Chapter 1
Salt Stress: Causes, Types and Responses of Plants

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1.1 Introduction

Abiotic factors like temperature, drought, salt stress, etc. results in the depletion of large number of food production in today's world and as a result these global changes have led to alarmist projections that seem to argue for additional strategies by which food supply can be guaranteed (Miflin 2000). Moreover, the increased productivity achieved in irrigated areas still do not benefit people because salinization following prolonged irrigation is unavoidable (Flowers and Yeo 1995; Postel 1999). These considerations have aroused strong interest in studying plant abiotic stress responses. Salinity has severely affected the agricultural productivity and the damaging effects of salt accumulation have influenced both ancient and modern civilizations. It is estimated that about 20% of the irrigated land in the present world is affected by salinity that is exclusively classified as arid and desert lands comprising

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25% of the total land of our planet (Yeo 1999). Saline soils with soluble salts affect plant growth at various stages leading to yield differences between crops and also the differences in their ion compositions at maturity. The loss of farmable land due to salinization directly affects the food requirement of the world population, which is projected to increase by 8.5 billion over the next 25 years. Since the cultivable land is declining day by day because of urbanization, there is need to use the uncultivable land for food production to feed teeming population. The maximum area of uncultivable land belongs to salt affected area. In developed and developing countries, the intensive use of agricultural practices has led to the degradations of farming land and water supplies. Preferably, use of crops that tolerate the high levels of salinity in the soils would be a practical contribution towards addressing the problem. Most crops tolerate salinity to a threshold level (Khan et al. 2006), a 'threshold' for a crop is defined as the value below which crop growth is generally not affected due to salinity.

According to Flowers et al. (1977) plants can be divided in to glycophytes and halophytes on the basis of their abilities to grow on different salt concentrations. Halophytes are the plants that grow and complete their life cycle on high concentration of salt, e.g. *Atriplex*, *Vesicaria*. Majority of the terrestrial plants including agricultural crops are glycophytic and cannot tolerate high concentration of salt. Plant growth and development is hampered due to salinity stress through: (1) low osmotic potential of soil solution (water stress), (2) nutritional imbalance, (3) specific ion effect (salt stress) or (4) a combination of these factors (Ashraf 1994). During the onset and development of salt stress within a plant, all the major processes such as photosynthesis, protein synthesis and energy and lipid metabolisms are affected.

Osmotic stress is caused due to the excess of Na^+ and Cl^- in the environment that decrease the osmotic potential of the soil solution and hence water uptake by the plant root. During osmotic stress plant also accumulate low molecular mass compounds known as compatible solutes or osmolytes like, proline, protein, mannitol, sorbitol, glycine betaine, etc. Salt induced osmotic stress is responsible for the oxidative stress caused by reactive oxygen species (ROS).

ROS, such as singlet oxygen ($_1O^2$), superoxide ions (O_2^-) and peroxides, the most widely distributed being hydrogen peroxide (H_2O_2) are toxic molecules (Apel and Hirt 2004; Triantaphylidès et al. 2008). ROS is capable of inducing damage to almost all cellular macromolecules including DNA (Jaleel et al. 2007a, b, c, 2008; Tuteja et al. 2009). ROS targets high-molecular mass molecules, such as membrane lipids or mitochondrial DNA, with the formation of lipid or nucleotide peroxides, especially at the level of thymine.

The harmful effect of ROS is primarily due to their ability to initiate a variety of autoxidative chain reactions on unsaturated fatty acids (Smirnoff 2000). Oxidative attack on proteins results in site specific amino acid modifications, fragmentation of the peptide chain, aggregation of cross linked reaction products and increased susceptibility to proteolysis (Ahmad et al. 2010b, c, 2011). ROS can also induce numerous lesions in DNA that cause deletions, mutations and other lethal genetic effects (Srivalli et al. 2003; Tuteja et al. 2009).

Table 1.1 Different classes of salinity

Salinity class	ECe range (dS/m)
Non-saline	0–2
Low salinity	2–4
Moderate salinity	4–8
High salinity	8–16
Severe salinity	16–32
Extreme salinity	>32

The toxic effects of ROS are counteracted by enzymatic as well as nonenzymatic antioxidative system such as: superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), ascorbic acid (AsA), tocopherol, glutathione and phenolic compounds, etc. (Shi and Zhu 2008; Sharma and Dietz 2009; Ashraf 2009; Ahmad et al. 2008a, b, 2010a, b, c, 2011, 2012b). Normally, each cellular compartment contains more than one enzymatic activity that detoxifies a particular ROS.

1.2 Salinity in India and World

In the arid and semi-arid regions, low rainfall coupled with ambiguity of its occurrence has been the major limiting factors in crop production. This is mainly true for India because most of the agricultural productive regions lie in hyper-arid to sub-humid regions where evaporation far exceeds the rainfall. The data collected for salt affected areas in different states by Soil Resource Maps has been published by the NBBS and LUP, Nagpur (Bhargava 2005). The NBSS and LUP (National Bureau of Soil Survey and Land Use Planning) had mapped saline soils into six classes on the basis of ECe (electrical conductivity of the saturation extract) viz., slight, moderate, moderately strong, strong, severe and very severe (Table 1.1). While compiling the figures for salt affected soils the values for ECe ranging between 2–4 dS/m were discarded because they constitute non-saline class as per norms evolved by (Richards 1954). Similarly, Bureau categorized the soil sodicity classes in three classes on the basis of ESP (exchangeable sodium percentage) namely high (< 5), moderate (5–15) and strong (>15). All the soils with less than 5 ESP have been considered non-sodic or non-alkali. But all black soils or vertisols with >5 ESP have been considered sodic or alkali. The Rann of Kutchchh (Bangalore), which has an area of 2.1507 million ha and comprises a saline marsh, has been separated in the Maps published by the Bureau. The figures so extracted have been presented in Table 1.2.

