and transgenic canola plants. The increase in SAT was limited to only 10% in transgenic plants growing in the presence of 150 mM NaCl, whereas wild type plants showed a marked increase in SAT activity of about 2.5 times. The salinity induced differences in SAT activity between wild type and transgenic plants were correlated with the leaf Cys concentrations because Cys content was found 1.5 times more in wild-type plants than transgenic plants. Cys can be converted into Met and further to S-adenosylmethionine (SAM) through reaction with ATP by SAM synthetase. In plants with S deficiency, the decline in chlorophyll together with decrease in SAM by many folds has been observed Nikiforova *et al.,* (2005). S-containing amino acid Met is an essential amino acid and executes central role in the initiation of mRNA translation of plants. Met is also a fundamental metabolite in plant cells as it directly or indirectly regulates a variety of cellular processes such as the precursor of SAM, which is the primary biological methyl group donor in cell wall synthesis, secondary metabolites, and chlorophyll synthesis, DNA replication Amir, (2010) ethylene, glycine betaine Khan *et al.,* (2012) nicotianamine and polyamine Sauter *et al.,* (2013). In addition, SAM is required for other methylation reaction of chlorophyll biosynthesis Nikiforova *et al.,* (2005). In addition, Met has nutritional importance in crop plants Galili *et al.,* (2005). Sanchez-Aguayo *et al.,* (2004) have established a relationship between the increased levels of SAM synthetase (enzyme in SAM synthesis from Met) content and salinity tolerance in tomato plants. Recently, Ogawa and Mitsuya, (2012) showed that utilization of S-methyl methionine was involved in salinity tolerance at the germination and early growth stages of Arabidopsis. Thus, plant development under stress conditions could be augmented with enhanced Met metabolism. The derivatives of methionine, ethylene and polyamines (PAs) have also been shown to induce salinity tolerance in plants. Cao *et al.,* (2008) have given an insight into the link between ethylene signaling pathway and salinity tolerance. They also showed that ethylene signaling modulates salt response at different levels, including membrane receptors, components in cytoplasm, and nuclear transcription factors in the pathway. Recently, Abbas and Morris, (2013) showed that MAPK signal transduction pathways are important to salt tolerance. The over expressed transgenic barley lines had constitutively higher levels of ethylene with jasmonic acid and showed tolerance to salinity; and after two weeks of salt treatment barley transgenic plants showed less reduction in growth. Polyamines are Met derivative plant growth regulators which include putrescine, cadaverine, spermidine and spermine. The tolerance of plants induced by PAs has been correlated with elevated levels of putrescine, spermidine or spermine Alcázar *et al.,* (2010). In a study, Yamaguchi *et al.,* (2006) have found that absence of spermine causes an imbalance in calcium homeostasis in the mutant plant in high salinity responses. In several other studies, putrescine, spermidine and spermine have shown potential in enhancing salt tolerance in plants Roy and Wu, (2001), (2002).

7.4. Vitamins

Vitamin generally links with the necessary dietary factors for animals. However, in general, plants are the only sources of vitamins. S is a core substance in nutritional vitamins i.e., biotin or vitamin H and thiamine or vitamin B1 Fig. (54).

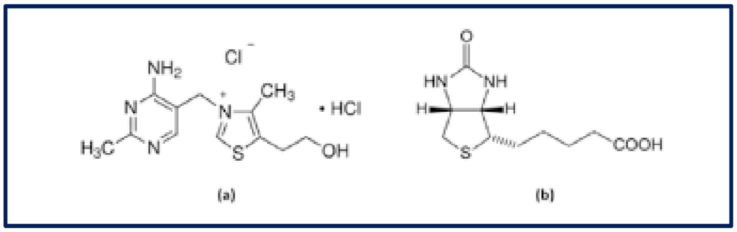


Fig. 54: Illustrates the structure of (a) thiamine hydrochloride and (b) biotin.

Biotin is a water-soluble vitamin biosynthesized by plants and is required by all living organisms for normal cellular functions and growth Che *et al.,* (2003). In plants, biotin plays a role as coenzyme that binds covalently to lysine residue of a group of enzymes and catalyzes many of reactions including carboxylation and decarboxylation Moss and Lane, (1971). Besides acting as a catalytic cofactor, biotin has a critical role in the enzymological mechanism of a number of enzymes that are essential in both catabolic and anabolic metabolic processes. Che et al. Che *et al.,* (2003) demonstrated that biotin has additional non-catalytic functions in regulating gene expression in Arabidopsis plants. Biotin controls expression of the biotin-containing enzyme, methyl crotonyl-coenzyme A (CoA) carboxylase by modulating the transcriptional, translational and/or post-translational regulation of this enzyme. Similarly, Li *et al.,* (2012) suggested that biotin deficiency resulted in spontaneous cell death and modulated defense gene expression. However, role of biotin under salinity is not well studied until date, but Hamdia, (2000) have studied the influence of biotin in ameliorating the effects of salinity on growth and metabolism in lupine plants. More research is needed to evaluate the role of biotin in salinity tolerance. Due to the abundance of thiamine in whole grains and green vegetables, plants represent the primary dietary source of thiamine in human and animal diets. Thiamine in the form of thiamine pyrophosphate (TPP), acts as a cofactor for several enzymes in key cellular metabolic pathways such as glycolysis, the pentose phosphate pathway and the tricarboxylic acid cycle (TCA); and in amino acid and isoprenoid biosynthesis Tunc-Ozdemir *et al.,* (2009). Another form of thiamine is thiamine diphosphate (TDP), a coenzyme in a number of metabolic reactions including acetyl-CoA synthesis, TCA cycle, anaerobic fermentation, oxidative pentose phosphate pathway, the Calvin cycle and plant pigment biosynthesis Friedrich, (1987), Rapala-Kozik *et al.,* (2008). Rapala-Kozik *et al.,* (2008) observed responses of Zea mays seedlings to abiotic stress including salinity and suggested the involvement of TDP-dependent enzymes metabolism under stress conditions. Total thiamine content in maize seedling leaves increased under salinity stress and the increase was found associated with changes in the relative distribution of free thiamine, thiamine monophosphate (TMP) and TDP suggesting a role of thiamine metabolism in the plants' response to salinity. In another study, Rapala-Kozik, *et al.,* (2008) has shown the involvement of biosynthesis of thiamine compounds and thiamine diphosphate-dependent enzymes in salinity and osmotic stress sensing and adaptation processes in Arabidopsis thaliana. El-Shintinawy and El-Shourbagy, (2001) observed that the addition of thiamine in 100 mM NaCl concentration alleviated the reduction of growth in plants and further they described that alleviation was correlated to the induction of 20 kDa and 24 kDa low molecular proteins in total protein content and increased contents of Cys and Met.

7.5. Thioredoxin System

Thioredoxins are small (12-13 KDa), ubiquitous and heat stable proteins found in all types of organisms. Thioredoxins are believed to regulate the cell redox with active disulfide bridge Schurmann and Jacquot, (2000) with a conserved pair of vicinal Cys (-Trp-Cys-Gly-Pro-Cys-Lys-) Holmgren, (1989) . There are two distinct families of thioredoxins based on sequence of amino acids. Family I: one distinct thioredoxin domain whereas family II: fusion of proteins with one or more thioredoxin domains with additional domains Gelhaye *et al.,* (2004). Furthermore, family I is classified into six major groups: the thioredoxins f, h, m, o, x and y in higher plants. Thioredoxins f, m, x and y belong to chloroplasts, whereas the thioredoxin o is found in plant mitochondria. Marti *et al.,* (2011) showed a role of mitochondrial thioredoxin PsTrxo1 as a component of the defense system induced by 150 mM salt in pea mitochondria. The increase in mitochondrial Trx activity was observed in response to NaCl treatment was correlated to mechanism by which plants respond to salinity Fig. (55), and protects mitochondria from oxidative stress together with antioxidant enzyme. Similarly, Fernandez Trijueque, (2012) by using pea seedlings mRNA expression profile of the plastic PsTRX m1showed that TRX is expressed in cotyledons. Furthermore, the response of plastid TRXs to NaCl and its potential in restoring growth of TRX-deficient yeast under saline conditions was studied. It was suggested that there was reserve mobilization in seedling cotyledons and physiological functions of PsTRX m1 in the salinity response during germination. Zhang, *et al.,* (2011) have reported that OsTRXh1 regulates the redox state of the apoplast and influences plant development and salinity responses.

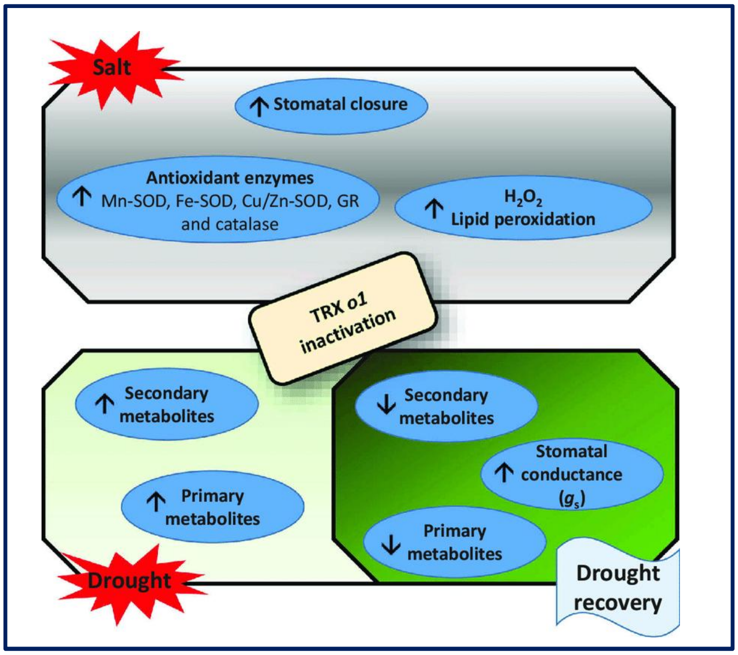


Fig. 55: Schematic model showing the main responses of TRX o1 mutant plants to salt and/or drought/drought recovery. Two independent studies have recently demonstrated that several physiological processes related to metabolism, stomatal function and antioxidant metabolism are affected in Arabidopsis thaliana plants with knockout of the mitochondrial TRX o1. 27, 29. The inactivation of TRX o1 leads to increases and decreases in both primary and secondary metabolism during drought and recovery, respectively27 (further details are found in the main text). Moreover, stomatal function is affected in the mutants under salinity and drought recovery: lower water loss and higher stomatal closure under salinity but higher stomatal conductance (gs) following drought recovery were observed. Although higher levels of H2O2 and lipid peroxidation were found in these plants, it seems that increased activities of antioxidative enzymes such as Mn-SOD, Fe-SOD, Cu/ZnSOD, GR and catalase are likely able to counteract TRX o1 deficiency in arabidopsis mutant plants under salinity. After Da Fonseca-Pereira *et al.,* (2019)

Da Fonseca-Pereira *et al.,* (2019), Redox reactions substantially influence the activity of several proteins and participate in the regulation of crucial cellular processes. Kocsy *et al.,* (2013). Accordingly, a growing body of evidence has highlighted the importance of the thioredoxins (TRXs) for the redox control of plant metabolism. Guggenberger *et al.,* (2017), Buchanan (2016) TRXs are small proteins containing a redox active disulfide group within its catalytic domain. Being widely distributed throughout most living cells, Yano, (2014). TRXs are involved in a variety of cellular redox reactions. Numerous isoforms of TRXs are present in plants, differing in both amino acid sequence and subcellular localization. Over 20 isoforms have been identified in the genome of Arabidopsis and grouped into seven subfamilies (f-, m-, h-, o-, x- y-, and z-types). Belin *et al.,* (2015), Thormählen *et al.,* (2015). The vast majority of TRXs isoforms are located in the chloroplast, but TRXs are also present in mitochondria (TRXs o and h) and cytosol (TRX h), where the presence of highly similar isoforms of NADPH-dependent TRX reductase (NTR), A and B, complete a functional TRX system. Montrichard *et al.,* (2009), Reichheld *et al.,* (2004), Non-plastid TRX system also includes proteins located at the nucleus (TRXs h-type in wheat seeds, Serrato and Cejudo, (2003), Pulido *et al.,* (2009) NTRA in Arabidopsis Marchal *et al.,* (2014) and pea Martí *et al.,* (2009) and TRX o1 in pea leaves Calderón *et al.,* (2017), endoplasmic reticulum Traverso *et al.,* (2013) (TRXs h2, h7, and h8) and attached to the plasma membrane Meng *et al.,* (2010) (TRX h9). The redox regulation of chloroplast function has received considerable attention over the last decades; however, the functional role of redox processes in other cell compartments remains unclear. For instance, the functional role of the extraplastidial NTR/TRX system remains poorly understood, most likely due to the extensive functional redundancies between

TRXs and glutaredoxins (GRXs) and also between NTRs found in both mitochondria and cytosol. Belin *et al.,* (2015); Reichheld *et al.,* (2010) The introduction of proteomics-based approaches to TRX studies have greatly contributed to the identification of putative TRX targets in plants, especially in the mitochondria. Montrichard *et al.,* (2009), Balmer *et al.,* (2004), Nietzel *et al.,* (2017). Since then, hundreds of putative targets involved in a broad spectrum of mitochondrial processes have been identified, including photorespiration, tricarboxylic acid (TCA) cycle and associated reactions, ATP synthesis, hormone synthesis, and stress-related reactions. Balmer *et al.,* (2004), Yoshida *et al.,* (2013). However, it is important to emphasize that such proteomic approaches provide substantial false-positive interactions and also lack the information whether the TRX-target interaction identified in vitro also occurs in vivo. Thus, further experiments with mutants and/or recombinant proteins are needed to fully elucidate the functionality of the TRX-target proteins interaction. In this vein, experimental validation successfully demonstrated that alternative oxidase (AOX) Gelhaye *et al.,* (2004) and some of the enzymes of the TCA cycle including isocitrate dehydrogenase, Yoshida and Hisabori, (2014) citrate synthase, Stevens *et al.,* (1997), Schmidtmann *et al.,* (2014) succinate dehydrogenase, and fumarase are regulated by the mitochondrial TRX system in vitro and/or in vivo. Daloso *et al.,* (2015). Furthermore, cytosolic malate dehydrogenase has also been demonstrated to be regulated by TRXs. Hara *et al.,* (2006). The mechanisms that coordinate mitochondrial TRX regulation and its implications for the dynamic of plant metabolism under different stresses conditions are poorly understood. However, the significance of mitochondrial redox metabolism in cellular signaling processes coupled with studies of different loss-of-function mutants have recently enabled us to grasp the importance of mitochondrial TRXs under stress conditions. Daloso *et al.,* (2015), Da Fonseca-Pereira *et al.,* (2019), Calderón *et al.,* (2018). In order to gain further insights into the physiological and metabolic function of the mitochondrial TRX/NTR system, we have recently investigated the significance of the mitochondrial TRX system under consecutive drought episodes. Using the Arabidopsis ntra ntrb double mutant and two independent mitochondrial trxo1 mutants, our study demonstrated that the lack of a functional mitochondrial NTR/TRX system enhances drought tolerance following single and multiple events of drought. Da Fonseca-Pereira *et al.,* (2019). Extensive metabolic and physiological analyses of these mutants revealed multiple and complex responses following both single and repetitive drought episodes. Da Fonseca-Pereira *et al.,* (2019) Notably, TRX o1 transcripts were more highly expressed under drought, an effect that was even stronger during repetitive drought/recovery events. Da Fonseca-Pereira *et al.,* (2019) Compelling evidence from several plant species indicates that AOX transcript and protein increase during drought (reviewed in Vanlerberghe *et al.,* (2016)). Given that TRX o1 may function in the reductive activation of AOX, Martí *et al.,* (2009) further investigation to elucidate whether the proposed protective role for TRX o1 under drought Da Fonseca-Pereira *et al.,* (2019) and salinity Ortiz-Espín *et al.,* (2017), Calderón *et al.,* (2018) is possibly also associated to the redox modulation of AOX. Notwithstanding, we further showed that the levels of a large number of secondary metabolites (glucosinolates, anthocyanins, flavonol glycosides, and hydroxycinnamates) increased in at least one of the TRX mutants following two cycles of drought. Da Fonseca-Pereira *et al.,* (2019). This result reinforces the idea that secondary metabolism is redox-regulated by TRX system. Daloso *et al.,* (2015), Bashandy *et al.,* (2009). What remains unclear and thus deserve further investigation is which enzymes of the secondary metabolism are the target of TRXs. Additionally; our study demonstrated that TRX mediated redox regulation seems to be crucial for stomatal function following the plant recovery from a second drought event, Da Fonseca-Pereira *et al.,* (2019). Similar to the situation observed under water limitation, compensatory readjustments were also observed in the responses of plants lacking the mitochondrial TRX o1 following salt stress. These responses included alterations in the glutathione redox state and/or up-regulation of AOX Martí *et al.,* (2011), and antioxidant enzymes. Ortiz-Espín *et al.,* (2017), Calderón *et al.,* (2018). Fig. (56). Moreover, Attrxo1 seeds germinated faster and accumulated higher H_2O_2 content under salinity, suggesting that TRX o1 could act as a sensor under salinity and/or an inducer of H_2O_2 accumulation. Ortiz-Espín *et al.,* (2017), the expression of the antioxidant enzymes AtPRXIIF and AtSRX was not altered during germination in either water or NaCl. Ortiz-Espín *et al.,* (2017), conversely, in pea plants the expression of TRX o1 and PRXIIF increased in response to shortterm salt stress Martí *et al.,* (2011), Barranco-Medina *et al.,* (2008) highlighting to the heterogeneity of the antioxidant system depending on the stress condition, which may in turn be related to specific TRX o1 targets following seed germination, a point that clearly deserves further investigation. Ortiz-Espín *et al.,* (2017), collectively, these observations are in good agreement with our proposal that perturbation of mitochondrial TRX affects cellular redox metabolism in general. It seems likely that in the absence of a functional mitochondrial TRX system the main mechanisms used to maintain redox homeostasis under drought/salt include an increased concentration of secondary metabolites and higher activities of enzymes of redox metabolism such as superoxide dismutase and catalase Fig. (56). Moreover, stomatal behavior allowing higher stomatal closure during salt stress Calderón *et al.,* (2018), and better recovery of stomatal conductance following rehydration Da Fonseca-Pereira *et al.,* (2019) Fig. (56) was shown to be a key factor for the maintenance of plant growth. To further elucidate the physiological performance of the TRX mutant lines after drought, here we compared the relationship between the ratio of electron transport rate (ETR) and net photosynthesis (AN) versus stomatal conductance (gs) (extracted from Da Fonseca-Pereira *et al.,* (2019). Both parameters can be employed as physiological status indicators. Flexas *et al.,* (2002), Flexas *et al.,* (2002) ETR/AN ratio reflects the energy transfer to the photosynthesis. Under optimum conditions, AN is the main sink, however, under stress AN is more sensitive and reduces faster than ETR, promoting the ratio increase and indicating an energy impairment that can be associated to ROS production. Flexas *et al.,* (2002) Accordingly, following drought recovery after drought (irrigation for 3 days) an inverse relationship between both parameters was observed, where WT plants displayed higher ETR/AN (indicating higher physiological stress) accompanied by lower gs; meanwhile TRX mutant lines showed comparatively lower ratios with higher gs for the same recovery period Fig. (56).

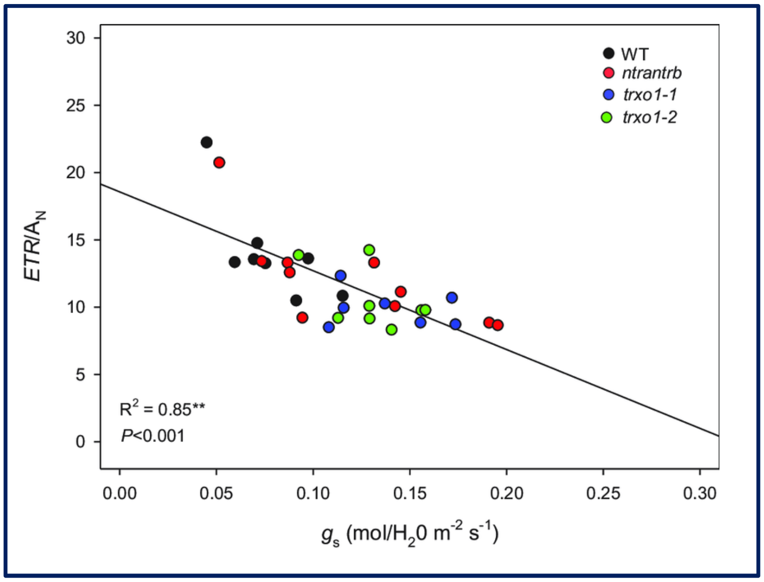


Fig. 56: Relationship between the ratio of electron transport rate (ETR) and net photosynthesis (AN) versus stomatal conductance (gs) in TRX Arabidopsis knockout mutants. The genotypes used here were ntra ntrb, trxo1-1 and trxo1-2, and wild-type plants (WT) during dehydration and following rehydration. Data was calculated from da Fonseca-Pereira et al. 2019.27 Regression coefficient and P value are shown.**Means the significant difference of the relationship between AN/ETR x gs. in a two-tailed Fisher's exact test (P< 0.001). After Da Fonseca-Pereira *et al.,* (2019)

In addition, Serrato *et al.,* (2004) reported a novel NADPH thioredoxin reductase (NTR) in the chloroplast. Deficiency of NTR caused hypersensitivity to salinity in Arabidopsis thaliana as Arabidopsis NTRC knockout mutant showed growth inhibition and hypersensitivity to salinity and suggested the role of NTRC gene in plant protection against oxidative stress.

7.6. Glutathione

Studies have shown the up-regulation of Cys synthesis in plants in response to salinity, suggesting a definite possible role of thiol in salt stress tolerance. Salinity creates over production of ROS and causes adverse effects on plant growth and metabolism that may be associated with the disturbances in osmotic potential of soil leading to osmotic stress or specific ion toxicity Munns and Tester, (2008) Fig. (57).

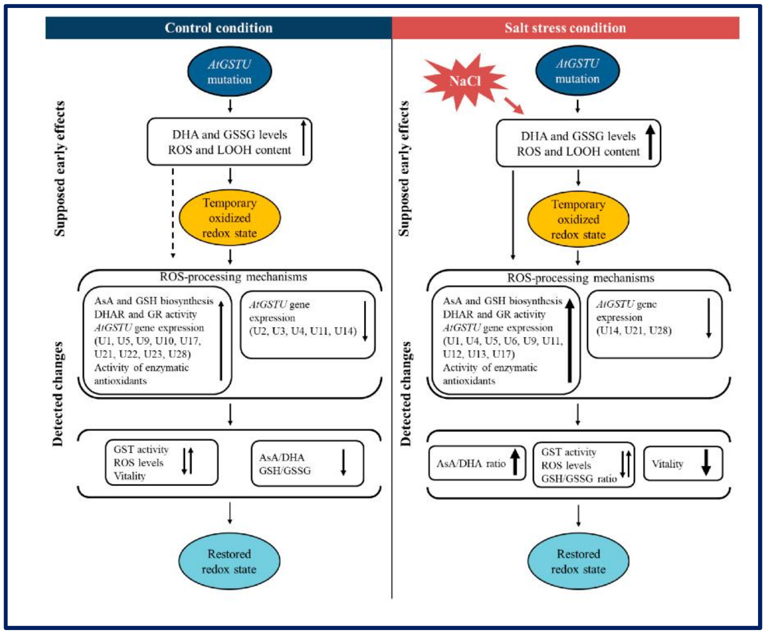


Fig. 57: Schematic model summarizing the results presented in this study. Mutation in a tau group glutathione transferase (AtGSTU) gene supposedly induced the accumulation of ROS and lipid peroxides, which led to a temporary oxidized redox state within the cells, accompanied by elevated Dehydroascorbate and oxidized glutathione levels. After Horváth *et al.,* (202)

Horváth *et al.,* (2020) reported that, high levels of reduced GSH are advantageous as they act as a strong buffer against ROS but would make the system less responsive to changes in redox potential that may be needed to up regulate the inducible defence components as reported by Schwarzländer *et al.,* (2008). Proteomic analysis of Arabidopsis roots subjected to the 150 mM NaCl treatment revealed an increase in the amount of important ROS-scavenging and detoxifying proteins, including APX, glutathione peroxidase, Class III peroxidases, SOD and GSTs Jiang *et al.,* (2006). In the present study, we found that the salt stress was accompanied by enhanced DHAR and GR activities. Knockout Atgstu24 also had higher DHAR activity and GSH content after salt treatment than wild-type plants and this could help to keep ROS under tight control and maintain a higher AsA/DHA and GSH/GSSG ratio. However, taking into account that the Atgstu24 mutant had slightly lower vitality than the other two genotypes, it can be assumed that these changes were not suitable to allow the plant to cope successfully with salt stress. Although the lack of AtGSTU24 increased the total GST activity under control conditions and it was slightly elevated even after salt treatment, the induction of several AtGSTU genes (AtGSTU3-6, AtGSTU9, AtGSTU11 and AtGSTU12) observed after salt treatment was in most cases lower than in Atgstu19 or wild-type plants. In the Atgstu19 mutant, the GSH content was also increased, but the GSH to GSSG ratio was lower than in Col-0. Interestingly, the calculated redox potential from the measured data revealed similar redox status in this mutant than in the wild type, both under control conditions and two days after application of the salt stress. By analyzing the redox status of Arabidopsis root tips using a roGFP1 redox sensor, Jiang *et al.,* (2016) demonstrated that the immersion of seedlings in 100 mM of NaCl for 3–24 h shifted the redox potential of the entire root toward the more oxidized status at the beginning, but it was re-established after 6 h and more negative redox potentials were detected compared to control roots, especially in the case of 24 h long treatment. Generally, the redox potential of roots depended on the strength and duration of the applied stress: while it might remain more negative in the case of mild (50 mM NaCl) stress, it became more oxidized in the presence of a higher (150 mM) salt concentration. However, after a few days, the salt-induced changes in redox potentials decreased and the differences in the redox status of seedlings practically disappeared Jiang *et al.,* (2016). Investigation of the redox status of five-day-old Atgstu19 and Atgstf8 mutants using a roGFP2 fluorescent probe revealed that the Atgstu19 mutant had the most oxidized redox status in all root zones and under all investigated conditions Horváth *et al.,* (2019).

Interestingly, the redox potential of the mutant roots showed smaller changes after applying 150 mM NaCl for 3 h than the wild type, due to the fact of their already more positive value under control conditions. It was concluded that their increased salt sensitivity can be associated with the decreased redox potential response Horváth *et al.,* (2019). The lower GSH/GSSG ratio and increased GSH level observed in several GST mutants and overexpressing lines Roxas *et al.,* (2000), Kilili *et al.,* (2004) and references above) suggest that altering the redox homeostasis can be part of a general mode of action in the mechanisms of GSTs. The dynamic interaction of GSTs with other glutathione-related enzymes might be how temporary redox status changes allow the regulation of normal cellular physiology. A schematic model illustrating predicted physiological and regulatory events in Atgstu mutants resulting in the observed changes in metabolite concentrations and enzyme activities under control conditions and after applying salt stress are summarized in Fig.(57) .To compensate these changes in Atgstu mutants the ascorbic acid and glutathione biosynthesis, the enzymatic antioxidant system (such as Dehydroascorbate reductase and glutathione reductase activity) was induced and the AtGSTU gene expression pattern was modified. The alteration of the ROS-processing network might help to maintain the ROS and redox homeostasis in the mutants. Salt stress presumably intensified the accumulation of ROS, LOOH and oxidized non-enzymatic antioxidants leading to further enhancement of the AsA and GSH biosynthesis, the activity of antioxidant enzymes (DHAR and GR) and the expression of several AtGSTU genes. Although these changes helped Atgstu mutants to restore the redox potential after NaCl treatment, the vitality of mutants was lower than in wild type. (An upward arrow indicates increase while a downward arrow shows decrease; the thickness of the arrows refers to the extent of the changes). Abbreviations: AsA, ascorbic acid; DHA, Dehydroascorbate; DHAR, Dehydroascorbate reductase; GSH, reduced glutathione; GR, glutathione reductase; GSSG, oxidized glutathione; GSTU, glutathione transferase tau group; LOOH, lipid peroxides; ROS, reactive oxygen species

In order to cope the salt-induced adverse effects, plants develop defense mechanisms that include the up-regulation of synthesis of GSH that has essential roles within the plant metabolism in reducing the adverse effects of salinity stress Nazar *et al.,* (2011). GSH is a low-molecular weight S metabolite (thiol), nonenzymic antioxidant found in most of the cells. Synthesis of GSH is well regulated by S in a demand driven manner. Sulfate withdrawal from the growing medium decreases the levels of sulfate, Cys and GSH in plants leading to the up-regulation of sulfate transport systems and key enzymes of S assimilatory pathway Lappartient and Touraine, (1996). It has been observed that increases in GSH synthesis are associated with up-regulation of the Cys synthesis. Similarly, S assimilation pathway enzymes have been found to be involved in the regulation of GSH synthesis. Queval *et al.,* (2009) reported that GSH accumulation was triggered by stress that resulted in the up-regulation of APR and SAT. Regulation of the GSH synthesis is dependent on the cell compartmentation as mitochondrial SAT is able to make major contribution to Cys synthesis under optimal conditions Haas *et al.,* (2008), Watanabe, *et al.,* (2008) whereas, the SAT in chloroplast was strongly induced during H_2O_2 triggered accumulation of GSH Queval *et al.,* (2009). Oxidation state of GSH homeostasis (GSH/GSSG) can maintain cellular redox of GSH in plant cells May *et al.,* (1998). The capacity of GSH to participate in the redox regulation in plant cells is, largely, dependent on its absolute concentration and the ratio of GSH/GSSG under salinity stress Nazar *et al.,* (2011); Khan *et al.,* (2012). The cellular GSH redox buffer present in cells forms major basis of redox homeostasis by which thiols proteins can maintain their redox state and can be reverted to their reduced form. Moreover, GSH is not only a redox buffer for cell, it also acts as an electron donor for scavenging of ROS in the major metabolic pathways of plants like photosynthesis, respiration or sulfate assimilation. Sensitivity of plants to salt plays a major role in the GSH-mediated tolerance. Recently, Nazar *et al.,* (2011) have shown that Vigna radiata cultivars differing in salt tolerance have different rate of GSH biosynthesis; the GSH content was higher in salt tolerant than salt sensitive cultivar. The salt sensitive cultivar showed greater oxidative damage than salt tolerant cultivar. A study on Lycopersicon esculentum has also shown that salt sensitive plants contained lesser GSH content and redox state than the salt tolerant plants Shalata *et al.,* (2001). Similar reports are also available in *Oryza sativa* Vaidyanathan *et al.,* (2003) and *Arachis hypogaea* Jain *et al.,* (2002). GSH biosynthesis and its turnover differed in salt tolerant *Lycopersicon esculentum* and its wild relative *Lycopersicon pennellii* Mittova *et al.,* (2003), and the salt tolerant plants were able to maintain favorable GSH/GSSG redox state within 15 days in response to salt stress. Wild type Brassica napus plants accumulated higher GSH upon salt stress suggesting its protective role against salt-induced oxidative damage, whereas transgenic plants did not show these antioxidative responses Ruiz and

Blumwald, (2002). In Nicotiana, tobacum transgenics overexpressing glyoxalase enzymes (NtglyI) and (NtglyII) either alone or together at 200 mM NaCl maintained higher GSH levels under salt stress. These plants showed enhanced basal activity of GSH and suffered minimal salinity stress induced oxidative damage measured as lipid peroxidation Yadav *et al.,* (2005) Fig. (58).

