

Causes of salinity and plant manifestations to salt stress: A review

Author Details

Sangeeta Yadav	Plant Physiology Section, Department of Botany, Aligarh Muslim University, Aligarh - 202 002, India
Mohd. Irfan	Plant Physiology Section, Department of Botany, Aligarh Muslim University, Aligarh - 202 002, India
Aqil Ahmad	Plant Physiology Section, Department of Botany, Aligarh Muslim University, Aligarh - 202 002, India
Shamsul Hayat (Corresponding author)	Plant Physiology Section, Department of Botany, Aligarh Muslim University, Aligarh - 202 002, India e-mail: shayat@lycos.com

Abstract

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Salinity in agricultural terms is the excess of salts above the level plant require. Most often it poses constrains in the growth hence productivity of the category of plants called glycophytes, wherein falls major crops, therefore is a serious concern. It is often recognized as excess of sodium ions (sodicity) that imparts life threatening consequences in plant due to mal-textured soil hindered porosity and aeration leads to physiological water deficit. Mingling with other edaphic/environmental factors viz. precipitation, temperature, flooding, soil profile, water table exaggerates the catastrophe synergistically. Improper irrigations system, leaching fraction added with land clearing and deforestation have been marked as the major cause. The present review underlines the different sources of salinity stress and their physiological manifestations, toxicity responses alongwith tolerance in plants and management strategies in affected landscapes.

Key words

Salinity stress, Planetolerance, Physiological manifestation, Management strategies

Introduction

Salinity is one of the most important abiotic stresses, limiting crop production in arid and semi-arid regions, where soil salt content is naturally high and precipitation can be insufficient for leaching (Zhao *et al.*, 2007). According to the FAO Land and Nutrition Management Service (2008), over 6% of the world's land is affected by either salinity or sodicity which accounts for more than 800 million ha of land (Table 1). Saline soils are defined by Ponnampertuma (1984) as those contain sufficient salt in the root zone to impose the growth of crop plants. However, since salt injury depends on species, variety, growth stage, environmental factors, and nature of the salts, it is difficult to define saline soils precisely. The USDA Salinity Laboratory defines a saline soil as having an electrical conductivity of the saturation extract (EC_c) of 4 dS m⁻¹ or more. EC_c is the electrical conductivity of the 'saturated paste extract', that is, of the solution extracted from a soil sample after being mixed with sufficient water to produce a saturated paste. The most widely accepted definition of a saline soil has been adopted from FAO (1996) as one that has an EC_c of 4 dS m⁻¹ or more and soils with EC_c's exceeding 15 dS m⁻¹ are considered strongly saline.

Traditionally, 4 levels of soil salinity based on saline irrigation water have been distinguished (Table 2), low salinity defined by electrical conductivity of less than 0.25 mmhos cm⁻¹ (in current terminology equal to 0.25 dS m⁻¹); medium salinity (0.25 to 0.75 dS m⁻¹); high salinity (0.75 to 2.25 dS m⁻¹), and very high salinity with an electrical conductivity exceeding 2.25 dS m⁻¹ (US Salinity Laboratory Staff, 1954).

The common cations associated with salinity are Na⁺, Ca²⁺ and Mg²⁺, while the common anions are Cl⁻, SO₄²⁻ and HCO₃⁻. Since Na⁺ in particular causes deterioration of the physical structure of soil and Na⁺ and Cl⁻ both are toxic to plants are therefore considered the most important ions (Dubey, 1997; Hasegawa *et al.*, 2000). Historically soils were classified as saline, sodic or saline-sodic based on the total concentration of salt and the ratio of Na⁺ to Ca²⁺ and Mg²⁺ in the saturated extract of the soil (Dudley, 1994).

Salinity occurs through natural or human induced processes that result in the accumulation of dissolved salts in the soil water to an extent that inhibits plant growth. Sodicity is a secondary result of salinity in clay soils, where leaching through either natural or human

induced processes has washed soluble salts into the subsoil and left sodium bound to the negative charges of the clay due to an increase in its concentration. There is competition for fresh water among the municipal, industrial and agricultural sectors in several regions. The consequence has been a decreased allocation of fresh water to agriculture (Tilman *et al.*, 2002). This phenomenon is expected to continue and to intensify in less developed, arid region countries that already have high population growth rates and suffer from serious environmental problems. For this reason there is increasing pressure to irrigate with water of certain salt content like ground water, drainage water and treated wastewater. The average salinity levels of the different class of water have been appended which could be planned and coordinated for the management of surface and groundwater, so as to maximize the efficient use of water resources (Table 3).

According to Carvajal *et al.* (1999); Yeo (1998) and Grattan and Grieve (1999) that the direct effect of salts on plant growth may be divided into three broad categories: (i) a reduction in the osmotic potential of the soil solution that reduces plant available water, (ii) a deterioration in the physical structure of the soil such that water permeability and soil aeration are diminished, and (iii) increase in the concentration of certain ions that have an inhibitory effect on plant metabolism (specific in toxicity and mineral nutrient deficiencies). The relative contribution of osmotic effects and specific in toxicities on yield is difficult to quantify. However, with most crops, Dasberg *et al.* (1991) reported that yield losses from osmotic stress could be significant before foliar injury is apparent. Various causes of salinity over globe and how plants response to their suboptimal and toxic doses along with tolerance strategies has illustrated in Fig. 1.

Causes of salinity

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.

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 sea water 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.

Depending on prevailing winds and distance from the sea-coast the rain water composition greatly varies. Table 4 shows

the rain water composition (measured as mg kg⁻¹ or ppm) from a northern hemisphere source (Encyclopedia Britannica). The composition of sea water is expressed as g kg⁻¹ or ppt (parts per thousands) and is almost uniform around the globe. The electrical conductivity of sea water is 55 dS m⁻¹ while that of rainwater is about 0.01 dS m⁻¹.

Anthropogenically induced salinity: Secondary salt affected soils are those that have been salinized by human caused factors, mainly as a consequence 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) 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, Ohara (1997) 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). Anthropogenic 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:

(a) Deforestation: It is recognized as a major cause of salinization and alkalization of soils as a result 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 gets 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).