At global scale more than 77 mha of land are salt affected and about 43 mha are attributed to secondary salinization as reported by FAO (2007). It is estimated that about one-third of the irrigated land in the major countries with irrigated agriculture is badly affected by salinity or is likely to be salinized in the near future.

Table 1.2 Distribution of saline/sodic soils in India (,000 ha)

State	Saline	Sodic	Total
Punjab	10.2	190.9	201.1
Haryana	175.2	255.7	430.9
Rajasthan	490.4	9.5	499.9
Dehli	21.2	Nil	21.2
Uttar Pradesh	128.9	3,394.1	3,523.0
Bihar	–	229.0	229.0
West Bengal	377.7	–	377.7
Maharashtra	317.3	114.6	431.9
Andhra Pradesh	312.7	217.2	529.9
Madhya Pradesh	1,743.4	26.6	1,770.0
Karnataka	100.0	10.0	110.0
Orissa	74.5	–	74.5
Tamil Nadu	50.0	46.2	96.2
Goa	1.0	–	1.0
A & N Islands	91.9	–	91.9
Karaikal	1.7	1.8	3.5
Pondicherry	1.5	1.9	3.4
Kerala	203.3	–	203.0
Jammu & Kashmir	40.0	20.2	60.0
Gujarat	3,598.4	846.2	4,444.6
Rann of Kutchchh	2,150.7	–	2,150.7
Total	9,889.7	5,363.7	15,253.4

Source: (Bhargava 2005)

Current estimates of the salt-affected soils as percent of the irrigated lands for different countries are: 27% for India, 28% for Pakistan, 13% for Israel, 20% for Australia, 15% for China, 50% for Iraq, and 30% for Egypt (Stockle 2001). In only New South Wales (NSW) state of Australia, salinity is estimated to affect 15% of the irrigated land.

There has been a sequential increase in the level and strength of salinity that affects soil. A number of major irrigation schemes throughout the world have suffered to some extent from the effect of salinity and/or sodocity. Many once-productive areas have become salt affected wastelands. Salt related problems occur within the boundaries of at least 75 countries (Szabolcs 1994). An alphabetical list of the countries with serious salinity problems include Australia, China, Egypt, India, Iraq, Mexico, Pakistan, the Soviet Union, Syria, Turkey and the United States (Rhoades 1998). It has been reported by different international organizations like ICID (International Commission on Irrigation and Drainage), UNEP (United Nations Environment Programme) and FAO (Food and Agriculture Organization) that salinization and water logging of the soil in arid and semi-arid regions are highly responsible for the loss of agricultural productivity on irrigated land. Therefore, the focus should be on urgent measures to combat desertification via modification of farming techniques and amelioration of salt affected and water logged soils with a resultant improvement in social and economic conditions of people dependent on agriculture (Rhoades 1998).

1.3 Causes and Types of Soil Salinity

Salinity has also been categorized as primary and secondary on the basis of their source of cause. Former occurs as natural salt in the landscape like salt marshes, salt lakes, tidal swamps or natural salts clads. While as latter results due to human activity such as urbanization and agriculture (irrigated and dry land). Following are the factors responsible for soil salinity:

For Primary salinity:

I. Weathering of rocks
II. Capillary rise from shallow brackish groundwater
III. Intrusion of sea water along the coast
IV. Salt laden sand blown by sea winds
V. Impeded drainage

Secondary salinization is due to human activities like:

I. Introduction of irrigation without proper drainage system
II. Industrial effluents
III. Overuse of fertilizers
IV. Removal of natural plant cover
V. Flooding with salt rich waters
VI. High water table and the use of poor quality ground water for irrigation

1.3.1 Types of Salinity

There are two types of salt affected soils:

(i) Sodic soils
(ii) Saline soils

The main differences between these two lies in the nature of anions and the pH of the soil. Studies demonstrate that carbonate or bicarbonate ions constitute the sodic soils with pH above 8.5, whereas chloride or sulphate ion dominates the saline soils with pH below 8.5. Some plants grow well in salt affected coastal areas, shores of backwaters lakes and marshy lands. The plants that thrive well in high salt concentrations are called halophytes. However, some plants that cannot withstand even 10% of seawater are called glycophytes or non-halophytes (Gorham 1995; Cherian et al. 1999; Parida and Das 2005; Yadav et al. 2011; Mane et al. 2011).