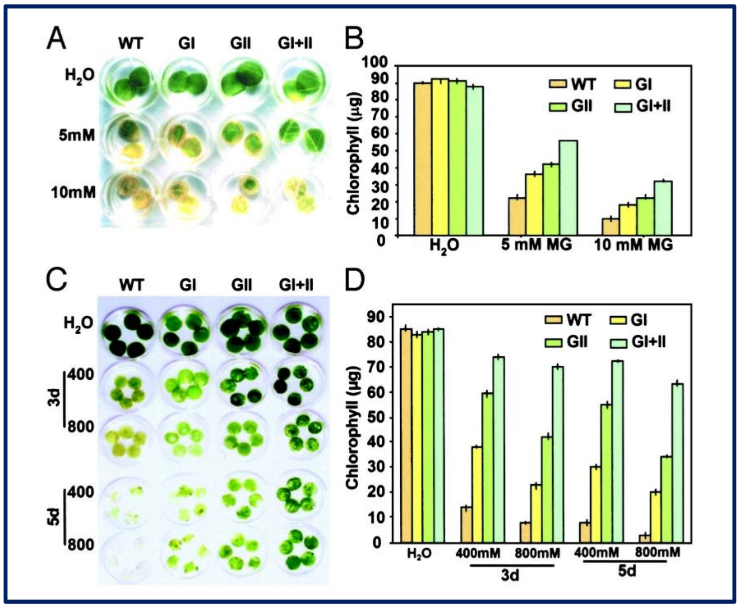


Fig. 58: Retardation of MG- and salt stress-promoted senescence in transgenic tobacco plants overexpressing either gly I (GI), gly II (GII), or both gly I and II in double transgenics (GIII), indicating the tolerance at cellular levels toward toxic levels of MG and salt. Phenotypic differences (A) and chlorophyll content (B) (gg of fresh weight) from MG-treated leaf discs of WT and various transgenic plants (GI, GII, and GIII) after incubation in 5 and 10 mM solutions of MG for 48 h are shown. Discs floated in water served as the experimental control. Phenotypic differences (C) and chlorophyll content (D) (g.g of fresh weight) from sodium chloride-treated leaf discs of WT and various transgenic plants (GI, GII, and GI+II) after incubation in 400 and 800 mM solutions of NaCl for 3 and 5 days are shown. Discs floated in water served as the experimental control. The standard deviation in each case is represented by the vertical bar in each graph (n = 3). Note the difference in retention of chlorophyll in WT and transgenic plants. After Singla-Pareek, (2003)

Singla-Pareek, (2003) reported that glyoxalase pathway involving glyoxalase I (gly I) and glyoxalase II (gly II) enzymes is required for glutathione-based detoxification of methylglyoxal. We had earlier indicated the potential of gly I as a probable candidate gene in conferring salinity tolerance. We report here that overexpression of gly I+ II together confers improved salinity tolerance, thus offering another effective strategy for manipulating stress tolerance in crop plants. We have overexpressed the gly II gene either alone in untransformed plants or with gly I transgenic background. Both types of these transgenic plants stably expressed the foreign protein, and the enzyme activity was higher. Compared with nontransformants, several independent gly II transgenic lines showed improved capability for tolerating exposure to high methylglyoxal and NaCl concentration and were able to grow, flower, and set normal viable seeds under continuous salinity stress conditions. Importantly, the double transgenic lines always showed a better response than either of the single gene-transformed lines and WT plants under salinity stress. Ionic measurements revealed higher accumulation of Na^+ and K^+ in old leaves and negligible accumulation of Na^+ in seeds of transgenic lines as compared with the WT plants. Comparison of various growth parameters and seed production demonstrated that there is hardly any yield penalty in the double transgenics under nonstress conditions and that these plants suffered only 5% loss in total productivity when grown in 200 mM NaCl. These findings establish the potential of manipulation of the glyoxalase pathway for increased salinity tolerance without affecting yield in crop plants.

In contrast, Jaleel *et al.,* (2007) reported that treatment of salinity at 80 mM concentration to Catharanthus roseus resulted in decreased GSH content when compared with control plants. A number of reports are available on the response of GSH to salt stress, but its mode of action in coping salt stress needs elaborative studies. The integrated knowledge on physiological, biochemical and molecular approaches may provide deeper insights towards the precise roles and mechanism of GSH involved in salt stress tolerance. Lipoic Acid Lipoic acid (LA) is derived from octanoic acid, contains two S atoms connected by a disulfide bond at C-6 and C-8 of its chemical structure and is soluble in both water and lipid phase. Its antioxidative property and protective nature, both in reduced form as dihydrolipoic acid (DHLA) and oxidised form as LA have been suggested Navari-Izzo *et al.,* (1988). Bast and Haenen, (1988) reported that DHLA can reduce GSH and can be a good tool for detoxification of ROS in a stressful environment. However, it can also have pro-oxidant properties by its iron-reducing ability and by its ability to generate S-containing radicals that can damage proteins Navari-Izzo *et al.,* (2002). Perez-Lopez *et al.,* (2010) have shown that the presence of LA in barley leaves occurred in the reduced as well as in oxidized forms under non-salinized and salinized conditions. They found that non-salinized conditions represent LA that was present mainly in reduced form i.e. DHLA and was partly involved in the tolerance of barley to elevated salinity. In the same report, the effects of salinity were mitigated and were correlated to a higher constitutive level of LA, which was believed to improve regeneration of DHA, and GSSG under salinity. Tarchoune *et al.,* (2013) explained the role of LA and DHLA in salinity tolerance in basil (Ocimum basilicum). They have shown that salt tolerance was dependent on cultivar and salt exposure time as adaptive response was associated with higher constitutive amounts of tocopherols with a maximum ability of roots to use DHLA to maintain growth-making basil tolerant to salinity. Glucosinolates are a class of secondary metabolites having S as integral part of its structure and mainly found in Brassica crops like oilseed rape, broccoli and cabbage. Although, physiological significance of glucosinolates in plants is not clear but it is assumed that glucosinolates has a role in plant-pathogen interaction Del *et al.,* (2013). Besides pathogen interaction, glucosinolates metabolism has role in tolerance of environmental factors including saline condition. Glucosinolates accumulation in response to environmental stress has been studied showing that some environmental factors can change the glucosinolates content and changes in the glucosinolate profile under stress is variable for plant adaptation. López-Berenguer *et al.,* (2008) showed the influence of salinity level for glucosinolates content and found that salinity level at 40 mM increased total glucosinolates content while it decreased at 80 mM concentration of salt stress suggesting that glucosinolates have potential to versatile role under salt stress. This variation in the glucosinolates content may be related to the developmental stage of plants Pang *et al.,* (2012). It has been suggested that increased glucosinolates was involved in osmotic adjustment and salt tolerance with low water potential in boroccoli plants López-Berenguer *et al.,* (2009). The glucoerucin (a type of glucosinolates) content in broccoli sprouts was increased by NaCl treatment whereas total glucosinolates reduced under salt stress. Salt treatment at 60 mmol/L for 5 d maintained higher biomass and comparatively higher content of glucosinolates in sprouts of broccoli Guo *et al.,* (2013). Allocation of glucosinolates could be one of the tolerance strategies to cope with stressful conditions with relative low energy cost. Bekaert *et al.,* (2012) has reported a direct allocation of glucosinolates production in Arabidopsis with an increase in photosynthetic energy. These all findings indicated that salt-induced increases in glucosinolates content may be involved in the salt stress response of plants but the effects of salinity on glucosinolates biosynthesis and metabolism need further attention at molecular and cellular levels.

Conclusions and Future prospects

Salinization of soils and water resources is likely to increase as global climate change continues. These natural resources are critical to crop food production and environmental and human health and thus further pressures and negative implications under salinization of agroecosystems are among the very realistic scenarios for the near future, Various preventive and proactive solutions have been applied over time in salt-stressed agroecosystems to improve plant nutrition.

- Some relatively new and modern approaches such as microbe–plant associations have been shown to be very effective in alleviating various agricultural constraints, including salt stress. Although in some cases, the full results are still unknown or contradictory (e.g., negative effects on some biota). Multidisciplinary approaches and solutions driven not only by plant and agri-environmental scientists, but also those from other areas (remote sensing, artificial intelligence, machine learning, big data analyses), can ensure very useful tools for detecting, protecting, and controlling salinization. A wide range of sustainable preventive and proactive (reclamation) approaches separately and/or in combination to improve plant salt resistance and crop nutrition under salt-affected conditions. The most applicative strategies are controlled water management over the applications of modern, low pressurized, and localized irrigation , and if necessary, surface/underground drainage systems . Both systems can help maintain salinized groundwater levels below the critical root zone level and leach concentrated salts from the rhizosphere.

- Salt-affected areas often overlap with water-stressed, organically depleted, and poorly structured sandy soils, which are knowingly compatible for implementation in land and water conservation practices and can additionally, underpin crop nutrition under saline conditions. Organic amendments promote the benefits of different organic amendments for plant growth particularly in saline/sodic soils creating the reduction of oxidative and osmotic stress. The selection of a sustainable reclamation technique and organic material is an extremely important factor for salinization management and mitigating salt stress in plants.
- Phytohormones might be a crucial metabolic engineering target for creating salt stress-tolerant crop plants; auxin can improve the growth performance in plants under salinity stress. Moreover, exogenous addition of salicylic acid can effectively increase endogenous auxin and abscisic acid content and improve the growth performance in salt-stressed , addition of jasmonic acid also seems to have the potential to alleviate salt-induced adverse impacts in plants.
- Microbial communities present in the rhizosphere are influenced by soil chemical conditions and plant interactions. It was confirmed that plant–micro symbiotic associations have crucial functions in plant nutrition, plant performance, resistance to biotic stresses, and adverse environmental conditions (nutrient imbalances, injuries by pathogens, soil acidity/alkalinity). Soil salinity (NaCl) could suppress certain plant–microbial associations and their population activity, and organic rhizodeposition. Metabolic profiles of the root, rhizosphere, and root exudates can be markedly compromised in response to NaCl exposure and can differ among plant cultivars. Confirmed antagonistic interrelations between soil salinity and microbial biomass C, resulting in a negative impact on microbe biomass /activity. Plant–microbe interrelations, notably with particular symbiotic-associated bacteria (e.g., N_2-fixing) and/or arbuscular mycorrhizal fungi (AMF), have been confirmed as up-and coming options for mitigating salt stress. N-fixing-associated bacteria (AB) groups, that act as plant growth promoters improving salinity tolerance by generating specific enzymes (e.g., 1-aminocyclopropane-1-carboxylate deaminase), metal-organic complexes (e.g., siderophores), and hormones, fixing atmospheric N_2 and solubilizing fewer mobile phosphates to more bioavailable forms.
- Arbuscular mycorrhizal fungi (AMF) belong to the phylum Glomeromycotan, one of the most important groups of soil microbes that can establish symbiotic inoculation with the roots of over 80% of terrestrial plant species. Occurring microbiota of saline soils and multiple beneficial implications for symbiotic associated glyco/halophytic species were confirmed in different study types. AMF such as Glomus claroideum, Glomus intraradices, Glomus macrocarpum, Glomus mosseae, Paraglomus occultum, and Rhizophagus intraradices in associated plant species with Olive, acacia and citrus trees, corn, Sesbania aegyptiaca can mitigate salt stress. Enhancing plant growth over improvement of water absorption capacity, nutrient acquisition and uptake, accumulation of different osmoregulator (proline, betaines, and polyamines, antioxidants) to adjust cell osmopotential, physiological processes and molecular performance.
- Foliar-stabilized silicic acid can be classified as a biostimulants and has been shown to be very efficient against abiotic and biotic stresses, which deserves much more attention in the future study.
- Effect of Si on the expression of SOS and HTK genes. However, the detailed regulatory mechanisms of Si on SOS signaling pathways and possible interaction between Si and other salt stress sensors remain obscure. Si transporters belong to the NIP sub-family of the aquaporin family.

References

Abass, M., and P.C. Morris, 2013. The *Hordeum vulgare* signalling protein MAP. kinase 4 is a regulator of biotic and abiotic stress responses. J. Plant Physiol., 170: 1353-1359.

Abbas, T., R.M. Balal, M.A. Shahid, M.A. Pervez, C.M. Ayyub, M.A. Aqueel, and M.M. Javaid, 2015. Silicon-induced alleviation of NaCl toxicity in okra (Abelmoschus esculentus. is associated with enhanced photosynthesis, osmoprotectants and antioxidant metabolism. Acta Physiol. Plant, 37, 6. [CrossRef]

Abbasi, F.M., and S. Komatsu, 2004. A. proteomic approach to analyze salt responsive proteins in rice leaf sheath. Proteomics, 4:2072–2081.

Abdallah, M.M., Z.A. Abdelgawad and H.S.M. El-Bassiouny 2016. Alleviation of the adverse effects of salinity stress by trehalose two rice varieties. South Africa Journal of Botany, 103: 275-282.

Abd-Elbar, O.H., R.E. Farag, S.S. Eisa, and S.A. Habib, 2012. Morpho-anatomical changes in salt stressed Kallar grass (*Leptochloa fusca* L. Kunth. Res. J. Agric. Biol. Sci., 8: 158–166.

Abdel-Haliem, M.E.F., H.S. Hegazy, N.S. Hassan, and D.M. Naguib, 2017. Effect of silica ions and nano silica on rice plants under salinity stress. Ecol. Eng., 99: 282–289. [CrossRef]

Abdelly, C., A. Debez, A. Samoui, and C. Grignon, 2011. Halophyte-fodder species association may improve nutrient availability and biomass production of the Sabkha ecosystem. In: Öztürk M. *et al.,* (eds) Sabkha ecosystems, tasks for vegetation science. Springer, D. ordrecht, the Netherlands, 85–94.

Abdelly, C., Z. Barhoumi, T. Ghanya, A. Debez, K. Ben Hamed, N. Sleimi, Z. Ouerghi, A. Smaoui, B. Huchzermeyer, and C. Grignon, 2006. Potential utilization of halophytes for the rehabilitation and valorization of salt-affected areas in Tunisia. In: Öztürk M, Waisel Y, K.han MA, Görk G. (eds) Biosaline agriculture and salinity tolerance in plants. Birkhäuser Verlag, Basel

Abdoli, S., K. Ghassemi-Golezani, and S. Alizadeh-Salteh, 2020. Responses of ajowan (*Trachyspermum ammi* L). to exogenous salicylic acid and iron oxide nanoparticles under salt stress. Environ. Sci. Pollut. Res. 27: 36939–36953.

Abdullah, Z., M.A. Khan, and T.J. Flowers 2001. Causes of sterility in seed set of rice under salinity stress. J. Agron. Crop Sci., 167:25–32.

Abebe, T., A.C. Guenzi, B. Martin, and J.C. Cushman 2003. Tolerance of mannitol-accumulating transgenic wheat to water stress and salinity. Plant Physiol., 131:1748–1755.

Abedi, T., A. Alemzadeh and S.A. Kazemeini, 2011. Wheat yield and grain protein response to nitrogen amount and timing. Australian Journal of Crop Science, 5 (3): 330-336.

Abrah´am, E., I.P. Salam´o, C. Koncz, and L. Szabados, 2011. “Identification of Arabidopsis and Thellungiella genes involved in salt tolerance by novel genetic system,” Acta Biologica Szegediensis, 55(1): 53–57.

Agarie S., N. Hanaoka, O. Ueno *et al.,* 1998. “Effects of silicon on tolerance to water deficit and heat stress in rice plants (*Oryza sativa* L)., monitored by electrolyte leakage,” Plant Production Science, 1(2): 96–103.

Agarwal S. and R. Shaheen, 2007. “Stimulation of antioxidant system and lipid peroxidation by abiotic stresses in leaves of Momordica charantia,” Brazilian Journal of Plant Physiology, 19(2): 149–161.

Agarwal, P.K., P.S. Shukla, K. Gupta, and B. Jha, 2013. Bioengineering for salinity tolerance in plants: state of the art. Mol. Biotechnol., 54:102–123.

Aghaei, K., A.A. Ehsanpour, and S. Komatsu, 2008. Proteome analysis of potato under salt stress. J. Proteome Res., 7:4858–4868.

Ahmad P. and S. Umar, 2011.Oxidative Stress: Role of Antioxidants in Plants, Studium Press, New Delhi, India.

Ahmad, H., S. Hayat, M. Ali, H. Liu, X. Chen, J. Li, *et al.,* 2020. The protective role of 28-homobrassinolide and glomus versiforme in cucumber to withstand saline stress. Plants, 9:42. doi: 10.3390/plants9010042

Ahmad, H., S. Hayat, M. Ali, T. Liu, and Z. Cheng, 2018. The combination of arbuscular mycorrhizal fungi inoculation (*Glomus versiforme*. and 28-homobrassinolide spraying intervals improves growth by enhancing photosynthesis, nutrient absorption, and antioxidant system in cucumber (Cucumis sativus L). under salinity. Ecol. E8: 5724–5740. doi: 10.1002/ece3.4112

Ahmad, P., A.A. Arafat, H. Abeer, F.A. Elsayed, G. Salih and P.T. Lam-Son 2016. Nitric Oxide Mitigates Salt Stress by Regulating Levels of Osmolytes and Antioxidant Enzymes in Chickpea, F. rontiers in Plant Science | www.frontiersin.org, 7: 347.

Ahmad, P., A.M. Abass, A.M. Nasser, L. Wijaya, P. Alam, and M. Ashraf, 2018. Mitigation of sodium chloride toxicity in *Solanum lycopersicum* L. by supplementation of jasmonic acid and nitric oxide. J. Plant Interact., 13: 64–72. [CrossRef]

Ahmad, P., and S. Sharma, 2008. Salt stress and phyto-biochemical responses of plants. Plant Soil Environ., 54:89–99.

Ahmad, P., C.A. Jaleel, and S. Sharma, 2010b. Antioxidative defence system, lipid peroxidation, prolinemetabolizing enzymes and biochemical activity in two genotypes of *Morus alba* L. subjectedto NaCl stress. Russ. J. Plant Physiol., 57:509–517.

Ahmad, P., C.A. Jaleel, M.A. Salem, G. Nabi, and S. Sharma, 2010a. Roles of enzymatic and non-enzymaticantioxidants in plants during abiotic stress. Crit. Rev. Biotechnol., 30:161–175.

Ahmad, P., C.A. Jeleel, M.M. Azooz, and G. Nabi, 2009. Generation of ROS. and non-enzymatic antioxidants during abiotic stress in Plants. Bot. Res. Intern., 2:11–20.

Ahmad, P., G. Nabi, and M. Ashraf, 2011. Cadmium-induced oxidative damage in mustard [Brassica juncea(L). Czern.& Coss.] plants can be alleviated by salicylic acid. South Afr. J. Bot., 77:36–44

Ahmad, P., K.R. Hakeem, A. Kumar, M. Ashraf, and N.A. Akram, 2012. Salt induced changes in photosyntheticactivity and oxidative defense system of three cultivars of mustard (Brassica juncea L). Afr. J. Biotechnol., 11:2694–2703.

Ahmad, R., C.J. Lim, and S.-Y. Kwon, 2013. "Glycine betaine: a versatile compound with great potential for gene pyramiding to improve crop plant performance against environmental stresses," Plant Biotechnology Reports, 7: 49–57.

Akbarimoghaddam, H., M. Galavi, A. Ghanbari, and N. Panjehkeh, 2011. Salinity effects on seed germination and seedling growth of bread wheat cultivars. Trakia, J. Sci., 9:43–50.

Akram, M., S. Akhtar, I. Javed, A. Wahid, and R. Rasul, 2002. Anatomical attributes of different wheat (*Triticum aestivum*. accessions/varieties to NaCl salinity. Int. J. Agric. Biol., 4, 166–168.

Akram, N.A., and M. Ashraf, 2011. Improvement in growth, chlorophyll pigments and photosynthetic performance in salt-stressed plants of sunflower (Helianthus animus L). by foliar application of 5-aminolevulinic acid. Agrochimica Pica, 55: 94–104.

Akram, N.A., M. Iqbal, A. Muhammad, M. Ashraf, F. Al-Qurainy, and S. Shafiq, 2018. Aminolevulinic acid and nitric oxide regulate oxidative defense and secondary metabolisms in canola (Brassica napus L). under drought stress. Protoplasma, 255: 163–174. [CrossRef] [PubMed]

Alam, P., A. Mohammed, A.A. Abdulaziz, A.A. Maged, and A. Thamer, 2022. Silicon Nanoparticle-Induced Regulation of Carbohydrate Metabolism, Photosynthesis, A.lam and ROS. Homeostasis in Solanum lycopersicum Subjected to Salinity Stress, A.CS. Omega, 7: 31834−31844

Alamgir A.N.M. and M. Yousuf Ali, 1999. "Effect of salinity on leaf pigments, sugar and protein concentrations and chloroplast ATPase activity of rice (*Oryza sativa* L).," Bangladesh Journal of Botany, 28(2): 145–149.

Alamri, S., Y. Hu, S. Mukherjee, T. Aftab, S. Fahad, and A. Raza, 2020. Silicon induced postponement of leaf senescence is accompanied by modulation of antioxidative defense and ion homeostasis in mustard (Brassica juncea. seedlings exposed to salinity and drought stress. Plant Physiol. Biochem. 157: 47–59. Doi: 10.1016/j.plaphy.2020.09.038

Alc´azar, R., F. Marco, J.C. Cuevas, *et al.,* 2006. "Involvement of polyamines in plant response to abiotic stress," Biotechnology Letters, 28(23): 1867–1876.

Alc´azar, R., J. C. Cuevas, J. Planas, *et al.,* 2011. "Integration of polyamines in the cold acclimation response," Plant Science, 180(1):31–38.

Alc´azar, R., J. Planas, T. Saxena, *et al.,* 2010. "Putrescine accumulation confers drought tolerance in transgenic Arabidopsis plants overexpressing the homologous Arginine decarboxylase 2 gene," Plant Physiology and Biochemistry, 48(7): 547–552.

Alcázar, R., T. Altabella, F. Marco, C. Bortolotti, M. Reymond, *et al.,* 2010. Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. Planta, 231: 1237-1249.

Aldesuquy, H., Z. Baka, and B. Mickky, 2014. Kinetin and spermine-mediated induction of salt tolerance in wheat plants: Leaf area, photosynthesis and chloroplast ultrastructure of flag leaf at ear emergence. Egypt. J. Basic Appl. Sci., 1: 77–87. [CrossRef]

Alet, A.I., D.H. S´anchez, J.C. Cuevas *et al.,* 2012. "New insights into the role of spermine in Arabidopsis thaliana under long-term salt stress," Plant Science, 182(1): 94–100.

Alharby, H.F., E.M.R. Metwali, M.P. Fuller, and A.Y. Aldhebiani, 2016. Impact of application of zinc oxide nanoparticles on callus induction, plant regeneration, element content and antioxidant enzyme activity in tomato (*Solanum lycopersicum* MilL). under salt stress. Arch. Biol. Sci., 68(4):723–735.

Ali, A., M. Mageed, I. Ahmed and S. Mariey, 2007. Genetic and molecular studies on barley salt tolerance. Afr. Crop Sci. Conf. Proc., 8: 669–682.

Ali, S., A. Mehmood, and N. Khan, 2021. Uptake, translocation, and consequences of nanomaterials on plant growth and stress adaptation. J. Nanomater, 1–17.

Allakhverdiev S. I., A. Sakamoto, Y. Nishiyama, M. Inaba, and N. Murata, 2000. “Ionic and osmotic effects of NaCl-induced inactivation of photosystems I. and II. Synechococcus sp.,” Plant Physiology, 123(3):1047–1056.

Allakhverdiev, S.I., A. Sakamoto, Y. Nishiyama, M. Inaba, and N. Murata, 2000. Ionic and osmotic effects of NaCl-induced inactivation of photosystems I. and II. in Synechococcus sp. Plant Physiol., 123:1047–1056.

Almutairi, Z.M., 2016a. Influence of silver nano-particles on the salt resistance of tomato (*Solanum lycopersicum* L). during germination. Int. J. Agri. Biol., 18(2):449–457. https://doi.org/10.17957/ IJAB/15.0114

Almutairi, Z.M., 2016b. Effect of nano-silicon application on the expression of salt tolerance genes in germinating tomato (*Solanum lycopersicum* L). seedlings under salt stress. Plant Omics Journal, 9(1):106–114.

Alvarez, S., E.L. Marsh, S.G. Schroeder, and D.P. Schachtman, 2008. Metabolomic and proteomic changes in the xylem sap of maize under drought. Plant Cell Environ., 31:325–340

Alvez, F.J.G., M. Baghour, G. Hao, O. Cagnac, M.P. Rodr´ıguez- Rosales, and K. Venema, 2012. “Expression of LeNHX. isoforms in response to salt stress in salt sensitive and salt tolerant tomato species,” Plant Physiology and Biochemistry, 51: 109–115.

Aly-Salama, K.H. and M.M. Al-Mutawa, 2009. “Glutathione-triggered mitigation in salt-induced alterations in plasmalemma of onion epidermal cells,” International Journal of Agriculture and Biology, 11(5): 639–642.

Amina, I., R. Saiema, A.M. Mudasir, W. Wasia, Z.M. Khalid, and A. Parvaiz, 2021. Ion homeostasis for salinity tolerance in plants: a molecular approach, Physiologia Plantarum, 171: 578–594. Scandinavian Plant Physiology Society, I.SSN. 0031-9317

Amir, R., 2010. Current understanding of the factors regulating methionine content in vegetative tissues of higher plants. Amino Acids, 39: 917-931.

Amirjani, M.R., 2011. Effect of salinity stress on growth, sugar content, pigments and enzyme activity of rice. Int. J. Bot., 7:73–81.

An, J., P. Hu, F. Li, H. Wu, Y. Shen, J.C. White, X. Tian, Z. Li, and J.P. Giraldo, 2020. Emerging investigator series: molecular mechanisms of plant salinity stress tolerance improvement by seed priming with cerium oxide nanoparticles. Environ. Sci. Nano, 7: 2214–2228.

Apel, K., and H. Hirt, 2004. Reactive oxygen species: metabolism, oxidative stress and signal transduction. Annu. Rev. Plant Biol., 55:373–399.

Apse, M.P., G.S. Aharon, W.A. Snedden, and E. Blumwald, 1999. Salt tolerance conferred by over-expression of a vacuolar Naþ/Hþ antiport in Arabidopsis. Science, 285:1256–1258.

Arafa, A.A., M.A. Khafagy, and M.F. El-Banna, 2009. The effect of glycinebetaine or ascorbic acid on grain germination and leaf structure of sorghum plants grown under salinity stress. Aust. J. Crop. Sci., 3:294–304.

Arenas-Huertero, C., B. Pérez, F. Rabanal, D. Blanco-Melo, C. De la Rosa, G. Estrada-Navarrete, F. Sanchez, A. Covarrubias, and J. Reyes, 2009. Conserved and novel miRNAs in the legume Phaseolus vulgaris in response to stress. Plant Mol. Biol., 70:385–401

Arfan, M., H.R. Athar, and M. Ashraf, 2007. Does exogenous application of salicylic acid through the rooting medium modulate growth and photosynthetic capacity in two differently adapted spring wheat cultivars under salt stress? J. Plant Physiol. 164, 685–694. doi: 10.1016/j.jplph.2006.05.010

Arif, Y., P. Singh, H. Siddiqui, A. Bajguz, and S. Hayat, 2020. Salinity induced physiological and biochemical changes in plants: an omic approach towards salt stress tolerance. In: Plant Physiology and Biochemistry, 156: 64–77.

Arnon, D.I. and P.R. Stout, 1939. “The essentiality of certain elements in minute quantity for plants with special reference to copper,” Plant Physiology, 14(2):371–375.

Aroca, R., R. Porcel, and J.M. Ruiz-Lozano, 2011. Regulation of root water uptake under abiotic stress conditions. J. Exp. Bot., 63, 43–57. [CrossRef] [PubMed]

Asada, K., 1994. Production and action of active oxygen species in photosynthetic tissue. In: Foyer CH, M.ullineaux PM. (eds) Causes of photooxidative stress and amelioration of defense systems in plants. CRC. Press, Boca Raton, 77–104.

Asada, K., 1999. "The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons," Annual Review of Plant Biology, 50: 601–639.

Asha, A.B., and R. Narain, 2020. Chapter 15 - Nanomaterials properties. In: Narain, R. (ed.), Polymer Science and Nanotechnology. Elsevier, 343–359.

Ashraf, M. and M.R. Foolad, 2007. "Roles of glycine betaine and proline in improving plant abiotic stress resistance," Environmental and Experimental Botany, 59(2): 206–216.

Ashraf, M. and P.J.C. Harris, 2004. Potential biochemical indicators of salinity tolerance in plants. Plant Sci., 166: 3- 16.

Ashraf, M., 2009. Biotechnological approach of improving plant salt tolerance using antioxidants as markers. Biotechnol. Adv., 27: 84-93.

Ashraf, M., and Q. Ali, 2008. Relative membrane permeability and activities of some antioxidant enzymes as the key determinants of salt tolerance in canola (*Brassica napus* L). Environ. Exp. Bot., 63: 266–273. doi: 10.1016/j.envexpbot.2007.11.008

Ashraf, M., and R. Sultana, 2000. Combination effect of NaCl salinity and nitrogen form on mineral composition of sunflower plants. Biol. Plant. 43: 615–619. doi: 10.1023/A:1002860202032 doi: 10.1105/tpc.109.210313

Ashraf, M., N.A. Akram, R.N. Arteca, and M.R. Foolad, 2010. "The physiological, biochemical and molecular roles of brassinosteroids and salicylic acid in plant processes and salt tolerance," Critical Reviews in Plant Sciences, 29(3): 162–190.

Askari, H., J. Edqvist, M. Hajheidari, M. Kafi, and G.H. Salekdeh, 2006. Effects of salinity levels onproteome of Suaeda aegyptiaca leaves. Proteomics, 6:2542–2554.

Askari-Khorasgani, O., S. Emadi, F. Mortazaienezhad, and M. Pessarakli, 2017. Differential responses of three chamomile genotypes to salinity stress with respect to physiological, morphological, and phytochemical characteristics. J. Plant Nutr., 40(18):2619–2630.