(b) 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 waste water from municipalities and sludge may contaminate the upper soil later causing salinization and/or alkalization (Bond, 1998).

(c) Contamination with chemicals: It often occurs in modern intensive agricultural systems, particularly in green houses and intensive farming systems.

(d) 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 gets 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 watertable, 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 1 dS 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). In the wheat/cotton rotation as practiced in the Sirsa District of India with critical salt tolerance levels of 6 dS m^{-1} for wheat and 7.7 dS m^{-1} for cotton, the leaching fraction can be as low as 5% in case of fresh groundwater ($\text{EC} < 1.5 \text{ dS m}^{-1}$) and should be 15% in case of moderately saline groundwater ($\text{EC} = 5.0 \text{ dS m}^{-1}$) (Leffelaar *et al.*, 2003)

The rocks with naturally high salt content after weathering add salinity in aquifers. Saline water is denser than fresh water therefore, with the increasing depth generally salinity increases. However, the regions have been observed where ground water is pumped up for irrigation salinity gradients get reversed through local irrigation (Kijine and Vander Velde, 1992). Rising water tables not only induce soil secondary salinization based on the upward movement of salts from saline aquifers and saline soils it also accelerates the water and salts into rivers water bodies, causing salinization in lowlands or in the aquifer flow system. 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.

Mechanisms of salt stress resistance: A variety of mechanisms contribute to salt tolerance (Gorham, 1995). Resistance is the ability of plants to adapt to salinity. It can be achieved by the ability of growing cells of a plant to avoid high ion concentrations or the ability of cells to cope with high ion concentrations (Greenway and Munns, 1980). Levitt (1980) characterized these mechanisms as avoidance and tolerance, and has used the term salt resistance to refer to a combination of tolerance and avoidance strategies. Examples of salt avoidance mechanisms include delayed germination or maturity until favorable conditions prevail; the exclusion of salt at the root zone or preferential root growth into nonsaline areas; compartmentalization of salt into and secretion from specialized organelles such as salt glands and salt hairs; or storage in older leaves (Hasegawa *et al.*, 1986). These tolerance mechanisms are discussed under separate headings.

Selective accumulation or exclusion of ions: Both glycophytes and halophytes cannot tolerate large amounts of salt in the cytoplasm and therefore under saline conditions they either restrict the excess salts in the vacuole or compartmentalize the ions in different tissues to facilitate their metabolic functions (Iyengar and Reddy, 1996; Zhu, 2003).

In general, exclusion mechanisms are effective at low to moderate levels of salinity, whereas ion accumulation is the primary mechanism used by halophytes at high salt levels, presumably in conjunction with the capacity to compartmentalize ions in the vacuole (Jeschke, 1984). Glycophytes limit sodium uptake, or partition sodium in older tissues, such as leaves, that serve as storage compartments which are eventually abscised (Cheeseman, 1988). Apse *et al.* (1999) reported that removal of sodium from the cytoplasm or compartmentalization in the vacuoles is done by a salt-inducible enzyme Na^+/H^+ antiporter.

Inclusion of ions in the cytoplasm can lead to osmotic adjustment that is generally accepted as an important adaptation to

Table - 1: Variation in salinity levels in the world, in million hectares (Mha)

Regions	Total area Mha	Saline soils		Sodic soils	
		Mha	%	Mha	%
Africa	1899	39	2.0	34	1.8
Asia, the Pacific & Australia	3107	195	6.3	249	8.0
Europe	2011	07	0.3	73	3.6
Latin America	2039	61	3.0	51	2.5
Near East	1802	92	5.1	14	0.8
North America	1924	05	0.2	15	0.8
Total	12781	397	3.1%	434	3.4

Source: FAO Land and plant nutrition service, 2008

salinity (Guerrier, 1996). The decrease of leaf osmotic potential would compensate the salt-induced lowering of water potential, helping to maintain turgor pressure and cell functions under adverse water conditions. Under salt stress, sugar beet accumulated more inorganic ions in the leaves (Ghoulam *et al.*, 2002). Such varieties are qualified as "includers" (Yeo, 1983). Similar results were reported in rice (Lutts *et al.*, 1996) and in sorghum (Colmer *et al.*, 1996). The tomato cultivar 'Daniela' responded to salinity by decreasing leaf osmotic potential more than 'Money maker' did and, in this sense, it was considered more adaptable to salty conditions than 'Money maker' (Romero-Aranda *et al.*, 2001). This accumulation of salt ions could play an important role in osmotic adjustment in stressed plants if they were efficiently compartmentalized. The ability to regulate salt concentration through compartmentalization is an important aspect to salt tolerance.

Synthesis of compatible solutes: The presence of salt in the growth media often results in the accumulation of low-molecular mass compounds, termed as compatible solutes, which do not interfere with normal biochemical reactions (Hasegawa *et al.*, 2000; Zhifang and Loescher, 2003). These compatible solutes include mainly proline and glycine betaine (Ghoulam *et al.*, 2002; Girija *et al.*, 2002; Khan *et al.*, 2000; Wang and Nii, 2000). It has been reported that proline levels increases significantly in leaves of rice (Lutts *et al.*, 1996), sugar beet (Ghoulam *et al.*, 2002), *Brassica juncea* (Yusuf *et al.*, 2008) and in the tolerant variety of sugarcane (Vasanth and Rajlakshmi, 2009). The increase in proline content was positively correlated to the level of salt tolerance. The proposed functions of proline under stress conditions include osmotic adjustment, protection of enzymes and membranes, as well as acting as a reservoir of energy and nitrogen for utilization during exposure to salinity (Bandurska, 1993; Perez-Alfocea *et al.*, 1993).

Exposure to saline stress results in the accumulation of nitrogen-containing compounds (NCC) such as amino acids, amides, proteins, polyamines and their accumulation is frequently correlated with plant salt tolerance (Mansour, 2000). For instance, glycine betaine content has been observed to increase in green gram (Sudhakar *et al.*, 1993); in amaranth (Wang and Nii, 2000) and in peanut (Girija *et al.*, 2002). According to Sakamoto *et al.* (1998), subcellular compartmentation of glycine betaine biosynthesis in rice is important for increased salt tolerance. These compounds

have been reported to function in osmotic adjustment, protection of cellular macromolecules, storage of nitrogen maintenance of cellular pH, detoxification of the cells and scavenging of free radicals.