1.4 Reclamation and Management Strategies

Reclamation is the process of restoring disturbed land into a cultivable soil. While as management is the sum total of all procedures to protect soil and increase its performance. This reclamation process of saline soil includes the following methods:

1.4.1 Physical Method

Physical method of reclamation of saline soil includes the following processes:

1.4.1.1 Scarping

Scraping is the temporary method for soil reclamation in which salt layer of soil surface is scrapped off by mechanical means and the lower layer with less salt content is used for cultivation. Since, with the lowering of ground level in relation to water table salt accumulates again, this method has resulted in limited success. Thus, it again intensifies the problem. This method is rarely used because it involves high cost (Gupta and Gupta 1987).

1.4.1.2 Flushing

Another method of desalinization is to flush the soil with water. In this method accumulated salt on the surface is washed away by water which is associated with very low permeability and high salinity content in their surface layer. This method has little practical significance and shows high efficiency at the beginning but gradually decreases as saline concentration begins to fall.

1.4.1.3 Leaching

In this method, the excess amount of salt can be removed by applying water onto the soil surface. The soluble salts dissolved and transported through the soil are consequently removed from the root zone through drainage. Nevertheless, the amount of liquid required for this process varies and depends on the various characteristics of the soil (Gupta and Gupta 1987). The quantity of soluble salt leached per unit volume of water applied describes the efficiency of leaching (Tanji 1990) and this depends on the (a) uptake of water (b) uniformity of distribution of water on the soil surface, and (c) sufficiency of drainage. The major factors like primary salt content, soil salinity requirement after leaching and depth of root zone becomes imperative to provide a reliable estimate of the quantity of water required for leaching. Leaching of the salts from the soil is usually done by two methods (a) continuous leaching (b) intermittent leaching.

Continuous ponding is the traditional method for leaching of salts from surface irrigated lands (Tanji 1990). In this method of leaching, the water flows in the macropores with salts in the micropores to diffuse to the mobile water. Being faster, this method is also extensively used when time becomes the limiting factor.

Intermittent ponding is most effective method for leaching when water is the limiting factor. Less than 30–35% of water is needed for intermitted ponding than continuous ponding, but the main disadvantage of this method is that it is much slower than continuous ponding method (Gupta and Gupta 1987).

1.4.2 Chemical Method

Gypsum, sulfuric acid and farm yard manure amendments are applied especially in sodic or saline sodic soils. Sodic and saline sodic soil reclamation needs a different approach than saline soils which might be more costly. Furthermore an increase in the infiltration rates is to be required in sodic soils for reclamation that can be achieved by mechanical and chemical measures. Gypsum is considered as one of the most helpful soil amendment to leach out cations (Na^+) from the soil. Gypsum is a slight soluble salt of calcium and sulphate and hence it will react slowly with the soil. The gypsum amount required will vary widely depending on the percentage of exchangeable sodium and soil texture.

It has been investigated that chemical amendment-based technology has been established to reclaim the alkali/sodic soils for proper regulation of salts in root zone (Singh 2009). This includes field leveling, bunding, soil sampling to know the sodicity status for working out amendment dose application of gypsum/pyrite as per the need of the soil followed by rice-wheat rotation for 3–4 years including sesbania as a green manure crop after wheat harvest in April.

1.4.3 Biological Method

Leaching and water quality appears to be limited for the knowledge of soil amendments. By biological reclamation the use of saline wastelands can be made possible through effective management strategies by using salt tolerant plants. To reclaim salt affected soils of unproductive agricultural lands by biological means may be a feasible choice. Agricultural land fed with rain water, lack of irrigation water, shallow and brackish groundwater suggests that the salt affected lands may better be cultivated with crops tolerant to low to moderate saline conditions. Several varieties of salt tolerant crops like rice, wheat and mustard have been developed with a good economic yield both in high pH alkali soils and in saline soils (Singh and Sharma 2006). Among these rice varieties like CSR10, CSR13, CSR19, CSR23, CSR27, and CSR30 can be cultivated in soils with pH ranging from 9.4 to 9.8 and EC values of 6–11 dSm^{-1}. Salt tolerant varieties with their level of tolerance to soil salinity and alkalinity has been shown in Table 1.3.

Table 1.3 Suggested salt tolerant varieties

		Adaptability	
Crop	Tolerant varieties	Sodic with pH	Saline with EC (dSm^{-1})
Rice	CSR 10[a], CSR 11, CSR 12, CSR 13[a]	9.8–10.2	6–11
	CSR19, CSR23[a], CSR27[a], CSR30[a], CSR1,	9.4–9.8	6–11
	CSR2, CSR3, CSR4[a], CST7-1[a],	9.4–9.8	6–9
Wheat	KRL 1–4[a], WH157	<9.3	6–10
	Raj3077, KRL19[a]	<9.3	6–10
Barley	DL200, Ratna, BH97, DL348	8.8–9.3	
Indian Mustard	Pusa Bold, Varuna	8.8–9.2	6–8
	Kranti, CS52[a], CSTR330-1,	8.8–9.3	6–9
	CST609-B 10, CS54[a]	8.8–9.3	6–9
Gram	Karnal Chana 1	<9.0	<6.0
Sugar beet	Ramonskaaya 06, Maribo Resistapoly	9.5–10	<6.5
Sugarcane	Co453, Co1341	<9.0	ECe–10

[a] Institute varieties released by central varietal released committee.
Source: (Singh 2009)