Askary, M., S.M. Talebi, F. Amini, and A.D.B. Bangan, 2016. Effect of NaCl and iron oxide nanoparticles on Mentha piperita essential oil composition. Environ. Exp. Biol., 14:27–32. https://doi. org/10.22364/eeb.14.05

Aslani, F., S. Bagheri, N. Muhd Julkapli, A.S. Juraimi, F.S.G. Hashemi, and A. Baghdadi, 2014. Effects of engineered nanomaterials on plants growth: an overview. Sci. World J., 641759.

Assaha D.V.M., U. Akihiro, S. Hirofumi, A. Rashid and W.Y. Mahmoud, 2017. The Role of Na+ and K+ Transporters in Salt Stress Adaptation in Glycophytes, Frontiers in Physiology | www.frontiersin.org, 8: 509.

Astolfi S, and S. Zuchi 2013. Adequate S. supply protects barley plants from adverse effects of salinity stress by increasing thiol contents. Acta Physiol Plant, 35: 175-181.

Aziz, A., M. Ashraf, S. Sikandar, M. Asif, N. Akhtar, S.M. Shahzad, and B.H. Babar, 2019. Optimizing sulfur for improving salt tolerance of sunflower Helianthus annuus L. Soil Environ., 38: 222–233. [CrossRef]

Bae, M.J., Y.S. Kim, I.S. Kim, Y.H. Choe, E.J. Lee, Y.H. Kim, H.M. Park, and H.S. Yoon, 2013. Transgenic rice overexpressing the Brassica juncea gamma-glutamyl cysteine synthetase gene enhances tolerance to abiotic stress and improves grain yield under paddy field conditions. Mol Breeding, 31: 931-945.

Baea, H., E. Herman, B. Bailey, H.J. Bae, and R. Sicher, 2005. Exogenous trehalose alters Arabidopsis transcripts involved in cell wall modification, abiotic stress, nitrogen metabolism, and plant defense. Physiol. Plant, 125:114–126

Bajgu, A., 2014. "Nitric oxide: role in plants under abiotic stress," in Physiological Mechanisms and Adaptation Strategies in Plants Under Changing Environment, 137–159, Springer.

Balestrazzi, A., C. Massimo, M. Anca, D. Mattia, and C. Daniela, 2011. Genotoxic stress and DNA. repair in plants: emerging functions and tools for improving crop productivity, Plant Cell Rep., 30:287–295 DOI. 10.1007/s00299-010-0975-9

Ballif, B.A., and J. Blenis, 2001. Molecular mechanisms mediating mammalian mitogen-activatedprotein kinase (MAPK. kinase (MEK. -MAPK. cell survival signals. Cell Growth Differ, 12:397–408

Balmer, Y., W.H. Vensel, C.K. Tanaka, W.J. Hurkman, E. Gelhaye, N. Rouhier, J.-P. Jacquot, W. Manieri, P. Schurmann, and M. Droux, 2004. Thioredoxin links redox to the regulation of fundamental processes of plant mitochondria. Proc Natl Acad Sci USA., 101:2642–2647. PMID: 14983062. Doi: 10.1073/ pnas.0308583101.

Bandehagh, A., G.H. Salekdeh, M. Toorchi, A. Mohammadi, and S. Komatsu 2011. Comparative proteomic analysis of canola leaves under salinity stress. Proteomics 11:1965–1975

Bar, Y., A. Apelbaum, U. Fi Kafka, and R. Goren 1997. Relationship between chloride and nitrate and its effect on growth and mineral composition of avocado and citrus plants. J. Plant Nutr., 20:715–731.

Barkla, B.J., R. Vera-Estrella, M. Hernandez-Coronado, and O. Pantoja, 2009. Quantitative proteomics of the tonoplast reveals a role for glycolytic enzymes in salt tolerance. Plant Cell, 21:4044–4058

Barrag´an V., E.O. Leidi, Z. Andr´es, *et al.,* 2012. “Ion exchangers NHX1 and NHX2 mediate active potassium uptake into vacuoles to regulate cell turgor and stomatal function in Arabidopsis,” Plant Cell, 24(3): 1127–1142,

Barranco-Medina, S., T. Krell, L. Bernier-Villamor, F. Sevilla, J.J. Lázaro, and K.J. Dietz, 2008. Hexameric oligomerization of mitochondrial peroxiredoxin PrxIIF. and formation of an ultrahigh affinity complex with its electron donor thioredoxin Trx-o. J. Exp. Bot., 59:3259–3269. PMID: 18632730. doi:10.1093/jxb/ern177.

Barroso, C., J.M. Vega, and C. Gotor, 1995. A. new member of the cytosolic O-acetylserine(thiollyase gene family in Arabidopsis thaliana. FEBS. Lett., 363: 1-5.

Barroso, C., L.C. Romero, F.J. Cejudo, J.M. Vega, and C. Gotor, 1999. Salt-specific regulation of the cytosolic O-acetylserine(thiollyase gene from Arabidopsis thaliana is dependent on abscisic acid. Plant Mol. Biol., 40: 729-736.

Bashandy, T., L. Taconnat, J.P. Renou, Y. Meyer, and J.P. Reichheld, 2009. Accumulation of flavonoids in an ntra ntrb mutant leads to tolerance to UV-C. Mol Plant; 2:249–258. PMID: 19825611. doi:10.1093/mp/ssn065.

Bast, A., and G.R. Haenen 1988. Interplay between lipoic acid and glutathione in the protection against microsomal lipid peroxidation. Biochim. Biophys. Acta., 963: 558-561.

Battaglia, M., Y. Olvera-Carillo, A. Garciarrubio, and A.A. Covarrubias 2008. The enigmatic LEA. proteins and other hydrophilins. Plant Physiol., 148:6–24.

Beck, M., G. Komis, A. Ziemann, D. Menzel, and J. Samaj, 2011. Mitogenactivated protein kinase 4 is involved in the regulation ofmitotic and cytokinetic microtubule transitions in Arabidopsis thaliana. New Phytol., 189:1069–1083.

Beck, M., G. Komis, J. Muller, D. Menzel, and J. Samaj 2010. Arabidopsis homologs of nucleus- and phragmoplast-localized kinase 2 and 3 and mitogen-activated protein kinase 4 are essential for microtubule organization. Plant Cell, 22:755–771.

Begara-Morales, J.C., B. S´anchez-Calvo, M. Chaki, *et al.,* 2014. “Dual regulation of cytosolic scorbate peroxidase (APX. by tyrosine nitration and S-nitrosylation,” Journal of Experimental Botany, 65(2):527–538.

Bekaert, M., P.P. Edger, C.M. Hudson, J.C. Pires, and G.C. Conant, 2012. Metabolic and evolutionary costs of herbivory defense: systems biology of glucosinolate synthesis. New Phytol., 196: 596-605.

Belin, C., T. Bashandy, J. Cela, V. Delorme-Hinoux, C. Riondet, and J.P. Reichheld, 2015. A. comprehensive study of thiol reduction gene expression under stress conditions in Arabidopsis thaliana. Plant Cell Environ. 38:299–314. PMID: 24428628. Doi: 10.1111/ pce.12276.

Ben Ahmed, C., B. Ben Rouina, S. Sensoy, M. Boukhriss, and F. Ben Abdullah, 2010. “Exogenous proline effects on photosynthetic performance and antioxidant defense system of young olive tree,” Journal of Agricultural and Food Chemistry, 58(7):4216–4222.

Ben Hamed, K., C. Magné, and C. Abdelly, 2014. From Halophyte Research to Halophytes Farming, See discussions, stats, and author profiles for this publication.
https://www.researchgate.net/publication/274072817

Ben Youssef, R., J. Nahida, B. Nadia, A. Alfonso, M. Cristina, P.A. Francisco and A. Chedly, 2021. The Efficiency of Different Priming Agents for Improving Germination and Early Seedling Growth of Local Tunisian Barley under Salinity Stress, Plant s, 10, 2264. https://doi.org/10.3390/plants10112264

Benzon, H.R.L., M.R.U. Rubenecia, V.U. Ultra, and S.C. Lee 2015. Nano-fertilizer affects the growth, development, and chemical properties of rice. IJAAR, 7(1):105–117

Berkowitz, O., M. Wirtz, A. Wolf, J. Kuhlmann, and R. Hell 2002. Use of biomolecular interaction analysis to elucidate the regulatory mechanism of the cysteine synthase complex from Arabidopsis thaliana. J. Biol. Chem., 277: 30629-30634.

Bhandal, I.S., and C.P. Malik, 1988. Potassium estimation, uptake, and its role in the physiology and metabolism of flowering plants. Int. Rev. Cytol., 110:205–254.

Binzel M.L., F.D. Hess, R.A. Bressan, and P.M. Hasegawa, 1988. "Intracellular compartmentation of ions in salt adapted tobacco cells," Plant Physiology, 86:607–614.

Blaha, G., U. Stelzl, C.M. Spahn, R.K. Agrawal, J. Frank, and K.H. Nierhaus, 2000. Preparation of functional ribosomal complexes and effect of buffer conditions on tRNA. positions observed by cryoelectron microscopy. Methods Enzymol., 317:292–309

Blumwald, E., 2000. Sodium transport and salt tolerance in plants. Curr. Opin. Cell Biol., 12: 431–434. [CrossRef]

Bohnert H.J., D.E. Nelson, and R.G. Jensen, 1995. "Adaptations to environmental stresses," Plant Cell, 7(7):1099–1111.

Bordi, A., 2010. The influence of salt stress on seed germination, growth and yield of canola cultivars. Not. Bot. Horti. Agrobo., 38:128–133.

Bosnic, P., D. Bosnic, J. Jasnic, and M. Nikolic, 2018. Silicon mediates sodium transport and partitioning in maize under moderate salt stress. Environ. Exp. Bot., 155:681–687. [CrossRef]

Bouchereau A., A. Aziz, F. Larher, and J. Martin-Tanguy, 1999. "Polyamines and environmental challenges: recent development," Plant Science, 140(2):103–125,

Brumós, J., J.M. Colmenero-Flores, A. Conesa, P. Izquierdo, G. Sánchez, D.J. Iglesias, M.F. López-Climent, A. Gómez-Cadenas, and M. Talón, 2009. Membrane transporters and carbon metabolism implicated in chloride homeostasis differentiate salt stress responses in tolerant and sensitive citrus stocks. Funct. Integr. Genomics, 9:293–309

Buchanan, B.B., 2016. The path to thioredoxin and redox regulation in chloroplasts. Annu Rev Plant Biol., 67:1–24. PMID: 27128465. Doi: 10.1146/annurev-arplant-043015-111949.

Bugos, R.C., A.D. Hieber, and H.Y. Yamamoto, 1998. Xanthophyll cycle enzymes are members of the lipocalin family, the first identified from plants. J. Biol. Chem., 273:15321–15324.

Bybordi, A., 2014 Influence of exogenous application of silicon and potassium on physiological responses, yield, and yield components of salt-stressed wheat. Commun. Soil Sci. Plan., 46: 109–122. [CrossRef]

Calderón, A., A. Ortiz-Espín, R. Iglesias-Fernández, and P. Carbonero, 2017. Redox Biology Thioredoxin (Trx o 1) interacts with proliferating cell nuclear antigen (PCNA) and its overexpression a ff ects the growth of tobacco cell culture. Redox Biol.; 11:688–700. PMID: 28183062. doi:10.1016/j.redox.2017.01.018.

Calderón, A., A. Sánchez-Guerrero, A. Ortiz-Espín, I. Martínez-Alcal á, D. Camejo, A. Jiménez, and F. Sevilla, 2018. Lack of mitochondrial thioredoxin o1 is compensated by antioxidant components under salinity in Arabidopsis thaliana plants. Physiol Plant., 164:251–267. PMID: 29446456. doi:10.1111/ppl.12708.

Campo, S., P. Baldrich, J. Messeguer, E. Lalanne, M. Coca, and B.S. Segundo, 2014. Overexpression of a calcium-dependent protein kinase confers salt and drought tolerance in rice by preventing membrane lipid peroxidation. Plant Physiol doi:10.1104/pp.113. 230268.

Cao, Y.R., S.Y. Chen, and J.S. Zhang, 2008. Ethylene signaling regulates salt stress response: An overview. Plant Signal Behav., 3: 761-763.

Cao, Z., L. Rossi, C. Stowers, W. Zhang, L. Lombardini, and X. Ma, 2017. The impact of cerium oxide nanoparticles on the physiology of soybean (Glycine max (L). Merr. under different soil moisture conditions. Environ Sci. Pollut. Res. Int., 25(1):930–939. https://doi.org/10.1007/s11356-017-0501-5

Carpıcı, E.B., N. Celık, and G. Bayram, 2009. Effects of salt stress on germination of somemaize (Zea mays L). cultivars Afr. J. Biotechnol., 8:4918– 4922

Chai Y.Y., C.D. Jiang, L. Shi, T.S. Shi, and W.B. Gu, 2010. "Effects of exogenous spermine on sweet sorghum during germination under salinity," Biologia Plantarum, 54(1):145–148.

Chakraborty, K., R.K. Sairam, and R.C. Bhattacharya, 2012. Differential expression of salt overly sensitive pathway genes determines salinity stress tolerance in Brassica genotypes. Plant Physiol. Biochem., 51:90–101

Chattopadhyay, A., P. Subba, A. Pandey, D. Bhushan, R. Kumar, A. Datta, S. Chakraborty, and N. Chakraborty, 2011. Analysis of the grasspea proteome and identification of stress-responsive proteins upon exposure to high salinity, low temperature, and abscisic acid treatment. Phytochemistry, 72:1293–1307.

Cha-Um, S. and C. Kirdmanee, 2010. "Effect of glycinebetaine on proline, water use, and photosynthetic efficiencies, and growth of rice seedlings under salt stress," Turkish Journal of Agriculture and Forestry, 34(6):517–527.

Chaves, M.M., J. Flexas, and C. Pinheiro, 2008. Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. Ann. Bot.-London, 103: 551–560. [CrossRef]

Chaves, M.M., J.P. Maroco, J.S. Pereira, 2003. Understanding plant responses to drought-from genes to the whole plant. Funct. Plant Biol., 30:239–264.

Che, P., L.M. Weaver, E.S. Wurtele, and B.J. Nikolau, 2003. The role of biotin in regulating 3-methylcrotonyl-coenzyme a carboxylase expression in Arabidopsis. Plant Physiol., 131: 1479-1486.

Cheeseman, J.M., 1988. Mechanism of salinity tolerance in plants. Plant Physiol., 87:547–550.

Chen S., J. Li, S. Wang, A. H¨uttermann, and A. Altman, 2001. "Salt, nutrient uptake and transport, and ABA. of Populus euphratica; a hybrid in response to increasing soil NaCl," Trees—Structure and Function, 15(3):186–194.

Chen, D., L. Yin, X. Deng, S. Wang, 2014. Silicon increases salt tolerance by influencing the two-phase growth response to salinity in wheat (Triticum aestivum L). Acta Physiol. Plant., 36, 2531–2535. [CrossRef]

Chen, M.-X., S.-C. Lung, Z.-Y. Du, and M.-L. Chye, 2014. Engineering plants to tolerate abiotic stresses. Biocatalysis and agricultural biotechnology, 3:81–87.

Chen, S., N. Gollop, and B. Heuer, 2009. Proteomic analysis of salt-stressed tomato (Solanum lycopersicum. seedlings: effect of genotype and exogenous application of glycine betaine. J. Exp. Bot., 60: 2005–2019.

Chen, W., X. Yao, K. Cai, and J. Chen, 2011. Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. Biol. Trace Element Res. 142, 67–76

Cheng, Y., Y. Qi, Q. Zhu, X. Chen, N. Wang, X. Zhao, H. Chen, X. Cui, L. Xu, and W. Zhang, 2009. New changes in the plasma-membrane-associated proteome of rice roots under salt stress. Proteomics, 9:3100–3114.

Chitteti, B., and Z. Peng, 2007. Proteome and phosphoproteome differential expression under salinity stress in rice (Oryza sativa. roots. J. Proteome Res., 6:1718–1727.

Choudhury, F.K., R.M. Rivero, E. Blumwald, and R. Mittler, 2017. Reactive oxygen species, abiotic stress and stress combination. Plant J., 90: 856–867. [CrossRef] [PubMed]

Chutipaijit, S., S. Cha-um, and K. Sompornpailin, 2011. High contents of proline and anthocyaninincrease protective response to salinity in Oryza sativa L. spp. indica. Aust. J. Crop Sci., 5:1191–1198

Ciftci-Yilmaz, S., M.R. Morsy, L. Song, A. Coutu, B.A. Krizek, M.W. Lewis, D. Warren, J. Cushman, E.L. Connolly, and R. Mittler, 2007. The EAR. motif of the Cys2/His2-typezinc finger protein Zat7 plays a key role in the defense response of Arabidopsis to salinity stress. J. Biol. Chem., 282:9260–9268.

Clause S.D. and J.M. Sasse, 1998. "Brassinosteroids: essential regulators of plant growth and development," Annual Review of Plant Biology, 49:427–451.

Colcombet, J., and H. Hirt, 2008. Arabidopsis MAPKs: a complex signalling network involved in multiple biological processes. Biochem. J., 413: 217–226.

Coleto, I., M. de la Peña, J. Rodríguez-Escalante, I. Bejarano, G. Glauser, P.M. Aparicio-Tejo, and D. Marino, 2017. Leaves play a central role in the adaptation of nitrogen and sulfur metabolism to ammonium nutrition in oilseed rape Brassica napus. BMC. Plant Biol., 17: 1–13. [CrossRef] [PubMed]

Colmenero-Flores, J.M., D.F.-N. Juan, C.-F. Paloma, P.-T. Procopio and A.R. Miguel, 2019. Chloride as a Beneficial Macronutrient in Higher Plants: New Roles and Regulation, I.nt. J. Mol. Sci., 20, 4686; doi: 10.3390/ijms20194686

Cona A., G. Rea, R. Angelini, R. Federico, and P. Tavladoraki, 2006. “Functions of amine oxidases in plant development and defence,” Trends in Plant Science, 11(2):80–88.

Conde, C., P. Silva, A. Agasse, R. Lemoine, S. Delrot, R. Tavares, and H. Geròs, 2007. Utilization and transport of mannitol in Olea europaea and implications for salt stress tolerance. Plant Cell Physiol., 48:42–53

Cooke, J., and M.R. Leishman, 2011. Is plant ecology more siliceous than we realize Trends Plant Sci. 16: 61–68.

Coskun, D., D.T. Britto, Y. Jean, L.M. Schulze, A. Becker, and H.J. Kronzucker, 2012. Silver ions disrupt K+ homeostasis and cellular integrity in intact barley (Hordeum vulgare L). roots. J. Exp. Bot., 63: 151–162. [CrossRef] [PubMed]

Coskun, D., R. Deshmukh, H. Sonah, J.G. Menzies, O. Reynolds, J.F. Ma, H.J. Kronzucker, and R.R. Belanger, 2019. The controversies of silicon’s role in plant biology. New Phytol., 221:67–85. [CrossRef]

Coucha, M., S.L. Elshaer, W.S. Eldahshaw, B.A. Mysona, and A.B. El-Remessy, 2015. Molecular mechanisms of diabetic retinopathy: Potential therapeutic targets. Middle East Afr J. Ophthalmol., 22(2):135–144. https://doi.org/10.4103/0974-9233. 154386

Crawford N.M., 2006. “Mechanisms for nitric oxide synthesis in plants,” Journal of Experimental Botany, 57(3):471– 478.

Da Fonseca-Pereira, P., D.M. Daloso, J. Gago, F.M.D.O. Silva, J.A. CondoriApfata, I. Florez-Sarasa, T. Tohge, J.-P. Reichheld, A. Nunes-Nesi, A.R. Fernie, and W.L. Araújo, 2019. The mitochondrial thioredoxin system contributes to the metabolic responses under drought episodes in arabidopsis. Plant Cell Physiol., 60:213–229. PMID: 30329109. 10. doi:10.1093/pcp/pcy194.

Da Fonseca-Pereira, P., M.D. Danilo, G. Jorge, N.-N. Adriano and L.A. Wagner, 2019. On the role of the plant mitochondrial thioredoxin system during abiotic stress, PLANT. SIGNALING. & BEHAVIOR. 2019, 14(6, e1592536 (5 pages. https://doi.org/10.1080/15592324.2019.1592536

Daloso, D.M., K. Müller, T. Obata, A. Florian, T. Tohge, A. Bottcher, C. Riondet, L. Bariat, F. Carrari, A. Nunes-Nesi, 2015. Thioredoxin, a master regulator of the tricarboxylic acid cycle in plant mitochondria. Proc. Natl. Acad. Sci., U.SA., 112:E1392–400. PMID: 25646482. doi:10.1073/pnas.1424840112.

Dang, Y.P., R.C. Dalal, D.G. Mayer, M. McDonald, R. Routely, G.D. Schwenke, S.R. Buck, I.G. Daniells, D.K. Singh, W. Manning, and N. Ferguson, 2008. High subsoil chloride concentrations reduce soil water extraction and crop yield on Vertisols in north-eastern Australia. Aust. J. Agric. Res., 59:321–330.

Dang, Y.P., R.C. Dalal, R. Routley, G.D. Schwenke, and I. Daniells, 2006. Subsoil constraints to grain production in the cropping soils of the northeastern region of Australia: an overview. Aust. J. Exp. Agric., 46:19–35.

Dani, V., W.J. Simon, M. Duranti, and R.R.D. Croy, 2005. Changes in the tobacco leaf apoplast proteome in response to salt stress. Proteomics, 5:737– 745

Dantas, B.F., R.L. De Sa, and C.A. Aragao, 2007. Germination, initial growth and cotyledon protein content of bean cultivars under salinity stress. Rev Bras de Sementes, 29:106–110

Das, P., I. Manna, A.K. Biswas, and M. Bandyopadhyay, 2018. Exogenous silicon alters ascorbate-glutathione cycle in two salt-stressed indica rice cultivars (MTU. 1010 and Nonabokra. Environ. Sci. Pollut. Res., 25: 26625–26642. [CrossRef]

Dassanayake, M., D.H. Oh, J.S. Haas, A. Hernandez, H. Hong, S. Ali, D.J. Yun, R.A. Bressan, J.K. Zhu, H.J. Bohnert, and J.M. Cheeseman, 2011. The genome of the extremophile crucifer Thellungiella parvula. Nat. Genet., 43:913–918.

Dawood, M.G., M.T. Abdelhamid, and U. Schmidhalter, 2014. Potassium fertiliser enhances the salt-tolerance of common bean (Phaseolus vulgaris L). J. Hortic. Sci. Biotechnol., 89: 185–192. [CrossRef]

De Lourdes Oliveira Otoch, M., A.C. Menezes Sobreira, M.E. Farias De Arag˜ao, E.G. Orellano, M. Da Guia Silva Lima, and D. FernandesDeMelo, 2001. "Saltmodulation of vacuolarH+-ATPase and H+-Pyrophosphatase activities in Vigna unguiculata," Journal of Plant Physiology, 158(5):545–551.

De Paola, D., F. Cattonaro, D. Pignone, and G. Sonnante, 2012. ThemiRNAome of globe artichoke: conserved and novel micro RNAs and target analysis. BMC. Genomics, 13:41.

De Souza Freitas, W.E., A.B. de Oliveira, R.O. Mesquita, H.H. de Carvalho, J.T. Prisco, and E. Gomes-Filho, 2019. Sulfur-induced salinity tolerance in lettuce is due to a better P. and K. uptake., lower Na/K. ratio and an efficient antioxidative defense system. Sci. Hortic. 257: 108764. [CrossRef]

Debona, D., F.A. Rodrigues, and L.E. Datno_, 2017. Silicon's role in abiotic and biotic plant stresses. Annu. Rev. Phytopathol., 55: 85–107. [CrossRef]

Debona, D., F.A. Rodrigues, and L.E. Datnoff, 2017. Silicon's role in abiotic and biotic plant stresses. Annu. Rev. Phytopathol., 55: 85–107

Deivanai, S., R. Xavier, V. Vinod, K. Timalata, and O.F. Lim, 2011. "Role of exogenous proline in ameliorating salt stress at early stage in two rice cultivars," Journal of Stress Physiology & Biochemistry, 7:157–174.

Del Carmen, M.-B.M., D.A. Moreno, and M. Carvajal 2013. The physiological importance of glucosinolates on plant response to abiotic stress in brassica. Int. J. Mol. Sci., 14: 11607-11625.

Delfani, M., M.B. Firouzabadi, N. Farrokhi, and H. Makarian, 2014.Some physiological responses of black-eyed pea to iron and magnesium nanofertilizers. Commun Soil Sci., Plant Anal., 45:530–540.

Delledonne M., Y. Xia, R. A. Dixon, and C. Lamb, 1998. "Nitric oxide functions as a signal in plant disease resistance," Nature, 394(6693):585–588.

Demetriou, G., C. Neonaki, E. Navakoudis, and K. Kotzabasis, 2007. Salt stress impact on the molecular structure and function of the photosynthetic apparatus—the protective role of polyamines. Biochim Biophys Acta-Bioenerget, 1767:272–280.

Desingh, R., and G. Kanagaraj, 2007. Influence of salinity stress on photosynthesis and antioxidative systems in two cotton varieties. Applied Plant Physiology, 33 (3– 4): 221–234.

Dietz, K.J., N. Tavakoli, C. Kluge *et al.,* 2001. "Significance of the Vtype ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level," Journal of Experimental Botany, 52(363):1969–1980.

Ding, D., L. Zhang, H. Wang, Z. Liu, Z. Zhang, and Y. Zheng, 2009. Differential expression of miRNAs in response to salt stress in maize roots. Ann. Bot., 103:29–38.

Dionisio-Sese, M.L., and S. Tobita 1998. Antioxidant responses of rice seedlings to salinity stress. Plant Sci., 135:1–9.

Djamei, A., A. Pitzschke, H. Nakagami, I. Rajh, and H. Hirt, 2007. Trojan horse strategy in Agrobacterium transformation: abusing MAPK. defense signaling. Science, 318:453–456

Dolan, L., and J. Davies, 2004. Cell expansion in roots. Curr. Opin. Plant Biol., 7: 33–39. [CrossRef]

Dolatabadian, A. and R.S. Jouneghani, 2009. Impact of Exogenous Ascorbic Acid on Antioxidant Activity and Some Physiological Traits of Common Bean Subjected to Salinity Stress, N.ot. Bot. Hort. Agrobot. Cluj., 37 (2): 165-172.

Dolatabadian, A., and R.J. Saleh Jouneghani, 2009. Impact of exogenous ascorbic acid on antioxidant activity and some physiological traits of common been subjected to salinity stress. Notulae Botanicae Horti Agrobotanici Cluj-Napoca, 37 (2): 165–172.

Dolatabadian, A., S.A.M. Modarressanavy, and F. Ghanati, 2011. Effect of salinity on growth, xylem structure and anatomical characteristics of soybean. Not. Sci. Biol., 3:41–45.

Dombrowski, J.E., J.C. Baldwin, and R.C. Martina, 2008. Cloning and characterization of a salt stress inducible small GTPase gene from the model grass species Lolium temulentum. J. Plant Physiol., 165:651– 661.

Dominguez-Solís, J.R., G. Gutierrez-Alcalá, J.M. Vega, L.C. Romero, and C. Gotor, 2001. The cytosolic O-acetylserine (thiollyase gene is regulated by heavy metals and can function in cadmium tolerance. J. Biol. Chem., 276: 9297-9302.

Domínguez-Solís, J.R., M.C. López-Martín, F.J. Ager, M.D. Ynsa, L.C. Romero, *et al.,* 2004. Increased cysteine availability is essential for cadmium tolerance and accumulation in Arabidopsis thaliana. Plant Biotechnol. J., 2: 469-476.

Dooki, A.D., F.J. Mayer-Posner, H. Askari, A.A. Zaiee, and G.H. Salekdeh, 2006. Proteomic responses of rice young panicles to salinity. Proteomics, 6: 6498–6507.

Droux, M., 2003. Plant serine acetyltransferase: new insights for regulation of sulphur metabolism in plant cells. Plant Physiol. Biochem., 41: 619-627.

Droux, M., 2004. Sulfur assimilation and the role of sulfur in plant metabolism: a survey. Photosynth Res 79: 331-348.

Droux, M., M.L. Ruffet, R. Douce, and D. Job, 1998. Interactions between serine acetyltransferase and O-acetylserine (thiol) lyase in higher plants--structural and kinetic properties of the free and bound enzymes. Eur. J. Biochem., 255: 235-245.

Duan J., J. Li, S. Guo, and Y. Kang, 2008. “Exogenous spermidine affects polyamine metabolism in salinity-stressed Cucumis sativus roots and enhances short-term salinity tolerance,” Journal of Plant Physiology, 165(15):1620–1635,

Dubchak, S., A. Ogar, J.W. Mietelski and K. Turnau, 2010. “Influence of silver and titanium nanoparticles on arbuscular mycorrhiza colonization and accumulation of radiocaesium in Helianthus annuus,” Span. J. Agric. Res., 8: s103–S108.

Eckardt, N.A., 2009. A. new chlorophyll degradation pathway. Plant Cell, 21:700.

El Sebai, T.N., M.M.S. Abdallah, H.M.S. El-Bassiouny, and F.M. Ibrahim 2016. Amelioration of The Adverse Effects of Salinity Stress by Using Compost, N.igella Sativa Extract or Ascorbic Acid in Quinoa Plants. International Journal of Pharm Tech Research. 9, (6): 127-144.

El-Bassiouny H.M.S., M.M.S. Abdallah, M.A.M. El-Enany, and M.Sh. Sadak, 2020. Nano-Zinc Oxide and Arbuscular mycorrhiza effects on physiological and biochemical aspects of wheat cultivars under saline conditions. Pakistan journal of biological sciences, 23 (4): 478-490.

El-Bassiouny, H.M.S. and M.Sh.S. Sadak, 2015. Impact of foliar application of ascorbic acid and α-tocopherol on antioxidant activity and some biochemical aspects of flax cultivars under salinity stress Acta Biologica Colombiana, 20(2):209-222

El-Mashad H. and I. A.A.A. Mohamed, 2012. “Brassinolide alleviates salt stress and increases antioxidant activity of cowpea plants (Vigna sinensis)” Protoplasma, 249(3):625–635.

El-Sharkawy, M.S., T.R. El-Beshsbeshy, E.K. Mahmoud, N.I. Abdelkader, R.M. Al-Shal, and A.M. Missaoui, 2017. Response of alfalfa under salt stress to the application of potassium sulfate nanoparticles. Am. J. Plant Sci., 8:1751–1773. https://doi.org/10.4236/ajps.2017.88120

El-Shintinawy, F., and M.N. El-Shourbagy, 2001. “Alleviation of changes in protein metabolism in NaCl-stressed wheat seedlings by thiamine,” Biologia Plantarum, 44(4):541–545,

El-Shintinawy, F., and M.N. El-Shourbagy, 2001. Alleviation of changes in protein metabolism in NaCl stressed wheat seed by thiamine. Biol. Plant, 44: 541-545.