Other compatible solutes that accumulate in plants under salt stress include (a) carbohydrates such as sugars (glucose, fructose, sucrose, fructans) and starch (Parida *et al.*, 2002; Kerepesi and Galiba, 2000), and their major functions have been reported to be osmotic adjustment, carbon storage, and radical scavenging, (b) Polyols are reported to make up a considerable percentage of compatible solutes and serve as scavengers of stress-induced oxygen radicals and are also involved in osmotic adjustment and osmoprotection (Bohnert *et al.*, 1995).

According to Greenway and Munns (1980), salt sensitivity in non-halophytes may result from either (i) inability of osmoregulation, which may result from either an insufficient uptake of salt ions or a lack of synthesis of organic solutes being used as osmotica, or (ii) injury caused by inorganic ions which are absorbed by the cell and are not compartmentalized. Parvaiz and Satyavati (2008) emphasized the need of appropriate biochemical markers of salt tolerance based on MAS (marker assisted selection) and QTL (quantitative trait loci) analyses.

Control of ion uptake by roots and transport into leaves: Plants regulate ionic balance to maintain normal metabolism. For example, uptake and translocation of toxic ions such as Na⁺ and Cl⁻ are restricted, and uptake of metabolically required ions such as K⁺ is maintained or increased. They do this by regulating the expression and activity of K⁺ and Na⁺ transporters and of H⁺ pump that generate the driving force for ion transport (Zhu *et al.*, 1993). It is well documented that a greater degree of salt tolerance in plants is associated with a more efficient system for the selective uptake of K⁺ over Na⁺ (Noble and Rogers, 1992; Ashraf and O'Leary, 1996). It has been reported that salt tolerant in a barley variety maintained cytosolic Na⁺, ten times lower than a more sensitive other variety (Carden *et al.*, 2003). The tomato cultivar 'Radha' seems to possess higher ability to select and translocate major nutrients (K⁺, Ca²⁺, Mg²⁺ and NO₃⁻) to young leaves under moderate salinity (Perez-Alfocea *et al.*, 1996). However, at higher salinity this did not occur for NO₃⁻. Thus, decreases in shoot growth observed in this genotype at high salinity could be explained not only by the great amount of toxic ions accumulated in the leaves but also by

Table - 2: Approximate soil salinity classes

Salinity rating	EC (dS m ⁻¹)	Level of effect
Slightly saline	1.5–2	Salinity effects usually minimal
Moderately saline	2–6	Yield of salt sensitive plants restricted
Highly saline	6–15	Only salt tolerant plants yield satisfactorily
Extremely saline	>15	Few salt tolerant plants yield satisfactorily

Source: FAO land and plant nutrition management service, 2008

Table - 3: Classification of salt water

Water class	EC (dS m ⁻¹)	TDS ¹ (g l ⁻¹)
Non-saline	< 0.7	< 0.5
Slightly saline	0.7-2.0	0.5-1.5
Moderately saline	2.0-10.0	1.5-7.0
Highly saline	10.0-20.5	7.0-15.0
Very highly saline	20.0-45.0	15.0-35.0
Brine	> 45.0	> 35.0

Source: Rhoades *et al.*, 1992. TDS¹ = Total dissolved solids, EC = Electrical conductivity

the decrease of NO₃⁻ in young leaves. Nitrate selectivity over Cl⁻ in shoot has been correlated with salt tolerance in tomato cultivars (Perez-Alfocea *et al.*, 1993).

The use of plant ionic status to identify salt tolerance has been shown to be applicable (Ashraf and Khanum, 1997), and its relationship with salt tolerance is considered strong enough to be exploited as a selection tool in the breeding of salt tolerant cultivars (Omielon *et al.*, 1991).

Changes in photosynthetic capacity under salinity: The reduction in photosynthetic rates in plants under salt stress is mainly due to the reduction in water potential. The aim of salt tolerance is, therefore, to increase water use efficiency under salinity. To this effect, some plants such as facultative halophyte (*Mesembryanthemum crystallinum*) shift their C₃ mode of photosynthesis to CAM (Cushman *et al.*, 1989). This change allows the plant to reduce water loss by opening stomata at night, thus decreasing respiratory water loss in day time. In salt-tolerant plant species such as *Atriplex lentiformis*, there is a shift from the C₃ to C₄ pathway in response to salinity (Zhu and Meinzer, 1999). The role of pigments particularly chlorophylls in trapping solar energy to reduce it in the carbon chains of organic photosynthates is central.

Table - 4: The rain water composition (mg kg⁻¹ or ppm)

Ion	Rainfall (local)		Sea water (global)	
	mg kg ⁻¹ (ppm)	μM (μmol l ⁻¹)	g 10 g ⁻¹ (ppt)	μM (μmol l ⁻¹)
Sodium (Na ⁺)	2.0	86	10.8	470
Chloride (Cl ⁻)	3.8	107	19.4	547
Sulfate (SO ₄ ²⁻)	0.6	6	2.7	28
Magnesium (Mg ²⁺)	0.3	11	1.3	53
Calcium (Ca ²⁺)	0.1	2	0.4	10
Potassium (K ⁺)	0.3	8	0.4	10
Total	7.0		35.0	

Source: Encyclopaedia Britannica.

The carbon fixed with the aid of chlorophyll and other pigments ultimately support the metabolic and energy reactions to be translated as growth and development. In addition to stomatal and nonstomatal factors the regulation of chlorophyll biosynthesis, metabolism and activity is of prime value for the most important physiological process, the photosynthesis. Salt stress, however, variously affects the biosynthesis-activity of these pigments. Measurement of chlorophyll fluorescence provides quantitative information about photosynthesis through non-destructive means. A variability of maximal chlorophyll fluorescence (the ratio of Fv/Fm) is the indicator of PSII efficiency (Maxwell *et al.*, 2000).

