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Biochemical Mechanisms to Defend Salinity Stress in Cabbage Family Members

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Abstract

Soil salinity is a major problem of this century. It effects crop productivity as well as plant growth and development. Salt ions are responsible for several types of plant organelle damage. Salinity stress is the most dangerous stress among all abiotic stresses in the environment. During salinity stress various cellular and biochemical mechanisms get up regulated to protect the plant. Cabbage family has a large number of plant species with significant variation of chromosome number as well as significant variation in salinity stress responses. This family has the model plant named *Arabidopsis thaliana* which is a salt susceptible plant where *the lungiella halophila* shows salt resistant. Members of the *Brassicaceae* family show a wide range of reaction to salt stress to survive. High salinity stress causes membrane rupture, electrolyte leakage, ionic and osmotic equilibrium disruption even the death of plants. Pathway like SOS (Salt Overly Sensitive) helps Cabbage plants to survive in this kind of conditions. Along with biochemical pathways, Cabbage (*Brassicaceae*) family plants always up regulate salt stress removing compounds like several carbohydrates, proteins, amino acids and queternary ammonium compounds which act as osmoprotectants. This chapter describes the cellular as well as biochemical responses of *Brassicaceae* family member plants to fight against salinity stress.

Keywords: Salt stress; Soil salinity; Cabbage family; *Brassicaceae*; Water balance; Osmoprotectants

Introduction

Salt is a natural component of soil. Soil salinity is the salt content of soil and upon a certain level of salt concentration in soil causes salinity stress to plant systems. Excess amount of salt in the land is harmful for plant growth and regulation. It is a major factor which left a mark on crop productivity. The process of continuous increasing content of salt in soil is known as salinization. Soil salinization is a precursor of desertification [1]. The most important ions responsible for soil salinity are: Na^+, K^+, Ca_2^+, Mg_2^+ and Cl^- [2,3]. If Na^+ predominates in the soil, soil becomes sodic. Sodic soils limit water infiltration and drainage mechanisms [4]. Major salt in this soil is Na_2Co_3. Previously these soils are known as alkali for the capability of alkaline hydrolysis. Acid sulfate soils are also one kind of soil. These soils have low pH in between 3.5 to 4.0. This soil is responsible for high salinity. Apart from high salinity this type of soil consists of Iron (Fe) and Aluminum (Al) toxicities. This type of soil lack phosphorus ions [5]. Degraded sodic soil is another type of soil which is produced by clay, organic compounds and washed out salts. For these reason this soil have dark colour and extreme compact layers. This type of soil also contains high Na^+. According to the capacity of salt tolerance, plants are defined to glycophytes (cannot tolerate salts) or halophytes (can tolerate salts) [6,7]. Most of the plants cannot tolerate salt. Crop producing plants like *Hordeum vulgare* (Barley), *Beta vulguris* (Sugar beet), *Spinacia oleracea* (Spinach), *Phoenix dactylifera* (Date palm) are highly salt tolerant. Where plants like *Triticum aestivum* (Wheat), *Lycopersicon esculentum* (Tomato), *Avena sativa* (Oat), *Medicago sativa* (Alfalfa), *Oryza sativa* (rice), *Zea mays*, *Solanum tuberosum* (Potato), *Daucus carota* (Carrot), *Allium cepa* (Onion), *Cucumis sativus* (Cucumber), *Punica granatum* (Pome granate), *Ficus carica* (Fig), *Olea europea* (Olive), *Vitis vinifera* (Grape). Few plants like *Pisum sativum* (Pea), *Phaseolus vulgaris* (Bean), *Malus domestica* (Apple), *Trifolium partense* (Red clover), *Saccharum officinarum* (Sugar cane), *Citrus aurantium* (Orange) etc. [8]. There are several measurement units according to the measurement procedures of salinity stress. In case of soil conductivity measurement dS m^{-1} unit is used, for irrigation and river water µS cm^{-1} unit used. For measuring total dissolved salts in river water mg L^{-1} unit is used and in laboratory methods mM unit is used.