Elstner, E.F., 1987. Metabolism of activated oxygen species. In: Davies DD. (ed.) The biochemistry of plants, vol II, B.iochemistry of metabolism. Academic, S.an Diego, 252–315

El-Tayeb, M.A., 2005. “Response of barley grains to the interactive effect of salinity and salicylic acid,” PlantGrowth Regulation, 45(3):215–224.

Etesami, H., and B.R. Jeong, 2018. Silicon (Si): review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants. Ecotoxicol. Environ. Saf., 147: 881–896.

Etesami, H., B.R. Jeong, and M. Rizwan, 2020. The use of silicon in stressed agriculture management: action mechanisms and future prospects. Metalloids in Plants: Advances and Future Prospects, 381–431.

Etesami, H., F. Hamideh, and R. Muhammad, 2021. Interactions of nanoparticles and salinity stress at physiological, biochemical and molecular levels in plants: A Review, E.cotoxicology and Environmental Safety 225 2021. 112769

Fancy, N.N., A.K. Bahlmann, and G.J. Loake, 2017. Nitric oxide functions in plant abiotic stress. Plant Cell Environ., 40: 462–472. [CrossRef] [PubMed]

FAO, 2009. High Level Expert Forum—How to Feed the World in 2050, E.conomic and Social Development, F.ood and Agricultural Organization of the United Nations, R.ome, I.taly.

Farooq, M., M. Hussain, A. Wakeel, and K.H.M. Siddique, 2015. Salt stress in maize: Effects, resistance mechanisms, and management. A Review. Agron. Sustain. Dev., 35: 461–481. [CrossRef]

Fatehi, F., A. Hosseinzadeh, H. Alizadeh, T. Brimavandi, and P.C. Struik, 2012. The proteome response of salt-resistant and salt-sensitive barley genotypes to long-term salinity stress. Mol. Biol. Rep., 39:6387–6397.

Fathi, A., M. Zahedi, and S. Torabian, 2017. Effect of interaction between salinity and nanoparticles (Fe2O3 and ZnO) on physiological parameters of Zea mays L. J. Plant Nutr., 40 (19):2745–2755. https://doi.org/10.1080/00103624.2013.863911

Fatma, M., A. Masood, T.S. Per, and N.A. Khan, 2016. Nitric oxide alleviates salt stress inhibited photosynthetic performance by interacting with sulfur assimilation in mustard. Front. Plant Sci., 7, 521. [CrossRef]

Fatma, M., A. Masood, T.S. Per, F. Rasheed, and N.A. Khan, 2016. Interplay between nitric oxide and sulfur assimilation in salt tolerance in plants. Crop J., 4: 153–161. [CrossRef]

Fatma, M., M. Asgher, A. Masood, and N.A. Khan, 2014.Excess sulfur supplementation improves photosynthesis and growth in mustard under salt stress through increased production of glutathione. Environ. Exp. Bot., 107: 55–63. [CrossRef]

Fatma, M., N. Iqbal, H. Gautam, Z. Sehar, A. Sofo, I. D'Ippolito, and N.A. Khan, 2021. Ethylene and sulfur coordinately modulate the antioxidant system and ABA. accumulation in mustard plants under salt stress. Plants, 10, 180. [CrossRef]

Fatma, M., N. Iqbal, H. Gautam, Z. Sehar, A. Sofo, I. D'Ippolito, and N.A. Khan, 2021. Ethylene and sulfur coordinately modulate the antioxidant system and ABA. accumulation in mustard plants under salt stress. Plants, 10, 180. [CrossRef]

Fatma, M., N. Iqbal, Z. Sehar, M.N. Alyemeni, P. Kaushik, N.A. Khan, and P. Ahmad, 2021. Methyl jasmonate protects the ps ii system by maintaining the stability of chloroplast d1 protein and accelerating enzymatic antioxidants in heat-stressed wheat plants. Antioxidants, 10, 1216. [CrossRef] [PubMed]

Fediuc, E., S.H. Lips, and L. Erdei, 2005. O-acetylserine (thiol) lyase activity in Phragmites and Typha plants under cadmium and NaCl stress conditions and the involvement of ABA. in the stress response. J. Plant Physiol., 162: 865-872.

Fernández-Torquemada, Y., and J.L. Sánchez-Lizaso, 2013. Effects of salinity on seed germination and early seedling growth of the Mediterranean seagrass Posidonia oceanica (L). Delile. Estuarine, C.oastal Shelf Sci., 119:64–70

Fernández-Trijueque, J., D. Barajas-López Jde, A. Chueca, R. Cazalis, M. Sahrawy, *et al.,* 2012. Plastid thioredoxins f and m are related to the developing and salinity response of post-germinating seeds of Pisum sativum. Plant Sci., 188- 189: 82-8.

Flam-Shepherd, R., W.Q. Huynh, D. Coskun, A.M. Hamam, D.T. Britto, and H.J. Kronzucker, 2018. Membrane fluxes, bypass flows, and sodium stress in rice: The influence of silicon. J. Exp. Bot., 69: 1679–1692. [CrossRef]

Fleck, A.T., S. Schulze, M. Hinrichs, A. Specht, F. Waßmann, L. Schreiber, and M.K. Schenk, 2015. Silicon promotes exodermal Casparian band formation in Si-accumulating and Si-excluding species by forming phenol complexes. PLoS. ONE, 10, e0138555. [CrossRef]

Fleck, A.T., T. Nye, C. Repenning, F. Stahl, M. Zahn, and M.K. Schenk, 2011. Silicon enhances suberization and lignification in roots of rice (Oryza sativa) J. Exp. Bot., 62, 2001–2011. [CrossRef] [PubMed]

Flexas, J., and H. Medrano, 2002. Drought-inhibition of photosynthesis in C3 Plants: stomatal and non-stomatal limitations Revisited. Ann Bot., 89:183–189. PMID: 12099349. doi:10.1093/aob/mcf027.

Flexas, J., J. Bota, J.M. Escalona, and B.M.H. Sampol, 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. Funct Plant Biol., 29: 461–471.

Flowers, T.J., 2004. "Improving crop salt tolerance," Journal of Experimental Botany, 55(396):307–319.

Flowers, T.J., M.A. Hajibagheri, and A.R. Yeo, 1991. Ion accumulation in the cell walls of rice plants growing under saline conditions: evidence for the Oertli hypothesis. Plant, C.ell and Environ 14:319–325.

Flowers, T.J., M.A. Hajibagheri, and N.J.W. Clipson, 1986. Halophytes. Quart. Rev. Biol., 61:313–337

Fluhr, R. and A.K. Mattoo, 1996. "Ethylene-biosynthesis and perception," Critical Reviews in Plant Sciences, 15:479–523,

Ford, C.W., 1984. "Accumulation of low molecular weight solutes in water-stressed tropical legumes," Phytochemistry, 23(5):1007–1015.

Foster, S.S.D. * and P.J. Chilton, 2003. Groundwater: the processes and global significance of aquifer degradation. Phil. Trans. R. Soc. Lond. B. 2003. 358,–1972 1957, 2003 The Royal Society DOI. 10.1098/rstb.2003.1380, Downloaded from rstb.royalsocietypublishing.org on July 13, 2011.

Foyer, C.H., H. Lopez-Delgado, J.F. Dat, and I.M. Scott, 1997. "Hydrogen peroxide- and glutathione-associated mechanisms of acclimatory stress tolerance and signalling," Physiologia Plantarum, 100(2):241–254.

Fragnire, C., M. Serrano, E. Abou-Mansour, J.-P. M´etraux, and F. L'Haridon, 2011. "Salicylic acid and its location in response to biotic and abiotic stress," FEBS. Letters, 585(12):1847–1852,

Franco-Navarro, J.D., J. Brumos, M.A. Rosales, P. Cubero-Font, M. Talon, and J.M. Colmenero-Flores, 2016. Chloride regulates leaf cell size and water relations in tobacco plants. J. Exp. Bot., 67: 873–891. [CrossRef] [PubMed]

Franco-Navarro, J.D., M.A. Rosales, R. Álvarez, P. Cubero-Font, P. Calvo, A. Díaz-Espejo, and J.M. Colmenero-Flores, 2019. Chloride as macronutrient increases water use efficiency by anatomically-driven reduced stomatal conductance and increased mesophyll diffusion to CO2 . Plant J., 99: 815–831.

Friedrich, W., 1987. Thiamin (Vitamin B1, aneurin) In: Handbuchder vitamine. (ed.) Urban, S.chwartzenberg, M.unich, 240-258.

Fukuda A. and Y. Tanaka, 2006. "Effects of ABA, auxin, and gibberellin on the expression of genes for vacuolar H+- inorganic pyrophosphatase,H+-ATPase subunitA, andNa+/H+ antiporter in barley," Plant Physiology and Biochemistry, 44(5-6):351–358.

Gabbay, K.H. 1973. The sorbitol pathway and the complications of diabetes. N. Engl J. Med. 288 (16):831–836.

Gabbay, K.H. 1975. Hyperglycemia, polyol metabolism and complications of diabetes mellitus. Ann Rev Med., 26:521–536.

Gadallah, M.A.A. 1999. Effects of proline and glycine betaine on Vicia faba response to salt stress. Biol Plant 42:249–257

Gain, P., M.A. Mannan, P.S. Pal, M.M. Hossain, and S. Parvin, 2004. Effect of salinity on some yield attributes of rice. Pak J. Biol. Sci., 7:760–762.

Galili, G., R. Amir, R. Hoefgen, and H. Hesse 2005. Improving the levels of essential amino acids and sulfur metabolites in plants. Biol. Chem., 386: 817-831.

Galston, A.W., R. Kaur-Sawhney, T. Altabella, and A.F.Tiburcio, 1997. "Plant polyamines in reproductive activity and response to abiotic stress," Botanica Acta, 110(3):197–207.

Gao, M., R. Tao, K. Miura, A.M. Dandekar, and A. Sugiura, 2001. Transformation of Japanese persimmon (Diospyros kaki Thunb. with apple cDNA. encoding NADP-dependent sorbitol-6-phosphate dehydrogenase. Plant Sci., 160:837–845

Gao, X., C. Zou, L. Wang, and F. Zhang, 2005. Silicon improves water use e_ciency in maize plants. J. Plant Nutr., 27, 1457–1470. [CrossRef]

Gao, Z., M. Sagi, and S.H. Lips, 1998. "Carbohydrate metabolism in leaves and assimilate partitioning in fruits of tomato (Lycopersicon esculentumL). as affected by salinity," Plant Science, 135(2):149–159.

Garcia-Olmedo, F., A. Molina, A. Segura, and M. Moreno, 1995. The defensive role of nonspecific lipid-transfer proteins in plants. Trends. Microbiol., 3:72–74

Garg, A.K., J.K. Kim, T.G. Owens, A.P. Ranwala, Y.D. Choi, L.V. Kochian, and R.J. Wu, 2002. Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. Proc. Natl. Acad. Sci. U. S. A., 99:15898–15903.

Garg, N., and G. Manchanda, 2008. Salinity and its effects on the functional biology of legumes. Acta Physiol Plant, 30:595–618.

Garg, N., and P. Bhandari, 2016. Interactive effects of silicon and arbuscular mycorrhiza in modulating ascorbate-glutathione cycle and antioxidant scavenging capacity in differentially salt-tolerant Cicer arietinum L. genotypes subjected to long-term salinity. Protoplasma, 253, 1325–1345. [CrossRef]

Garg, N., and P. Bhandari, 2016. Silicon nutrition and mycorrhizal inoculations improve growth, nutrient status, K.+/Na+ ratio and yield of Cicer arietinum L. genotypes under salinity stress. Plant Growth Regul., 78, 371–387. [CrossRef]

Gaupels, F., G.T. Kuruthukulangarakoola, and J. Durner, 2011. Upstream and downstream signals of nitric oxide in pathogen defence. Curr. Opin. Plant Biol., 14, 707–714. [CrossRef]

Geilfus C.M., 2018a. Chloride (CL) From nutrient to toxicant. Plant and Cell Physiology, 59, 877–886

Geissler N, S. Hussin, H.W. Koyro, 2010. Elevated atmospheric CO2 concentration enhances salinity tolerance in Aster tripolium L. Planta, 231:583–594

Gelhaye E, N. Rouhier, J. Gérard, Y. Jolivet, J. Gualberto, *et al.,* 2004. A. specific form of thioredoxin h occurs in plant mitochondria and regulates the alternative oxidase. Proc. Natl. Acad. Sci. U. S. A. 101: 14545-14550.

Gelhaye, E., N. Rouhier, J. Gérard, Y. Jolivet, J. Gualberto, N. Navrot, P.-I. Ohlsson, G. Wingsle, M. Hirasawa, and D.B. Knaff, 2004. A. specific form of thioredoxin h occurs in plant mitochondria and regulates the alternative oxidase. Proc. Natl. Acad. Sci., USA., 101:14545–14550. PMID: 15385674. Doi: 10.1073/ pnas.0405282101.

Gerlich, S.C., J.W. Berkley, K. Stephan, and K. Stanislav, 2018. Sulfate Metabolism in C4 Flaveria Species Is Controlled by the Root and Connected to Serine Biosynthesis, Plant Physiology, 178:565–582, www.plantphysiol.org American Society of Plant Biologists. All Rights Reserved.

Ghanem, A.E., E. Mohamed, A.M. Kasem, and A.A. El-Ghamery, 2021. Differential salt tolerance strategies in three halophytes from the same ecological habitat: Augmentation of antioxidant enzymes and compounds. Plants, 10, 1100. [CrossRef]

Ghassemi, F., A.J. Jakeman, and H.A. Nix, 1995. Salinisation of land and water resources: Human causes, extent, management and case studies. UNSW. Press, S.ydney, A.ustralia, and CAB. International, Wallingford, U.K. Godoy JA, L.unar S, T.orres-Schumann J, M.oreono J, R.odrigo RM, P.intor-Toro JA. 1994. Expression, tissue distribution and subcellular

Gigolashvili, T. and K. Stanislav, 2014. Transporters in plant sulfur metabolism, F.rontiers in Plant Science, F.rontiers website link: www.frontiersin.org

Gill, S.S., M. Tajrishi, M. Madan, and N. Tuteja, 2013. "A. DESDbox helicase functions in salinity stress tolerance by improving photosynthesis and antioxidant machinery in rice (Oryza sativa L. cv. PB1.," Plant Molecular Biology, 82(1-2):1–22.

Gilroy, S., M. Bialasek, N. Suzuki, M. Gorecka, A. Devireddy, S. Karpinski, and R. Mittler, 2016. ROS, calcium and electric signals: key mediators of rapid systemic signaling in plants. Plant Physiol. 171: 1606–1615.

Gohari, G., F. Safai, S. Panahirad, A. Akbari, F. Rasouli, M.R. Dadpour, and V. Fotopoulos, 2020b. Modified multiwall carbon nanotubes display either phytotoxic or growth promoting and stress protecting activity in Ocimum basilicum L. in a concentration-dependent manner. Chemosphere, 249: 126171.

Gomathi, R., and P. Rakkiyapan, 2011. Comparative lipid peroxidation, leaf membrane thermostability, and antioxidant system in four sugarcane genotypes differing in salt tolerance. Int. J. Plant Physiol. Biochem. 3: 67–74.

Gomes-Filho, E., C.RF. Machado Lima, J.H. Costa, A.C. da Silva, M. daGuia Silva Lima, C.F. de Lacerda, and J.T. Prisco 2008. Cowpea ribonuclease: properties and effect of NaCl-salinity on its activation during seed germination and seedling establishment. Plant Cell. Rep., 27:147–157.

Gong, H.J., D.P. Randall, and T.J. Flowers, 2006 Silicon deposition in the root reduces sodium uptake in rice (Oryza sativa L). Seedlings by reducing bypass flow. Plant. Cell Environ. 29: 1970–1979. [CrossRef]

Gorbe, E., and A. Calatayud, 2012. Applications of chlorophyll fluorescence imaging technique in horticultural research: A Review. Sci. Hortic.-Amsterdam, 138:24–35. [CrossRef]

Gou, T., X. Chen, R. Han, J. Liu, Y. Zhu, and H. Gong, 2020. Silicon can improve seed germination and ameliorate oxidative damage of bud seedlings in cucumber under salt stress. Acta Physiol. Plant. 42: 1–11

Grattan, S.R., and C.M. Grieve, 1999. Salinity-mineral nutrient relations in horticultural crops. Sci Hortic 78:127–157.

Greenway, H., and R. Munns, 1980. Mechanisms of salt tolerance in nonhalophytes. Annu. Rev. Plant Physiol., 31:149–190

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat., 111:1169–1194.

Gro, F., J. Durner, and F. Gaupels, 2013. “Nitric oxide, antioxidants and prooxidants in plant defence responses,” Frontiers in Plant Science, 4, article 419.

Gu, M.F., N. Li, X.H. Long, M. Brestic, H.B. Shao, J. Li, and S. Mbarki, 2016. Accumulation capacity of ions in cabbage (Brassica oleracea L). Supplied with sea water. Plant Soil Environment 62(7):314–320. https://doi.org/10.17221/771/2015-PSE

Guan, B., J. Yu, X. Chen, W. Xie, and Z. Lu, 2011. Effects of salt stress and nitrogen application on growthand ion accumulation of Suaeda salsa plants. Intl Conf Remote Sens Environ Transport Engin, 24– 26 June, 8268–8272.

Guerriero, G., F.M. Sutera, N. Torabi-Pour, J. Renaut, J.-F. Hausman, R. Berni, H.C. Pennington, M. Welsh, A. Dehsorkhi, and L.R. Zancan, 2021. Phyto-courier, a silicon particle-based nano-biostimulant: evidence from cannabis sativa exposed to salinity. ACS. Nano 15, 3061–3069.

Guerriero, G., J. Hausman, and S. Legay, 2016 Silicon and the plant extracellular matrix. Front. Plant Sci., 7, 463. [CrossRef]

Gueta-Dahan, Y., Z. Yaniv, B.A. Zilinskas, and G. Ben-Hayyim, 1997. Salt and oxidative stress: similarand specific responses and their relation to salt tolerance in citrus. Planta, 204:460–469.

Guggenberger, P., I. Thormählen, D.M. Daloso, and A.R. Fernie, 2017. The unprecedented versatility of the plant thioredoxin system. Trends Plant Sci., 22:249–262. PMID: 28139457.doi:10.1016/ j.tplants.2016.12.008.

Gunes, A., A. Inal, E.G. Bagci and D.J. Pilbeam. 2007. Silicon mediated changes of some physiological and enzymatic parameters symptomatic for oxidative stress in spinach and tomato grown in sodic- B. toxic soil. Plant Soil, 290: 103- 114.

Guo, R.F., G.F. Yuan, and Q.M. Wang 2013. Effect of NaCl treatments on glucosinolate metabolism in broccoli sprouts. J. Zhejiang Univ. Sci. B., 14: 124-131.

Guo, Y., Q.-S. Qiu, F.J. Quintero *et al.,* 2004. “Transgenic Evaluation of Activated Mutant Alleles of SOS2 Reveals a Critical Requirement for Its Kinase Activity and C-Terminal Regulatory Domain for Salt Tolerance in Arabidopsis thaliana,” Plant Cell, 16(2):435–449,

Gupta, B., and B.R. Huang, 2014 Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. Int. J. Genom., 6: 727–740. [CrossRef] [PubMed]

Gupta, K. J., M. Stoimenova, and W.M. Kaiser, 2005. “In higher plants, only root mitochondria, but not leaf mitochondria reduce nitrite to NO, in vitro and in situ,” Journal of Experimental Botany, 56(420):2601–2609.

Gupta, K., A. Dey, and B. Gupta, 2013. “Plant polyamines in abiotic stress responses,” Acta Physiologiae Plantarum, 35(7):2015–2036

Gupta, K., A. Dey, and B. Gupta, 2013. “Polyamines and their role in plant osmotic stress tolerance,” in Climate Change and Plant Abiotic Stress Tolerance, N. Tuteja and S. S. Gill, (Eds.)1053–1072, Wiley-VCH,Weinheim, G.ermany.

Gurmani, A.R., A. Bano, S.U. Khan, J. Din, and J.L. Zhang, 2011. “Alleviation of salt stress by seed treatment with abscisic acid (ABA) 6-benzylaminopurine (BA) and chlormequat chloride (CCC) optimizes ion and organic matter accumulation and increases yield of rice (Oryza sativa L).,” Australian Journal of Crop Science, 5(10):1278–1285.

Gururani, M.A., J. Venkatesh, and L.S.P. Tran, 2015. Regulation of photosynthesis during abiotic stress-induced photoinhibition. Mol. Plant, 8:1304–1320. doi: 10.1016/j.molp.2015.05.005

Haas, F.H., C. Heeg, R. Queiroz, A. Bauer, M. Wirtz, *et al.,* 2008. Mitochondrial serine acetyltransferase functions as a pacemaker of cysteine synthesis in plant cells. Plant Physiol., 148: 1055-1067.

Halfter, U., M. Ishitani, and J.K. Zhu, 2000. The Arabidopsis SOS2 protein kinase physically interacts with and is activated by the calciumbinding protein SOS3. Proc Natl. Acad. Sci., U. S. A. 97:3735–3740.

Halliwell, B., and J.MC. Gutteridge, 1985. Free radicals in biology and medicine. Clarendon, Oxford

Halliwell, B., and J.MC. Gutteridge, 1989. Free radicals in biology and medicine, 2nd edn. Clarendon, Oxford. halophyte and cryophyte Arabidopsis relative model system and its applicability to molecular genetic analyses of growth and development of extremophiles. Plant Physiol 135:1718–1737.

Hamdia, M.A., 2000. Physiological studies on the influence of biotin or pyridoxine in amelioration the effect of salinity in lupine plants. Bull. Fac. Sci. Assiut Univ., 29: 283-291.

Hameed, M., M. Ashraf, and N. Naz, 2009. Anatomical adaptations to salinity in cogon grass [Imperata cylindrica (L). Raeuschel] from the salt range, P.akinstan. Plant Soil, 322: 229–238. [CrossRef]

Hanfrey, C., S. Sommer, M.J. Mayer, D. Burtin, and A.J. Michael, 2001. "Arabidopsis polyamine biosynthesis: absence of ornithine decarboxylase and the mechanism of arginine decarboxylase activity," Plant Journal, 27(6):551–560.

Hanson, A.D., B. Rathinasabapathi, J. Rivoal, M. Burnet, M.O. Dillon, and D.A. Gage, 1994. "Osmoprotective compounds in the Plumbaginaceae: a natural experiment in metabolic engineering of stress tolerance," Proceedings of the National Academy of Sciences of the United States of America, 91(1):306–310.

Hanzawa, Y., A. Imai, A.J. Michael, Y. Komeda, and T. Takahashi, 2002. "Characterization of the spermidine synthase-related gene family in Arabidopsis thaliana," FEBS. Letters, 527(1–3):176–180.

Hara, S., K. Motohashi, F. Arisaka, P.GN. Romano, N. Hosoya-Matsuda, N. Kikuchi, N. Fusada, and T. Hisabori, 2006. Thioredoxin-h1 reduces and reactivates the oxidized cytosolic malate dehydrogenase dimer in higher plants. J. Biol Chem., 281:32065–32071. PMID: 16945919. doi:10.1074/jbc.M605784200.

Hasanuzzaman, M., and M. Fujita 2011b. Exogenous silicon treatment alleviates salinity-induced damage in Brassica napus L. seedlings by upregulating the antioxidant defense and methylglyoxal detoxification system. Abstract of Plant Biology 2011, A.merican Society of Plant Biology. http://abstracts.aspb.org/pb2011/public/P10/P10001.html.

Hasanuzzaman, M., and M. Fujita, 2011a. Selenium pretreatment upregulates the antioxidant defense and methylglyoxal detoxification system and confers enhanced tolerance to drought stress in rapeseed seedlings. Biol. Trace Elem. Res., 143:1758–1776.

Hasanuzzaman, M., K. Nahar, and M. Fujita, 2014. "Regulatory role of polyamines in growth, development and abiotic stress tolerance in plants," in Plant Adaptation to Environmental Change: Significance of Amino Acids and Their Derivatives, 157–193.

Hasanuzzaman, M., M. Fujita, M.N. Islam, K.U. Ahamed, and K. Nahar, 2009. Performance of four irrigatedrice varieties under different levels of salinity stress. Int. J. Integr. Biol., 6:85–90.

Hasanuzzaman, M., M.H.M. Bhuyan, K. Parvin, T.F. Bhuiyan, T.I. Anee, K. Nahar, M. Hossen, F. Zulfiqar, M. Alam, and M. Fujita, 2021. Regulation of ROS. metabolism in plants under environmental stress: A Review of recent experimental evidence. Int. J. Mol. Sci., 21: 8695. [CrossRef]

Hasanuzzaman, M., M.H.M.B. Bhuyan, F. Zulfiqar, A. Raza, S.M. Mohsin, J.A. Mahmud, M. Fujita, and V. Fotopoulos, 2020. Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. Antioxidants 9, 681. [CrossRef] [PubMed]

Hasanuzzaman, M., M.H.R. Rakib, C.M. Abdul Awal, R. Khussboo, N. Farzana, R. Mira, N. Kamrun and F. Masayuki, 2021. Regulation of Reactive Oxygen Species and Antioxidant Defense in Plants under Salinity, I.nt. J. Mol. Sci. 2021, 22, 9326. https://doi.org/10.3390/ijms22179326

Hasanuzzaman, M., N. Kamrun, and F. Masayuki, 2013. Chapter 2 Plant Response to Salt Stress and Role of Exogenous Protectants to Mitigate Salt-Induced Damages in Ecophysiology and Responses of Plants under Salt Stress Parvaiz Ahmad M.M. Azooz M.N.V. Prasad Editors ISBN. 978-1-4614-4746-7 ISBN. 978-1-4614-4747-4 (eBook) DOI. 10.1007/978-1-4614-4747-4 Springer New York Heidelberg Dordrecht London.

Hasegawa, P.M., 2013. “Sodium (Na+) homeostasis and salt tolerance of plants,” Environmental and Experimental Botany, 92:19–31.

Hasegawa, P.M., R.A. Bressan, J.-K. Zhu, and H.J. Bohnert, 2000. “Plant cellular andmolecular responses to high salinity,” Annual Review of Plant Biology, 51:463–499,

Hashimoto, T., K. Tamaki, K.-I. Suzuki, and Y. Yamada, 1998. “Molecular cloning of plant spermidine synthases,” Plant and Cell Physiology, 39(1):73–79,

Hattori, T., S. Inanaga, E. Tanimoto, A. Lux, M. Luxová, and Y. Sugimoto, 2003. Silicon-induced changes in viscoelastic properties of sorghum root cell walls. Plant Cell Physiol., 44: 743–749. [CrossRef] [PubMed].

He, T. and G.R. Cramer, 1996. “Abscisic acid concentrations are correlated with leaf area reductions in two salt-stressed rapidcycling Brassica species,” Plant and Soil, 179(1): 25–33.

Hell, R., 2003. Metabolic regulation of cysteine synthesis, sulfur assimilation. The plant sulfate transporter family: Specialized functions, integration with whole plant nutrition. In: Sulfur transport, assimilation in plants: Regulation interaction, signaling. (ed.) Davidian J-C, G.rill D, D.e Kok LJ, S.tulen I, H.awkesford MJ, S.chnug E, Rennenberg H. Backhuys Publishers, Leiden, 21-31.

Hern´andez-Hern´andez, H., A. Ju´arez-Maldonado, A. Benavides-Mendoza, H. Ortega- Ortiz, G. Cadenas-Pliego, D. S´anchez-Aspeytia, and S. Gonz´alez-Morales, 2018. Chitosan-PVA. and copper nanoparticles improve growth and overexpress the SOD. and JA. genes in tomato plants under salt stress. Agronomy 8, 175.

Hezaveh, T.A., L. Pourakbar, F. Rahmani, and H. Alipour, 2019. Interactive effects of salinity and ZnO. nanoparticles on physiological and molecular parameters of rapeseed (Brassica napus L). Commun. Soil Sci. Plant Anal. 50: 698–715.

Holmgren, A., 1989. Thioredoxin and glutaredoxin systems. J. Biol Chem., 264: 13963-13966.

Hong, Z., K. Lakkineni, Z. Zhang, D.PS. Verma 2000. Removal of feedback inhibition of 1 pyrroline-5-carboxylase synthetase (P5CS) results in increased proline accumulation and protection of plants from osmotic stress. Plant Physiol., 122:1129–1136.

Hoque, M.A., M.N.A. Banu, E. Okuma *et al.,* 2007. “Exogenous proline and glycinebetaine increase NaCl-induced ascorbateglutathione cycle enzyme activities, and proline improves salt tolerance more than glycinebetaine in tobacco Bright Yellow-2 suspension-cultured cells,” Journal of Plant Physiology, 164(11):1457–1468.

Hoque, M.A., M.N.A. Banu, Y. Nakamura, Y. Shimoishi, and Y. Murata, 2008. “Proline and glycinebetaine enhance antioxidant defense and methylglyoxal detoxification systems and reduce NaCl-induced damage in cultured tobacco cells,” Journal of Plant Physiology, 165(8):813–824.

Horváth, E., B. Krisztina, G. Ágnes, R. Riyazuddin, C. Gábor, and C. Dorottya and C. Jolán, 2020. Compensation of Mutation in Arabidopsis glutathione transferase (AtGSTU) Genes under Control or Salt Stress Conditions, I.nt. J. Mol. Sci., 21, 2349; doi:10.3390/ijms21072349 www.mdpi.com/journal/ijms.

Horváth, E., K. Bela, B. Holinka, R. Riyazuddin, Á. Gallé, Á. Hajnal, Á. Hurton, A. Fehér, and J. Csiszár, 2019. The Arabidopsis glutathione transferases, A.tGSTF8 and AtGSTU19 are involved in the maintenance of root redox homeostasis affecting meristem size and salt stress sensitivity. Plant Sci., 283: 366–374. [CrossRef]

Hosseinpour, A., K. Haliloglu, K. Tolga Cinisli, G. Ozkan, H.I. Ozturk, A. Pour- Aboughadareh, and P. Poczai, 2020. Application of zinc oxide nanoparticles and plant growth promoting bacteria reduces genetic impairment under salt stress in tomato (Solanum lycopersicum L. ‘Linda’. Agriculture, 10, 521.

Hu, Y., and U. Schmidhalter 2005. Drought and salinity: a comparison of their effects onmineral nutrition of plants. J. Plant Nutr Soil Sci., 168:541–549.

Hundertmark, M., and D.K. Hincha 2008. LEA. (late embryogenesis abundant. proteins and their encoding genes in Arabidopsis thaliana. BMC. Genomics, 9:118–139.

