CIBTech Journal of Biotechnology ISSN: 2319–3859 (Online)
An Open Access, Online International Journal Available at http://www.cibtech.org/cjb.htm
2015 Vol. 4 (1) January-March, pp.33-46/Hapani and Marjadi
Review Article

SALT TOLERANCE AND BIOCHEMICAL RESPONSES AS A STRESS INDICATOR IN PLANTS TO SALINITY: A REVIEW

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ABSTRACT

Salinity affects plant growth and development in various ways through its impact on photosynthesis, water relations and nutrient absorption. The ability of plants to tolerate salts is determined by many biochemical pathways which enable acquisition of water, protect chloroplast functions and maintain ion homeostasis. Essential pathways include those that lead to synthesis of osmotically active metabolites, specific proteins and certain free radical enzymes to control ion and water flux and support scavenging of oxygen radicals. It is highlighted that the fundamental mechanism of salinity's effects on plant function is the increase in the osmotic pressure of the plant's environment that inhibits the absorption of water and nutrients. There is a need to determine the underlying biochemical mechanisms of salinity tolerance so as to provide plant breeders with appropriate indicators.

Keywords: *Salinity Stress, Soil, Plants Responses, Biochemical Indicators*

INTRODUCTION

Abiotic stresses, in particular drought and salinity, not only compromise crop quality and limit yield, but also restrict the geographical range over which crop production is viable (Thakur *et al*., 2010). Soil salinity has been a major concern to global agriculture throughout human history (Lobell *et al*., 2007). In recent times, it is a serious problem and is increasing steadily in many parts of the world, particularly in arid and semi arid areas (Abdel, 2010). Saline soils occupy 7% of the earth's land surface (Ruiz-Lozano *et al*., 2001) and increased salinization of arable land will result up to 50% land loss by the middle of the 21st century (Wang *et al*., 2003). At present, out of 1.5 billion hectares of cultivated land around the world, about 77 million hectares (5 %) is affected by excess salt content (Sheng *et al*., 2008). The deleterious effects of salinity on plant growth are associated with (1) low osmotic potential of soil solution, (2) nutritional imbalance (Attia *et al*., 2011), (3) specific ion effect (Munns and Tester, 2008), or 4) a combination of these factors (Arzani, 2008). All of these cause adverse pleiotropic effects on plant growth and development at physiological and biochemical levels and at the molecular level (Munns, 2002; Tester and Davenport, 2003; Winicov, 1998).

The most important aspect of plant responses leading to salt stress tolerance is the regulation of uptake and distribution of Na^+ ions (Tester and Davenport, 2003). Along osmotic homeostasis, maintenance of ionic homeostasis is an important strategy for achieving enhanced tolerance to environmental stresses (Sun *et al.*, 2009). Despite a great deal of research into salinity tolerance of plants, the metabolic sites at which salt stress damages plants and the adaptive mechanisms utilized by plants to survive under saline stress are still not well understood. The main problem is due to the lack of well defined plant indicators for salinity tolerance that could practically be used by plant breeders for improvement of salinity tolerance in a number of important agricultural crops. This is partly due to the fact that the mechanisms of salt tolerance are very complex and variation occurs not only amongst the species but in many cases, also among cultivars within a single species (Ashraf, 2002; Ashraf and Harris, 2004; Khan *et al*., 2006; Shafi *et al*., 2011 a, b; Bakht *et al*., 2006; 2011).

Researchers have suggested that plant species possesses distinctive indicators of salt tolerance at the whole plant, tissue or cellular levels (Munns, 2002; Ashraf, 2002). Nonetheless, parallels have been drawn between different biochemical indicators and plant tolerance. For ex., Glycine betaine (quaternary ammonium compound) and proline (amino acid) play a key role in mediating osmotic adjustment and protecting the subcellular structures in stressed plants. In various studies a positive correlation between the accumulation of these two compatible solutes and stress tolerance has been observed (Yamada *et al*., 2003; Yang *et al*., 2003).