Plants often experience several abiotic stresses like salinity, drought, cold and freezing etc. This stress causes serious crop loss. Among them high salinity level is the major threat for crop production. Large amount of land area affected with high salinity is increasing day by day (Table 1). 45 million hectares (Mha) of land which equals to the 20% of total land have been damaged by salt world wide and 1.5 Mha are taken out of production every year due to high salinity [9]. It is expected that 50% of agricultural land will be lost due to high salinity in between middle of the twenty first century [10]. Actually Na^+ and Cl^- causes most negative effects on plant growth and metabolism. These ions cause major physiological disorders in plants, i.e. membrane damage, metabolic dysfunction, nutrient imbalance etc. The effect of salt stress depends on the time and concentration of salt, plant genotypes and age of the plant also. There are mainly two types of soil salinity. These are of two types like, Natural or primary salinity and Secondary salinity. Primary salinity of the crop lands occurs by long term exposure to salinity. This is a natural process in the coastal region. Primary salinity may also occur by break down of rocks. Break down of rocks involves Na^+, Cl^-, Ca_2^+, Mg_2^+ sometimes So_4^{2-}, Co_3^{2-}. Secondary salinity is the process of increasing amount of salt by several human activities. It may come from agricultural land farming. It also comes from poor quality ground water. Based on the nature, characteristics and ability of plant growth in saline conditions, major types of soils have been coiled [11]. Saline soils are this type of soil where soluble salts are NaCl and Na_2So_4. This type of soil has negative effect on plant growth.

Region	Area (10^6 ha)
Africa	69.5
Near and Middle East	53.1
Asia and Far East	19.5
Latin America	59.4
Australia	84.7
North America	16
Europe	20.7

Table 1: Percentage of salinity affected parts of different continents of world.

Salt stress always creates ionic as well as osmotic stress [12]. These stresses cause several changes in the plant body. Root and shoot growth decreases in salt sensitive plants in the presence of high salt concentration. In the presence of the high salinity Na^+ is accumulated in leaves [3]. In older leaves, Na^+ causes necrosis. High Na^+ hampers the nutrient uptake in the plant body [12]. Na^+ interfering with other transporters like K^+ ion channels in the root plasma membrane. Root growth inhibition occurs in presence of high Na^+ concentration. For that reason, uptake of different macro and micro nutrients like Fe, Zn and P can be inhibited. Growth of mycorrhizal fungi and other microorganisms can be inhibited by high Na^+ in the soil. Leaves are more dangerous than roots in the in case of Na^+ accumulation. High accumulation of Na^+ and Cl^- occurs in the leaves. Na^+ is moved into the shoot by rapid movement through xylem. Na^+ is moved into root by phloem. High level of Na^+ or Na^+: K^+ ratio can disturb various enzymatic processes in the cytoplasm. K^+ activates more than fifty enzymes. Studies show that plasma membrane is the site of injury and disruption of protein synthesis occurs in high level of Na^+. Osmotic damage i.e. removal of water from the cells in presence of high saline condition is natural in the plant body.

Brassicaceae Family and their Unique Relationship in Between

Brassicaceae is one of the major crops producing family of the angiosperms. *Cruciferae* was the old name of *Brassicaceae* family which means 'cross bearing', describing the four petals of *Brassicaceae* family. This family contains 330 genera and 3700 species according to Royal Botanic Gardens Kew. *Brassicaceae* family is often called as cabbage family for producing several types of winter crops. The family contains well known crop species like *Brassica rapa* (turnip, Chinese cabbage), *Brassica oleracea* (broccoli, cabbage, cauliflower), *Brassica napus* (rapeseed), *Raphanus sativus* (common raddish), *Armoracia rusticana* (horse raddish) and many others (Table 2). Model plant *Arabidopsis thaliana* (thale cress) belong to this family.

Name of the plant	Status in salt stress	References
Arabidopsis thaliana	Susceptible	(Orsini et al. 2010)
Brassica rapa	Tolerant	(Su et al. 2013)
Brassica nigra	Salt sensitive	(Pareek et al. 2008)
Brassica juncea	Tolerant	(Pareek et al. 2008)
Brassica napus	Tolerant	(Pareek et al. 2008)
Sinapis elba	Tolerant	(Su et al. 2013)
Eruca sativa	Tolerant	(Su et al. 2013)
Thellungiella halophila	Tolerant	(Orsini et al. 2010)
Thellungiella parvula	More tolerant than *T. halophila*	(Orsini et al. 2010)

Table 2: Members of cabbage family and their responses towards salt stress [13-15].