Hussain, K., K. Nawaz, A. Majeed *et al.,* 2011. “Role of exogenous salicylic acid applications for salt tolerance in violet (Viola Odorata L).,” Sarhad Journal of Agriculture, 27:171–175.

Hussain, S., Z. Bai, J. Huang, X. Cao, L. Zhu, C. Zhu, J. Zhang, 2019. 1-Methylcyclopropene modulates physiological, biochemical, and antioxidant responses of rice to different salt stress levels. Front. Plant Sci., 10, 124. [CrossRef] [PubMed]

Hussain, S.J., N.A. Khan, N.A. Anjum, A. Masood, and M.I.R. Khan, 2021. Mechanistic elucidation of salicylic acid and sulphur-induced defence systems, nitrogen metabolism, photosynthetic, and growth potential of mungbean (Vigna radiata. under salt stress. J. Plant Growth Regul., 40, 1000–1016. [CrossRef]

Hussin S, N. Geissler, and H.W. Koyro, 2013. Effect of NaCl salinity on Atriplex nummularia (L). with special emphasis on carbon and nitrogen metabolism. Acta Physiol Plant, 35:1025–1038.

Ibrar, M., M. Jabeen, J. Tabassum, F. Hussain, and I. Ilahi 2003. Salt tolerance potential of Brassica juncea Linn. J. Sci. Tech. Univ. Peshawar, 27:79– 84.

Inan G, Q. Zhang, P. Li, Z. Wang, Z. Cao, H. Zhang, C. Zhang, T.M. Quist, S.M. Goodwin, J. Zhu, H. Shi, B. Damsz, T. Charbaji, Q. Gong, S. Ma, M. Fredricksen, D.W. Galbraith, M.A. Jenks, D. Rhodes, P.M. Hasegawa, H.J. Bohnert, R.J. Joly, R.A. Bressan, and J.K. Zhu, 2004. Salt cress. An immunity, jasmonic acid, and ethylene levels in Arabidopsis. Plant Cell, 19:2213–2224.

Iqbal, M.N., R. Rasheed, M.Y. Ashraf, M.A. Ashraf, and I. Hussain, 2018. Exogenously applied zinc and copper mitigate salinity effect in maize (Zea mays L). by improving key physiological and biochemical attributes. Environ. Sci. Pollut. Res. 25: 23883–23896.

Iqbal, N., S. Umar, N.A. Khan, and F.J. Corpas, 2021. Nitric oxide and hydrogen sulfide coordinately reduce glucose sensitivity and decrease oxidative stress via ascorbate-glutathione cycle in heat-stressed wheat (Triticum aestivum L). Plants Antioxidants, 10, 108. [CrossRef]

Isa, M., S. Bai, T. Yokoyama, J.F. Ma, Y. Ishibashi, T. Yuasa, and M. Iwaya-Inoue, 2010. Silicon enhances growth independent of silica deposition in a low-silica rice mutant, lsi1. Plant Soil, 331, 361–375. [CrossRef]

Ishitani M., J. Liu, U. Halfter, C.-S. Kim, W. Shi, and J.- K. Zhu, 2000. “SOS3 function in plant salt tolerance requires Nmyristoylation and calcium binding,” Plant Cell, 12(9):1667–1677.

Ivanov, A., and M. Velitchkova, 2014. “Chapter 27: Mechanisms of stimulation of photosystem I. activity in chloroplast membranes under heat stress. Correlation between P700 Photooxidation and Thermostability of Thylakoid Membrane Organization,” in Contemporary Problems of Photosynthesis, 2, eds S. I. Allakhverdiev, A. B. Rubin and V. A. Shuvalov (Moscow–Izhevsk: Izhevsk Institute of Computer Science., 377–395.

Iyengar, E.R.R., and M.P. Reddy, 1996. Photosynthesis in highly salt-tolerant plants. In: Pessaraki M. (ed.) Handbook of photosynthesis. Marcel Dekker, New York, 897–909.

Jacoby, R.P., A.H. Millar, and N.L. Taylor, 2010. Wheat mitochondrial proteomes provide new links between antioxidant defense and plant salinity tolerance. J. Proteome Res., 9:6595–6604.

Jahan, B., M.F. Al Ajmi, M.T. Rehman, and N.A. Khan, 2020. Treatment of nitric oxide supplemented with nitrogen and sulfur regulates photosynthetic performance and stomatal behavior in mustard under salt stress. Physiol. Plant, 168: 490–510. [PubMed]

Jahan, B., M.F. Al Ajmi, M.T. Rehman, and N.A. Khan, 2020. Treatment of nitric oxide supplemented with nitrogen and sulfur regulates photosynthetic performance and stomatal behavior in mustard under salt stress. Physiol. Plant, 168: 490–510. [PubMed].

Jahan, B., N. Iqbal, M. Fatma, Z. Sehar, A. Masood, A. Sofo, I. D’Ippolito, and N.A. Khan, 2021. Ethylene supplementation combined with split application of nitrogen and sulfur protects salt-inhibited photosynthesis through optimization of proline metabolism and antioxidant system in mustard (Brassica juncea L). Plants, 10, 1303. [CrossRef] .

Jahan, B., N. Iqbal, M. Fatma, Z. Sehar, A. Masood, A. Sofo, I. D’Ippolito, and N.A. Khan, 2021. Ethylene supplementation combined with split application of nitrogen and sulfur protects salt-inhibited photosynthesis through optimization of proline metabolism and antioxidant system in mustard (Brassica juncea L). Plants, 10, 1303. [CrossRef].

Jahan, B., R. Faisal, S. Zebus, F. Mehar, I. Noushina, M. Asim, A.A. Naser and A.Kh. Nafees, 2021. Coordinated Role of Nitric Oxide, E.thylene, N.itrogen, and Sulfur in Plant Salt Stress Tolerance, Stresses, 1: 181–199. https://doi.org/10.3390/stresses1030014 https://www.mdpi.com/journal/stresses.

Jain, M., D. Choudhary, R.K. Kale, and N. Bhalla-Sarin, 2002. Salt- and glyphosateinduced increase in glyoxalase I. activity in cell lines of groundnut (Arachis hypogaea) Physiol Plant, 114: 499-505.

Jaleel, C.A., P. Manivannan, G.M. Lakshmanan, R. Sridharan, and R. Panneerselvam, 2007. NaCl as a physiological modulator of proline metabolism and antioxidant potential in Phyllanthus amarus. C.R. Biol., 330: 806-813.

James, R.A., C. Blake, C.S. Byrt, and R. Munns, 2011. "Major genes for Na+ exclusion, N.ax1 and Nax2 (wheatHKT1;4 and HKT1;5., decrease Na+ accumulation in bread wheat leaves under saline and waterlogged conditions," Journal of Experimental Botany, 62(8):2939–2947.

Janowitz, T., H. Kneifel, and M. Piotrowski, 2003. "Identification and characterization of plant agmatine iminohydrolase, the last missing link in polyamine biosynthesis of plants," FEBS. Letters, 544(1–3):258–261.

Jayakannan, M., J. Bose, O. Babourina *et al.,* 2013. "Salicylic acid improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing salt-inducedK+ loss via aGORK. channel," Journal of Experimental Botany, 64(8):2255–2268.

Jeschke, W.D., A.D. Peuke, J.S. Pate, and W. Hartung, 1997. "Transport, synthesis and catabolism of abscisic acid (ABA) in intact plants of castor bean (Ricinus communis L). under phosphate deficiency andmoderate salinity," Journal of Experimental Botany, 48(314):1737–1747,

Jiang, C., M. Johkan, M. Hohjo, S. Tsukagoshi, and T. Maruo, 2017. A correlation analysis on chlorophyll content and SPAD. value in tomato leaves. Hortic. Res., 71: 37–42.

Jiang, K., C. Schwarzer, E. Lally, S. Zhang, S. Ruzin, T. Machen, S.J. Remington, and L. Feldman, 2006. Expression and characterization of a redox-sensing green fluorescent protein (reduction-oxidation-sensitive green fluorescent protein. in Arabidopsis. Plant Physiol., 141: 397–403. [CrossRef] [PubMed]

Jiang, K., J. Moe-Lange, L. Hennet, and L.J. Feldman, 2016. Salt stress affects the redox status of Arabidopsis root meristems. Front. Plant Sci., 7, 81. [CrossRef] [PubMed]

Jiang, Y., B. Yang, N.S. Harris, and M.K. Deyholos, 2007. Comparative proteomic analysis of NaCl stress-responsive proteins in Arabidopsis roots. J. Exp. Bot., 58:3591–3607.

Jobe, T.O., I. Zenzen, K.P. Rahimzadeh, and S. Kopriva, 2019. Integration of sulfate assimilation with carbon and nitrogen metabolism in transition from C3 to C4 photosynthesis. J. Exp. Bot., 70: 4211–4221. [CrossRef]

Juan, M., R.M. Rivero, L. Romero, and J.M. Ruiz, 2005. Evaluation of some nutritional and biochemical indicators in selecting salt-resistant tomato cultivars. Environ. Exp. Bot. 54: 193–201. doi: 10.1016/j.envexpbot.2004.07.004

Kalaji, H.M., B.K. Govindjee, J. Koscielniakd, and K. Zük-Gołaszewska, 2011. Effects of salt stress on photosystem II. efficiency and CO2 assimilation of two Syrian barley landraces. Environ. Exp. Bot., 73:64–72

Kalaji, H.M., K. Bosa, J. Ko´scielniak, and K. Zuk-Gołaszewska, 2011. Effects of salt stress on photosystem II. efficiency and CO 2 assimilation of two Syrian barley landraces. Environ. Exp. Bot., 73:64–72. [CrossRef].

Kamala, G., D. Abhijit and G. Bhaskar 2013. Plant polyamines in abiotic stress responses. Acta Physiol Plant, DOI. 10.1007/s11738-013-1239-4.

Karunakaran, G., R. Suriyaprabha, P. Manivasakan, R. Yuvakkumar, V. Rajendran, P. Prabu, and N. Kannan, 2013Effect of nanosilica and silicon sources on plant growth promoting rhizobacteria, soil nutrients and maize seed germination. IET. Nanobiotechnol., 7:70–77. [CrossRef]

Kaur, G., S. Kumar, H. Nayyar, and H.D. Upadhyaya, 2008. Cold stress injury during the pod-fillingphase in chickpea (Cicer arietinum L). : effects on quantitative and qualitative components of seeds. J. Agron. Crop. Sci., 194:457–464.

Kav, N.N.V., S. Srivastava, L. Goonewardende, and S.F. Blade, 2004. Proteome level changes in the roots of Pisum sativum in response to salinity. Ann. Appl. Biol., 145:217–230.

Kaveh, H., H. Nemati, M. Farsi, and S.V. Jartoodeh, 2011. How salinity affect germination and emergence of tomato lines. J. Biol. Environ. Sci., 5: 159–163.

Kerepesi, I. and G. Galiba, 2000. "Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings," Crop Science, 40(2):482–487.

Keskin, B.C., A.T. Sarikaya, B. Y¨uksel, and A.R. Memon, 2010. “Abscisic acid regulated gene expression in bread wheat (Triticum aestivum L)” Australian Journal of Crop Science, 4(8):617–625.

Keutgen, A.J., and E. Pawelzik 2009. Impacts of NaCl stress on plant growth and mineral nutrient assimilation in two cultivars of strawberry. Environ Exp. Bot., 65:170–176

Khan M. A., I. A. Ungar, and A. M. Showalter, 2000. “Effects of sodium chloride treatments on growth and ion accumulation of the halophyte haloxylon recurvum,” Communications in Soil Science and Plant Analysis, 31(17-18):2763–2774,

Khan, M.A., and D.J. Weber, 2008. Ecophysiology of high salinity tolerant plants (tasks for vegetation science., 1st edn. Springer, A.msterdam

Khan, M.A., and Y. Rizvi, 1994. Effect of salinity, temperature and growth regulators on the germination and early seedling growth of Atriplex griffithii var. Stocksii. Can J. Bot., 72:475–479.

Khan, M.A., I.A. Ungar, and A.M. Showalter, 2000. Effects of salinity on growth, water relations and ion accumulation of the subtropical perennial halophyte, A.triplex griffithii var. stocksii. Ann. Bot., 85:225–232.

Khan, M.A., M.U. Shirazi, M.A. Khan, S.M. Mujtaba, E. Islam, S. Mumtaz, *et al.,* 2009. Role of proline, K./NA. ratio and chlorophyll content in salt tolerance of wheat (Triticum aestivum L). Pakistan J. Bot. 41: 633–638.

Khan, M.I.R., N. Iqbal, A. Masood, and N.A. Khan, 2012. Variation in salt tolerance of wheat cultivars: Role of glycinebetaine and ethylene. Pedosphere, 22:746-754.

Khan, M.M., R.S.M. Al-Mas'oudi, F. Al-Said, and I. Khan, 2013. Salinity effects on growth, electrolyte leakage, chlorophyll content and lipid peroxidation in cucumber (Cucumis sativus L). 2013 International Conference on Food and Agricultural Sciences IPCBEE. vol.55, I.ACSIT. Press, S.ingapore doi:10.7763/IPCBEE.2013. V55. 6.

Khan, M.N., M. Mobin, Z.K. Abbas, K.A. AlMutairi, and Z.H. Siddiqui, 2017. Role of nanomaterials in plants under challenging environments. Plant Physiol. Biochem., 110: 194–209.

Khan, M.R., V. Adam, T.F. Rizvi, B. Zhang, F. Ahamad, I. Jo´sko, Y. Zhu, M. Yang, and C. Mao, 2019b. Nanoparticle–plant interactions: two-way traffic. Small 15, 1901794.

Khanna-Chopra, R., K.S. Vimal, L. Nita, and P. Ashwani, 2019. Proline – A. Key Regulator Conferring Plant Tolerance to Salinity and Drought, C.hapter 5, DOI: 10.1201/9780203705315-5.

Khodarahmpour, Z., M. Ifar, and M. Motamedi, 2012. Effects of NaCl salinity on maize (Zea mays L). at germination and early seedling stage. Afr. J. Biotechnol., 11:298–304.

Kibria, M.G. and H.Md.Anamul, 2019. A Review on Plant Responses to Soil Salinity and Amelioration Strategies, D.OI: 10.4236/ojss. 911013 Nov. 1, O.pen Journal of Soil Science.

Kibria, M.G., M.A. Hossain, Y. Murata, and M.A. Hoque, 2017. Antioxidant Defense Mechanisms of Salinity Tolerance in Rice Genotypes. Rice Science, 24: 155-162. https://doi.org/10.1016/j.rsci.2017.05.001

Kilili, K.G., N. Atanassova, A. Vardanyan, N. Clatot, K. Al-Sabarna, P.N. Kanellopoulos, A.M. Makris, and S.C. Kampranis, 2004. Differential roles of tau class glutathione S-transferases in oxidative stress. J. Biol. Chem., 279, 24540–24551. [CrossRef] [PubMed]

Kim, D.W., R. Rakwal, G.K. Agrawal, Y.H. Jung, J. Shibato, N.S. Jwa, Y. Iwahashi, H. Iwahashi, D.H. Kim, I.S. Shim, K. Usui 2005. A. hydroponic rice seedling culture model system for investigating proteome of salt stress in rice leaf. Electrophoresis, 26:4521–4539.

Kim, S.H., D.H. Woo, J.M. Kim, S.Y. Lee, W.S. Chung, and Y.H. Moon, 2011. Arabidopsis MKK4 mediates osmotic-stress response via its regulation of MPK3 activity. Biochem Biophys Res Commun 412:150– 154

Kim, Y.H., A. Latif Khan, M. Waqas *et al.,* 2013. “Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress,” Journal of Plant Growth Regulation,

Kim, Y.H., A.L. Khan, M. Waqas, J.K. Shim, D.H. Kim, K.Y. Lee, and I.J. Lee, 2014. Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress. J. Plant Growth Regul., 33: 137–149.

Kim, Y.H., A.L. Khan, M. Waqas, J.K. Shim, D.H. Kim, K.Y. Lee, and I.J. Lee, 2014. Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress. J. Plant Growth Regul., 33: 137–149. [CrossRef]

Kinoshita, J.H., 1990. A thirty year journey in the polyol pathway. Exp. Eye. Res., 50(6):567–573. https://doi.org/10.1016/0014-4835 (90) 90096-D.

Knott, J.M., P. R¨omer, and M. Sumper, 2007. "Putative spermine synthases from Thalassiosira pseudonana and Arabidopsis thaliana synthesize thermospermine rather than spermine," FEBS. Letters, 581(16):3081–3086.

Kocsy, G., I. Tari, R. Vanková, B. Zechmann, Z. Gulyás, P. Poór, and G. Galiba, 2013. Redox control of plant growth and development. Plant Sci., 211:77–91. PMID: 23987814. doi:10.1016/j.plantsci.2013.07.004.

Kopriva, S., 2006. Regulation of sulfate assimilation in Arabidopsis and beyond. Ann Bot 97: 479-495.

Kopriva, S., and H. Rennenberg, 2004. Control of sulphate assimilation and glutathione synthesis: interaction with N. and C. metabolism. J. Exp. Bot., 55: 1831- 1842.

Koprivova, A., and S. Kopriva, 2008. Lessons from investigation of regulation of APS. reductase by salt stress. Plant Signal. Behav. 3: 567-569.

Kopyra, M. and E.A. Gw´o´zd´z, 2003. "Nitric oxide stimulates seed germination and counteracts the inhibitory effect of heavy metals and salinity on root growth of Lupinus luteus," Plant Physiology and Biochemistry, 41(11-12):1011–1017.

Kosová, K., I.T. Prášil, and P. Vítámvás, 2013. Protein contribution to plant salinity response and tolerance acquisition a review. Int. J. Mol. Sci., 14:6757–6789.

Kosová, K., P. Vítámvás, and I.T. Prášil, 2010. The role of dehydrins in plant stress response. In:Handbook of Plant and CropStress. Pessarakli M. (ed.) CRC. Press, T.aylor and Francis: Boca Raton, FL, USA, 239– 285.

Kosova, K., P.V. ´ ´ıtamv ´ as, I.T. Pr ´ a´˜sil, and J. Renaut, 2011. "Plant proteome changes under abiotic stress—contribution of proteomics studies to understanding plant stress response," Journal of Proteomics, 74(8):1301–1322.

Kov´acs, Z., L. Simon-Sarkadi, A. Szucs, and G. Kocsy, 2010. "Differential effects of cold, osmotic stress and abscisic acid on polyamine accumulation inwheat,"Amino Acids, 38(2):623–631.

Krueger, S., A. Donath, M.C. Lopez-Martin, R. Hoefgen, C. Gotor, *et al.,* 2010. Impact of sulfur starvation on cysteine biosynthesis in T-DNA. mutants deficient for compartment-specific serine-acetyltransferase. Amino Acids, 39: 1029-1042.

Kumar, D., and S. Chattopadhyay, 2018. Glutathione modulates the expression of heat shock proteins via the transcription factors BZIP10 and MYB21 in Arabidopsis. J. Exp. Bot., 69: 3729–3743. [CrossRef]

Kumar, G., R.S. Purty, M.P. Sharma, S.L. Singla-Pareek, and A. Pareek, 2009. Physiological responses among Brassica species under salinity stress show strong correlation with transcript abundance for SOS. pathway-related genes. J. Plant Physiol., 166:507–520.

Kumar, M., H. Etesami, and V. Kumar, 2019. Saline Soil-based Agriculture by Halotolerant Microorganisms. Springer. Kumar, V., G.uleria, P., K.umar, V., Y.adav, S.K., 2013. Gold nanoparticle exposure induces growth and yield enhancement in Arabidopsis thaliana. Sci. Total Environ. 461–462, 462–468.

Kumar, N.C., K.L. Milan, K.T. Rahul, D. Devanshu, B.K. Hemant, U.P. Virupaksh, K. Amarjeet, V. Girimalla, K. Dharmendra, B. Vinay, K.M. Jitendra, M. Vikas, M.S. Rahul, K. Jae-Yean and P. Dibyajyoti, 2021. Salinity Stress in Potato: Understanding Physiological, B.iochemical and Molecular Responses, L.ife 2021, 11, 545. https://doi.org/10.3390/life11060545 https://www.mdpi.com/journal/life

Kumar, S.A., S.I. Alam, N. Sengupta, and R. Sarin, 2011. Differential proteomic analysis of salt response in Sorghum bicolor leaves. Environ. Exp. Bot., 71:321–328.

Kumari, S., V. Panjabi, H.R. Kushwaha, S.K. Sopory, S.L. Singla-Pareek, and A. Pareek, 2009. Transcriptome map for seedling stage specific salinity stress response indicates a specific set of genes as candidate for saline tolerance in Oryza sativa L. Funct Integr Genomics, 9:109–123.

Kurth, E., G.R. Cramer, A. Lauchli, and E. Epstein, 1986. Effects of NaCl and CaCl2 on cell enlargement and cell production in cotton roots. Plant Physiol., 82:1102–1106.

Kusano, T., K. Yamaguchi, T. Berberich, and Y. Takahashi, 2007. “Advances in polyamine research in 2007,” Journal of Plant Research, 120(3):345–350.

Kyriakis, J.M., and J. Avruch, 2012. Mammalian MAPK. Signal transduction pathways activated by stress and inflammation: a 10-year update. Physiol. Rev., 92:689–737.

Laane, H., 2017. The effects of the application of foliar sprays with stabilized silicic acid: An overview of the results from 2003-2014. Silicon-Neth., 9: 803–807. [CrossRef]

Laane, H., 2018. The effects of foliar sprays with diferent silicon compounds. Plants, 7, 45. [CrossRef] [PubMed].

Lancaster, J.R., 2015. Nitric oxide: A. brief overview of chemical and physical properties relevant to therapeutic applications. Future Sci. OA, 1. [CrossRef]

Lappartient, A.G., and B. Touraine, 1996. Demand-Driven Control of Root ATP. Sulfurylase Activity and SO42- Uptake in Intact Canola (The Role of PhloemTranslocated Glutathione. Plant Physiol., 111: 147-157.

Latef, A.A.H.A., M.FA. Ahmed, and K.E. Abdel Fattah, 2017. The possible roles of priming with ZnO. nanoparticles in mitigation of salinity stress in lupine (Lupinus termis) plants. J. Plant Growth Regul., 36(1):60–70. https://doi.org/10.1007/s00344-016-9618-x

Lauchli, A., and S.R. Grattan, 2007. Plant growth and development under salinity stress. In: Jenks MA, H.asegawa PM, Mohan JS. (eds) Advances in molecular breeding towards drought and salt tolerant crops. Springer, B.erlin, 1–32.

Lawlor, D.W. 2009. Musings about the effects of environment on photosynthesis. Ann. Bot. 103: 543–549. doi: 10.1093/aob/mcn256

Lea-Cox, J.D., and J.P. Syvertsen, 1993. Salinity reduces water use and nitrate- N-use efficiency of citrus. Ann. Bot., 72:47–54

Lee, S.M., E.J. Lee, E.J. Yang, J.E. Lee, A.R. Park, W.H. Song, and O.K. Park, 2004b. Proteomic identification of annexins, calcium-dependent membrane binding proteins that mediateosmotic stress and abscisic acid signal transduction in Arabidopsis. Plant Cell, 16:1378–1391.

Lee, Y.S., S.R. Park, H.J. Park, and Y.W. Kwon, 2004a. Salt stress magnitude can be quantified by integrating salinity with respect to duration. Proceedings of 4th International Crop Sci. Congress. Brisbane, Aust 26 Sept-1 Oct pp 1–5.

Leustek, T., M.N. Martin, J.A. Bick, and J.P. Davies, 2000. Pathways And Regulation Of Sulfur Metabolism Revealed Through Molecular And Genetic Studies. Annu. Rev. Plant Physiol Plant Mol. Biol., 51: 141-165.

Li, B., L. He, S. Guo *et al.,* 2013. “Proteomics reveal cucumber Spd-responses under normal condition and salt stress,” Plant Physiology and Biochemistry, 67:7–14.

Li, H., J. Chang, H. Chen, Z. Wang, X. Gu, C. Wei, Y. Zhang, J. Ma, J. Yang, and X. Zhang, 2017. Exogenous melatonin confers salt stress tolerance to watermelon by improving photosynthesis and redox homeostasis. Front. Plant Sci., 8: 295. [CrossRef]

Li, H., Y. Dong, H. Yin, N. Wang, J. Yang, X. Liu, Y. Wang, J. Wu, and X. Li 2011a. Characterization of the stress associated micro RNAs in Glycine max by deep sequencing. BMC. Plant Biol. 11:170.

Li, H., Y. Zhu, Y. Hu, W. Han, and H. Gong, 2015. “Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture,” Acta Physiologiae Plantarum, 37(4):1–9.

Li, H., Y. Zhu, Y. Hu, W. Han, and H. Gong, 2015. Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture. Acta Physiol. Plant., 37, 71. [CrossRef]

Li, J., G. Brader, E. Helenius, T. Kariola, and E.T. Palva, 2012. Biotin deficiency causes spontaneous cell death and activation of defense signaling. Plant J. 70: 315- 326.

Li, Q., G. Yan and Y. An, 2020. Sulfur Homeostasis in Plants, Int. J. Mol. Sci., 21, 8926; doi: 10.3390/ijms21238926 www.mdpi.com/journal/ijms

Li, T.X.Y.Z., Y. Zhang, H. Liu, Y.T. Wu, W.L. Bin, and H.X. Zhang, 2010. Stable expression of arabidopsis vacuolar Na+/H+ antiporter gene AtNHX1, and salt tolerance in transgenic soybean for over six generations. Chinese Sci. Bull., 55: 1127–1134. doi: 10.1007/s11434-010-0092-8.

Li, W., C. Zhang, Q. Lu, X. Wen, and C. Lu 2011b. The combined effect of salt stress and heat shock on proteome profiling in Suaeda salsa. J. Plant Physiol., 168:1743–1752.

Li, Y., W. Zhang, J. Cui, D. Lang, M. Li, Q. Zhao, and X. Zhang, 2016 Silicon nutrition alleviates the lipid peroxidation and ion imbalance of Glycyrrhiza uralensis seedlings under salt stress. Acta Physiol. Plant, 38, 96. [CrossRef]

Liang, X., H. Wang, Y. Hu, L. Mao, L. Sun, T. Dong, W. Nan, and Y. Bi, 2015Silicon does not mitigate cell death in cultured tobacco BY-2 cells subjected to salinity without ethylene emission. Plant Cell Rep., 34: 331–343. [CrossRef] [PubMed]

Liang, Y., 1999. Effects of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. Plant Soil, 209: 217–224. [CrossRef]

Liang, Y., Q. Chen, Q. Liu, W. Zhang, and R. Ding, 2003Exogenous silicon (Si. increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (Hordeum vulgare L). J. Plant Physiol., 160: 1157–1164. [CrossRef] [PubMed]

Liang, Y., W. Sun, Y.G. Zhu and P. Christie, 2007. Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environ. Pollut., 147: 422-428

Liang, Y., W. Zhang, Q. Chen, R. Ding, 2005. Effects of silicon on H+-ATPase and H+-PPase activity, fatty acid composition and fluidity of tonoplast vesicles from roots of salt-stressed barley (Hordeum vulgare L). Environ. Exp. Bot., 53: 29–37. [CrossRef]

Liang, Y., W. Zhang, Q. Chen, Y. Liu, and R. Ding, 2006. Effect of exogenous silicon (Si. on H+-ATPase activity, phospholipids and fluidity of plasma membrane in leaves of salt-stressed barley (Hordeum vulgare L). Environ. Exp. Bot., 57: 212–219. [CrossRef]

Lin, H., Y. Yang, R. Quan, I. Mendoza, Y. Wu, W. Du, S. Zhao, K.S. Schumaker, J.M. Pardo, and Y. Guoa, 2009. Phosphorylation of SOS3-like calcium binding protein8 by SOS2 protein kinase stabilizes their protein complex and regulates salttolerance in Arabidopsis. Plant Cell, 21: 1607–1619.

Linghe, Z., and M.C. Shannon, 2000. Salinity effects on seedling growth and yield components of rice. Crop Sci., 40:996–1003.

Liska, A.J., A. Shevchenko, U. Pick, and A. Katz, 2004. Enhanced photosynthesis and redox energy production contribute to salinity tolerance in Dunaliella as revealed by homology-based proteomics. Plant Physiol., 136:2806–2817.

Liu, H.H., X. Tian, Y.J. Li, C.A. Wu, and C.C. Zheng, 2008. Microarray-based analysis of stress-regulated microRNAs in Arabidopsis thaliana. RNA. 14:836–843.

Liu, J., M. Ishitani, U. Halfter, C.-S. Kim, and J.-K. Zhu, 2000. “The Arabidopsis thaliana SOS2 gene encodes a protein kinase that is required for salt tolerance,” Proceedings of the National Academy of Sciences of theUnited States ofAmerica, 97(7):3730– 3734.

Liu, J., M. Ishitani, U. Halfter, C.S. Kim, J.K. Zhu. 2000. The Arabidopsis thaliana SOS2 gene encodes a protein kinase that is required for salt tolerance. Proc Natl Acad Sci USA. 97:3730–3734.

Liu, J.H., W. Wang, H. Wu, X. Gong, and T. Horiguchi, 2015. Polyamines function in stress tolerance: from synthesis to regulation. Front Plant Sci., 6:827. https://doi.org/10.3389/fpls.2015.00827.

Liu, P., L. Yin, S. Wang, M. Zhang, X. Deng, and S. Zhang, 2015. Enhanced root hydraulic conductance by aquaporin regulation accounts for silicon alleviated salt-induced osmotic stress in Sorghum bicolor L. Environ. Exp. Bot. 111:42–51. doi: 10.1016/j.envexpbot.2014.10.006

Liu, P., L. Yin, S. Wang, M. Zhang, X. Deng, S. Zhang, and K. Tanaka, 2015Enhanced root hydraulic conductance by aquaporin regulation accounts for silicon alleviated salt-induced osmotic stress in Sorghum bicolor L. Environ. Exp. Bot., 111: 42–51. [CrossRef]

Liu, P., L. Yin, X. Deng, S. Wang, K. Tanaka, and S. Zhang, 2014. Aquaporin-mediated increase in root hydraulic conductance is involved in silicon-induced improved root water uptake under osmotic stress in Sorghum bicolor L. J. Exp. Bot., 65: 4747–4756. [CrossRef]

Liu, R., and R. Lai, 2015. Potentials of engineered nanoparticles as fertilizers for increasing agronomic productions. Sci. Total Environ., 51:131–139.

Localization of dehydrin TAS14 in salt-stressed tomato plants. Plant Mol. Biol., l26:1921–1934.

López-Berenguer, C., M.C. Martínez-Ballesta, C. García-Viguera, and M. Carvajal, 2008. Leaf water balance mediated by aquaporins under salt stress and associated glucosinolate synthesis in broccoli. Plant Sci., 174: 321-328.