While determining the role of various antioxidants in the salt tolerance of tomato, Mittova *et al.*, (2002) found that higher salt tolerance of wild tomato (*Lycopersicon pennellii*) as compared to cultivated tomato (*L. esculentum*) was correlated with increased activities of anti-oxidative enzymes like SOD (superoxide dismutase), APX (ascorbate peroxidase), and POD (guiacol peroxidase).

Thus we can say that the compatible solutes that usually participate in osmotic adjustment vary between species and plant developmental stage and consist of sugars (glucose and fructose), sugar alcohols (glycerol), complex sugars (trehalose, raffinose and fructans), sulfonium compounds (choline osulfate, dimethyl sulfonium propironate) and amino quaternary compounds (glycine betaine and proline) and it is also observed that plants have developed efficient antioxidant system which can protect them under various environmental stress conditions.

This review has been focused upon salt tolerance mechanism which is acquired by the plants and includes mainly biochemical responses of plants under salt stress which can be used as stress indicator at the cellular and sub cellular level.

Salt Tolerance

Salt tolerance is the ability of a plant to grow and complete its life cycle on a substrate that contains high concentrations of soluble salt.

Plants have classified into halophytes and glycophytes depending on their sensitivity to salinity. 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 facultative (Parida and Das, 2005).

Almost all major crop species as well as most wild species are glycophytes. Although individual responses to high salinity may differ, several lines of evidence suggest that all plants use the same general salt tolerance regulatory mechanisms, and differences between halophytic and glycophytic species are a quantitative rather than qualitative nature (Omami, 2005; Zhu, 2001).

Mechanism of salt tolerance: Plants have evolved several mechanisms to acclimatize to salinity. It is possible to distinguish three types of plant response or tolerance: (Munns and Tester, 2008)