In isolated chloroplasts, the photoreduction of ferricyanide is stimulated progressively with increasing concentrations of NaCl up to 30 to 50 mM (Baker, 1978; Smillie *et al.*, 1976), an effect possibly related to a cation-dependent alteration in membrane ultra-structure that changes the distribution of absorbed light energy in favor of PSII at the expense of PSI (Baker, 1978). These changes are to be expected with decreased PSII activity but they also indicate the absence of significant inhibition by salt on reactions of photosynthesis after PSII, otherwise quenching ought to have decreased (Bradbury and Baker, 1981). One possible effect of high salinity is the formation of a water deficit and consequent depression of growth (Greenway and Munns, 1980).

Besides, measurements of the plant tissue take only a few seconds to record, and portable measuring equipment is available commercially. Measurement of chlorophyll fluorescence furnishes quite different information on the effect of salinity on plant photosynthetic metabolism. The growth under salinity stress is checked at the cost of elicitation of defense strategies. The regulation of chlorophyll biosynthesis could be well defending strategy. Since the chlorophyll biosynthesis is an offshoot of mevalonic acid pathway, an important pathway of secondary metabolism, the pathways from this keypoint (α -levulunate) probably are diverted either towards the biosynthesis of compatible osmolytes for purpose of osmoregulation (as discussed before) or for growth regulators. In beans grown under saline conditions, older leaves showed higher Cl⁻ concentrations than younger leaves (Greenway *et al.*, 1966). Older leaves lost Chl and with loss of Chl the variable Chl fluorescence decreased. The younger leaves showed the opposite effect for Chl fluorescence with increases in the magnitude

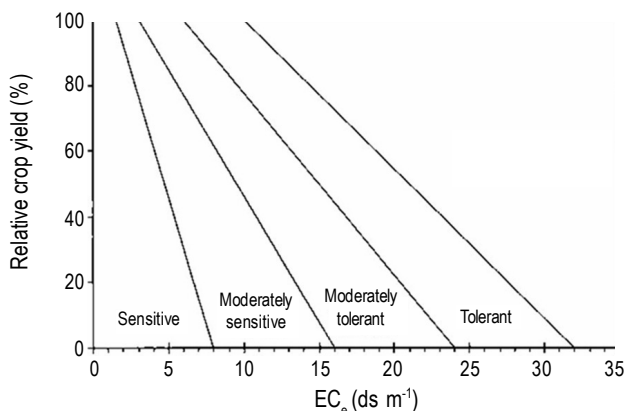


Fig. 2: Division for classifying crop tolerance to salinity. Tanji and Neeltje (2002)

and. Although photosystem activity was lost in salt-stressed leaves, this could be attributed mostly to Chl degradation as some PSII activity remained, as evidenced by the persistence of a Chl (Smillie and Norr, 1982).

Induction of antioxidative enzymes under salt stress: All environmental or manmade stresses have been reported to lead to the production of reactive oxygen species (ROS) that cause oxidative damage (Smirnov, 1993; Schwanz *et al.*, 1996). Plants possess efficient systems for scavenging active oxygen species that protect them from destructive oxidative reactions (Foyer *et al.*, 1994). As part of this system, antioxidative enzymes are key elements in the defense mechanisms. Garratt *et al.* (2002) has listed some of these enzymes as catalase (CAT), glutathione reductase (GR), superoxide dismutase (SOD) and glutathione-S-transferase (GST). Superoxide dismutase that metabolizes oxygen (O_2) radicals to hydrogen peroxide (H_2O_2) thus protecting cells from damage. Catalase, ascorbate peroxidase, and a variety of peroxidases catalyze the subsequent breakdown of H_2O_2 to water and oxygen (Chang *et al.*, 1984; Garratt *et al.*, 2002). Plants with high levels of antioxidants have been reported to have greater resistance to this oxidative damage (Szychalla and Desborough, 1990). Garratt *et al.* (2002) and Mittova *et al.* (2002, 2003) reported an increase in the activity of antioxidative enzymes in plants under salt stress. They found a correlation between these enzyme levels and salt tolerance. Similarly, many changes have been detected in the activity of antioxidant enzymes in plants exposed to salinity. The activity of antioxidant enzymes was reported to increase under saline conditions in shoot cultures of rice (Fadzilla *et al.*, 1997), wheat (Meneguzzo *et al.*, 1999) and pea (Hernandez *et al.*, 1999), but decreased in wheat roots (Meneguzzo and Navarilzo, 1999) or SOD was unaffected in cucumber (Lechno *et al.*, 1997). The variations in these observations maybe due to the fact that the effects of salinity depend on a number of factors, for example, salt type, their concentration, plant genotype, growth stage and/or environmental conditions (Shannon *et al.*, 1994). The mechanism by which salinity affects the antioxidant responses is not yet clear. Meneguzzo and Navarilzo (1999), however, proposed that it might be via the change in membrane integrity caused by high Na^+ to Ca^{2+} ratio.

Salinity and induction of plant hormones: The level of plant hormones such as ABA and cytokinins increase with high salt concentration (Vaidyanathan *et al.*, 1999). Abscisic acid (ABA) causes alteration in the expression of stress-induced genes which are predicted to play an important role in the mechanism of salt tolerance in rice (Gupta *et al.*, 1998). The inhibitory effects of NaCl on photosynthesis, growth and translocation of assimilates has been found to be alleviated by ABA (Popova *et al.*, 1995). Although the nature of ABA receptor(s) remains unknown Leung and Giraudat (1998) pointed out that there is substantial evidence of the involvement of ABA in reversible protein phosphorylation and modification of cytosolic calcium levels and pH. Chen *et al.* (2001) reported that the increase of Ca^{2+} uptake is associated with the rise of ABA under salt stress and thus contributes to membrane integrity maintenance, which enables plants to regulate uptake and transport under high levels of external salinity in the longer terms. ABA has been reported to reduce ethylene release and leaf abscission under salt stress in citrus probably by decreasing the accumulation of toxic Cl^- ions in leaves (Gomezcadenas *et al.*, 2002). Zhang (2009) proposed that the signaling cascades of ABA and BR primarily cross-talk after BR perception, but before their transcriptional activation. They explained a large proportion of BR-responsive genes are also regulated by ABA.