López-Berenguer, C., M.C. Martínez-Ballesta, D.A. Moreno, M. Carvajal, and C. GarcÃa-Viguera, 2009. Growing hardier crops for better health: Salinity tolerance and the nutritional value of broccoli. J. Agric. Food Chem., 57: 572-578.

Lòpez-Climent, M.F., V. Arbona, R.M. Pérez-Clemente, and A. Gòmez-Cadenas, 2008. Relationship between salt tolerance and photosynthetic machinery performance in citrus. Environ. Exp. Bot., 62:176–184.

López-Martín, M.C., L.C. Romero, and C. Gotor, 2008. Cytosolic cysteine in redox signaling. Plant Signal Behav., 3: 880-881.

Lopez-Martin, M.C., M. Becana, L.C. Romero, and C. Gotor 2008a. Knocking out cytosolic cysteine synthesis compromises the antioxidant capacity of the cytosol to maintain discrete concentrations of hydrogen peroxide in Arabidopsis. Plant Physiol., 147: 562-572.

Lotfi, R., and K. Ghassemi-Golezani, 2015. Influence of salicylic acid and silicon on seed development and quality of mung bean under salt stress. Seed Sci. Technol., 43: 52–61. [CrossRef]

Lu, C., C. Mo-Xian, L. Rui, Z. Lin, H. Xuanxuan, L. Shouxu, D. Xinhua, J. Yong, X. Jiandi, Z. Jianhua, Z. Xiangyu and L. Ying-Gao, 2019.Abscisic Acid Regulates Auxin Distribution to Mediate Maize Lateral Root Development Under Salt, F.rontiers in Plant Science | www.frontiersin.org, 10(716).

Lu, S.F., Y.H. Sun, and V.L. Chiang, 2008. Stress-responsive microRNAs in Populus. Plant J., 55:131–151.

Lu, Y., H. Lam, E. Pi, Q. Zhan, S. Tsai, C. Wang, Y. Kwan, and S. Ngai, 2013. Comparative metabolomics in Glycine max and Glycine soja under salt stress to reveal the phenotypes of their offspring. J. Agric. Food Chem., 61:8711–8721.

Luyckx, M., J.F. Hausman, S. Lutts, and G. Guerriero, 2017. Silicon and plants: Current knowledge and technological perspectives. Front. Plant Sci., 8, 411. [CrossRef]

Ma, J.F., 2002. Arice mutant defective in Si uptake. Plant Physiol., 130: 2111–2117. [CrossRef] [PubMed]

Ma, J.F., and N. Yamaji, 2015. A cooperative system of silicon transport in plants. Trends Plant Sci. 20: 435–442. Doi: 10.1016/j.tplants.2015.04.007.

Ma, L., H. Zhang, L. Sun *et al.,* 2012. "NADPH. oxidase Atrboh D. and Atrboh F. function in ROS-dependent regulation of Na+/K+ homeostasis in Arabidopsis under salt stress," Journal of Experimental Botany, 63(1):305–317.

Ma, Y., L. Kuang, X. He, W. Bai, Y. Ding, Z. Zhang, Y. Zhao, and Z. Chai, 2010. Effects of rare earth oxide nanoparticles on root elongation of plants. Chemosphere, 78: 273–279.

Mahajan, S., G.K. Pandey, and N. Tuteja 2008. Calcium and salt-stress signaling in plants: shedding light on SOS. pathway. Arch. Biochem. Biophys., 471:146–158.

Mahdieh, M., N. Habibollahi, M.R. Amirjani, M.H. Abnosi, and M. Ghorbanpour, 2015. Exogenous silicon nutrition ameliorates saltinduced stress by improving growth and efficiency of PSII. in Oryza sativa L. cultivars. J. Soil Sci. Plant Nutr., 15: 1050–1060. [CrossRef]

Makela, P., J. Karkkainen, and S. Somersalo, 2000. "Effect of glycinebetaine on chloroplast ultrastructure, chlorophyll and protein content, and RuBPCO. activities in tomato grown under drought or salinity," Biologia Plantarum, 43(3):471– 475.

Malakar, P. and D. Chattopadhyay, 2021. Adaptation of plants to salt stress: the role of the ion transporters, J.ournal of Plant Biochemistry and Biotechnology, 30(4):668–683 https://doi.org/10.1007/s13562-021-00741-6

Manaa, A., H.B. Ahmed, B. Valot, J.P. Bouchet, S. Aschi-Smiti, M. Causse, and M. Faurobert, 2011. Salt and genotype impact on plant physiology and root proteome variations in tomato. J. Exp. Bot. 62:2797–2813.

Mane, A.V., B.A. Karadge, and J.S. Samant, 2010. Salinity induced changes in photosynthetic pigments and polyphenols of Cymbopogon Nardus (L). Rendle. J. Chem. Pharm. Res., 2:338–347.

Mantri, N., V. Patade, S. Penna, R. Ford, and E. Pang, 2012. Abiotic stress responses in plants: present and future. In: Ahmad P, Prasad MNV. (eds) Abiotic stress responses in plants: metabolism, productivity and sustainability. Springer, N.ew York, 1–19.

Marchal, C., V. Delorme-Hinoux, L. Bariat, W. Siala, C. Belin, J. SaezVasquez, C. Riondet, J.P. Reichheld, 2014. NTR/NRX. define a new thioredoxin system in the nucleus of Arabidopsis thaliana cells. Mol Plant. 7:30–44. PMID: 24253198. doi:10.1093/mp/ sst162.

Maron, L.G., 2019. From foe to friend: The role of chloride as a beneficial macronutrient. Plant J., 99: 813–814. [CrossRef] [PubMed]

Marschner, H., 1995. “Functions of mineral nutrients: macronutrients,” in Mineral Nutrition of Higher Plants, H. Marschner, (Ed.). 379–396, G.ulf Professional Publishing, Houston, Tex, U.SA, 2nd edition,

Mart´ınez-Atienza, J., X. Jiang, B. Garciadeblas *et al.,* 2007. “Conservation of the salt overly sensitive pathway in rice,” Plant Physiology, 143(2):1001–1012.

Martí, M.C., E. Olmos, J.J. Calvete, I. Díaz, S. Barranco-Medina, J. Whelan, J.J. Lázaro, F. Sevilla, and A. Jiménez, 2009. Mitochondrial and nuclear localization of a novel pea thioredoxin: identification of its mitochondrial target proteins. Plant Physiol., 150:646–657. PMID: 19363090. doi:10.1104/pp.109.138073.

Martí, M.C., I. Florez-Sarasa, D. Camejo, M. Ribas-Carbó, J.J. Lázaro, *et al.,* 2011. Response of mitochondrial thioredoxin PsTrxo1, antioxidant enzymes, and respiration to salinity in pea (Pisum sativum L). leaves. J. Exp. Bot., 62: 3863- 3874.

Martí, M.C., I. Florez-Sarasa, D. Camejo, M. Ribas-Carbó, J.J. Lázaro, F. Sevilla, and A. Jiménez, 2011. Response of mitochondrial thioredoxin PsTrxo1, antioxidant enzymes, and respiration to salinity in pea (Pisum sativum L). leaves. J. Exp. Bot., 62:3863–3874. PMID: 21460385. doi:10.1093/jxb/err076.

Martínez-Atienza, J., X. Jiang, B. Garciadeblas, I. Mendoza, J.K. Zhu, J.M. Pardo, and F.J. Quintero, 2007. Conservation of the salt overly sensitive pathway in rice. Plant Physiol 143:1001–1012

Martínez-Ruiz, A., S. Cadenas, and S. Lamas, 2011. Nitric oxide signaling: Classical, less classical and nonclassical mechanisms. Free Radic. Biol. Med., 51: 17–29. [CrossRef]

Mass, E.V., 1986. Salt tolerance of plants. Appl. Agric. Res., 1:12–26.

Mastronardi, E., P. Tsae, X. Zhang, C.M. Monreal, and M.C. DeRosa, 2015. Strategic role of nanotechnology in fertilizers: potential and limitations. In: Rai M, Ribeiro C, Mattoso L, D.uran N. (eds) Nanotechnologies in food and agriculture. Springer, Berlin.

Mathebula, S.D., 2015. Polyol pathway: A. possible mechanism of diabetes complications in the eye. Afr Vis Eye Health., 74 (1):a13. https://doi.org/10.4102/aveh. v74i1.13.

Matoh, T., P. Kairusmee, and E. Takahashi, 1986. Salt-induced damage to rice plants and alleviation effect of silicate. Soil Sci. Plant Nutr., 32: 295–304. [CrossRef]

Matysik, J., A. Alia, B. Bhalu, and P. Mohanty, 2002. “Molecular mechanisms of quenching of reactive oxygen species by proline under stress in plants,” Current Science, 82(5):525– 532.

May, M.J., T. Vernoux, C. Leaver, M. Van Montagu, and D. Inze, 1998. Glutathione homeostasis in plants: implications for environmental sensing and plant development. J. Exp. Bot., 49: 649-667.

Mendoza, I., F. Rubio, A. Rodriguez-Navarro, and J.M. Pardo, 1994. The protein phosphatise calcineurin is essential for NaCl tolerance of Saccharomyces cerevisiae. J. Biol. Chem., 269:8792–8796.

Meng, L., J.H. Wong, L.J. Feldman, P.G. Lemaux, and B.B. Buchanan, 2010. A. membrane-associated thioredoxin required for plant growth moves from cell to cell, suggestive of a role in intercellular communication. Proc Natl Acad Sci USA., 107:3900–3905. PMID: 20133584. doi:10.1073/pnas.0913759107.

Merrick, B.A., and M.E. Bruno, 2004. Genomic and proteomic profiling for biomarkers and signature profiles of toxicity. Curr. Opin. Mol. Ther., 6:600–607.

Meyer, A.J., and R. Hell, 2005. Glutathione homeostasis and redox-regulation by sulfhydryl groups. Photosynth Res., 86: 435-457.

Mir, R.A., A.B. Basharat, Y. Henan, T.I. Sheikh, R. Ali, A.R. Masood, C. Sidra, A. Mohammed, A.S. Parvaze and M.Z. Sajad, 2022. Multidimensional Role of Silicon to Activate Resilient Plant Growth and to Mitigate Abiotic Stress, F.rontiers in Plant Science | www.frontiersin.org, 13 : 819658.

Mishra, S., A.B. Jha, and R.S. Dubey, 2011. “Arsenite treatment induces oxidative stress, upregulates antioxidant system, and causes phytochelatin synthesis in rice seedlings,” Protoplasma, 248(3):565–577.

Mittal, D., K. Gurjeet, S. Parul, Y. Karmveer and A.A. Syed, 2020. Nanoparticle-Based Sustainable Agriculture and Food Science: Recent Advances and Future Outlook, Frontiers in Nanotechnology | www.frontiersin.org, 2:579954.

Mittal, S., N. Kumari, and V. Sharma, 2012. Differential response of salt stress on Brassica juncea: photosynthetic performance, pigment, proline, D.1 and antioxidant enzymes. Plant Physiol., Biochem., 54:17–26.

Mittal, S., N. Kumari, and V. Sharma, 2012. Differential response of salt stress on Brassica juncea: photosynthetic performance, pigment, proline, D.1 and antioxidant enzymes. Plant Physiol. Biochem. 54: 17–26. doi: 10.1016/j.plaphy.2012.02.003.

Mittler, R. and E. Blumwald, 2015. The roles of ROS. and ABA. in systemic acquired acclimation. Plant Cell, 27: 64–70.

Mittler, R., S. Vanderauwera, M. Gollery, and F. Van Breusegem, 2004 Reactive oxygen gene network of plants. Trends Plant Sci., 9: 490–498. [CrossRef]

Mittova, V., F.L. Theodoulou, G. Kiddle, L. GÃ³mez, M. Volokita, *et al.,* 2003. Coordinate induction of glutathione biosynthesis and glutathione-metabolizing enzymes is correlated with salt tolerance in tomato. FEBS. Lett., 554: 417-421.

Mittova, V., M. Guy, M. Tal, and M. Volokita, 2004. Salinity upregulates the antioxidative system in rootmitochondria and peroxisomes of the wild salt-tolerant tomato species Lycopersicon pennellii. J. Exp. Bot., 55:1105–1113.

Molassiotis, A.N., T. Sotiropoulos, G. Tanou, G. Kofidis, G. Diamantidis and I. Therios, 2006. Antioxidant and anatomical responses in shoot culture of the apple rootstock MM. 106 treated with NaCl, K.Cl, mannitol or sorbitol. Biol. Plant, 50: 61-68

Moln´ar, ´A., M. Papp, D. Zolt´an Kov´acs, P. B´elteky, D. Ol´ah, G. Feigl, R. Sz˝oll˝osi, Z. R´azga, A. ¨Ord¨og, L. Erdei, A. R´onav´ari, Z. K´onya, and Z. Kolbert, 2020. Nitro-oxidative signalling induced by chemically synthetized zinc oxide nanoparticles (ZnO) NPs. in Brassica species. Chemosphere, 251: 126419.

Monirifar, H., and M. Barghi, 2009. Identification and selection for salt tolerance in alfalfa (Medicago sativa L). ecotypes via physiological traits. Not. Sci. Biol. 1: 63–66. doi: 10.15835/nsb113498

Montrichard, F., F. Alkhalfioui, H. Yano, W.H. Vensel, W.J. Hurkman, and B.B. Buchanan, 2009. Thioredoxin targets in plants: the first 30 years. J. Proteomics., 72:452–474. PMID: 19135183.doi:10.1016/j. jprot.2008.12.002.

Moon, H., B. Lee, G. Choi, S. Shin, D.T. Prasad, O. Lee, S.S. Kwak, D.H. Kim, J. Nam, J. Bahk, J.C. Hong, S.Y. Lee, M.J. Cho, C.O. Lim, and D.J. Yun, 2003. NDP. kinase 2 interacts with two oxidative stress-acivated MAPKs to regulate cellular redox state and enhancesmultiple stress tolerance in transgenic plants. Proc. Natl. Acad. Sci., U. S. A., 100:358–363.

Moons, A., G. Bauw, E. Prinsen, M. van Montagu, and D. van Der Straeten, 1995. Molecular and physiological responses to abscisic acid and salts in roots of salt-sensitive and salt-tolerant Indica rice varietites. Plant Physiol., 107:177–186

Moradbeygi, H., R. Jamei, R. Heidari, and R. Darvishzadeh, 2020. Investigating the enzymatic and non-enzymatic antioxidant defense by applying iron oxide nanoparticles in Dracocephalum moldavica L. plant under salinity stress. Sci. Hortic., 272: 109537.

Moschou, P.N., K.A. Paschalidis, and K.A. Roubelakis- Angelakis, 2008. “Plant polyamine catabolism: the state of the art,” Plant Signaling and Behavior, 3(12):1061–1066.

Moss, J., and M.D. Lane, 1971. The biotin-dependent enzymes. Adv. Enzymol. Relat Areas Mol. Biol., 35: 321-442.

Muchate, N.S., C.N. Ganesh, S.R. Nilima, P. Suprasanna and D.N. Tukaram, 2016. Plant Salt Stress: Adaptive Responses, T.olerance Mechanism and Bioengineering for Salt Tolerance, Bot. Rev. 82:371–406 DOI. 10.1007/s12229-016-9173-y

Muhammad, I., S. Abdullah, A. Muhammad, Y. Qing-Hua, A. Husain and B.L. Feng, 2021. Mechanisms Regulating the Dynamics of Photosynthesis Under Abiotic Stresses, F.rontiers in Plant Science | www.frontiersin.org, 11:615942.

Müller, J., M. Beck, U. Mettbach, G. Komis, G. Hause, D. Menzel, and J. Samaj, 2010. Arabidopsis MPK6 is involved in cell division plane control during early root development, and localizes to the pre-prophase band, phragmoplast, trans-Golgi network and plasma membrane. Plant J. 61:234–248.

Muneer, S., Y.G. Park, A. Manivannan, P. Soundararajan, and B.R. Jeong, 2014. Physiological and proteomic analysis in chloroplasts of Solanum lycopersicum L. under silicon efficiency and salinity stress. Int. J. Mol. Sci. 15: 21803–21824.

Munir N. and F. Aftab, 2011. “Enhancement of salt tolerance in sugarcane by ascorbic acid retreatment,” African Journal of Biotechnology, 10(80):18362–18370.

Munns R. and M. Tester, 2008. “Mechanisms of salinity tolerance,” Annual Review of Plant Biology, 59:651–681.

Munns R. and M. Tester, 2008. “Mechanisms of salinity tolerance,” Annual Review of Plant Biology, 59:651–681

Munns R., 1993. Physiological processes limiting plant growth in saline soil:some dogmas and hypotheses. Plant Cell Environ., 16:15–24.

Munns R., 1993. Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. Plant Cell Environ., 16:15–24.

Munns R., 2005. Genes and salt tolerance: bringing them together. New Phytol., 167:645–663.

Munns R., and M. Gilliham, 2015. Salinity tolerance of crops – what is the cost? New Phytologist, 208: 668–673.

Munns, R., 2002. Comparative physiology of salt and water stress. Plant Cell Environ., 25:239–250.

Munns, R., 2005. “Genes and salt tolerance: bringing them together,” New Phytologist, 167(3):645–663.

Munns, R., and M. Gilliham, 2015. Salinity tolerance of crops what is the cost? New Phytol., 208(3):668–673.

Munns, R., and M. Tester, 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol., 59: 651-681.

Munns, R., and M. Tester, 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol., 59: 651–681. [CrossRef]

Muranaka, S., K. Shimizu, and M. Kato, 2002. Ionic and osmotic effects of salinity on single-leaf photosynthesis in two wheat cultivars with different drought tolerance. Photosynthetica, 40: 201–207. doi: 10.1023/A:1021337 522431

Murty, P.S.S., and K.S. Murty, 1982. Spikelet sterility in relation to nitrogen and carbohydrate contents in rice. Ind. J. Plant Physiol., 25:40–48.

Musa, A. and M. Sowbiya, 2021. Silicon Supplementation Modulates Physiochemical Characteristics to Balance and Ameliorate Salinity Stress in Mung Bean.

Naderi, M.R., and A. Danesh-Shahraki, 2013. Nanofertilizers and their roles in sustainable agriculture. Int J. Agric. Crop Sci., 5:2229–2232.

Nahar, K., and M. Hasanuzzaman, 2009. Germination, growth, nodulation and yield performance of three mung bean varieties under different levels of salinity stress. Green Farming, 2:825–829.

Najafpour, M.M., M.Z. Ghobadi, A.W. Larkum, J.R. Shen, and S.I. Allakhverdiev, 2015. The biological water-oxidizing complex at the nano-bio interface. Trends Plant Sci. 20: 559–568. doi: 10.1016/j.tplants.2015.06.005.

Nalousi, A.M., S. Ahmadiyan, A. Hatamzadeh, and M. Ghasemnezhad, 2012. “Protective role of exogenous nitric oxide against oxidative stress induced by salt stress in bell-pepper (Capsicum annum L).,” American-Eurasian Journal of Agricultural & Environmental Science, 12(8):1085–1090.

Navakoudis, E., C. L¨utz, C. Langebartels, U. L¨utz-Meindl, and K. Kotzabasis, 2003. “Ozone impact on the photosynthetic apparatus and the protective role of polyamines,” Biochimica et Biophysica Acta—General Subjects, 1621(2):160–169.

Navari-Izzo, F., M.F. Quartacci, and S.gherri, 2002. Lipoic acid: a unique antioxidant in the detoxification of activated oxygen species. Plant Physiol. Biochem., 40: 463-470.

Navari-Izzo, F., R. Izzo, and M.F. Quartacci, 1988. Phospholipid and sterol alterations associated with salinity and water stress in maize roots. Plant Physiol (Life Science Advance). 7: 137-142.

Navarro, L., P. Dunoyer, and F. Jay, 2006. A. plant miRNA. Contributes to antibacterial resistance by repressing auxin signaling. Science, 312: 436–439.

Nazar, R., N. Iqbal, A. Masood, S. Syeed, and N.A. Khan, 2011. Understanding the significance of sulfur in improving salinity tolerance in plants. Environ. Exp. Bot., 70: 80-87.

Nazar, R., N. Iqbal, S. Syeed, and N.A. Khan, 2011. “Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars,” Journal of Plant Physiology, 168(8):807–815.

Nazar, R., N. Iqbal, S. Syeed, and N.A. Khan, 2011. Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars. J. Plant Physiol., 168: 807-815.

Nazar, R., N. Iqbal, S. Syeed, and N.A. Khan, 2011. Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars. J. Plant Physiol., 168: 807–815. [CrossRef] [PubMed].

Ndimba, B.K., S. Chivasa, W.J. Simon, and A.R. Slabas, 2005. Identification of Arabidopsis salt and osmotic stress responsive proteins using two dimensional difference gel electrophoresis and mass spectrometry. Proteomics, 5:4185–4196.

Nietzel, T. J. Mostertz, F. Hochgräfe, and M. Schwarzländer, 2017. Redox regulation of mitochondrial proteins and proteomes by cysteine thiol switches. Mitochondrion; 33:72–83. PMID: 27456428. doi:10.1016/j.mito.2016.07.010.

Nikiforova, V.J., J. Kopka, V. Tolstikov, O. Fiehn, L. Hopkins, *et al.,* 2005. Systems rebalancing of metabolism in response to sulfur deprivation, as revealed by metabolome analysis of Arabidopsis plants. Plant Physiol., 138: 304-318.

Nishikawa, T., D. Edelstein, and M. Brownlee, 2000. The missing link: A. single unifying mechanism for diabetic complications. Kidney Int., 58 (Suppl):S26–S30. https://doi.org/10.1046/j.1523-1755.2000.07705.x.

Niu Xiaomu, N.X., R.A. Bressan, P.M. Hasegawa, and J.M. Pardo, 1995. "Ion homeostasis in NaCl stress environments," Plant Physiology, 109(3):735–742,

Noji, M., K. Saito, 2007. Metabolic engineering of sulfur assimilation in plants. In: applications of plant metabolic engineering. (ed.) Verpoorte R, A.lfermann AW, J.ohnson TS. Springer, Netherlands, 297-309.

Noreen, Z., M. Ashraf, and N.A. Akram, 2010. Salt-induced modulation in some key gas exchange characteristics and ionic relations in pea (Pisum sativum L). and their use as selection criteria. Crop Pasture Sci. 61: 396–378. doi: 10.1071/CP09255.

Nounjana, N., P.T. Nghiab, and P. Theerakulpisuta, 2012. Exogenous proline and trehalose promote recovery of rice seedlings from salt-stress and differentially modulate antioxidant enzymes and expression of related genes. J. Plant Physiol., 169:596–604.

Nxele, X., A. Klein, and B.K. Ndimba, 2017. Drought and salinity stress alters ROS. accumulation, water retention, and osmolyte content in sorghum plants. S. Afr. J. Bot., 108: 261–266. [CrossRef]

Oates, P.J., 2002. Polyol pathway and diabetic peripheral neuropathy. Int. Rev. Neurobiol., 50:325–392.

Oertli, J.J., 1968. Extracellular salt accumulation a possible mechanism of salt injury in plants. Agrochimica, 12:461–469.

Oertli, J.J., 1991. Nutrient management under water and salinity stress. In: Proceeding of the symposium on nutrient management for sustained productivity. Dept Soils Punjab Agric UnverLudhiana, India, 138–165.

Ogawa, S., and S. Mitsuya 2012. S-methylmethionine is involved in the salinity tolerance of Arabidopsis thaliana plants at germination and early growth stages. Physiol. Plant, 144: 13-19.

Oh, D.-H., S.Y. Lee, R.A. Bressan, D.-J. Yun, and H.J. Bohnert, 2010. "Intracellular consequences of SOS1 deficiency during salt stress," Journal of Experimental Botany, 61(4):1205–1213.

Ohnishi, N., and N. Murata, 2006. Glycine betaine counteracts the inhibitory effects of salt stress on the degradation and synthesis of D1 proteinduring photoinhibition in Synechococcussp. PCC. 7942. Plant Physiol., 141:758–765

Omoto, E., M. Taniguchi, and H. Miyake, 2010. Effects of salinity stress on the structure of bundle sheath and mesophyll chloroplasts in NAD-malic enzyme and PCK. type C4 plants. Plant Prod. Sci. 13: 169–176. doi: 10.1626/pps.13.169.

Ortiz-Espín, A., R. Iglesias-Fernández, A. Calderón, P. Carbonero, F. Sevilla, and A. Jiménez, 2017. Mitochondrial AtTrxo1 is transcriptionally regulated by AtbZIP9 and AtAZF2 and affects seed germination under saline conditions. J. Exp Bot PMID: 28184497; 68:1025–1038. doi:10.1093/jxb/erx012.

Othman, Y., G. Al-Karaki, A.R. Al-Tawaha, and A. Al-Horani, 2006. Variation in germination and ion uptake in barley genotypes under salinity conditions. World J. Agric., Sci 2:11–15.

Pang, Q., J. Guo, S. Chen, Y. Chen, L. Zhang, M. Fei, S. Jin, M. Li, Y. Wang, and X. Yan, 2012. Effect of salt treatment on the glucosinolate-myrosinase system in Thellungiella salsuginea. Plant soil 355: 363-374.

Pang, Q., S. Chen, S. Dai, Y. Chen, Y.Wang, and X. Yan, 2010. "Comparative proteomics of salt tolerance in Arabidopsis thaliana and Thellungiella halophila," Journal of Proteome Research, 9(5):2584–2599.

Pang, Q., S. Chen, S. Dai, Y. Wang, Y. Chen, and X. Yan, 2010. Comparative proteomics of salt tolerance in Arabidopsis thaliana and Thellungiella halophila. J. Proteome Res 9:2584–2599

Pannaga, K., R. Kosala, F. Rochus, H.S. Prakash, S. Lukas and M.K. Mathew, 2009. The role of root apoplastic transport barriers in salt tolerance of rice (Oryza sativa L)., Plant a 2009. 230:119–134 DOI. 10.1007/s00425-009-0930-6.

Paramo, L.A., A.A. Feregrino-P´erez, Guevara, R., Mendoza, S., and Esquivel, K., 2020. Nanoparticles in agroindustry: applications, toxicity, challenges, and trends. Nanomaterials, 10: 1654.

Parida, A.K., A.B. Das, and B. Mittra, 2004. Effects of salt on growth, ion accumulation photosynthesis and leaf anatomy of the mangrove, B.ruguiera parviflora. Trees-Struct Funct., 18:167–174.

Parida, A.K., A.B. Das, and P. Mohanty, 2004. "Investigations on the antioxidative defence responses to NaCl stress in a mangrove, B.ruguiera parviflora: differential regulations of isoforms of some antioxidative enzymes," Plant Growth Regulation, 42(3):213–226.

Parida, A.K., and A.B. Das 2005. Salt tolerance and salinity effect on plants: a review. Ecotoxicol. Environ., Saf., 60:324–349.

Parida, A.K., and A.B. Das, 2005. Salt tolerance and salinity effects on plants: A Review. Ecotoxicol. Environ. Saf., 60: 324–349. [CrossRef] [PubMed].

Parihar, P., S. Samiksha, S. Rachana, P.S. Vijay and M.P. Sheo 2015. Effect of salinity stress on plants and its tolerance strategies: a review, Environ Sci. Pollut. Res., 22:4056–4075 DOI. 10.1007/s11356-014-3739-1.

Parihar, P., S. Singh, R. Singh, V.P. Singh, and S.M. Prasad, 2015. Effect of salinity stress on plants and its tolerance strategies: A Review. Environ. Sci. Pollut. Res., 22: 4056–4075. [CrossRef] [PubMed].

Paz, R.C., H. Reinoso, F.D. Espasandin, F.A. González Antivilo, P.A. Sansberro, R.A. Rocco, O.A.Ruiz, and A.B. Menendez, 2014. Akaline, saline and mixed saline–alkaline stresses induce physiological and morpho-anatomical changes in Lotus tenuis shoots. Plant Biol., 16: 1042–1049. [PubMed]

Peng, H., Z.hang, J., 2009. Plant genomic DNA. methylation in response to stresses: potential applications and challenges in plant breeding. Prog. Nat. Sci., 19: 1037–1045.

Peng, Z., M.Wang, F. Li, H. Lv, C. Li, and G. Xia, 2009. Aproteomic study of the response to salinity and drought stress in an introgression strain of bread wheat. Mol Cell Proteomics 8:2676–2686

Per, T.S., N.A. Khan, A. Masood, and M. Fatma, 2016. Methyl jasmonate alleviates cadmium-induced photosynthetic damages through increased S-assimilation and glutathione production in mustard. Front. Plant Sci., 7, 1933. [CrossRef]

Per, T.S., N.A. Khan, P.S. Reddy, A. Masood, M. Hasanuzzaman, M.I.R. Khan, and N.A. Anjum, 2017. Approaches in modulating proline metabolism in plants for salt and drought stress tolerance, P.hytohormones, mineral nutrients and transgenics. Plant Physiol. Biochem., 115:126–140. [CrossRef]

Pereira, A.D.E.S., C.O. Halley, F.F. Leonardo and S. Catherine, 2021. Nanotechnology Potential in Seed Priming for Sustainable Agriculture, Nanomaterials, 11: 267. https://doi.org/10.3390/nano11020267 www.mdpi.com/journal/nanomaterials

Pérez-López, U., A. Robredo, M. Lacuesta, C. Sgherri, A. Mena-Petite, *et al.,* 2010. Lipoic acid and redox status in barley plants subjected to salinity and elevated CO2. Physiol Plant, 139: 256-268.

Persak, H., and A. Pitzschke, 2013. Tight interconnection and multi-level control of Arabidopsis MYB44 in MAPK. cascade signalling. PLoS. One 8:e57547.

Perveen, S., M. Shahbaz, and M. Ashraf, 2010. Regulation in gas exchange and quantum yield of photosystem II. (PSII) in salt-stressed and non-stressed wheat plants raised from seed treated with triacontanol. Pakistan J. Bot. 42: 3073–3081.

Pinheiro, H.A., J.V. Silva, L. Endres, V.M. Ferreira, C.A. de Câmara, F.F. Cabral, *et al.,* 2008. Leaf gas exchange, chloroplastic pigments and dry matter accumulation in castor bean (Ricinus communis L. seedlings subjected to salt stress conditions. Ind. Crops Prod. 27: 385–392. doi: 10.1016/j.indcrop.2007.10.003.

Piotr, S., and K. Grazyna, 2005. Antioxidant defense in the leaves of C3 and C4 plants under salinity stress. Physiol Plant, 125:31–40.

Pitzschke, A., A. Djamei, F. Bitton, and H. Hirt, 2009. A. major role of the MEKK1-MKK1/2-MPK4 pathway in ROS. signalling. Mol. Plant, 2: 120–137.

Popova, L.P., Z.G. Stoinova, and L.T. Maslenkova, 1995. "Involvement of abscisic acid in photosynthetic process in Hordeum vulgare L. during salinity stress," Journal of Plant Growth Regulation, 14(4):211–218.