Different members of *Brassica* show a unique relationship in between. This relationship states the triangle of U theory. The triangle of U theory is a theory about the evolutionary relationship between the members of plant genus *Brassica*. This theory states that genome of three ancestral species of *Brassica* combined to create the new vegetables of *Brassica*. It was confirmed by the studies in genetic level. Study of DNA and protein confirmed the theory of triangle of U. It shows three *Brassica* species were derived from three ancestral genomes. This is defined by the notations AA, BB, CC. This ancestral genome singly produces three crop species of *Brassicaceae* family. AA produced *Brassica rapa*, BB produced *Brassica nigra* and CC produced *Brassica oleracea* (Table 3). These crops are diploid in nature. All these species can exist as crop separately. But the interspecific breeding between these three species develop tetraploid *Brassica* species. These hybrid plants contain four genomes which are derived from two different species like AABB called amphidiploids.

Species	Varieties	Chromosomes (2n)	Genome
Brassica carinata	HC209, HC210	34	BBCC
Brassica juncea	RH8813,CS52	36	AABB
Brassica napus	HNS9605	38	AACC
Brassica oleracea	PT30, PT303	18	CC
Brassica camprestis	BSH1	20	AA
Brassica nigra	-	16	BB

Table 3: Different species of *Brassica* and their ploidy level.

Biochemical Responses to Fight Against Salinity Stress by Ion Homeostasis in Cabbage Family

At the cellular level, the Salt Overly Sensitive signaling pathway (SOS) takes part in defending salinity stress. This SOS pathway is comprised of SOS1, SOS2, SOS3 which maintains ion homeostasis. Several types of transporters are required in sodium homeostasis [16]. The influx of Na^+ is regulated by AtHKT1 gene. AtHKT1 is a low affinity sodium ion transporter. But efflux of sodium ion is catalyzed by SOS1 (Salt Overly Sensitive 1) which is a plasma membrane Na^+/H^+ antiporter. Vacuolar membrane transporters, like tonoplast Na^+/H^+ antiporter. AtNHX1 is important in regulating sodium ion homeostasis. That mechanism is performed by sequestering all Na^+

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ions in the vacuole. Probably SOS1 is involved in plant body for sensing Na^+ ion. Carboxyl terminus of AtNHX1 always present in the vacluole. Na^+ sensors are involved in regulating Ca_2^+ level which helps in SOS signal transduction machinery [3]. SOS3 is a calcium binding protein which activates SOS2 kinase. This SOS2 kinase is then phosphorylated and then activates SOS1. SOS1 is the plasma membrane Na^+/H^+ antiporter [3]. Na^+ is not important in plant cell; salt concentration decreases the growth of plants. Under physiological conditions, plants always maintain a high K^+/Na^+ concentration. Three classes of low affinity k^+ ion channels have been identified. The K^+ inward rectifying channels (KIRC) activates K^+ influx. K^+ outward rectifying channels (KORCs) play an important role in Na^+ influx in the plant cell. KORCs channel shows a high affinity of K^+ over Na^+. Voltage independent cation channels (VIC) have a high Na^+/K^+ selectivity. These channels are not gated by voltage. This insists ion uptake i.e. Na^+ ion uptake in the plant cells.

Sodium ions can enter in the cell through a large number of carriers. Carrier's poses high as well as low affinity to K^+ ions. AtHKT1 is a regulator of Na^+ influx in plant roots. The process of Na^+ storage into vacuoles provides efficient mechanism to avoid the toxic effects of high sodium concentration. The transport of Na^+ ions is regulated by Na^+/H^+ antiports. That process is driven by electro chemical gradient of protons. These protons are formed by vacuolar H^+ translocating enzymes, the H^+ ATPase and the H^+-PPiase.