Exogenous treatment of 24-epibrassinosteroids (Ali *et al.*, 2008) and salicylic acid (Yusuf *et al.*, 2008) protects *Brassica juncea* against salinity stress. SA has shown to enhance antioxidant enzymes activity (Yusuf *et al.*, 2008) and induce H_2O_2 production to work as a signaling molecule. Pretreatment of H_2O_2 has been reported to induce salt tolerance in barley seedlings (Fedina *et al.*, 2009). However, exogenous treatment of salicylic acid, H_2O_2 and Ca^{2+} induced salinity tolerance has been indicated its association with endogenous level of H_2O_2 homeostasis in naked oat seedlings (Xu *et al.*, 2008). Higher levels of jasmonates were also found to accumulate in salt-tolerant tomato cultivars compared to the salt-sensitive ones (Hilda *et al.*, 2003). Jasmonates have been reported to have important roles in salt tolerance. However, it is yet not known whether SA and JA are synthesized de-novo in the osmotically stressed mesophyll cells of leaves under regulation of ABA or it is transported as methylated inactive form from root to shoots. They are generally considered to mediate signaling, such as defense responses, flowering and senescence (Hilda *et al.*, 2003). However, factors involved in the salicylate and jasmonate signal-transduction pathway remain unclear.

The effect of salinity on plants: Salinization severely affects the agricultural productivity. The disastrous effects of irrigation-induced soil salinization in the Runn of Kachh represent amongst the most extreme examples in India. In agricultural land water-logging and salt accumulations affect plant growth adversely to reduce potential crop production. Plants can be killed in the advanced stages and the land rendered unusable. The salinization of agricultural land at extensive scale causes massive economic loss at the global level. The annual global income losses due to salinization of agricultural land could reach US\$11.4 billion in irrigated land and US\$1.2

Table - 5: Relative tolerance level of some important economic crops

Crop		Salt tolerance parameters				References
Common name	Botanical name [†]	Tolerance based on	Threshold (EC_e) $dS\ m^{-1}$	Slope % $dS^{-1}\ m^{-1}$	Rating	
Fibre, grain and special crops						
Artichoke, Jerusalem	<i>Helianthus tuberosus</i> L.	Tuber yield	0.4	9.6	MS	Newton <i>et al.</i> , 1991
Barley [#]	<i>Hordeum vulgare</i> L.	Grain yield	8.0	5.0	T	Ayars <i>et al.</i> , 1952; Hassan <i>et al.</i> , 1970
Canola or rapeseed	<i>Brassica campestris</i> L. [syn. <i>B. rapa</i> L.]	Seed yield	9.7	14	T	Francois, 1994a
Canola or rapeseed	<i>B. napus</i> L.	Seed yield	11.0	13	T	Francois, 1994a
Chickpea	<i>Cicer arietinum</i> L.	Seed yield	-	-	MS	Manchanda and Sharma, 1989; Ram <i>et al.</i> , 1989
Corn	<i>Zea mays</i> L.	Ear FW	1.7	12	MS	Bernstein and Ayars, 1949b; Kaddah and Ghowail, 1964
Cotton	<i>Gossypium hirsutum</i> L.	Seed cotton yield	7.7	5.2	T	Bernstein, 1955, 1956; Bernstein and Ford, 1959a
Flax	<i>Linum usitatissimum</i> L.	Seed yield	1.7	12	MS	Hayward and Spurr, 1944
Millet, channel	<i>Echinochloa turmerana</i> (Domin) J.M. Black	Grain yield	-	-	T	Shannon <i>et al.</i> , 1981
Oats	<i>Avena sativa</i> L.	Grain yield	-	-	T	Mishra and Shitole, 1986
Peanut	<i>Arachis hypogaea</i> L.	Seed yield	3.2	29	MS	Shalhevet <i>et al.</i> , 1969
Rice, paddy	<i>Oryza sativa</i> L.	Grain yield	3.0	12	S	Ehrler, 1960; Narale <i>et al.</i> , 1969; Pearson, 1959; Venkateswarlu <i>et al.</i> , 1972
Rye	<i>Secale cereale</i> L.	Grain yield	11.4	10.8	T	Francois <i>et al.</i> , 1989
Safflower	<i>Carthamus tinctorius</i> L.	Seed yield	-	-	MT	Francois and Bernstein, 1964b
Sorghum	<i>Sorghum bicolor</i> (L.) Moench	Grain yield	6.8	16	MT	Francois <i>et al.</i> , 1984
Soybean	<i>Glycine max</i> (L.) Merrill	Seed yield	5.0	20	MT	Abel and McKenzie, 1964; Bernstein <i>et al.</i> , 1955; Bernstein and Ogata, 1966
Sugar beet	<i>Beta vulgaris</i> L.	Storage root	7.0	5.9	T	Bower <i>et al.</i> , 1954
Sugar cane	<i>Saccharum officinarum</i> L.	Shoot DW	1.7	5.9	MS	Bernstein <i>et al.</i> , 1966; Dev and Bajwa, 1972; Syed and El-Swaify, 1972
Sunflower	<i>Helianthus annuus</i> L.	Seed yield	4.8	5.0	MT	Cheng, 1983; Francois, 1996
Triticale	<i>X Triticosecale</i> Wittmack	Grain yield	6.1	2.5	T	Francois <i>et al.</i> , 1988
Wheat	<i>Triticum aestivum</i> L.	Grain yield	6.0	7.1	MT	Asana and Kale, 1965; Ayers <i>et al.</i> , 1952; Hayward and Uhvits, 1944
Wheat (semi-dwarf)	<i>T. aestivum</i> L.	Grain yield	8.6	3.0	T	Francois <i>et al.</i> , 1986
Wheat, Durum	<i>T. turgidum</i> L. var. <i>durum</i> Desf.	Grain yield	5.9	3.8	T	Francois <i>et al.</i> , 1986
Alfalfa	<i>Medicago sativa</i> L.	Shoot DW	2.0	7.3	MS	Bernstein and Francois, 1973; Bernstein and Ogata, 1966; Bower <i>et al.</i> , 1969; Brown and Hayward, 1956; Gauch and Magistad, 1943; Hoffman <i>et al.</i> , 1975
Bentgrass, creeping	<i>Agrostis stolonifera</i> L.	Shoot DW	-	-	MS	Younger <i>et al.</i> , 1967
Bermudagrass	<i>Cynodon dactylon</i> (L.) Pers.	Shoot DW	6.9	6.4	T	Bernstein and Ford, 1959b; Bernstein and Francois, 1962; Langdale and Thomas, 1971
Broad bean	<i>Vicia faba</i> L.	Shoot DW	1.6	9.6	MS	Ayers and Eberhard, 1960
Gram, Black or Urd bean	<i>Vigna mungo</i> (L.) Hepper [syn. <i>Phaseolus mungo</i> L.]	Shoot DW	-	-	S	Keating and Fisher, 1985
Pigeon pea	<i>Cajanus cajan</i> (L.) Huth [syn. <i>C. indicus</i> (K.) Spreng.]	Shoot DW	-	-	S	Subbarao <i>et al.</i> , 1991; Keating and Fisher, 1985
Sesbania	<i>Sesbania exaltata</i> (Raf.) V.L. Cory	Shoot DW	2.3	7.0	MS	Bernstein, 1956
Vegetables and fruit crops						
Bean, common	<i>Phaseolus vulgaris</i> L.	Seed yield	1.0	19	S	Bernstein and Ayers, 1951; Hoffman and Rawlins, 1970; Magistad <i>et al.</i> , 1943; Nieman and Bernstein, 1959; Osawa, 1965