Pravin V. Jadhav, P.rashant B. Kale, M.angesh P.M., C.G. Deepti, S.D. Mahendra, S.M. Shyam, S.N. Ravindra, S.M. Shyamsundar, V. Philips, G.M. Joy and G.D. Raviprakash, 2018. Abiotic Stress Tolerance Mechanisms in Plants, P.ages 1–84 Edited by: Gyanendra K. Rai, R.anjeet Ranjan Kumar and Sreshti Bagati Copyright © Narendra Publishing House, Delhi, India.

Prodhan, M.A., P.M. Finnegan, and H. Lambers, 2019. How does evolution in phosphorus-impoverished landscapes impact plant nitrogen and sulfur assimilation? Trends Plant Sci. 24: 69–82. [CrossRef]

Pulido, P., R. Cazalis, F.J. Cejudo, and A. Ame, 2009. An antioxidant redox system in the nucleus of wheat seed cells suffering oxidative stress. Plant J., 132–145. PMID: 18786001. doi:10.1111/j.1365- 313X.2008.03675.x.

Qadir, M., and S. Schubert, 2002. Degradation processes and nutrient constraints in sodic soils. Land Degrad. Dev., 13:275–294

Qiu, Q.S., Y. Guo, F.J. Quintero, J.M. Pardo, K.S. Schumaker, and J.K. Zhu, 2004. Regulation of vacuolar Naþ/Hþ exchange in Arabidopsis thaliana by the salt-overly sensitive (SOS) pathway. J. Biol. Chem., 279:207–215.

Quan, R., H. Lin, I. Mendoza, Y. Zhang, W.Cao, Y. Yang, M. Shang, S. Chen, J.M. Pardo, and Y. Guo, 2007. SCaBP8/CBL10, a putative calcium sensor, interacts with theprotein kinase SOS2 to protect Arabidopsis shoots from salt stress. Plant Cell, 19:1415–1431.

Queval, G., D. Thominet, H. Vanacker, M. Miginiac-Maslow, and B. GakiÃ¨re, *et al.,* 2009. H2 O2 - activated up-regulation of glutathione in Arabidopsis involves induction of genes encoding enzymes involved in cysteine synthesis in the chloroplast. Mol. Plant, 2: 344-356.

Quintero, F.J., M. Ohta, H. Shi, J.-K. Zhu, and J.M. Pardo, 2002. "Reconstitution in yeast of the Arabidopsis SOS. signaling pathway for Na+ homeostasis," Proceedings of the National Academy of Sciences of the United States of America, 99(13):9061–9066.

Qureshi, A.S., M. Qadir, N. Heydari, H. Turral and A. Javadi, 2007. A Review of management strategies for salt-prone land and water resources in Iran. Colombo, S.ri Lanka: International Water Management Institute. 30p. (IWMI) Working Paper 125.

Rahman, S., H. Miyake, and Y. Takeoka, 2002. "Effects of exogenous glycinebetaine on growth and ultrastructure of salt-stressed rice seedlings (Oryza sativa L).," Plant Production Science, 5(1):33–44,

Rahman, S.U., W. Xiaojie, S. Muhammad, B. Owais, L. Yanliang, and C. Hefa, 2022. A Review of the influence of nanoparticles on the physiological and biochemical attributes of plants with a focus on the absorption and translocation of toxic trace elements, E.nvironmental Pollution 310 119916

Rahnama, A., R.A. James, K. Poustini, and R. Munns, 2010. "Stomatal conductance as a screen for osmotic stress tolerance in durum wheat growing in saline soil," Functional Plant Biology, 37(3):255–263.

Rais, L., A. Masood, A. Inam, and N. Khan, 2013. Sulfur and nitrogen co-ordinately improve photosynthetic efficiency, growth and proline accumulation in two cultivars of mustard under salt stress. J. Plant Biochem. Physiol., 1. [CrossRef]

Rambla, J.L., F. Vera-Sirera, M.A. Bl´azquez, J. Carbonell, and A. Granell, 2010. “Quantitation of biogenic tetraamines in Arabidopsis thaliana,” Analytical Biochemistry, 397(2):208–211,

Rania M.A.N., A.K. Hedaya, E.G. Ahmed, J.A. Juan, S. Agnieszka, U. Christian and T.A. Magdi, 2020 . Physiological and a natomical Mechanisms in Wheat to Cope with Salt Stress Induced by Seawater, Plant s, 9, 237; doi: 10.3390/plants9020237 www.mdpi.com/journal/plants

Rapala-Kozik, M., E. Kowalska, and K. Ostrowska, 2008. Modulation of thiamine metabolism in Zea mays seedlings under conditions of abiotic stress. J. Exp. Bot., 59: 4133-4143.

Rapala-Kozik, M., N. Wolak, A.K. Kujda and M. Banas, 2012. The upregulation of thiamine (vitamin B1. biosynthesis in Arabidopsis thaliana seedlings under salt and osmotic stress conditions is mediated by abscisic acid at the early stages of this stress response. BMC. Plant Biol., 12: 1-21.

Rasheed, F., A.A. Naser, M. Asim, S. Adriano, and A.K. Nafees, 2020. The key roles of salicylic acid and sulfur in plant salinity stress tolerance, Journal of Plant Growth Regulation https://doi.org/10.1007/s00344-020-10257-3.

Rasoulnia, A., M.R. Bihamta, S.A. Peyghambari, H. Alizadeh, and A. Rahnama, 2011. Proteomic response of barley leaves to salinity. Mol. Biol. Rep., 38:5055–5063.

Rastogi, A., M. Zivcak, O. Sytar, H.M. Kalaji, X. He, S. Mbarki, and M. Brestic, 2017. Impact of metal and metal oxide nanoparticles on plant: a critical review. Front Chem., 5:78. https://doi.org/10.3389/ fchem.2017.00078.

Rawia Eid, A., L.S. Taha, and S.M.M. Ibrahiem, 2011. “Alleviation of adverse effects of salinity on growth, and chemical constituents of marigold plants by using glutathione and ascorbate,” Journal of Applied Sciences Research, 7:714–721.

Raza, S.H., H.U.R. Athar, and M. Ashraf, 2006. Influence of exogenously applied glycinebetaine on the photosynthetic capacity of two differently adapted wheat cultivars under salt stress. Pakistan J. Bot. 38: 341–351.

Reddy, M.P., S. Sanish, and E.R.R. Iyengar, 1992. “Photosynthetic studies and compartmentation of ions in different tissues of Salicornia brachiata Roxb. under saline conditions,” Photosynthetica, 26:173–179.

Reichheld, J.P., C. Riondet, V. Delorme, F. Vignols, and Y. Meyer, 2010. Thioredoxins and glutaredoxins in development. Plant Sci., 178:420–423. doi:10.1016/j.plantsci.2010.03.001.

Reichheld, J.P., E. Meyer, M. Khafif, G. Bonnard, and Y. Meyer, 2005. AtNTRB. is the major mitochondrial thioredoxin reductase in Arabidopsis thaliana. FEBS. Lett., 579:337–342. doi:10.1016/j. febslet.2004.11.094.

Renberg, L., A.I. Johansson, T. Shutova, H. Stenlund, A. Aksmann, J.A. Raven, P. Gardeström, T. Moritz, and G. Samuelsson, 2010. A. metabolomic approach to study major metabolite changes during acclimation to limiting CO2 in Chlamydomonas reinhardtii. Plant Physiol., 154: 187–196.

Rico, C.M., M.I. Morales, R. McCreary, H. Castillo-Michel, A.C. Barrios, J. Hong, A. Tafoy, W.Y. Lee, A. Varela-Ramirez, J.R. Peralta-Videa, and J.L. Gardea-Torresdey, 2013. Cerium oxide nanoparticles modify the antioxidative stress enzyme activities and macromolecule composition in rice seedlings. Environ. Sci. Technol., 47(24):14110–14118. https://doi.org/10.1021/es4033887

Riffat, A.L.I.A., M. Sajid, and A. Ahmad, 2020. Alleviation of adverse effects of salt stress on growth og maize Zea mays L. by sulfur supplementation. Pak. J. Bot., 523: 763–773.

Rocha, F., E.L.-B. Manuel, P. Paulo and M.-R. Miriam, 2020. Cyanobacteria as a Nature-Based Biotechnological Tool for Restoring Salt-Affected Soils, A.gronomy 10, 1321; doi:10.3390/agronomy10091321 www.mdpi.com/journal/agronomy

Rodriguez, M.C., M. Petersen, and J. Mundy, 2010. Mitogen-activated protein kinase signaling in plants. Annu. Rev. Plant Biol., 61:621–649.

Rogers, M.E., C.M. Grieve, and M.C. Shannon, 2003. Plant growth and ion relations in lucerne (Medicagosativa L). in response to the combined effects of NaCl and P. Plant Soil, 253:187–194.

Romero, L., A. Belakbir, L. Ragala, and J. M. Ruiz, 1997. Response of plant yield and leaf pigments to saline conditions: effectiveness of different rootstocks in melon plants (Cucumis melo L). Soil Sci. Plant Nutr. 43, 855–862. doi: 10.1080/00380768.1997.10414652

Romero, L.C., J.R. Domínguez-Solis, G. Gutierrez-Alcala, and C. Gotor, 2001. Salt regulation of O-acetylserine(thiollyase in Arabidopsis thaliana and increased tolerance in yeast. Plant Physiol Biochem., 39: 643-647.

Romero-Aranda, M.R., O. Jurado, and J. Cuartero, 2006. Silicon alleviates the deleterious salt Effect on tomato plant growth by improving plant water status. J. Plant Physiol., 163: 847–855. [CrossRef] [PubMed].

Romero-Aranda, R., T. Soria, and S. Cuartero, 2001. Tomato plant-water uptake and plant-water relationships under saline growth conditions. Plant Sci., 160:265–272.

Rossi, L., W. Zhang, L. Lombardini, and X. Ma, 2016. The impact of cerium oxide nanoparticles on the salt stress responses of Brassica napus L. Environ. Pollut., 219:28–36.

Roxas, V.P., S.A. Lodhi, D.K. Garrett, J.R. Mahan, and R.D. Allen, 2000. Stress tolerance in transgenic tobacco seedlings that overexpress glutathione S-transferase/glutathione peroxidase. Plant Cell. Physiol., 41: 1229–1234. [CrossRef]

Roy, M. and R. Wu, 2002. “Overexpression of S-adenosylmethionine decarboxylase gene in rice increases polyamine level and enhances sodium chloride-stress tolerance,” Plant Science, 163(5):987–992.

Roy, M. and R. Wu, 2002. Overexpression of S-adenosylmethionine decarboxylase gene in rice increases polyamine level and enhances sodium chloride-stress tolerance. Plant Sci., 163: 987-992.

Roy, M., and R. Wu, 2001. Arginine decarboxylase transgene expression and analysis of environmental stress tolerance in transgenic rice. Plant Sci., 160: 869-875.

Roy, S.J., S. Negr˜ao, and M. Tester, 2014. “Salt resistant crop plants,” Current Opinion in Biotechnology, 26:115–124.

Rozeff, N., 1995. Sugarcane and salinity—a review paper. Sugarcane, 5:8–19.

Rozema, J. and T. Flowers, 2008. “Ecology: crops for a salinized world,” Science, 322(5907):1478–1480.

Ruiz, J.M., and E. Blumwald 2002. Salinity-induced glutathione synthesis in Brassica napus. Planta, 214: 965-969.

Sabaghnia, N., and M. Janmohammadi, 2014. Effect of nano-silicon particles application on salinity tolerance in early growth of some lentil genotypes. Ann UMCS. Biol., 69:39–55.

Sabir, P., M. Ashraf, M. Hussain, and A. Jamil, 2009. Relationship of photosynthetic pigments and water relations with salt tolerance of proso millet (Panicum Miliaceum L). accessions. Pakistan J. Bot., 41: 2957–2964.

Sachdev, S. and S. Ahmad, 2021. Role of Nanomaterials in Regulating Oxidative Stress in Plants Springer Nature Switzerland AG. 2021 J. M. Al-Khayri *et al.,* (eds), N.anobiotechnology, https://doi.org/10.1007/978-3-030-73606-4_13.

Sadak, S.h., A.A. Abd El-Monem, H.M.S. El-Bassiouny and Nadia M. Badr, 2012. Physiological response of sunflower (Helianthus annuus L). to exogenous arginine and putrescine treatments under salinity Stress. Journal of Applied Sciences Research, 8(10): 4943-4957.

Sade, N., M. Gebretsadik, R. Seligmann, A. Schwartz, R. Wallach, and M. Moshelion, 2010. The role of tobacco aquaporin1 in improving water use efficiency, hydraulic conductivity, and yield production under salt stress. Plant Physiol. 152, 245–254. doi: 10.1104/pp.109.145854.

Sah, S.K., K.R. Reddy, and J. Li, 2016. Abscisic acid and abiotic stress tolerance in crop plants. Front. Plant Sci., 7, 571. [CrossRef].

Saha, P., P. Chatterjee, and A.K. Biswas, 2010. NaCl pretreatment alleviates salt stress by enhancement of antioxidant defense system and osmolyte accumulation in mungbean (Vigna radiata L.Wilczek. Indian J. Exp. Biol., 48:593–600.

Sairam, R.K. and A. Tyagi, 2004. “Physiology and molecular biology of salinity stress tolerance in plants,” Current Science, 86(3):407–421

Sairam, R.K., and A. Tyagi, 2004. Physiology and molecular biology of salinity stress tolerance in plants. Curr. Sci., 86: 407-412.

Sairam, R.K., K.V. Roa, and G.C. Srivastava, 2002. Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. Plant Sci., 163:1037–1046.

Sakamoto, A., and M.N. Alia, 1998. Metabolic engineering of rice leading to biosynthesis of glycine betaine and tolerance to salt and cold. Plant Mol. Biol., 38:1011–1019.

Salim, B., A. Abou El-Yazied, Y. Salama, A. Raza, and H.S. Osman, 2021. Impact of silicon foliar application in enhancing antioxidants, growth, flowering and yield of squash plants under deficit irrigation condition. Ann. Agricult. Sci. 66: 176–183.

Samajova, O., O. Plihal, M. Al-Yousif, H. Hirt, and J. Samaj, 2013. Improvement of stress tolerance in plants by genetic manipulation of mitogen activated protein kinases. Biotechnol. Adv., 31:118–128.

Sánchez-Aguayo, I., J.M. RodrÃguez-GalÃ¡n, R. GarcÃa, J. Torreblanca, and J.M. Pardo, 2004. Salt stress enhances xylem development and expression of S-adenosylL-methionine synthase in lignifying tissues of tomato plants. Planta, 220: 278- 285.

Sanders, D., 2000. “Plant biology: the salty tale of Arabidopsis,” Current Biology, 10(13):R486–R488,

Santos, C.V., 2004. Regulation of chlorophyll biosynthesis and degradation by salt stress in sunflower leaves. Sci. Hortic. 103, 93–99. doi: 10.1016/j.scienta.2004.04.009.

Santos, M.R.D., M.A. Martinez, S.L.R. Donato, and E.F. Coelho, 2014. ’Tommy Atkins’ mango yield and photosynthesis under water deficit in semiarid region of Bahia. Rev. Brasil. Engenharia Agrícola Ambiental, 18:899–907.

Sattar, A., M.A. Cheema, T. Abbas, A. Sher, M. Ijaz, and M. Hussain, 2017. Separate and combined effects of silicon and selenium on salt tolerance of wheat plants. Russ. J. Plant Physl., 64: 341–348. [CrossRef]

Sauter, M., B. Moffatt, M.C. Saechao, R. Hell, and M. Wirtz, 2013. Methionine salvage and S-adenosylmethionine: essential links between sulfur, ethylene and polyamine biosynthesis. Biochem J., 451: 145-154.

Sawada, H., I.-S. Shim, and K. Usui, 2006. “Induction of benzoic acid 2-hydroxylase and salicylic acid biosynthesis-Modulation by salt stress in rice seedlings,” Plant Science, 171(2): 263– 270.

Saxena, S.C., H. Kaur, P. Verma *et al.,* 2013. “Osmoprotectants: potential for crop improvement under adverse conditions,” in PlantAcclimation to Environmental Stress):197–232, S.pringer, New York, N.Y., USA.

Schmidtmann, E., A.-C. König, A. Orwat, D. Leister, M. Hartl, and I. Finkemeier, 2014. Redox regulation of Arabidopsis mitochondrial citrate synthase. Mol Plant; 7:156–169. PMID: 24198232. doi:10.1093/mp/sst144.

Schroeder, J.I., E. Delhaize, W.B. Frommer *et al.,* 2013. “Using membrane transporters to improve crops for sustainable food production,” Nature, 497:60–66.

Schurmann, P., and J.P. Jacquot, 2000. Plant thioredoxin systems revisited. Annu Rev Plant Physiol Plant Mol. Biol., 51: 371-400.

Schwarzländer, M., M.D. Fricker, C. Müller, L. Marty, T. Brach, J. Novak, L.J. Sweetlove, R.Hell, and A.J. Meyer, 2008. Confocal imaging of glutathione redox potential in living plant cells. J. Microsc., 231: 299–316. [CrossRef] [PubMed]

Schweighofer, A., V. Kazanaviciute, E. Scheikl, M. Teige, R. Doczi, H. Hirt, M. Schwanninger, M. Kant, R. Schuurink, F. Mauch, A. Buchala, F. Cardinale, and I. Meskienea, 2007. The PP2C-type phosphatase AP2C1, which negatively regulates MPK4and MPK6, modulates seedlings. Plant Sci., 175:631–641.

Seemann, J.R., and C. Critchley, 1985. Effects of salt stress on the growth, ion contents, stomatal behaviour and photosynthetic capacity of a salt sensitive species, P.haseolus vulgaris L. Planta, 164:66–69.

Sehar, Z., A. Masood, and N.A. Khan, 2019. Nitric oxide reverses glucose-mediated photosynthetic repression in wheat (Triticum aestivum L). under salt stress. Environ. Exp. Bot., 161: 277–289. [CrossRef]

Semida, W.M., R.S. Taha, M.T. Abdelhamid, and M.M. Rady, 2014. Foliar-applied α-tocopherol enhances salt-tolerance in Vicia faba L. plants grown under saline conditions. S. Afr. J. Bot., 95: 24–31. [CrossRef]

Semiz, G.D., A. Ünlukara, E. Yurtseven, D.L. Suarez, and I. Telci, 2012. Salinity impact on yield, water use,mineral and essential oil contentof fennel (Foeniculum vulgare MilL). J. Agric Sci., 18:177–186.

Sengupta, S., and A.L. Majumder, 2009. Insight into the salt tolerance factors of a wild halophytic rice Porteresia coarctata: a physiological and proteomic approach. Planta, 229:911–929.

Serrato, A.J., and F.J. Cejudo, 2003. Type-h thioredoxins accumulate in the nucleus of developing wheat seed tissues suffering oxidative stress. Planta; 217:392–399. PMID: 14520565. Doi: 10.1007/ s00425-003-1009-4.

Serrato, A.J., J.M. Pérez-Ruiz, M.C. Spínola, and F.J. Cejudo 2004. A. novel NADPH. thioredoxin reductase, localized in the chloroplast, which deficiency causes hypersensitivity to abiotic stress in Arabidopsis thaliana. J. Biol. Chem., 279: 43821-43827.

Seth, C.S., T. Remans, E. Keunen, M. Jozefczak, H. Gielen, K. Opdenakker, and A. Cuypers, 2012. Phytoextraction of toxic metals: A. central role for glutathione. Plant Cell Environ. 35: 334–346. [CrossRef]

Sewelam, N., K. Kazan, and P.M. Schenk, 2016Global plant stress signaling: Reactive oxygen species at the cross-road. Front. Plant Sci., 7, 187. [CrossRef]

Shabala, S., O. Babourina, and I. Newman, 2000. Ion-Specific Mechanisms of Osmoregulation in Bean Mesophyll Cells. Journal of Experimental Botany, 51: 1243-1253. https://doi.org/10.1093/jexbot/51.348.1243

Shalata, A., V. Mittova, M. Volokita, M. Guy, and M. Tal, 2001. Response of the cultivated tomato and its wild salt-tolerant relative Lycopersicon pennellii to salt-dependent oxidative stress: The root antioxidative system. Physiol Plant, 112: 487-494.

Shanker, A.K., and B. Venkateswarlu 2011. Abiotic stress in plants—mechanisms and adaptations. In: TechJaneza Trdine 9, 51000 Rijeka, Croatia.

Sharma, A., V. Kumar, B. Shahzad, M. Ramakrishnan, G.P. Singh Sidhu, A.S. Bali, *et al.,* 2020. Photosynthetic response of plants under different abiotic stresses: a review. J. Plant Growth Regul. 39: 509–531. doi: 10.1007/s00344-019-10018-x

Shevyakova, N.I., L.I. Musatenko, L.A. Stetsenko, *et al.,* 2013. "Effects of abscisic acid on the contents of polyamines and proline in common bean plants under salt stress," Russian Journal of Plant Physiology, 60:200–211.

Shi, H., and J.K. Zhu, 2002. SOS4, a pyridoxal kinase gene, is required for root hair development in Arabidopsis. Plant Physiol., 129:585–593.

Shi, H., F.J. Quintero, J.M. Pardo, and J.-K. Zhu, 2002. "The putative plasma membrane Na+/H+ antiporter SOS1 controls longdistance Na+ transport in plants," Plant Cell, 14(2):465–477.

Shi, H., M. Ishitani, C. Kim, and J.-K. Zhu, 2000. "The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter," Proceedings of the National Academy of Sciences of the United States of America, 97(12): 6896–6901.

Shi, H., M. Ishitani, C. Kim, and J.K. Zhu, 2000. The Arabidopsis thaliana salt tolerance gene SOS1 encodes a putative Na+/H+ antiporter. Proc. Natl. Acad. Sci. USA. 97:6896–6901.

Shi, Y., Y. Wang, T.J. Flowers, and H. Gong, 2013. "Silicon decreases chloride transport in rice (Oryza sativa L). in saline conditions," Journal of Plant Physiology, 170(9):847–853.

Shi, Y., Y. Zhang, H. Yao, J. Wu, H. Sun, and H. Gong, 2014Silicon improves seed germination and alleviates oxidative stress of bud seedlings in tomato under water deficit stress. Plant Physiol. Biochem., 78: 27–36. [CrossRef]

Shrivastava, P., and R. Kumar, 2014. Soil salinity: a serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. Saudi Journal of Biological Science, 22: 123–131.

Shu, S., S.R. Guo, and L.Y. Yuan, 2012. "A Review: polyamines and photosynthesis," in Advances in Photosynthesis—Fundamental Aspects, M. M. Najafpour, (E.d.)439–464, I.nTech, R.ijeka, Croatia.

Shulaev, V., D. Cortes, G. Miller, and R. Mittler 2008. Metabolomics for plant stress response. Physiol Plant, 132:199–208.

Siddiqui, H., K.B.M. Ahmed, F. Sami, and S. Hayat, 2020. Silicon nanoparticles and plants: current knowledge and future perspectives. Sustain. Agric. Rev., 41: 129–142.

Siddiqui, M.H., and M.H. Al-Whaibi, 2014. Role of nano-SiO2 in germination of tomato (Lycopersicum esculentum seeds milL). Saudi J. Biol. Sci., 21:13–17.

Siddiqui, M.H., M.H. Al-Whaibi, M. Faisal, and A.A. Al Sahli, 2014. Nano-silicon dioxide mitigates the adverse effects of salt stress on Cucurbita pepo L. Environ. Toxicol. Chem., 33:2429–2437.

Silberbush, M., J. Ben-Asher, and J.E. Ephrath, 2005. A. model for nutrient and water flow and their uptake by plants grown in a soilless culture. Plant Soil, 271(1-2):309–319.

Singh, A., I. Hussain, N.B. Singh, and H. Singh, 2019. Uptake, translocation and impact of green synthesized nanoceria on growth and antioxidant enzymes activity of Solanum lycopersicum L. Ecotoxicol. Environ. Saf. 182, 109410.

Singh, M., V.P. Singh, and S.M. Prasad, 2016. Responses of photosynthesis, nitrogen and proline metabolism to salinity stress in Solanum lycopersicum under different levels of nitrogen supplementation. Plant Physiol. Biochem., 109: 72–83. [CrossRef]

Singh, S., V.P. Singh, S.M. Prasad, S. Sharma, N. Ramawat, and N.K. Dubey, 2019. Interactive effect of silicon (Si. and salicylic acid (SA) in maize seedlings and their mechanisms of cadmium (Cd. toxicity alleviation. J. Plant Growth Regul. 38: 1587–1597.

Singha, R.K., S. Debanjana, S. Milan, N.M. Udit, C. Jyoti, P.B. Laxmi, L. Devidutta, C. Subhash, K. Vivek, D.I. Prajjal, P. Saurabh, V. Pavla, G. Aayushi, B. Marian and E. Ayman, 2021. Crucial Cell Signaling Compounds Crosstalk and Integrative Multi-Omics Techniques for Salinity Stress Tolerance in Plants, F.rontiers in Plant Science, www.frontiersin.org, 12: 670369.

Singla-Pareek, S.L., M.K. Reddy and S.K. Sopory, 2003. Genetic engineering of the glyoxalase pathway in tobacco leads to enhanced salinity tolerance, P.NAS. December 9, 100 (25) 14673.

Snapp, S.S., C. Shennan, and A.V. Bruggen 1991. Effects of salinity on severity of infection by Phytophthora parasitica Dast., ion concentrations and growth of tomato, L.ycopersicon esculentum Mill. New Phytologist, 119: 275–284.

Sobhanian, H., N. Motamed, F.R. Jazii, T. Nakamura, and S. Komatsu, 2010a. Salt stress induced differential proteome and metabolome response in the shoots of Aeluropus lagopoides (Poaceae., a halophyte C4 plant. J. Proteome Res., 9:2882–2897.

Sobhanian, H., R. Razavizadeh, Y. Nanjo, A.A. Ehsanpour, F.R. Jazii, N. Motamed, and S. Komatsu, 2010b. Proteome analysis of soybean leaves, hypocotyls and roots under salt stress. Proteome Sci., 8:19.

Sofy, M.R., K.M. Elhindi, S. Farouk, and M.A. Alotaibi, 2020. Zinc and paclobutrazol mediated regulation of growth, upregulating antioxidant aptitude and plant productivity of pea plants under salinity. Plants, 9: 1197.

Solani, D.M., 2018. Biochemical changes in diabetic retinopathy triggered by Hyperglycaemia: A Review. African Vision and Eye Health ISSN: (Online) 2410-1516, (Print) 2413-3183.

Soliman, A.S., S.A. El-feky, and E. Darwish, 2015. Alleviation of salt stress on Moringa peregrina using foliar application of nanofertilizers. J. Hortic. For., 7(2):36–47.

Soundararajan, P., I. Sivanesan, S. Jana, and B.R. Jeong, 2014. "Influence of silicon supplementation on the growth and tolerance to high temperature in Salvia splendens," Horticulture, E.nvironment, and Biotechnology, 55(4):271–279.

Soylemezoglu, G., K. Demir, A. Inal, and A. Gunes, 2009. Effect of silicon on antioxidant and stomatal response of two grapevine (Vitis vinifera L). rootstocks grown in boron toxic, saline and boron toxic-saline soil. Sci. Hortic.-Amsterdam, 123: 240–246. [CrossRef]

Stevens, F.J., A.D. Li, S.S. Lateef, and L.E. Anderson, 1997. Identification of potential inter-domain disulfides in three higher plant mitochondrial citrate synthases: paradoxical differences in redox-sensitivity as compared with the animal enzyme. Photosyn Res., 185–197. doi:10.1023/A:1005991423503.

Sugimoto, M., and K. Takeda, 2009. Proteomic analysis of specific proteins in the root of salt-tolerant barley. Biosci. Biotechnol. Biochem., 73:2762– 2765.

Sun, C., Z. Yuxue, L. Lijuan, L. Xiaoxia, L. Baohai, J. Chongwei and L. Xianyong, 2021. Molecular functions of nitric oxide and its potential applications in horticultural crops https://doi.org/10.1038/s41438-021-00500-7.

Sundby, C., and B. Andersson, 1985. Temperature-induced reversible migration along the thylakoid membrane of photosystem II. regulates it association with LHC-II. FEBS. Lett. 191: 24–28. doi: 10.1016/0014-5793(85) 80986-8

Sung, C.H. and J.K. Hong, 2010. "Sodium nitroprusside mediates seedling development and attenuation of oxidative stresses in Chinese cabbage," Plant Biotechnology Reports, 4(4):243–251,

Sunkar, R., and J.K. Zhu 2004. Novel and stress-regulated microRNAs and other small RNAs from Arabidopsis. Plant Cell, 16:2001–2019.

Szabolcs, I. 1974. Salt affected soils in Europe. Martinus Nijhoff, The Hague, 63.

Sze, H., X. Li, and M.G. Palmgren, 1999. Energization of plant membranes by Hþ-pumping ATPases: regulation and biosynthesis. Plant Cell, 11: 677–689.

Tada, Y., and T. Kashimura, 2009. Proteomic analysis of salt-responsive proteins in the mangrove plant, B.ruguiera gymnorhiza. Plant Cell Physiol., 50:439–446.

Taffouo, V.D., O.F. Wamba, E. Youmbi, G.V. Nono, and A. Akoa, 2010. Growth, yield, water status and ionic distribution response of three Bambara groundnut (Vigna subterranea L). verdc. landraces grown under saline conditions. Int. J. Bot. 6: 53–58. doi: 10.3923/ijb.2010.53.58.

Tahir, M.A., T. Aziz, M. Farooq, and G. Sarwar, 2012. "Siliconinduced changes in growth, ionic composition, water relations, chlorophyll contents and membrane permeability in two saltstressed wheat genotypes," Archives of Agronomy and Soil Science, 58(3):247–256.

Taji, T., M. Seki, M. Satou, T. Sakurai, M. Kobayashi, K. Ishiyama, Y. Narusaka, M. Narusaka, J.K. Zhu, and K. Shinozaki, 2004. Comparative genomics in salt tolerance between Arabidopsis and Arabidopsis-related halophyte salt cress using Arabidopsis microarray. Plant Physiol., 35: 1697–1709.

Takahashi T. and J.-I. Kakehi, 2010. "Polyamines: ubiquitous polycations with unique roles in growth and stress responses," Annals of Botany, 105(1):1–6.

Takahashi, E., J.F. Ma and Y. Miyake, 1990. The possibility of silicon as an essential element for higher plants. Comm. Agric. Food Chem., 2: 99-122.

Takahashi, H., S. Kopriva, M. Giordano, K. Saito, and R. Hell, 2011. Sulfur assimilation in photosynthetic organisms: molecular functions and regulations of transporters and assimilatory enzymes. Annu. Rev. Plant Biol., 62: 157-184.