(a) The tolerance to osmotic stress

(b) The Na^+ exclusion from leaf blades

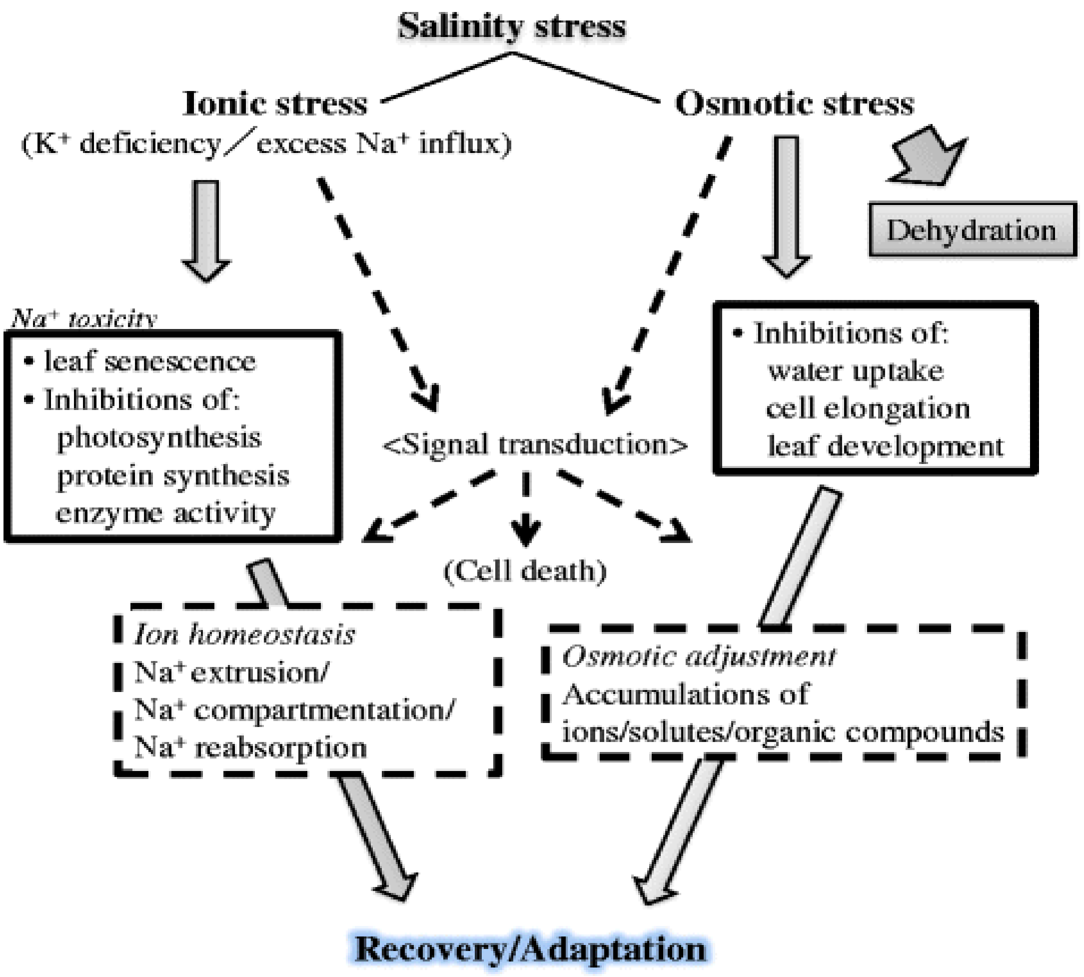

Figure 1: Mechanism of salt tolerance in plants (Horie *et al*., 2012)

1. Osmotic tolerance: The growth of salt-stressed plants is mostly limited by the osmotic effect of salinity, irrespective of their capacity to exclude salt that results in reduced growth rates and stomatal conductance (James *et al*., 2008). If the accumulation of salts reach to the toxic level, the old leaves die (usually old expanded leaves) and the young leaves, no more supported by photosynthesis, undergo a reduction of growth and new leaves production. It has been demonstrated that the plant's response to the osmotic stress is independent of nutrient levels in the growth medium (Hu *et al*., 2007). In response to osmotic stress, plants produce osmolytes like glycine betaine, trehalose or proline, which protect them from dehydration or protein denaturation. However, oxidative stress is an outcome of ionic stress lead to the production of different enzymatic or non-enzymatic antioxidants, which protect plants from harmful effects of reactive oxygen species (Turan *et al.*, 2012).

2. Na+ exclusion: It involves the ability to reduce the ionic stress on the plant by minimizing the amount of Na^+ that accumulates in the cytosol of cells, particularly those in the transpiring leaves. Na^+ exclusion from leaves is associated with salt tolerance in cereal crops including rice, durum wheat, bread wheat and barley (James *et al*., 2011). Salt stress can also induce the accumulation of ABA, which, by means of ABI1 and ABI2, can negatively regulate SOS2 or SOS1 and NHX1 (Silva and Gerós, 2009).