Bean, lima	<i>P. lunatus</i> L.	Seed yield	-	-	MT [*]	Mahmoud et al., 1988
Bean, mung	<i>Vigna radiata</i> (L.) R. Wilcz.	Seed yield	1.8	20.7	S	Minhas et al., 1990
Beet, red	<i>Beta vulgaris</i> L.	Storage root	4.0	9.0	MT	Bernstein et al., 1974; Hoffman and Rawlins, 1971; Magistad et al., 1943
Broccoli	<i>Brassica oleracea</i> L. (Botrytis Group)	Shoot FW	2.8	9.2	MS	Bernstein and Ayers, 1949a; Bernstein et al., 1974
Cabbage	<i>B. oleracea</i> L. (Capitata Group)	Head FW	1.8	9.7	MS	Bernstein and Ayars, 1949a; Bernstein et al., 1974; Osawa, 1965
Carrot	<i>Daucus carota</i> L.	Storage root	1.0	14	S	Bernstein and Ayars, 1953a; Bernstein et al., 1974; Lagerwerff and Holland, 1960; Magistad et al., 1943; Osawa, 1965
Cauliflower	<i>Brassica oleracea</i> L. (Botrytis Group)		-	-	MS [*]	
Corn, sweet	<i>Zea mays</i> L.	Ear FW	1.7	12	MS	Bernstein and Ayars, 1949b
Cowpea	<i>Vigna unguiculata</i> (L.) Walp.	Seed yield	4.9	12	MT	West and Francois, 1982
Cucumber	<i>Cucumis sativus</i> L.	Fruit yield	2.5	13	MS	Osawa, 1965; Ploegman and Bierhuizen, 1970
Eggplant	<i>Solanum melongena</i> L. var <i>esculentum</i> Nees.	Fruit yield	1.1	6.9	MS	Heuer et al., 1986
Garlic	<i>Allium sativum</i> L.	Bulb yield	3.9	14.3	MS	Francois, 1994b
Gram, black or Urd bean	<i>Vigna mungo</i> (L.) Hepper [syn. <i>Phaseolus mungo</i> L.]	Shoot DW	-	-	S	Keating and Fisher, 1985
Lettuce	<i>Lactuca sativa</i> L.	Top FW	1.3	13	MS	Ayars et al., 1951; Bernstein et al., 1974; Osawa, 1965
Muskmelon	<i>Cucumis melo</i> L. (Reticulatus Group)	Fruit yield	1.0	8.4	MS	Mangal et al., 1988
Okra	<i>Abelmoschus esculentus</i> (L.) Moench	Pod yield	-	-	MS	Masih et al., 1978; Paliwal and Maliwal, 1972
Onion (bulb)	<i>Allium cepa</i> L.	Bulb yield	1.2	16	S	Bernstein and Ayars, 1953b; Bernstein et al., 1974; Hoffman and Rawlins, 1971; Osawa, 1965
Onion (seed)		Seed yield	1.0	8.0	MS	Mangal et al., 1989
Pea	<i>Pisum sativum</i> L.	Seed FW	3.4	10.6	MS	Cerda et al., 1982
Pepper	<i>Capsicum annuum</i> L.	Fruit yield	1.5	14	MS	Bernstein, 1954; Osawa, 1965
Pigeon pea	<i>Cajanus cajan</i> (L.) Huth [syn. <i>C. indicus</i> (K.) Spreng.]	Shoot DW	-	-	S	Keating and Fisher, 1985; Subbarao et al., 1991
Potato	<i>Solanum tuberosum</i> L.	Tuber yield	1.7	12	MS	Bernstein and Ayers, 1951
Pumpkin	<i>Cucurbita pepo</i> L. var <i>Pepo</i>		-	-	MS [*]	
Radish	<i>Raphanus sativus</i> L.	Storage root	1.2	13	MS	Hoffman and Rawlins, 1971; Osawa, 1965
Spinach	<i>Spinacia oleracea</i> L.	Top FW	2.0	7.6	MS	Osawa, 1965
Squash, scallop	<i>Cucurbita pepo</i> L. var <i>meloepo</i> (L.) Alef.	Fruit yield	3.2	16	MS	Francois, 1985
Squash, zucchini	<i>C. pepo</i> L. var <i>meloepo</i> (L.) Alef.	Fruit yield	4.9	10.5	MT	Francois, 1985; Graifenberg et al., 1996
Strawberry	<i>Fragaria x Ananassa</i> Duch.	Fruit yield	1.0	33	S	Ehlig and Bernstein, 1958; Osawa, 1965
Sweet potato	<i>Ipomoea batatas</i> (L.) Lam.	Fleshy root	1.5	11	MS	Greig and Smith, 1962; USSL ^{††}
Tepary bean	<i>Phaseolus acutifolius</i> Gray		-	-	MS [*]	Goertz and Coons, 1991; Hendry, 1918; Perez and Minguez, 1985
Tomato	<i>Lycopersicon lycopersicum</i> (L.) Karst. ex Farw. [syn. <i>Lycopersicon esculentum</i> Mill.]	Fruit yield	2.5	9.9	MS	Bierhuizen and Ploeman, 1967; Hayward and Long, 1943; Lyon, 1941;
Turnip Turnip (greens)	<i>Brassica rapa</i> L. (Rapifera Group)	Storage root Top FW	0.9 3.3	9.0 4.3	MS MT	Francois, 1984
Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. and Nakai	Fruit yield	-	-	MS [*]	De Forges, 1970