Tang, X., X. Mu, H. Shao, H. Wang, and M. Brestic, 2015. Global plant-responding mechanisms to salt stress: physiological and molecular levels and implications in biotechnology. Crit. Rev. Biotechnol., 35(4):425–437. https://doi.org/10.3109/07388551.2014.889080

Tarchoune, I., C. Sgherri, O. Baâtour, R. Izzo, M. Lachaal, *et al.,* 2013. Effects of oxidative stress caused by NaCl or Na2 SO4 excess on lipoic acid and tocopherols in Genovese and Fine basil (Ocimum basilicum) Ann. Applied Bio., 163: 23-32.

Tarczynski, M.C., R.G. Jensen, and H.J. Bohnert 1993. Stress protection of transgenic plants by production of the osmolyte mannitol. Science, 259:508–510.

Tavakkoli, E., F. Fatehi, S. Coventry, P. Rengasamy, and G.K. McDonald, 2011. Additive effects of Na+ and Cl− ions on barley growth under salinity stress. J. Exp. Bot., 62:2189–2203.

Tayefi-Nasrabadi, H., G. Dehghan, B. Daeihassani, A. Movafegi, and A. Samadi, 2011. Some biochemical properties of guaiacol peroxidases as modified by salt stress in leaves of salt-tolerant and salt-sensitive safflower (Carthamus tinctorius L.cv) cultivars. African J. Biotechnol. 10:751–763. doi: 10.5897/ AJB10.1465.

Thakur, P., S. Kumar, J.A. Malik, J.D. Berger, and H. Nayyar, 2010. Cold stress effects on reproductive development in grain crops: an overview. Environ. Exp. Bot., 67:429–443.

Thomas, C.R., S. George, A.M. Horst, Z.X. Ji, R.J. Miller, J.R. Peralta-Videa, T.A. Xia, S. Pokhrel, L. Madler and J.L. Gardea-Torresdey, 2011. Nanomaterials in the environment: from materials to high-through put screening to organisms. ACS. Nano 5:13–20.

Thomas, J.C., M. Sepahi, B. Arendall, and H.J. Bohnert, 1995. "Enhancement of seed germination in high salinity by engineeringmannitol expression in Arabidopsis thaliana," Plant, C.ell and Environment, 18(7):801–806.

Thormählen I, T. Meitzel, J. Groysman, A.B. Öchsner, E. von Roepenack-Lahaye, B. Naranjo, F.J. Cejudo, and P. Geigenberger, 2015. Thioredoxin f1 and NADPH-dependent thioredoxin reductase C. have overlapping functions in regulating photosynthetic metabolism and plant growth in response to varying light conditions. Plant Physiol., 169:1766–1786. PMID: 26338951. Doi:10.1104/ pp.15.01122.

Thorne, S.J., E.H. Susan and J.M.M. Frans, 2020. Is Silicon a Panacea for Alleviating Drought and Salt Stress in Crops. Frontiers in Plant Science | www.frontiersin.org, A.ugust, 11:1221.

Tian, X., M. He, Z. Wang, J. Zhang, Y. Song, Z. He, and Y. Dong, 2015. Application of nitric oxide and calcium nitrate enhances tolerance of wheat seedlings to salt stress. Plant Growth Regul., 77: 343–356. [CrossRef]

Tisi, A., R. Angelini, and A. Cona, 2008. "Wound healing in plants: cooperation of copper amine oxidase and flavin-containing polyamine oxidase," Plant Signaling and Behavior, 3(3):204–206.

Tolaymat, T., A. Genaidy, W. Abdelraheem, D. Dionysiou, and C. Andersen, 2017. The effects of metallic engineered nanoparticles upon plant systems: an analytic examination of scientific evidence. Sci. Total Environ., 579: 93–106.

Tortella, G.R., O. Rubilar, N. Dur´an, M.C. Diez, M. Martínez, J. Parada, and A.B. Seabra, 2020. Silver nanoparticles: toxicity in model organisms as an overview of its hazard for human health and the environment. J. Hazard. Mater., 390: 121974.

Traverso, J.A., C. Micalella, A. Martinez, S.C. Brown, B. Satiat-Jeunemaître, T. Meinnel, and C. Giglione, 2013. Roles of N-terminal fatty acid acylations in membrane compartment partitioning: Arabidopsis h-Type thioredoxins as a case study. Plant Cell, 25:1056– 1077. PMID: 23543785. doi:10.1105/tpc.112.106849.

Tripathi, D.K., K. Vishwakarma, V.P. Singh, V. Prakash, S. Sharma, S. Muneer, M. Nikolic, R.Deshmukh, M. Vaculík, and F.J. Corpas, 2020b. Silicon crosstalk with reactive oxygen species, phytohormones and other signaling molecules. J. Hazard. Mater., 124820.

Tripathi, D.K., P. Rai, G. Guerriero, S. Sharma, F.J. Corpas, and V.P. Singh, 2020a. Silicon induces adventitious root formation in rice (Oryza sativa L). under arsenate stress with the involvement of nitric oxide and indole-3-acetic acid. J. Exp. Bot.

Tripathi, D.K., S. Singh, V.P. Singh, S.M. Prasad, N.K. Dubey, and D.K. Chauhan, 2018. Silicon nanoparticles more effectively alleviated UV-B. stress than silicon in wheat (Triticum aestivum. seedlings. Plant Physiol. Biochem., 110: 70–81.

Tripathi, D.K., S.hweta, S. Singh, S. Singh, R. Pandey, V.P. Singh, N.C. Sharma, S.M. Prasad, N.K.Dubey, and D.K. Chauhan, 2017a. An overview on manufactured nanoparticles in plants: Uptake, translocation, accumulation and phytotoxicity. Plant Physiol. Biochem., 110: 2–12.

Tripathi, D.K., V.P. Singh, P. Ahmad, D.K. Chauhan, and S.M. Prasad, 2016. Silicon in plants: advances and future prospects. Florida, F.L: CRC. Press.

Tuna, A.L., C. Kaya, D. Higgs, B. Murillo-Amador, S. Aydemir, and A.R. Girgin, 2008Silicon improves salinity tolerance in wheat plants. Environ. Exp. Bot., 62: 10–16. [CrossRef]

Tuna, L.A., C. Kaya, M. Ashraf, H. Altunlu, I. Yokas, and B. Yagmur 2007. The effects of calcium sulphate on growth, membrane stability and nutrient uptake of tomato plants grown under salt stress. Environ. Exp. Bot., 59:173–178.

Tunc-Ozdemir, M., G. Miller, L. Song, J. Kim, A. Sodek, *et al.,* 2009. Thiamin confers enhanced tolerance to oxidative stress in Arabidopsis. Plant Physiol., 151: 421-432.

Tutej, N., M. Tarique, and R. Tutej, 2014. Rice SUV3 is a bidirectional helicase that binds both DNA. and RNA. BMC. Plant Biol. 14:283. doi: 10.1186/s12870-014-0283-6

Tuteja, N., R.K. Sahoo, B. Garg, and R. Tuteja, 2013. "OsSUV3 dual helicase functions in salinity stress tolerance by maintaining photosynthesis and antioxidant machinery in rice (Oryza sativa L. cv.) IR64.," The Plant Journal, 76(1):115–127.

Ulfat, M., H. Athar, M. Ashraf, N.A. Akram, and A. Jamil 2007. Appraisal of physiological and biochemical selection criteria for evaluation of salt tolerance in canola (Brassica napus L). Pak. J. Bot., 39:1593– 1608s

Urano, K., Y. Kurihara, M. Seki, and K. Shinozaki 2010. 'Omics' analyses of regulatory networks in plant abiotic stress responses. Curr. Opin. Plant Biol., 13:132–138.

Urano, K., Y. Yoshiba, T. Nanjo *et al.,* 2003. "Characterization of Arabidopsis genes involved in biosynthesis of polyamines in abiotic stress responses and developmental stages," Plant, C.ell and Environment, 26(11):1917–1926.

Urano, K., Y. Yoshiba, T. Nanjo, T. Ito, K. Yamaguchi-Shinozaki, and K. Shinozaki, 2004.Arabidopsis stress-inducible gene for arginine decarboxylase AtADC2 is required for accumulation of putrescine in salt tolerance," Biochemical and Biophysical Research Communications, 313(2):369–375.

Vaidyanathan, H., P. Sivakumar, R. Chakrabarty, and G. Thomas 2003. Scavenging of reactive oxygen species in NaCl stressed rice (Oryza sativa L). differential response in salttolerant and sensitive varieties. Plant Sci., 165: 1411-1418.

Van der Werf, A., A. Kooijman, R. Welschen, and H. Lambers, 1988. Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of Carex diandra and Carex acutiformis. Physiologia Plantarum, 72: 483–491.

Van Oosten, M.J., A. Sharkhuu, G. Batelli, R. A. Bressan, and A. Maggio, 2013. "The Arabidopsis thaliana mutant air1 implicates SOS3 in the regulation of anthocyanins under salt stress," Plant Molecular Biology, 83:405–415.

Vanlerberghe, G.C., G.D. Martyn, and K. Dahal, 2016. Alternative oxidase: a respiratory electron transport chain pathway essential for maintaining photosynthetic performance during drought stress. Physiol Plant., 157:322–337. PMID: 27080742. Doi: 10.1111/ ppl.1245 .

Veeranagamallaiah, G., G. Jyothsnakumari, M. Thippeswamy, P.C.O. Reddy, G.K. Surabhi, G. Sriranganayakulu, Y. Mahesh, B. Rajasekhar, C. Madhurarekha, and C. Sudhakar, 2008. Proteomic analysis of salt stress responses in foxtail millet (Setaria italica L. cv) Prasad.

Veiga, T.A.M., S.C. Silva, A.C. Francisco, E.R. Filho, P.C. Vieira, J.B. Fernandes, *et al.,* 2007. Inhibition of photophosphorylation and electron transport chain in thylakoids by lasiodiplodin, a natural product from Botryosphaeria rhodina. J. Agricult. Food Chem. 55: 4217–4221. doi: 10.1021/ jf070082b.

Vieira Santos, C.L., A. Campos, H. Azevedo, and G. Caldeira, 2001. In situ and in vitro senescence induced by KCI. stress: nutritional imbalance, lipid peroxidation and antioxidant metabolism. J. Exp. Bot. 52, 351–360. doi: 10.1093/jexbot/52.355.351.

Vincent, D., A. Ergül, M.C. Bohlman, E.A. Tattersall, R.L. Tillett, M.D. Wheatley, R. Woolsey, D.R. Quilici, J. Joets, K. Schlauch, D.A. Schooley, J.C. Cushman, and G.R. Cramer 2007. Proteomic analysis reveals differences between Vitis. Vinifera L. cv. Chardonnay and cv. Cabernet Sauvignon and their responses to water deficit and salinity. J. Exp. Bot., 58:1873–1892.

Vorasoot, N., P. Songsri, C. Akkasaeng, S. Jogloy, and A. Patanothai 2003. Effect of water stress on yield and agronomic characters of peanut. Songklanakarin J. Sci. Technol., 25:283–288.

Wahid, A., R. Rao, and E. Rasul, 1997. Identification of salt tolerance traits in sugarcane lines. Field Crop Res., 54:9–17.

Walia, A., J.S. Lee, G. Wasteneys, and B. Ellis, 2009. Arabidopsis mitogenactivated protein kinaseMPK18 mediates cortical microtubule functions in plant cells. Plant J., 59:565–575

Wang, B., U. L¨uttge, and R. Ratajczak, 2001. "Effects of salt treatment and osmotic stress on V-ATPase and V-PPase in leaves of the halophyte Suaeda salsa," Journal of Experimental Botany, 52(365):2355–2365.

Wang, M.C., Z.Y. Peng, C.L. Li, F. Li, C. Liu, and G.M. Xia, 2008a. Proteomic analysis on a high salt tolerance introgression strain of Triticum aestivum/Thinopyrum ponticum. Proteomics, 8:1470–1489.

Wang, S., P. Liu, D. Chen, L. Yin, H. Li, and X. Deng, 2015Silicon enhanced salt tolerance by improving the root water uptake and decreasing the ion toxicity in cucumber. Front. Plant Sci., 6, 759. [CrossRef] [PubMed]

Wang, W., B. Vinocur, and A. Altman, 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta, 218:1–14.

Wang, X., P. Fan, H. Song, X. Chen, X. Li, and Y. Li, 2009. Comparative proteomic analysis of differentially expressed protein in shoots of Salicornia europea, under different salinity. J. Proteome Res., 8:3331– 3345.

Wang, X., P. Yang, Q. Gao, X. Liu, T. Kuang, S. Shen, and Y. He, 2008b. Proteomic analysis of the response to high-salinity stress in Physcomitrella patens. Planta, 228:167–177.

Wang, X.S., and J.G. Han, 2007. Effects of NaCl and silicon on ion distribution in the roots, shoots and leaves of two alfalfa cultivars with different salt tolerance. Soil Sci. Plant Nutr., 53:278–285. [CrossRef]

Wang, Y. and N. Nii, 2000. "Changes in chlorophyll, ribulose bisphosphate carboxylase-oxygenase, glycine betaine content, photosynthesis and transpiration in Amaranthus tricolor leaves during salt stress," Journal of Horticultural Science and Biotechnology, 75(6):623–627.

Watanabe, M., M. Kusano, A. Oikawa, A. Fukushima, M. Noji, *et al.,* 2008. Physiological roles of the beta-substituted alanine synthase gene family in Arabidopsis. Plant Physiol 146: 310-320.

Weisany, W., Y. Sohrabi, G. Heidari, A. Siosemardeh, and K.G. Golezani, 2012. Changes in antioxidant enzymes activity and plant performance by salinity stress and zinc application in soybean (Glycine max L). Plant OMICS. 5(2):60–67.

White, P.J., and M.R. Broadley, 2001. Chloride in soils and its uptake and movement within the plant: a review. Ann. Bot., 88:967–988.

Winicov, I., and J.R. Seemann, 1990. Expression of genes for photosynthesis and the relationship to salt tolerance of alfalfa (Medicago sativa) cells. Plant Cell Physiol. 31: 1155–1161. doi: 10.1093/oxfordjournals.pcp.a078029.

Wirtz, M., and M. Droux, 2005. Synthesis of the sulfur amino acids: cysteine and methionine. Photosynth. Res., 86: 345-362.

Witzel, K., A. Weidner, G.K. Surabhi, A. Börner, and H.P. Mock, 2009. Salt stress-induced alterations in the root proteome of barley genotypes with contrasting response towards salinity. J. Exp. Bot., 60: 3546–3557.

Wu, D., S. Cai, M. Chen, L. Ye, Z. Chen, H. Zhang, F. Dai, F. Wu, and G. Zhang, 2013. Tissue metabolic responses to salt stress in wild and cultivated barley. PLoS. One, 8:e55431.

Wu, J., H.-P. Mock, R.F.H. Giehl, B. Pitann, and K.H. Mühling, 2019. Silicon decreases cadmium concentrations by modulating root endodermal suberin development in wheat plants. J. Hazard. Mater. 364, 581–590. Doi: 10.1016/j. jhazmat.2018.10.052.

Wu, J., J. Guo, Y. Hu, and H. Gong, 2015. Distinct physiological responses of tomato and cucumber plants in silicon-mediated alleviation of cadmium stress. Front. Plant Sci., 6, 453. [CrossRef]

Wu, Q.S., and Y.N. Zou, 2009. Adaptive responses of birch-leaved pear (Pyrus betulaefolia. seedlings to salinity stress. Not. Bot. Horti Agrobot. Cluj Napoca 37: 133–138. doi: 10.15835/nbha3713109.

Wu, X., Z. Zhu, X. Li, and D. Zha, 2012. Effects of cytokinin on photosynthetic gas exchange, chlorophyll fluorescence parameters and antioxidative system in seedlings of eggplant (Solanum melongena L). under salinity stress. Acta Physiol. Plant, 34: 2105–2114. [CrossRef]

Wyn, J.R.G., C.J. Brady, and J. Speirs, 1979. Ionic and osmotic relations in plant cells. In: Laidman DL, W.yn Jones RG. (eds) Recent advances in the biochemistry of cereals. Academic Press, L.ondon, 63–103.

Xiong, J., G. Fu, L. Tao, and C. Zhu, 2010. "Roles of nitric oxide in alleviating heavy metal toxicity in plants," Archives of Biochemistry and Biophysics, 497(1-2):13–20.

Xu, C., T. Sibicky, and B. Huang 2010. Protein profile analysis of salt responsive proteins in leaves and roots in two cultivars of creeping bent grass differing in salinity tolerance. Plant Cell Rep., 29: 595–615.

Xu, C.X., Y.P. Ma, and Y.L. Liu, 2015. Effects of silicon (Si) on growth, quality and ionic homeostasis of aloe under salt stress. S. Afr. J. Bot., 98: 26–36. [CrossRef]

Xu, G., H. Magen, J. Tarchitzky, and U. Kafkafi, 2000. Advances in chloride nutrition of plants. Adv Agron., 68:97–150.

Xu, S., B. Hu, Z. He, F. Ma, J. Feng, W. Shen, and J. Yan, 2011. Enhancement of salinity tolerance during rice seed germination by presoaking with hemoglobin. Int J. Mol. Sci., 12:2488–2501.

Yadav, S.K., S.L. Singla-Pareek, M. Ray, M.K. Reddy and S.K. Sopory, 2005. Transgenic tobacco plants overexpressing glyoxalase enzymes resist an increase in methylglyoxal and maintain higher reduced glutathione levels under salinity stress. FEBS. Letters, 579: 6265-6271.

Yamaguchi, K., Y. Takahashi, T. Berberich *et al.,* 2006. "The polyamine spermine protects against high salt stress in Arabidopsis thaliana," FEBS. Letters, 580(30):6783–6788,

Yamaguchi, K., Y. Takahashi, T. Berberich, A. Imai, A. Miyazaki, *et al.,* 2006. The polyamine spermine protects against high salt stress in Arabidopsis thaliana. FEBS. Lett., 580: 6783-6788.

Yamori, W., 2016. Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. J. Plant Res. 129: 379–395. [CrossRef]

Yamori, W., 2016. Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. J. Plant Res., 129: 379–395. [CrossRef]

Yan, A., and Z. Chen, 2019. Impacts of silver nanoparticles on plants: a focus on the phytotoxicity and underlying mechanism. Int. J. Mol. Sci. 20: 1003.

Yang, Q., Z.Z. Chen, X.F. Zhoua, H.B. Yina, X. Lia, X.F. Xina, X.H. Honga, J.K. Zhu, and Z. Gong, 2009. Over-expression of SOS. (salt overly sensitive. genes increases salt tolerance in transgenic Arabidopsis. Mol. Plant, 2:22–31.

Yang, Y., and Y. Guo, 2018. Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol., 217: 523–539. [CrossRef]

Yang, Y., and Y. Guo, 2018. Unraveling salt stress signaling in plants. J. Integr. Plant Biol., 60, 796–804. [CrossRef]

Yano, H., 2014. Ongoing applicative studies of plant thioredoxins. Mol. Plant, 7:4–13. PMID: 23966635. doi:10.1093/mp/sst124.

Yassen, A., E. Abdallah, M. Gaballah, and S. Zaghloul, 2017. Role of silicon dioxide nano fertilizer in mitigating salt stress on growth, yield and chemical composition of cucumber (Cucumis sativus L). Int J. Agric Res 12:130–135. https://doi.org/10.3923/ijar.2017.130.135.

Ye, Y., I.A. Medina-Velo, K. Cota-Ruiz, F. Moreno-Olivas, and J.L. Gardea-Torresdey, 2019. Can abiotic stresses in plants be alleviated by manganese nanoparticles or compounds? Ecotoxicol. Environ. Saf. 184, 109671. You, J., C.han, Z., 2015. ROS. regulation during abiotic stress responses in crop plants. Front. Plant Sci. 6, 1092.

Ye, Y., K. Cota-Ruiz, J.A. Hern´andez-Viezcas, C. Vald´es, I.A. Medina-Velo, R.S. Turley, J.R.Peralta-Videa, and J.L. Gardea-Torresdey, 2020a. Manganese nanoparticles control salinity-modulated molecular responses in Capsicum annuum L. through priming: a sustainable approach for agriculture. ACS. Sustain. Chem. Eng. 8: 1427–1436.

Yen, H.E., S.-M. Wu, Y.-H. Hung, and S.-K. Yen, 2000. "Isolation of 3 salt-induced low-abundance cDNAs from light-grown callus ofMesembryanthemum crystallinum by suppression subtractive hybridization," Physiologia Plantarum, 110(3):402– 409.

Yin, J., J. Jia, Z. Lian, Y. Hu, J. Guo, H. Huo, Y. Zhu, and H. Gong, 2019. Silicon enhances the salt tolerance of cucumber through increasing polyamine accumulation and decreasing oxidative damage. Ecotoxicol. Environ. Saf., 169: 8–17. [CrossRef]

Yin, L., S. Wang, J. Li, K. Tanaka, and M. Oka, 2013. Application of silicon improves salt tolerance through ameliorating osmotic and ionic stresses in the seedling of Sorghum bicolor. Acta Physiol. Plant., 35: 3099–3107. [CrossRef]

Yin, L., S. Wang, K. Tanaka, S. Fujihara, A. Itai, X. Den, and S. Zhang, 2016. Silicon-mediated changes in polyamines participate in silicon-induced salt tolerance in Sorghum bicolor L. Plant Cell Environ., 39: 245–258. [CrossRef]

Yiu, J.-C., L.-D. Juang, D. Y.-T. Fang, C.-W. Liu, and S.-J. Wu, 2009. "Exogenous putrescine reduces flooding-induced oxidative damage by increasing the antioxidant properties of Welsh onion," Scientia Horticulturae, 120(3):306–314.

Yokotani, N., T. Ichikawa, Y. Kondou, M.Matsui, H. Hirochika, M. Iwabuchi, and K. Oda, 2009. Tolerance to various environmental stresses conferred by the salt-responsive rice gene ONAC063 in transgenic Arabidopsis. Planta, 229:1065–1075.

Yoshida, K., and T. Hisabori, 2014. Mitochondrial isocitrate dehydrogenase is inactivated upon oxidation and reactivated by thioredoxin-dependent reduction in Arabidopsis. Front. Environ. Sci., 2:1–7. doi:10.3389/fenvs.2014.00038.

Yoshida, K., K. Noguchi, K. Motohashi, and T. Hisabori, 2013. Systematic exploration of thioredoxin target proteins in plant mitochondria. Plant Cell Physiol., 54:875–892. PMID: 23444301. doi:10.1093/pcp/pct037.

Yu, J., S. Chen, Q. Zhao, T. Wang, C. Yang, C. Diaz, G. Sun, and S. Dai, 2011. Physiological and proteomic analysis of salinity tolerance in Puccinellia tenuiflora. J. Proteome Res 10:3852–3870.

Zargar, S.M., R. Mahajan, J. A. Bhat, M. Nazir, and R. Deshmukh, 2019. Role of silicon in plant stress tolerance: opportunities to achieve a sustainable cropping system. 3 Biotech 9:73. Doi: 10.1007/s13205-019-1613-z.

Zargar, S.M., R. Mahajan, J.A. Bhat, M. Nazir, and R. Deshmukh, 2019Role of silicon in plant stress tolerance: Opportunities to achieve a sustainable cropping system. 3 Biotech., 9, 73. [CrossRef]

Zhang, C.J., B.C. Zhao, W.N. Ge, Y.F. Zhang, Y. Song, *et al.,* 2011. An apoplastic h-type thioredoxin is involved in the stress response through regulation of the apoplastic reactive oxygen species in rice. Plant Physiol., 157: 1884-1899.

Zhang, F., Y. Wang, Y. Yang, H. Wu, D. Wang, and J. Liu, 2007. "Involvement of hydrogen peroxide and nitric oxide in salt resistance in the calluses from Populus euphratica," Plant, C.ell and Environment, 30(7):775–785.

Zhang, J.L. and H. Shi, 2013. "Physiological and molecular mechanisms of plant salt tolerance," Photosynthesis Research, 115:1–22.

Zhang, M.H., Z.H. Qin, and X. Liu 2005. Remote sensed spectral imagery to detect late blight in field tomatoes. Precision Agriculture, 6: 489–508.

Zhang, N.N., H. Zou, X.Y. Lin, Q. Pan, W.Q. Zhang, J.H. Zhang, and J. Chen, 2020. Hydrogen sulfide and rhizobia synergistically regulate nitrogen N. assimilation and remobilization during N. deficiency-induced senescence in soybean. Plant Cell Environ. 43: 1130–1147. [CrossRef] [PubMed]

Zhang, W., W.J. Peumans, A. Barre, C.H. Astoul, P. Rovira, P. Rougé, P. Proost, P. Truffa-Bachi, A.A.H. Jalali, and E.J.M. van Damme, 2000. Isolation and characterization of a jacalin-related mannose-binding lectin from salt-stressed rice (Oryza sativa) plants Planta, 210:970–978.

Zhang, W.Q., Y.Z. Huang, and L.J. Zhao, 2009. Effect of silicon on the germination of Si mutant rice and wild rice seeds under salt stress. Asian J. Ecotoxicol., 4: 867–873.

Zhang, Y., L. Wang, Y. Liu, Q. Zhang, Q. Wei, and W. Zhang, 2006. "Nitric oxide enhances salt tolerance inmaize seedlings through increasing activities of proton-pump and Na+/H+ antiport in the tonoplast," Planta, 224(3):545–555.

Zhao, F., C.P. Song, J. He, and H. Zhu, 2007. Polyamines improve K+/Na+ homeostasis in barley seedlings by regulating root ion channel activities. Plant physiol., 145: 1061–1072. [CrossRef]

Zhao, G., Y. Zhao, W. Lou, J. Su, S. Wei, X. Yang, R. Wang, R. Guan, H. Pu, and W. Shen, 2019. Nitrate reductase-dependent nitric oxide is crucial for multi-walled carbon nanotube-induced plant tolerance against salinity. Nanoscale, 11: 10511–10523.

Zhao, L., B. Peng, J.A. Hernandez-Viezcas, C. Rico, Y. Sun, J.R. Peralta-Videa, X. Tang, G. Niu, L. Jin, A. Varela-Ramirez, J.Y. Zhang, and J.L. Gardea-Torresdey, 2012. Stress response and tolerance of Zea mays to CeO2 nanoparticles: cross talk among H2O2, heat shock protein and lipid peroxidation. ACS. Nano 6:9615–9622. https://doi.org/10.1021/nn302975.

Zhao, L., F. Zhang, J. Guo, Y. Yang, B. Li, and L. Zhang, 2004. "Nitric oxide functions as a signal in salt resistance in the calluses from two ecotypes of reed," Plant Physiology, 134(2):849– 857.

Zhao, X., P. Wei, Z. Liu, B. Yu, and H. Shi, 2017. Soybean Na+/H+ antiporter GmsSOS1 enhances antioxidant enzyme activity and reduces Na+ accumulation in Arabidopsis and yeast cells under salt stress. Acta Physiol. Plant., 39, 19. [CrossRef]

Zhou, J., F. Li, J. Wang, Y. Ma, K. Chong, and Y. Xu, 2009. Basic helix-loophelix transcription factor from wild rice (OrbHLH2) improves tolerance to salt and osmotic stress in Arabidopsis. J. Plant Physiol., 166: 1296–1306.

Zhu Z., G. Wei, J. Li, Q. Qian, and J. Yu, 2004. "Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (Cucumis sativus L)" Plant Science, 167(3):527–533.

Zhu, J.K. 2004. Plant salt tolerance and the SOS. pathway. In: Proceedings of the XLVIII. Italian Society of Agricultural Genetics: SIFV-SIGA. Joint Meeting, L.ecce, I.taly (15–18 September, 2004) I.SBN. 88- 900622-5-8.

Zhu, J.K., 2001. Plant salt tolerance. Trends Plant Sci., 6:66–71.

Zhu, J.-K., 2003. "Regulation of ion homeostasis under salt stress," CurrentOpinioninPlant Biology, 6(5): 441–445.

Zhu, J.K., 2016. Abiotic stress signaling and responses in plants. Cell, 167: 313–324. [CrossRef]

Zhu, J.K., J. Liu, and L. Xiong, 1998. Genetic analysis of salt tolerance in Arabidopsis. Evidence for a critical role of potassium nutrition. Plant Cell, 10:1181–1191.

Zhu, Y.X., and H.J. Gong, 2014. Beneficial effects of silicon on salt and drought tolerance in plants. Agron. Sustain. Dev., 34: 455–472. [CrossRef]

Zhu, Y.-X., G. Hai-Jun and Y. Jun-Liang, 2019. Role of Silicon in Mediating Salt Tolerance in Plants: A Review, Plant s, 8, 147; doi: 10.3390/plants8060147 www.mdpi.com/journal/plants

Zhu, Y.X., H.J. Gong, and J.L. Yin, 2019a. Role of silicon in mediating salt tolerance in plants: a review. Plants 8:147. Doi: 10.3390/plants8060147.

Zhu, Y.X., J. Guo, R. Feng, J.H. Jia, W.H. Han, and H.J. Gong, 2016. The regulatory role of silicon on carbohydrate metabolism in Cucumis sativus L. under salt stress. Plant Soil, 406: 231–249. [CrossRef]

Zhu, Y.X., X.B. Xu, Y.H. Hu, W.H. Han, J.L. Yin, H.L. Li, and H.J. Gong, 2015. Silicon improves salt tolerance by increasing root water uptake in Cucumis sativus L. Plant Cell Rep., 34: 1629–1646. [CrossRef]

Zhu, Z., G. Wei, J. Li, Q. Qian, and J. Yu, 2004. Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (Cucumis sativus L). Plant Sci., 167: 527–533. [CrossRef]

Zhu, Z.J., G.Q. Wei, J. Li, Q.Q. Qian, and J.Q. Yu, 2004. Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of saltstressed cucumber (Cucumis sativus L). Plant Sci., 167:527–533.

Zi, Z., W. Liebermeister, and E. Klipp, 2010. A quantitative study of the Hog1 MAPK. Response to fluctuating osmotic stress in Saccharomyces cerevisiae. PLoS. One 5:e9522.

Ziaf, K., M. Amjad, M.A. Pervez, Q. Iqbal, I.A. Rajwana, and M. Ayyub, 2009. Evaluation of different growth and physiological traits as indices of salt tolerance in hot pepper (Capsicum annuum L). Pakistan J. Bot. 41: 1797–1809.

Zorb, C., C.-M. Geilfus and K.-J. Dietz, 2019. Salinity and crop yield, Plant Biology 21 (Suppl. 1. 31–38) 2018 German Society for Plant Sciences and The Royal Botanical Society of the Netherlands.

Zörb, C., R. Herbst, C. Forreite, and S. Schubert, 2009. Short-term effects of salt exposure on the maize chloroplast protein pattern. Proteomics, 9: 4209–4220.

Zörb, C., S. Schmitt, and K.H. Mühling, 2010. Proteomic changes inmaize roots after short-term adjustment to saline growth conditions. Proteomics, 10:4444–4449.

Zulfiqar, F., and M. Ashraf, 2021. Nanoparticles potentially mediate salt stress tolerance in plants. Plant Physiol. Biochem. 160: 257–268.