Different plasma membrane potassium carriers can mediate the influx of Na^+ in the cells. AKT1 is a low-affinity K^+ channel with a higher K^+/Na^+ selectivity. HKT1 is a high affinity K^+/Na^+ symporter. Outward rectifying channels such as NORC, are activated by Ca_2^+ and do not discriminate between Na^+ and K^+. Voltage Independent Channels (VIC) has a higher Na^+/K^+ selectivity. The main mechanism for Na^+ extrusion is powered by plasma membrane H^+-ATPase. The electro chemical gradient for H^+ is used by a Na^+/H^+ antiporter that couples the down-hill movement of H^+ with the active extrusion of Na^+ [3].

Figure 1 is showing the current model of SOS signaling pathway in *Arabidopsis* which is actually a web of signaling components consists of several stress responsible inputs and outputs. This pathway plays a significant role in changing the cellular, organellar and developmental features.

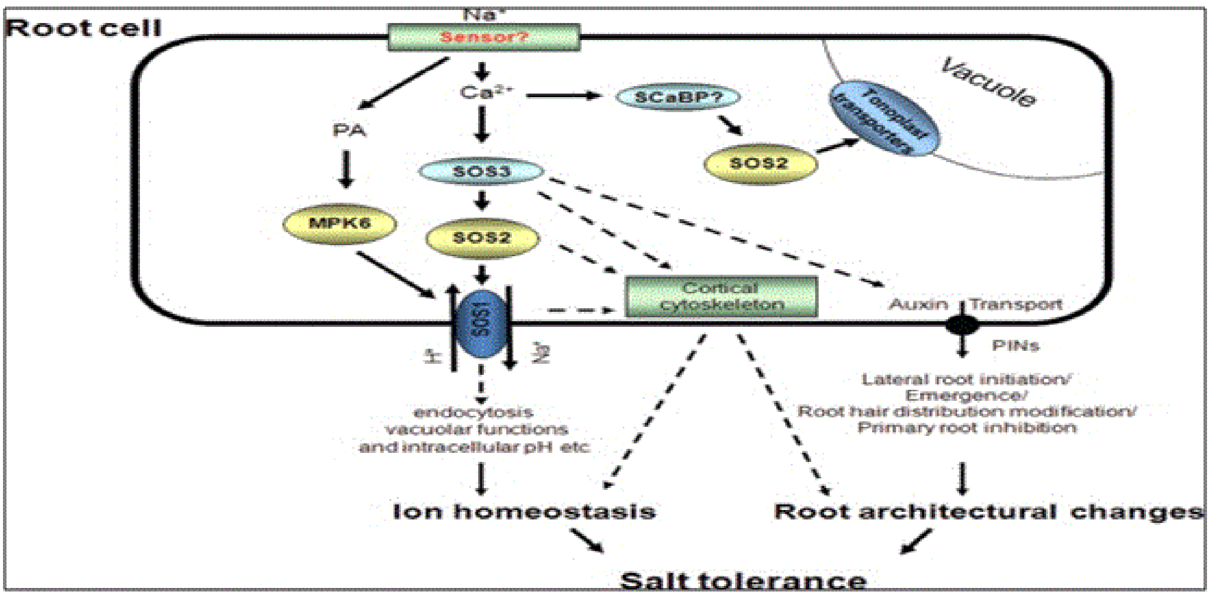

Figure 1: The current model of SOS Signaling in root cortex/epidermal cells for the maintenance of homeostasis, regulation of various cellular processes and lateral root development [3].

Osmolytes and Osmoprotectants in *Brassicaceae* to Defend Salt Stress

During high stress condition plants always try to maintain internal water potential below that of soil. In stress condition plants need to maintain turgor and water uptake from the soil. For these reasons, plants need to maintain an osmotic, either by the uptake of soil solutes or by synthesizing different metabolites. These metabolites are known as compatible solutes. These compatible solutes never interfere with the normal biochemical processes in the plant cell [17]. They are low molecular compounds and they always replace water in the plant cell in the biochemical reactions. Accumulation of these solutes varies between species to species. Basically these solutes contain sugars (glucose and fructose) and sometimes sugar alcohols (glycerols and methylated inositols) and complex sugars like trehalose, raffinose and fructans. Different sulfonium compounds like choline osulfate, dimethyl sulfonium propionate are also produced.