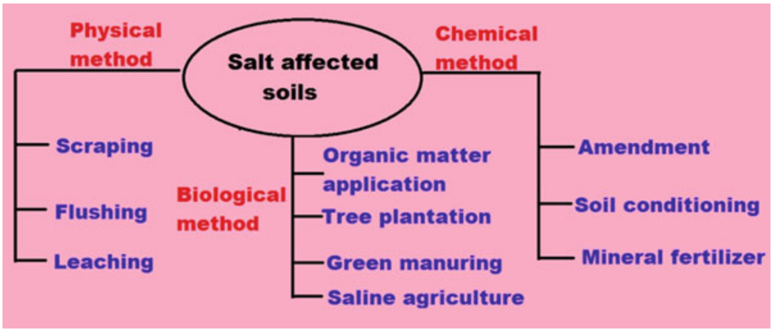

Fig. 1.1 Integrated management practices for the reclamation of salt affected soils

The biological reclamation techniques provide the earnings to the farmers without the need of costly drainage and reclamation work. Salt-tolerant trees and shrub species especially *Atriplex, Eucalyptus*, *Chenopodium*, *Suaeda*, *Salicornia*, *Kochia*, *Sesbania*, *Salsola, Juncus* and others can be grown efficiently in those areas of the land that cannot be restored (Aronson 1985; Le-Houerou 1986). For land reclamation purpose several investigators have studied the cultivation of salinity and sodocity-tolerant plants like grasses (Qadir et al. 1996), agronomic and horticultural crops (Ahmad et al. 1992, 2006, 2008a, b, 2010a, 2012a; Azooz et al. 2011), forest species. Furthermore this process can be made more effective by combining various ameliorative methods. As a result the outcome of this interaction becomes more impressive rather applied singly (Fig. 1.1).

1.5 Plant Adaptations to Salt Stress

Under osmotic stress, plants accumulate osmotically active compounds called osmolytes in order to lower the osmotic potential. These are referred to as compatible metabolites because they do not apparently interfere with the normal cellular metabolism of the cell (Ahmad and Sharma 2008; Ahmad and Prasad 2012a, b). The primary function of compatible solutes is to maintain cell turgor and thus providing the driving gradient for water uptake. Recent studies indicate that compatible solutes can also act as free-radical scavengers or chemical chaperones by directly stabilizing membranes and/or proteins (Mc Neil et al. 1999; Diamant et al. 2001). Glycerol and sucrose helps by were discovered by empirical methods to protecting the biological macromolecules against the damaging effects of salinity. Later, a systematic examination of the molecules, which accumulate in halophytes and halo-tolerant organisms, led to the identification of a variety of molecules also able to provide protection (Arabawa and Timasheff 1985; Wiggins 1990). These molecules are not highly charged, but are polar, highly soluble and have a larger hydration shell. Such molecules will be preferentially solubilized in the bulk water of the cell where they could interact directly with the macromolecules.

1.5.1 Glycine-Betaine

Plants synthesise glycine betaine-a major osmolyte that have been widely observed in various plant species conferring salt-tolerance (Rhodes and Hanson 1993; Hanson et al. 1994; Ahmad and Sharma 2008; Chen and Murata 2011; Koyro et al. 2012). Highly tolerant species, i.e., *Spartina* and *Distichlis* show highest accumulation, low tolerant accumulate average levels while as sensitive one's show low levels of accumulation of glycine-betaine (Rhodes et al. 1989). Glycinebetaine is synthesized from choline in two steps, the first being catalyzed by choline mono-oxygenase leading to synthesis of betaine aldehyde, which is further oxidized by betaine-aldehyde dehydrogenase (Ahmad and Sharma 2008; Chen and Murata 2011; Koyro et al. 2012). Genetic evidence showed that glycine-betaine has been obtained to develop the salinity tolerance for barley and maize (Rhodes et al. 1989; Grumet and Hanson 1986). Among these two plants, isogenic barley lines show different abilities to adjust osmotically. Transgenic rice plants expressing betaine-aldehyde dehydrogenase converted high levels of exogenously applied betaine aldehyde to glycine-betaine than did wild-type plants. The elevated level of glycinebetaine in transgenic plants conferred significant tolerance against salt, cold and heat stress (Chen and Murata 2011). Transgenic plants expressing bacterial gene for the synthesis of GB is given in table 1.4.

Table 1.4 Transgenic plants expressing bacterial gene for the synthesis of GB and their tolerance to salt stress

Gene	Plant species	Tolerance to	Reference
codA	*Arabidopsis*	Salt, Chilling stress	Hayashi et al. 1997
cox	*Arabidopsis*	Salt, drought, freezing	Huang et al. 2000
codA	*Arabidopsis*	Salt	Sulpice et al. 2003
codA	*Brassica juncea*	Salt	Prasad et al. 2000
codA	*Diospyras kaki*	Salt	Gao et al. 2000
codA	*Lycopersicon esculantum*	Chilling, salt	Park et al. 2004
cox	*Nicotiana tabacum*	Salt	Huang et al. 2000
codA	*Oryza sativa*	Salt	Mohanty et al. 2002
cox	*Oryza sativa*	Salt	Su et al. 2006
codA	*Soalnum tuberosum*	Salt, drought	Ahmad et al. 2008
BADH	*Nicotiana tabacum*	Salt	Zhou et al. 2008
BADH	*Nicotiana tabacum*	Salt	Yang et al. 2008
CMO	*Nicotiana tabacum*	Salt, drought	Zhang et al. 2008
BADH	*Lycopersicon esculantum*	Salt	Zhou et al. 2007
CMO	*Oryza sativa*	Salt	Shirasawa et al. 2006
OsCMO	*Nicotiana tabacum*	Salt	Luo et al. 2012
SoBADH	*Ipomoea batatas*	Salt	Fan et al. 2012