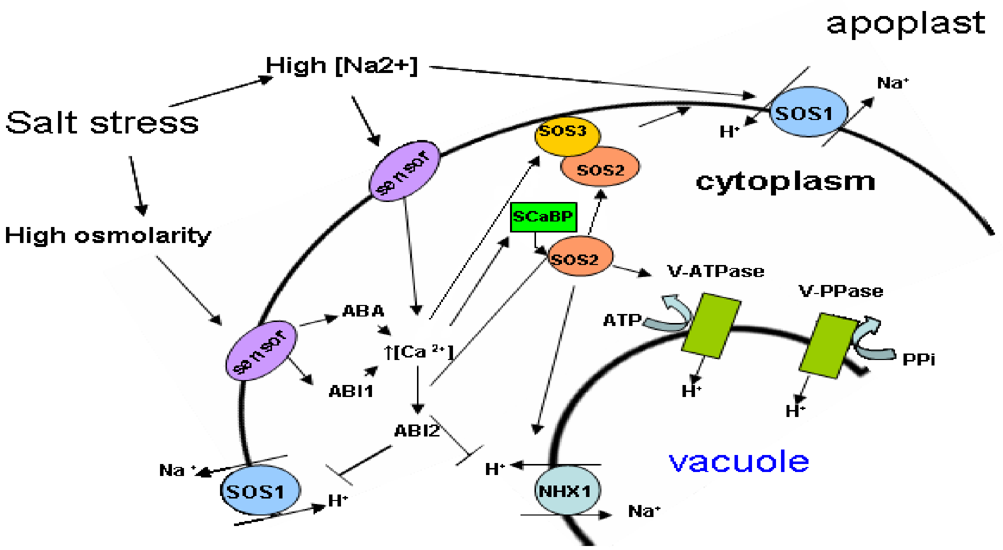

Figure 2: Signalling pathways responsible for Na+ extrusion in Arabidopsis under salt stress (Silva and Gerós, 2009)

Biochemical Effects of Salt Stress in Plants

Salinity Effects on Protein

Salt-induced proteins in plants have been classified into two major groups (Mansour, 2000), i.e., (1) salt stress proteins, which accumulate only due to salt stress, and (2) stress associated proteins, that accumulates in response to various abiotic stress like heat, cold, drought, water logging, and high and low mineral nutrients. Proteins accumulation also provides a storage form of nitrogen that is re-utilized later (Singh *et al.*, 1987) and also plays a role in osmotic adjustment. Large number of cytoplasmic proteins causes alterations in cytoplasmic viscosity of the cell stimulated by salinity (Hasegawa *et al*., 2000). Proteins may be synthesized de novo in response to salt stress or may be present constitutively at low concentration and increase when plants are exposed to salt stress (Parvaiz and Satyawati, 2008).

Salt tolerant shows higher soluble proteins than salt sensitive species of barley, sunflower, finger millet, and rice (Ashraf and Harris, 2004). Several researches showed that soluble protein contents of leaves decreased in response to salinity (Agastian *et al*., 2000; Parida *et al*., 2002; Wang and Nil, 2000).

Salinity Effects on Amino Acids

According to Mansour (2000) many amino acids including proline, alanine, arginine, glycine, serine, leucine, and valine and the non-protein amino acids (citrulline and ornithine) and amides (glutamine and asparagine) accumulate in plants exposed to salt stress. Salt tolerant varieties of sunflower (Ashraf and Tufail, 1995), safflower (Ashraf and Fatima, 1995), *Eruca sativa* (Ashraf, 1994) and *Lens culinaris* (Hurkman *et al*., 1991) have shown higher amount of total free amino acids than salt sensitive ones.

Proline is a major amino acid that accumulates in plant at a higher rate than other amino acids (Torabi *et al*., 2010; Abraham *et al*., 2003). Accumulation of proline occurred in the cytosol and accomplished osmotic adjustment (Ketchum *et al*., 1991). Proline accumulation affects membrane maintenance and also alleviated the effects of NaCl on cell membrane interruption (Mansour, 1998). Maggio *et al*., (2002) noted proline as a signaling/regulatory molecule able to activate multiple responses that are components of the adaptation process. There are two alternative routes in proline biosynthesis in higher plants: the L-ornithine and the L-glutamate pathways. It is also known that, as in plants, both ornithine and glutamate are precursors of proline biosynthesis in microorganisms and mammals. Two enzymes: pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR), play major roles in proline biosynthetic pathway which was shown in Figure 3.

There are different reports in terms of effects of salinity on proline in tolerant and sensitive genotypes among species. Torabi *et al.*, (2010) and Petrusa and Winicov (1997) noted that salt tolerant alfalfa lines had two times more free proline content in root than sensitive lines and also increasing the proline in tolerant lines were more rapid than sensitive lines. Kaymakanova *et al.*, (2008) indicated that with increasing salinity the amount of proline increased in bean (Phaseolus vulgaris L.).