Sugar plays a good role in maintaining osmotic balance in stress conditions. Sugar contributes up to 50% of the osmotic conditions in the salt sensitive plants [18]. Carbohydrates like glucose, sucrose, fructose are accumulated in the plant body in presence of osmotic stress. Starch accumulation in the stress plays a good role in osmotic adjustment, radical scavenging and carbon storage [19]. Trehalose is a di-saccharide produced under salt stress. These di-saccharides protect membranes and cells from water deficiency. Trehalose protects plant cells from protein denaturation and apoptic cell death.

Several proteins are produced in the salt stress. These types of proteins produced in the salt stress store in the cell as a nitrogen source [20]. These proteins play a good role in osmotic adjustment. In plant body osmotic stress produces different soluble proteins, which proteins are accumulated in the vegetative tissues. These proteins are related to Late Embryogenesis Abundant protein or LEA protein.

Amino acids like alanine, arginine, serine, leucine, valine, glycine, imino acids, proline, non-protein amino acids like citruline and ornithine are up regulated in the plant body. Different amides like glutamine and asparagines are also accumulated in the plant body under high saline conditions [21]. Proline which occurs in large amount in the plant body acts as an osmoticum and maintains the water balance in the plant body. Proline accumulation normally occurs in the cytosol. Later proline plays a good role in osmotic adjustment. Membrane stability and membrane disruption in presence of high sodium concentration is given by proline in the plant body under stress conditions. Proline does not suppress the enzyme activities. Basically, proline acts as a signal or regulatory molecule which help plant body top recover stress conditions. There are two alternative pathways present which helps the plant body in proline biosynthesis. Both Ornithine and Glutamate are the precursors of proline biosynthesis. Two enzymes like pyrroline-5-carboxylase synthetase (P5CS) and pyrroline-5-carboxylase reductase (P5CR) plays important role in proline biosynthesis (Figure 2).