1.5.2 Polyamines

Any stress factor like osmotic stress, low pH, potassium deficiency, nutrient deficiency or light leads to accumulation of polyamines. Among polyamines, putrescine accumulation is correlated with increased argenine decarboxylase (ADC) activity in oats. Similar studies reports that transgenic carrot cells over expressing ornithine decarboxylase (ODC) cDNA considerably show that these cells were significantly more tolerant to both salt stress as well as water stress (Bohnert et al. 1995). It has been demonstrated that increased ethylene synthesis and seed germination leads to the suppression of polyamine biosynthesis (Gallardo et al. 1995). Lin and Kao (1995) observed that spermidine increases and putrescine decreases in the shoot and roots of rice seedlings and their accumulation including spermine with ADC activity signifies a specific role in salt-tolerance (Ahmad et al. 2012b). Polyamines such as spermine and spermidine are derived from methionine and ornithine while as putriscine from arginine. The first step involves the decarboxylation of ornithine catalysed by ODC (Ahmad et al. 2012b). Furthermore polyamines and their corresponding enzyme activities are substantially enhanced under salt and drought stress (Lefevre and Lutts 2000). Nuclear DNA is found to be stabilized by histones in eukaryotic organisms while as putrescine and polyamines take over the role of histones in bacteria besides the regulation of DNA in plant mitochondria and chloroplasts. Moreover polyamines stimulate several protein biosynthesis mostly through nucleic acid interaction. They also play a key role in stabilization of bio-membranes.

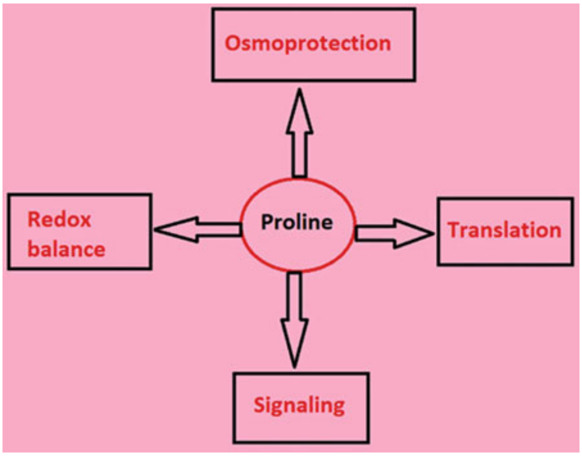

Fig. 1.2 Multiple function of proline

1.5.3 Proline

Proline plays a key role in osmoregulation in plants subjected to hyperosmotic stresses, primarily drought and salinity stress (Ahmad and Jhon 2005; Ahmad et al. 2006, 2010a, 2012a; Ahmad and Sharma 2010). Accumulation of proline is a means of adaptation to abiotic stress and has been observed in rye grass for the first time by Kemble and MacPherson (1954). There are various other compatible solutes including glycine betaine (Mc Cue and Hanson 1990), and polyols that have been shown to accumulate in plants subjected to osmotic stress conditions (Adams et al. 1992). Proline accumulation influences stress tolerance in different ways (Fig. 1.2). Proline acts as a molecular chaperone protecting protein integrity and thereby increase the activities of many enzymes. Besides plants, proline accumulation has been found most widely distributed osmolyte in eubacteria, protozoa, marine invertebrates and algae (Mc Cue and Hanson 1990). Investigations shows that enhancement of proline is due to the stimulation of biosynthetic pathway in plants. Glutamate or ornithine is utilized for the synthesis of proline, glutamate being the primary precursor in osmotically stressed cells (Ahmad and Sharma 2008; Koyro et al. 2012). Transcripts corresponding to both cDNAs that accumulate against NaCl stress are found to play a regulatory key to build up strategies for overproduction of proline in a selected plant species. Furthermore the intermediates of proline biosynthetic pathways also enhance the expression of numerous genes that are regulated osmotically in rice (Iyer and Caplan 1998). Evidence also shows that proline degradation in the mitochondria is linked to respiratory electron transport system as well as ATP production. Expression of P5CS transgenic rice from moth-bean led to stress-induced overproduction of the P5CS enzyme and proline accumulation in transgenic rice plants under the control of an inducible promoter. While as second generation (RI) transgenic plants observed an enhancement of biomass in response to salt and water stress (Zhu et al. 1998.). Table 1.5 shows response of different plants towards proline accumulation under salt stress.