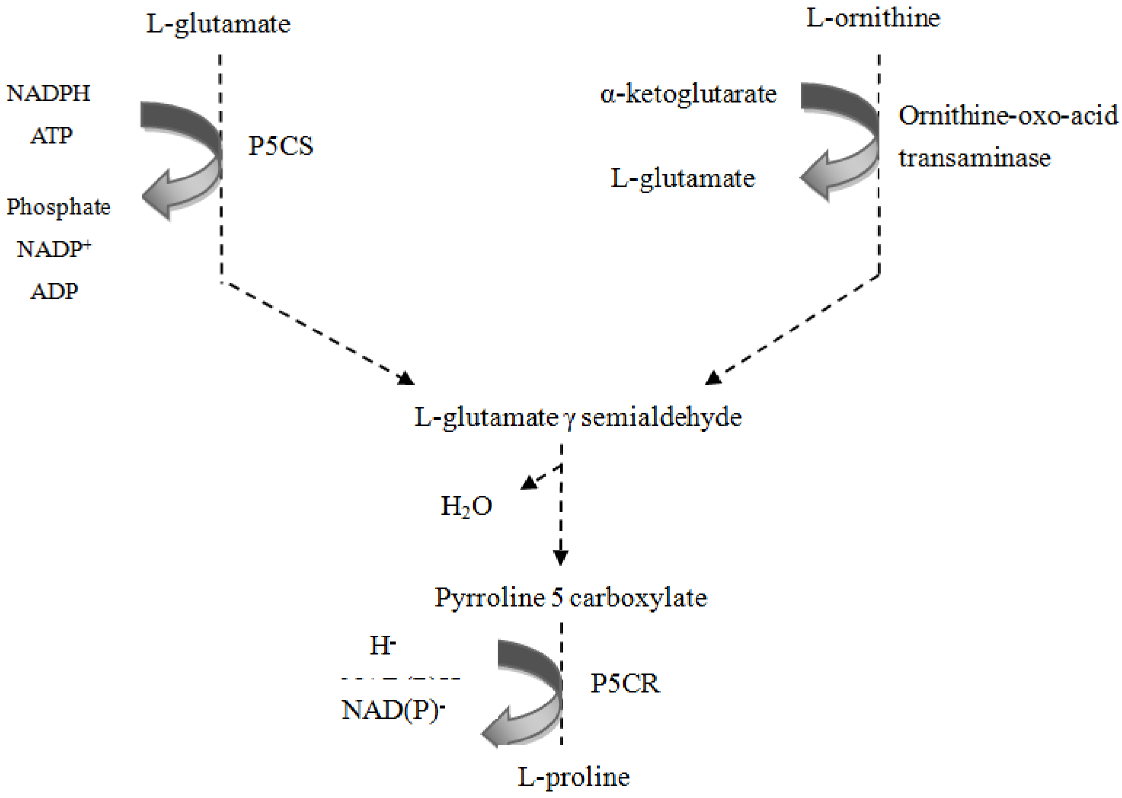

Figure 3: Biosynthetic pathway of proline

Salinity Effects on Carbohydrates

The accumulation of soluble carbohydrates in plants has been widely reported as a response to salinity or drought, despite a significant decrease in net CO2 assimilation rate (Murakezy *et al.*, 2003). When glycophytes are exposed to high salinity, the increase in soluble sugars contributes up to 50% increase in osmotic potential (Parvaiz and Satyawati, 2008).

Trehalose as a disaccharide accumulates in various abiotic stresses and protects membranes and proteins in cells exposed to stress caused by water deficit and reduced aggregation of denatured proteins. Also trehalose inhibit apoptotic cell death and there are some proofs that trehalose is present in trace amounts in vascular plants, but some roles of trehalose are still unknown (Yamada *et al*., 2003). Role of sugars in adaptation of plants to salinity have been concluded to be universally associated with salt tolerance. However, this does not rule out a significant role of soluble sugars in salt tolerance nor a potential role for soluble sugar accumulation as an indicator for salt tolerance in breeding programs for some species.