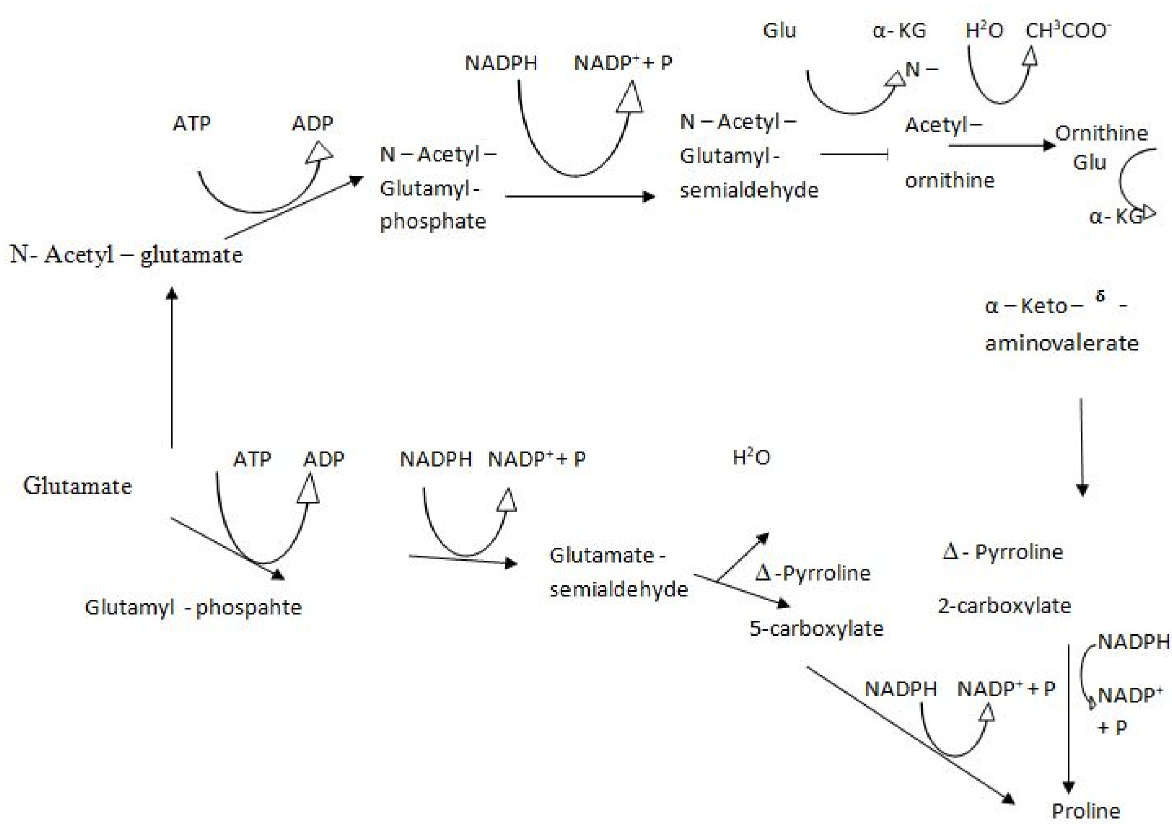

Figure 2: Proline biosynthesis by glutamate and ornithine pathways in plants [19].

This querternary ammonium compounds play a correlation with the plant body and salt stress. Glycine betaine, β alanine betaine and proline betaine are this type of compounds. These organic compounds act as osmoprotectants. These organic compounds are actually located in chloroplasts. They play a good role in protecting chloroplast specially the thylakoid membrane. They always maintain photosynthetic efficiency and plasma membrane integrity. Among all these organic compounds glycine betaine is the most important and abundantly occurred compound. In higher plants glycine betaine is synthesized in chloroplast from serine via ethanol amine, choline and lastly betaine aldehyde. Choline is converted to betaine aldehyde by choline mono oxygenase enzyme (CMO) [19]. Betaine aldehyde is then converted to glycine betaine with the help of betaine aldehyde de hydrogenase enzyme. Many other pathways like N-methylation of glycine is also observed. Glycine betaine is accumulated under stress condition in many plants like rice, shorghum, spinach, barley, tomato, carrot, potato etc. Actually glycine betaine protects plant photosystem II [19]. The concentration of glycine betaine differs among different species. For example, synthesis of glycine betaine is tenfold higher in sorghum than maize. Glycine betaine concentration always increases in the plant body under stress conditions, it always increases in the shoots. But in the roots glycine betaine concentration remain same under the stress conditions (Figure 3).

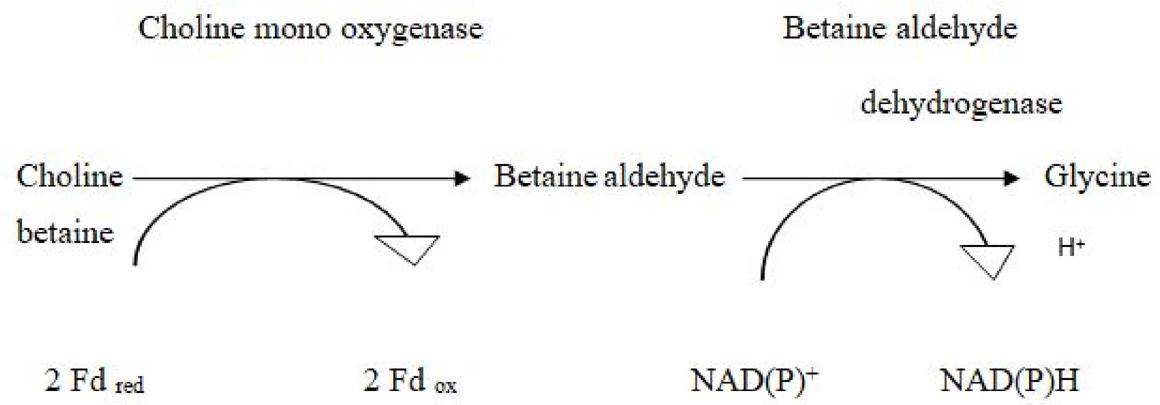

Figure 3: Biosynthetic pathway of Glycine betaine [19].

In natural conditions, accumulation of glycine betaine is very less in the plant system to fight against the adverse environmental conditions. Exogenous application of glycine betaine in the low accumulating plant system can increase the survival rate in the plant system. Foliar application of glycine betaine is not so positive in good yield, physiological processes.