Table 1.5 Responses of biochemical attributes under salt stress

	Species	Response to salinity	References
Soluble protein	*Pisum sativum*	Increase	Ahmad and Jhon 2005
	Oryza sativa	Decrease	Alamgir and Ali 1999
	Vicia faba	Decrease	Gadallah 1999
	Amaranthus tricolor	Decrease	Wang and Nil 2000
	Bruguiera parviflora	Decrease	Parida et al. 2002
	Pancratium maritimum	Increases at low salinity Decrease at high salinity	Khedr et al. 2003
	Arabidopsis thaliana	Increase	Quintero et al. 1996
	Morus alba	Increase	Ahmad and Sharma 2010
	Brassica juncea var. Bio902	Increase	Mittal et al. 2012
	Brassica juncea var. Urvashi	Decrease	Mittal et al. 2012
	Beta vulgarus	Decrease	Jamil et al. 2012a
	Oryza sativa	Decrease	Jamil et al. 2012b
	Portulaca oleraceae	Decrease	Rahdari et al. 2012
	Setaria italica	Increase	Hendawy et al. 2012
	Portulaca oleraceae	Increases	Rahdari et al. 2012
	Prunus species	Decrease	Sorkheh et al. 2012
	Borago officinalis	Decrease	Enteshari et al. 2011
Proline	*Pisum sativum*	Increase	Ahmad and Jhon 2005
	Portulaca oleraceae	Increases	Rahdari et al. 2012
	Matricaria chamomilla	Increases	Heidari and Sarani 2012
	Borago officinalis	Increases	Enteshari et al. 2011
	Brassica juncea var. Bio902	Increase	Mittal et al. 2012
	Brassica juncea var. Urvashi	Decrease	Mittal et al. 2012
	Suaeda maritima	Increase	Rajaravindran and Natarajan 2012
	Lycopersicon esculantum	Increase	Babu et al. 2012
	Morus alba	Increase	Ahmad and Sharma 2010
Carbohydrates	*Portulaca oleraceae*	Increases	Rahdari et al. 2012
	Matricaria chamomilla	Increases	Heidari and Sarani 2012
	Beta vulgaris L.	Increases	Dadkhah 2010
	Borago officinalis	Decrease	Enteshari et al. 2011
	Prosopis alba	Increase in soluble carbohydrate	Meloni et al. 2004
	Morus alba	Increase	Ahmad and Sharma 2010

1.5.4 Carbohydrates

Osmotic potential accounts more than 50% of sugar in glycophytes subjected to saline conditions (Cram 1976). Despite a significant decrease in net CO_2 assimilation rate its accumulation in plants have been widely reported (Murakeozy et al. 2003).

Accumulation of carbohydrates plays a central role in osmoprotection, osmotic adjustment, carbon storage and radical scavenging under salt stress (Ahmad and Sharma 2008; Koyro et al. 2012). Trehalose, have shown to accumulate and protects membranes and proteins in cells against water deficit and reduced aggregation of denatured proteins (Singer and Lindquist 1998). At the same time suppressive effect has been observed by trehalose on apoptotic cell death (Yamada et al. 2003) suggesting the presence of trace amounts in vascular plants, including major crops, though the definite role of this osmolyte in metabolism is still unclear.

Role of sugars in adaptation of plants to salinity have been concluded to be universally associated with salt tolerance. However, this does not signify the role of indicator for salt tolerance in breeding programs for some species. Table 1.5 shows response of different plants towards carbohydrate accumulation under salt stress.

1.5.5 Proteins

Salt-induced proteins in plants have been classified into two major groups (Mansour 2000), i.e., salt stress proteins, which accumulate only due to salt stress, and stress associated proteins, that accumulates in response to various abiotic stress like heat, cold, drought, water logging, and high and low mineral nutrients. Protein accumulation also provides a storage pool of nitrogen to be re-utilized later (Singh et al. 1987) and also a key role in osmotic adjustment. Large number of cytoplasmic proteins cause alterations in cytoplasmic viscosity of the cells stimulated by salinity (Hasegawa et al. 2000). Proteins have shown to increase on exposure to salt stress and can be synthesized *de novo* in response to salt stress or may be present constitutively at low concentration (Pareek et al. 1997). Protein with 26 kDa named as osmotin have been detected in tobacco in response to salt stress (Singh et al. 1987). In salt stressed *Mesembryanthemum crystallinum* another osmotin-like protein was also observed to increase as compared to non-stressed plants (Thomas and Bohnert 1993). In barley, two 26 kDa polypeptides, identified as germin which is not immunologically related to osmotin, have been found to increase in response to salt stress (Hurkman et al. 1991). Similar reports have been found in radish with 22 kDa protein (Lopez et al. 1994). Salt tolerant shows higher soluble proteins than salt sensitive species of barley (Hurkman et al. 1989), sunflower, finger millet (Uma et al. 1995), and rice (Pareek et al. 1997). Table 1.5 shows response of different plants towards protein accumulation under salt stress.

1.6 Reactive Oxygen Species and Antioxidants

Adaptation of the plant cell to high salinity involves osmotic adjustment and the compartmentation of toxic ions, whereas an increasing body of evidence suggests that high salinity also induces the generation of reactive oxygen species (ROS) and oxidative stress (Savouré et al. 1999; Ahmad et al. 2008a, b, 2010a, b, c, 2011, 2012a). The oxygen in the atmosphere enabled respiratory mechanism and electron transport system which use molecular oxygen (O) as final electron acceptor, which led to the formation of ROS in cells (Temple et al. 2005; Ahmad et al. 2008a, b, 2010a, b, c, 2011, 2012a). Although, atmospheric oxygen is relatively non-reactive, it can give rise to reactive oxygen intermediates which include superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH^-) and singlet oxygen ($^1O_2$) (Scandalios 2005).