Salinity Effects on Quaternary Ammonium Compounds

The quaternary ammonium compounds (QACs) that function as effective compatible osmolytes in plants subject to salt stress are glycinebetaine, ß-alaninebetaine, prolinebetaine, choline *O*-sulfate, hydroxyprolinebetaine, and pipecolatebetaine. In several plant species, a positive correlation between leaf osmotic potential and glycinebetaine, ß-alaninebetaine and prolinebetaine has been observed. These compounds have osmoprotective effects in the cell as well. Under salt stress, glycinebetaine occurs most abundantly from all QACs. In higher plants, GB is synthesized in chloroplast from serine via ethanolamine, choline, and betaine aldehyde (Rhodes and Hanson, 1993). Choline is converted to betaine aldehyde, by choline monooxygenase (CMO), which is then converted to GB by betaine aldehyde dehydrogenase (BADH) (Figure 4). Although other pathways such as direct *N*-methylation of glycine is also known, the pathway from choline to glycine betaine has been identified in all GB-accumulating plant species (Ashraf and Foolad, 2007).

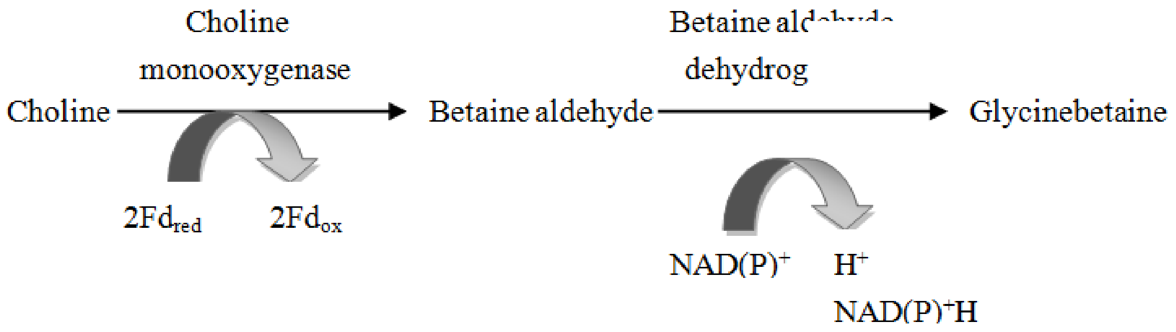

Figure 4: Biosynthetic pathway of Glycinebetaine

Positive effects of exogenous application of GB on plant growth and final crop yield under salt stress have been reported in a number of crops such as tobacco, wheat, maize, barley, sorghum, soybean and common beans (Ashraf and Foolad, 2007). Many researchers demonstrate positive effects of exogenous application of GB on plant growth and final crop yield examples include tobacco, wheat, barely, sorghum, soyabean.

Salinity Effects on Polyols

Polyols, the polyhydric alcohols, are among the compatible solutes involved in osmoregulation and are thought to play a role in plant salt tolerance (Bohnert and Shen, 1999). They exist in both acyclic and cyclic forms and are widely distributed in the plant kingdom. The most common polyols in plants include acyclic forms, mannitol, glycerol, sorbitol, and cyclic (cyclitols) forms ononitol and pinitol. In general, they are thought to accumulate in the cytoplasm of some halophytes to overcome the osmotic disturbances caused by high concentrations of inorganic ions compartmentalized in vacuoles. Polyols make up a considerable percentage of all assimilated CO2 as scavengers of stress-induced oxygen radicals (Bohnert *et al*., 1995). Mannitol, a sugar alcohol that may serve as a compatible solute to cope with salt stress, is synthesized via the action of a mannose-6-phosphate reductase (M6PR) in celery (Zhifang and Loescher, 2003) and its accumulation increases when plants are exposed to low water potential. The accumulation is regulated by inhibition of competing pathways and decreased mannitol consumption and catabolism (Stoop *et al.,* 1996). Studies using transgenic tobacco and *Arabidopsis* have shown improved growth of mannitol accumulating plants under stress (Thomas *et al.,* 1995). Mannitol improves tolerance to stress through scavenging of hydroxyl radicals (OH°) and stabilization of macromolecular structures. In tobacco, mannitol protects the thiol-regulated enzymes phosphoribulokinase, thioredoxin, ferrodoxin and glutathione from OH° (Shen *et al*., 1997). Abebe *et al.,* (2003), however, state that the amount of mannitol accumulated in response to stress was small and its effect on osmotic adjustment was less than that of other carbohydrates.