MT= Moderately tolerant, MS= Moderately sensitive, S= Sensitive, T= Tolerant, *= Estimated ratings, FW= Fresh weight, DW= Dry Weight, - = Not Estimated

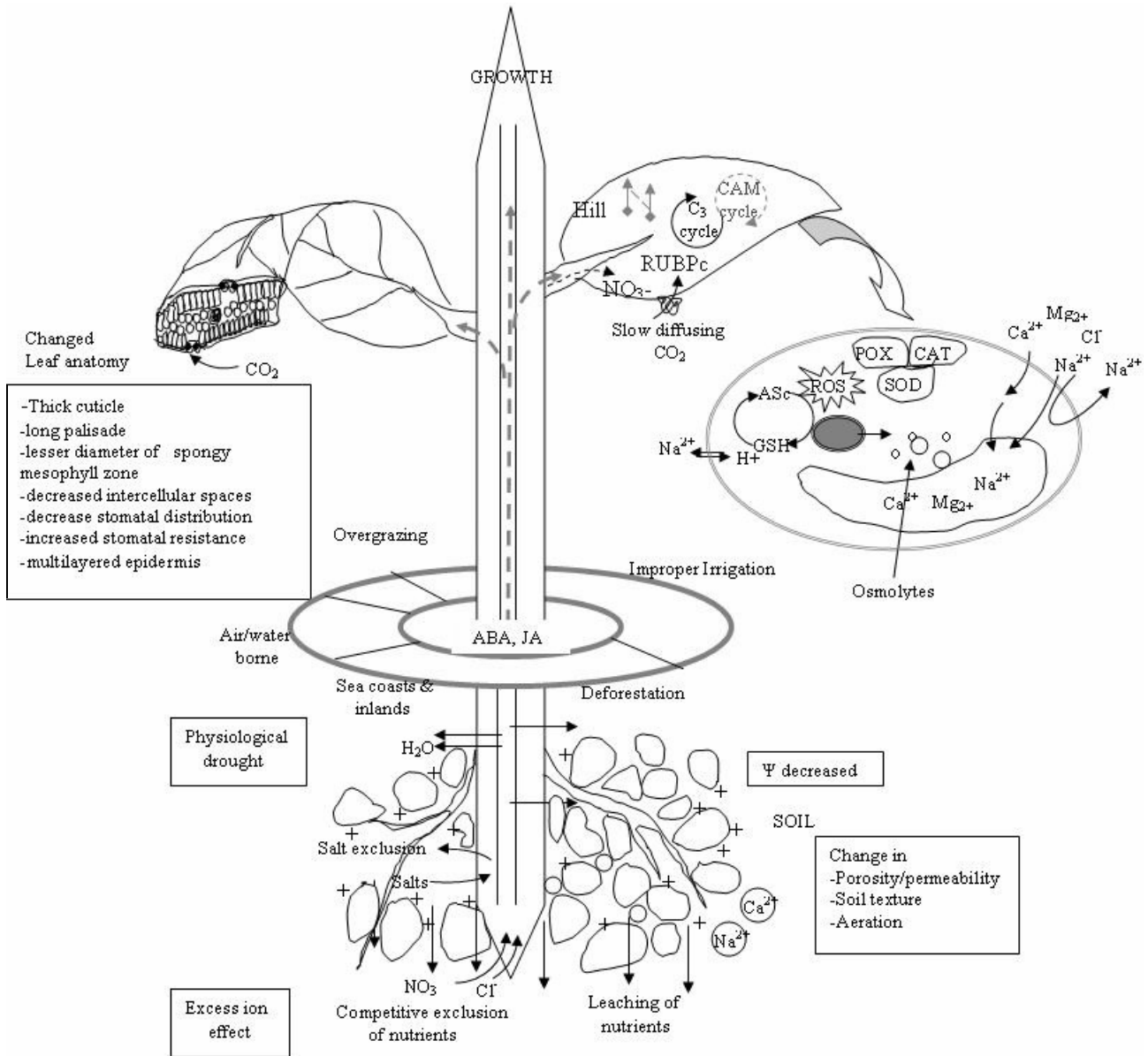


Fig. 1: Causes of salinity and plant manifestations to salt stress.

billion in non-irrigated areas (Ghassemi *et al.*, 1995). Soil salinity also causes other economic loss as through its direct effects on potable water and infrastructure corroding roads and buildings (Abdel-Dayem, 2005). Salinity directly and indirectly affects the environment by inducing changes in vegetation cover and physical and chemical soil properties. Consequently, loss of biodiversity, shrinking of wildlife (Barnum, 2005) and ecosystems disruption lead to loss of ecosystem resilience (Barrett-Lennard *et al.*, 2005) that affect local climate, water and mineral cycles.

Salts in the soil water may inhibit plant growth for two reasons:

- (i) The presence of salt in the soil solution reduces the ability of the plant to take up water, and this leads to reduction in growth

rate. This is referred to as the osmotic or water deficit effect of salinity (physiological drought).

- (ii) If excessive amount of salt enters the plant in its 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).

According to Dubey (1997) and Yeo (1998) salt causes both ionic and osmotic effects on plants and most of the known responses of plants to salinity are linked to these effects. The general response of plants to salinity is reduction in growth (Romero-Aranda *et al.*, 2001; Ghoulam *et al.*, 2002). The initial and primary effect of salinity, especially at low to moderate concentrations, is due to its

osmotic effects (Munns and Terment, 1986; Jacoby, 1994). Osmotic effects of salts on plants are a result of lowering of the soil water potential due to increasing solute concentration in the root zone.