ROS are produced continuously by photosynthesis, photorespiration and CO_2 assimilation in plants. ROS will act as damaging, protective or signaling factor depends on the delicate equilibrium between ROS production and scavenging at the proper site and time (Ahmad et al. 2008a, b, 2010a). Plant cells have developed a comprehensive array of antioxidant defense to prevent the formation of ROS or to limit their damaging effects.

1.6.1 Antioxidants

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). Although a wide range of genetic adaptations to saline conditions has been observed and a number of significant physiological responses have been associated with tolerance, underlying mechanisms of salt tolerance in plants are still poorly understood. The effects of various environmental stresses in plants are known to be mediated, at least in part, by an enhanced generation of reactive oxygen species (ROS) including $^{\cdot}O_2$, H_2O_2, and $^{\cdot}OH$ (Hernandez et al. 2000; Benavides et al. 2000; Ahmad et al. 2008a, b, 2010b, c, 2011). These ROS are highly reactive and can alter normal cellular metabolism through oxidative damage to membranes, proteins, and nucleic acids; they also cause lipid peroxidation, protein denaturation, and DNA mutation (Imlay 2003; Ahmad et al. 2008a, b, 2010b, c, 2011). To prevent damage to cellular components by ROS, plants have developed a complex antioxidant system. The primary components of this system include carotenoids, ascorbate, glutathione, and tocopherols, in addition to enzymes such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), peroxidases, and the enzymes involved in ascorbate–glutathione cycle (Foyer and Halliwell 1976), such as ascorbate peroxidase (APX) and glutathione reductase (GR) (Ahmad et al. 2008a, b, 2010b, c, 2011). Many components of this antioxidant defense system can be found in various subcellular compartments (Hernandez et al. 2000; Ahmad et al. 2011). The scavenging of ROS by increased activation of antioxidant enzymes can improve salt tolerance (Alscher et al. 2002). A relationship between salt tolerance and increased activation of antioxidant enzymes has been demonstrated in Plantago (Sekmen et al. 2007), pea (Hernandez et al. 2000; Ahmad et al. 2008a, b), Arabidopsis, rice (Dionisio-Sese and Tobita 2007), tomato, soybean, maize (Azevedo Neto et al. 2006), broad bean (Azooz et al. 2011), mustard (Ahmad 2010; Ahmad et al. 2010a, 2012a).

Under salt stress, increase in activity of SOD, APX, GR, DHAR, CAT and POX as well as higher antioxidant activity in tolerant species/varieties have been reported by various workers (Ahmad et al. 2010a, 2012a; Azooz et al. 2011; Koyro et al. 2012).

Superoxide dismutase (SOD) is the first defense agent against ROS being the major scavenger of $^{\cdot}O_2^-$ (Almoguera et al. 1995). High SOD activity protects the plant against the superoxide radical, it cannot be considered solely responsible for membrane protection against peroxidation because it converts $O^{2\bullet-}$ to H_2O_2, which is also a ROS. Current studies have shown 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* (Sudhakar et al. 2001; Ahmad et al. 2010a), *Triticum aestivum* (Sairam et al. 2002), *Lycopersicon* sp (Mittova et al. 2002), *Pisum sativum* (Ahmad et al. 2008a, b), *Vicia faba* (Azooz et al. 2011) and *Brassica juncea* (Ahmad 2010; Ahmad et al. 2010a, 2012a). Earlier studies suggested that the increased SOD activity enables the plant to resist the potential oxidative damage caused by NaCl salinity exposure (Khan et al. 2002; Panda and Khan 2003; Ahmad and Umar 2011).

Ascorbate peroxidase is a hydrogen peroxide-scavenging enzyme found in higher plants, algae, and some cyanobacteria (Asada 1992). Ascorbate peroxidase (APX) is a multigenic family with various isoforms in which cytosolic APX plays a fundamental role in non-photosynthetic tissues, by preventing H_2O_2 dependent inhibition of cytosolic enzymes (Verniquet et al. 1991). APX in the mechanisms of salt tolerance has been substantiated at protein level (Elkahouia et al. 2005; Masood et al. 2006; Koca et al. 2007). APX activity had a key role in response to salt stress in the comparison of the activities of antioxidant enzymes in salt-sensitive and salt-tolerant cultivars (Gueta-Dahan et al. 1997; Ahmad et al. 2008a, b, 2010a, 2012a; Ahmad and Umar 2011).

GR is one of the three enzymes, which catalyze reactions that maintain large pool of GSH and ascorbate in the H_2O_2 scavenging path way in chloroplasts (Yousuf et al. 2012). There are reports showing that GR activity increased in NaCl-tolerant pea variety as compared to NaCl-sensitive pea (Hernandez et al. 2000). The salt treatment had little effect on the activity of glutathione reductase (Lee et al. 2001), and it was suggested that its lower activity in the stressed roots could be due to some acclimation or an inability to maintain a high GSH/GSSG ratio (Mittova et al. 2000; Khan and Panda 2008).