Polyols are poly-hydric alcohols, they play very good role in fighting against the plant stress. These polyols act as compatible solutes and help in osmoregulation in salt stress [22]. They exist in the plant cell in both cyclic and acyclic forms. The most common polyols found in the plant body in acyclic forms are mannitol, glycerol and sorbitols. Cyclic forms are found in the plant body ononitol, pinitol. Generally they get accumulated in the cytoplasm of the halophytic plant body. This is for protecting the plant cell from osmotic disturbance for the presence of high inorganic salts sequestered in the vacuoles. Polyols help in scavenging stress induced oxygen radicals. Mannitol is a sugar alcohol which acts as osmoregulator in salt stress. Mannitol serves as a compatible solute in adverse environmental conditions by synthesizing mannose-6- phosphate reductase. Studies on *Arabidopsis* plant shows that mannitol accumulation occurs in the plant body under high salt concentration. Mannitol improves tolerance in stress by scavenging hydroxyl radicals (OH^*) and stabilization of macromolecular structures. *Arabidopsis thaliana* is a non mannitol producer, was transformed with Celery leaf M6PR gene under the control of CaMV 35S promoter. In all transgenic *Arabidopsis* M6PR plants mannitol get accumulated in the plant body from 0.5 to 6 μmol/gm fresh weight. Another one compound named 1-O-β-D-glucopyranosyl-D-mannitol is also accumulated in the mature transgenic plants, which is not found in Celery or *Arabidopsis*. This novel compound is accumulated in the vegetative tissues of the mature plants up to 4 μmol/gram fresh tissues. But it is not accumulated in the flowers or in the seeds. In the absence of NaCl all the transgenic plants are phenotypically same as the wild types. But in the presence of sodium salts the transgenics show higher tolerance than the wild types. The M6PR transgenics show tolerance upto 300 mM NaCl where wild type plants show tolerance upto 150 mM NaCl [17].

Antioxidants are few compounds which help plant body from oxidation. Free radicals which are scientifically known as Reactive Oxygen Species (ROS) generates from oxidation. Plants defense against reactive oxygen species by producing many antioxidant enzymes. These anti-oxidant enzymes are like catalase, peroxidase, ascorbate peroxidase, Mono Dehydro Ascorbate Reductase (MDHAR) superoxide dismutase, glutathione reductase etc. These enzymes can scavange Reactive Oxygen Species (ROS). The higher concentration of NaCl increases the activities of Super Oxide Dismutase (SOD) and glutathione reductase. Salt stress decreases the activities of catalase and ascorbate peroxidase. Salt stress also decreases total ascorbate, total glutathione and α-tocopherol. Salt stress has a little effect in glutathione reductase enzyme activity level. The non-enzymatic anti-oxidants like such as vitamin C, vitamin E, carotenoids, lipoic acids are produced under stress conditions [23].

Conclusion

Among several types of abiotic stresses salinity stress is the most destructive type of plant stress. It takes part in crop loss and several problems in farm land. *Brassicaceae* family plants have the ability to tolerate salt stress is by maintaining several biochemical pathways and physiological and cellular mechanisms. From the discovery of SOS pathway, it is quite easy to interpret signaling mechanisms related to salt stress. Along with the model plant *Arabidopsis thaliana*, the whole *Brassicaceae* family performs several mechanisms to fight against salinity stress using these weapons. In this way, they protect their chlorophyll content, stabilize membrane structure and protect several enzymes as well as maintain ion homeostasis. Essentially active pathways in salinity stress help in producing compounds which are helpful in osmotic balance. Sugars like glucose, fructose, complex sugars like trehalose, raffinose and sugar alcohols like glycerols and methylated inositols take part in maintaining osmotic balance. Polyols like mannitols, glycerols, sorbitols and pinitols also play in osmoregulation mechanism. Accumulation of different types of essential carbohydrates, proteins and amino acids help in maintaining osmotic balance and survival. We hope that, this chapter will open a new avenue in agriculture field for defending salinity stress in cellular and biochemical perspectives.

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