Salinity Effects on Polyamines

Polyamines are polyvalent compounds containing two or more amino groups. The most common polyamines in higher plants are putrescine, spermidine and spermine, with the diamines, diaminopropane and cadaverine occurring but less commonly (Mansour 2000). They can be classified into two groups on the basis of their biological role (Kuznetsov *et al.,* 2002). The first group includes putrescine and cadaverine, whose function is similar to that of auxins and gibberellins, i.e. cell elongation and root formation. The second group comprises spermidine and spermine, which, like cytokinins, regulate cell division, organogenesis, and plant senescence. At neutral pH, polyamines are polycations and can frequently bind to polyanions in the cell such as DNA, RNA and phospholipids, thereby stabilizing these macromolecules. They also stabilize protoplasts, activate cell division during embryogenesis and delay senescence in most plants (Genard *et al.,* 1991). Furthermore, the contribution of polyamines to osmotic adjustment appears to be small compared with other nitrogenous compounds. Nevertheless, in pea seedlings, all three common polyamines alleviated the inhibitory effect of salt stress (Ivanova *et al*., 1991). The synthesis of polyamines in plants occur by two alternative pathways, namely ornithine decarboxylase (ODC) catalysed reaction and second is from arginine (Arg) as a result of the action of Arg decarboxylase via agmatine. The polyamines in plants are not only found in the cytoplasm, but also in certain organelles like mitochondria, chloroplasts and vacuoles (Kusano *et al*., 2008). A few plant species, including *Arabidopsis thaliana* , lack the ODC pathway (Kusano *et al*., 2007). The genes encoding enzymes for the polyamine biosynthesis pathway have been cloned and characterized from various plant species (Liu *et al*., 2007; Kusano *et al*., 2008). Polyamines and the activities of their major metabolic enzymes were studied in *Brassica campestris* in response to stress (Das *et al*., 1995). It was found that prolonged stress caused only small changes in polyamine level, and activities of arginine and ornithine decarboxylases, and polyamine oxidase, whereas short-term stress caused a significant increase in polyamine level and enzyme activities.

Salinity Effects on Antioxidants

Plants have an effective system for scavenging active oxygen species that protect them from harmful oxidative reactions (Foyer *et al*., 1994; Mittova *et al*., 2004). Anioxidative enzymes such as catalase (CAT), glutathione reductase (GR), superoxide dismutase (SOD) and glutatione-S transferase are the main enzymes to protect cells (Garratt *et al*., 2002; Mittova *et al*., 2003). Whereas superoxide dismutase, metabolizes oxygen (O2) radicals to hydrogen peroxide (H2O2), then protecting cells from damage and catalase, ascorbate peroxidase, and a variety of peroxidases catalyze the subsequent breakdown of H2O2 to water and oxygen (Garratt *et al*., 2002; Mittova *et al*., 2002; Mittova *et al*., 2003). Several researchers showed that when plants are exposed to salinity the activity of antioxidant increase, in rice (Lee *et al*., 2001), wheat (Meneguzzo *et al*., 1999) and lentil (Bandeolu *et al*., 2004). Recent studies have demonstrated that over expression of mitochondrial Mn-SOD in transgenic *Arabidopsis thaliana* (Wang *et al*., 2004) and chloroplastic Cu/Zn-SOD in transgenic *Nicotiana tabacum* (Badawi *et al*., 2004) can provide enhanced tolerance to salt stress. Similar results have been found in *Morus alba* (Ramajulu and Sudhakar, 2001), *Triticum aestivum* (Sairam and Tyagi, 2004) and *Lycopersicon sp*. (Mittova *et al*., 2002). Bacterial catalase and Glutathione-STransferase / glutathione peroxidase were reported to increase the performance of plants under stress (Roxas *et al*., 2000).