Catalase is the main scavenger of H_2O_2 in peroxisomes, converting it to water and molecular oxygen (Willekens et al. 1995). CAT activity has been found to increase under salt stress in soybean (Comba et al. 1998), tobacco (Bueno et al. 1998), cucumber (Lechno et al. 1997), mulberry (Sudhakar et al. 2001; Ahmad et al. 2010a) and mustard (Ahmad et al. 2012a). Azevedo Neto et al. (2006) also found higher CAT activity in two maize cultivars differing in salt tolerance.

In plant cells, the most important reducing substrate for H_2O_2 detoxification is ASC. Ascorbic acid is an important antioxidant, which reacts not only with H_2O_2 but also with O^{2-}, OH and lipid hydroperoxidases (Reddy et al. 2004; Ahmad et al. 2008a, b, 2010a, b, c, 2011). Ascorbic acid can act as the “terminal antioxidant” because the redox potential of the AA/monodehydro ascorbate (MDA) pair is lower than that of most of the bioradicals (Scandalios et al. 1997). Several studies have revealed that ascorbic acid plays an important role in improving plant tolerance to abiotic stress (Shalata and Neumann 2001; Athara et al. 2008; Ahmad et al. 2008a, b, 2009, 2010b, c, 2011; Ahmad and Umar 2011).

Glutathione plays an important role in the protection against oxidative stress (Ahmad et al. 2008a, b, 2009, 2010b, c, 2011). It is involved in the ascorbate/glutathione cycle and in the regulation of protein thiol-disulphide redox status of plants in response to abiotic and biotic stress (Mullineaux and Rausch 2005; Yousuf et al. 2012). Ruiz and Blumwald (2002) and Mullineaux and Rausch (2005) reported that glutathione content in wild canola plants increased under salt stress, this suggests a possible protective mechanism against salt induced oxidative damage.

1.7 Conclusion and Future Perspective

Plants always experience the fluctuations of environment that causes stress and leads to crop loss worldwide. Salt stress is one of the most damaging abiotic stresses caused due various factors including human activities. In arid and semi-arid regions the salinity is intensified due to fertilizers and irrigation with saline ground water. Salinity in soils affect water availability due to limitation of water uptake of the plants. The ions Na^+ and Cl^- also hampers the assimilation, transport and distribution of essential mineral nutrients within the plant. It has been observed that nutrient assimilation especially K^+ and Ca^{2+} is reduced in the rooting medium under high levels of the NaCl, which ultimately leads to ion imbalances of K^+, Ca^{2+} and Mg^{2+} compared to Na^+. It has been reported that salinity is responsible for the inhibition of cell division and cell enlargement in plants. Overall growth of the plant is also affected with salinity that is why plants showed stunted growth under saline environment. Osmotic damage due to osmotic stress could occur as a result of high concentrations of Na^+ in the leaf apoplast, since Na^+ enters leaves in the xylem stream and is left behind as water evaporates. During stress conditions plants need to maintain internal water potential below that of soil and maintain turgor and water uptake for growth. This requires an increase in osmotica, either by uptake of soil solutes or by synthesis of metabolic (compatible) solutes.

Accumulation of different compatible solutes have been reported during salt stress in different plants. The compatible solutes protect the plants from stress through different courses, including contribution to cellular osmotic adjustment, detoxification of reactive oxygen species, protection of membrane integrity, and stabilization of enzymes/proteins. Some solutes perform an extra function of protection of cellular components from dehydration injury and are called as osmoprotectants. These solutes include proline, sucrose, polyols, trehalose and quaternary ammonium compounds (QACs) such as glycine betaine, alaninebetaine, proline, etc.

Apart from osmotic stress salt is responsible for the generation of ROS in cells that leads to oxidative stress. The generation of these ROSs is due to the imbalance between the production and scavenging machinery of ROS. The unquenched ROS react spontaneously with organic molecules and cause membrane lipid peroxidation, protein oxidation, enzyme inhibition and DNA and RNA damage.

Under severe stress conditions this ROS ultimately leads to cell death. Plants have evolved mechanisms that allow them to adapt and survive under abiotic stress. The production of ROS is however kept under tight control by a versatile and cooperative antioxidant system that modulates intracellular ROS concentration and sets the redox-status of the cell. Plants overexpressing antioxidant enzymes have been engineered with the aim of increasing stress tolerance by directly modifying the expression of these ROS scavenging enzymes. Many workers have reported the positive effects of SOD, CAT, APX, GR, MDHAR, AsA, glutathione, etc. in combating oxidative damage to the cell. There can be no doubt that transgenic plants will be invaluable in assessing the precise role that main antioxidants and ROS play in the functional network that controls stress tolerance.

One of the most important problems before the plant biologists is to develop stress tolerant plants with maximum yield. Since the development of modern biotechnology, a vast research has been carried out to understand the various approaches that plants have adopted to overcome the environmental stresses. Transgenic research proved to be invaluable tool for the development of stress tolerant crops. The advancement in omics is being used in elucidating important plant processes in response to various abiotic stresses. The road to engineering such tolerance into sensitive species is still far from us. Much effort is still required to uncover in detail each product of genes induced by salt stress and signal transduction pathways. Plant biologists should look forward for defined set of markers to predict tolerance towards a particular type of stress with a definite degree of assurance.

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