Table 1: Salt-stress-accumulating products and their function(s) in conferring tolerance (Parida *et al*., 2005)

Product group	**Specific compound**	**Suggested function(s)**
Proteins	Osmotin	Pathogenesis-related proteins, Osmoprotection, Radical detoxification
	SOD/Catalase	
Amino acids	Proline	Osmotic adjustment
	Ectoine	Osmoprotection
Sugars	Glucose, fructose, sucrose, fructans and starch	Osmotic adjustment, Osmoprotection, carbon storage and radical scavenging
Quaternary amines	Glycine betaine	Osmoprotection
	ß-Alanine betaine	Preservation of thylakoid and plasma membrane integrity
	Dimethyl-sulfonio propionate	Osmoprotection
	Choline-o-sulfate	Osmoprotection
	Trigonelline	Osmoprotection
Polyols	Acyclic (e.g., manitol)	Carbon storage, osmotic adjustment
	Cyclic (e.g., pinitol)	Osmoprotection, osmotic adjustment
		Retention of photochemical efficiency of PSII
		Radical scavenging
Polyamines	Spermine, Spermidine	Ion balance, Chromatin protection

Table 2: Response of biochemical parameters with suitable examples under salt stress

Specific compound	**Plant species**	**Response to salinity**	**References**
Soluble protein	*Brassica juncea* var.	Increase	Mittal *et al*., (2012)
	Bio902	Decrease	Mittal *et al*., (2012)
	Brassica juncea	Increase	Hendawy *et al*., (2012)
	var.Urvashi	Decrease	Rahdari *et al*., (2012)
	Setaria italic	Increases	Rahdari *et al*., (2012)
	Portulaca oleraceae	Increase	Ahmad and Sharma (2010)
	Portulaca oleraceae	Increase	Ahmad and Jhon (2005)
	Morus alba		
	Pisum sativum		
Proline	*Saueda maritime*	Increase	Rajaravindran and Natarajan
	Brassica juncea var.	Increase	(2012)
	Bio902	Decrease	Mittal *et al*., (2012)
	Brassica juncea	Increases	Mittal *et al*., (2012)
	var.Urvashi	Decrease	Rahdari *et al*., (2012)
	Portulaca oleraceae	Increases	Enteshari *et al*., (2011)
	Borago officinalis		Enteshari *et al*., (2011)
	Borago officinalis		
Carbohydrates	*Portulaca oleraceae*	Increases	Rahdari *et al*., (2012)
	Matricaria chamomilla	Increases	Heidari and Sarani (2012)
	Borago officinalis	Decrease	Enteshari *et al*., (2011)
	Beta vulgaris L.	Increases	Daskhan (2010)
	Morus alba	Increase	Ahmad and Sharma (2010)

CONCLUSION

Plants exhibit a variety of responses to salt stress, which are depicted by symptomatic and quantitative changes in growth and morphology.

The ability of the plant cope with or adjust to the salt stress varies across and within species as well as at different developmental stages. In addition to genetic means to developing plants with improved salt tolerance, attempts have been made to induce salt tolerance in a range of plant species using different approaches. Also while some notable progress has been reported as to the development of crop plants with improved salt tolerance via traditional breeding, the prospect for genetic engineering plants with salt tolerance is also good considering accumulating molecular information on the mechanisms of tolerance and contributing factors.

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