At high salinity, some symptoms of plant damage may be recognized, such as necrosis and leaf tip burn due to Na^+ or Cl^- ions (Wahome et al., 2001). High ionic concentrations may disturb membrane integrity and function; interferes with internal solute balance and nutrient uptake, causing nutritional deficiency symptoms similar to those that occur in the absence of salinity (Grattan and Grieve, 1999).

Sodium and chloride, usually the most prevalent ions in saline soils or water, account for most of the deleterious effects that can be related to specific ion toxicities (Levitt, 1980). The degree to which growth is reduced by salinity differs greatly with species and to a lesser extent with varieties (Bolarin et al., 1991; Ghoulam et al., 2002). The severity of salinity response is also mediated by environmental interactions such as relative humidity, temperature radiation and air pollution (Shannon et al., 1994). Salt stress affects all the major processes such as growth, water relations, photosynthesis and mineral uptake.

(a) Water relations: According to Sohan et al. (1999) and Romero-Aranda et al. (2001) increase of salt in the root medium can lead to a decrease in leaf water potential and, hence, may affect many plant processes. Osmotic effects of salt on plants are as a result of lowering of the soil water potential due to increase in solute concentration in the root zone. At very low soil water potentials, this condition interferes with plants ability to extract water from the soil and maintain turgor (Sohan et al., 1999). 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.

Salt treatment caused a significant decrease in relative water content (RWC) in sugarbeet varieties (Ghoulam et al., 2002). According to Katerji et al. (1997), a decrease in RWC indicates a loss of turgor that results in limited water availability for cell extension processes.

(b) Leaf anatomy: Salinity has been reported to cause anatomical changes in the leaves of a number of plants. Leaves of bean, cotton and *Atriplex* are reported to increase in epidermal thickness, mesophyll thickness, palisade cell length, palisade diameter, and spongy cell diameter with increasing salinity (Longstreth and Nobel, 1979). In contrast both epidermal and mesophyll thickness and intercellular spaces decreased significantly in NaCl treated leaves of the mangrove *Bruguiera parviflora* (Parida et al., 2004). In tomato plants salinity reduced the stomatal density (Romero-Aranda et al., 2001).

(c) Photosynthesis: Growth of plants is dependent on photosynthesis and, therefore, environmental stresses affecting growth also affect photosynthesis (Salisbury and Ross, 1992; Dubey, 1997; Taiz and Zeiger, 1998). Studies conducted by a number of

authors with different plant species showed that photosynthetic capacity was suppressed by salinity (Dubey, 1997; Kao et al., 2001; Ashraf, 2001; Romero-Aranda et al., 2001). A positive association between photosynthetic rate and yield under saline conditions has been found in different crops such as *Gossypium hirsutum* (Pettigrew and Meredith, 1994) and *Asparagus officinalis* (Faville et al., 1999). Fisarakis et al. (2001) found that inhibition of vegetative growth in plants submitted to salinity was associated with a marked inhibition of photosynthesis. In contrast, there are many studies in which no or little association between growth and photosynthetic capacity is evident, as in *Triticum repens* (Rogers and Noble, 1992) and *Triticum aestivum* (Hawkins and Lewis, 1993).

The effect of salinity on photosynthetic rate depends on salt concentration and plant species. There is evidence that at low salt concentration salinity may stimulate photosynthesis. For instance, in *B. parviflora*, Parida et al. (2004) reported that photosynthetic rate increased at low salinity and decreased at high salinity, whereas stomatal conductance remained unchanged at low salinity and decreased at high salinity.

Iyengar and Reddy (1996) attributed the decrease in photosynthetic rate to salinity induced factors:

(1) Dehydration of cell membranes which reduce their permeability to CO_2 . High salt concentration in soil and water create high osmotic potential which reduces the availability of water to plants. Decrease in water potential causes osmotic stress, which reversibly inactivates photosynthetic electron transport via shrinkage of intercellular spaces.

(2) Salt toxicity caused particularly by Na^+ and Cl^- ions: According to Banuls et al. (1991), Cl^- inhibits photosynthetic rate through its inhibition of NO_3^- -N uptake by the roots. Fisarakis et al. (2001) found that NO_3^- -N was significantly reduced in salt-stressed sultana vines and this reduction was correlated with photosynthetic reduction. The reduced NO_3^- -N uptake combined with osmotic stress may explain the inhibitory effect of salinity on photosynthesis.

(3) Reduction of CO_2 supply because of the closure of stomata: The reduction in stomatal conductance results in restricting the availability of CO_2 for carboxylation reactions (Brugnoli and Bjorkman, 1992). Iyengar and Reddy (1996) reported that stomatal closure minimizes loss of water through transpiration and this affects light-harvesting and energy-conversion systems thus leading to alteration in chloroplast activity. Higher stomatal conductance in plants is known to increase CO_2 diffusion into the leaves and thereby favor higher photosynthetic rates. Higher net assimilation rates could in turn favor higher crop yields as was found by Radin et al. (1994) in Pima cotton (*Gossypium barbadense*). However, the results for photosynthetic rate and stomatal conductance presented by Ashraf (2001) for six Brassica species did not show any significant relationship. There are also reports of nonstomatal inhibition of photosynthesis under salt stress. Iyengar and Reddy (1996) reported that this nonstomatal inhibition is due to increased resistance to CO_2 diffusion in the liquid phase from the mesophyll wall to the site

of CO₂ reduction in the chloroplast, and reduced efficiency of RuBPCase.

Other causes of reduced photosynthetic rates due to salinity have been identified by Iyengar and Reddy (1996) as: (4) enhanced senescence induced by salinity, (5) changes in enzyme activity, induced by alterations in cytoplasmic structure and (6) negative feedback by reduced sink activity.

Although the rate of photosynthesis is reduced under salt stress, this is not the cause of reduction in the rate of cell expansion as suggested by several lines of evidence. According to Yeo *et al.* (1991) and Alarcon *et al.* (1994) growth is reduced more rapidly and at lower concentrations of sodium in the leaf than is photosynthesis. This means that plants can withstand a certain loss in photosynthetic rate without any impact on growth. The relationship between photosynthesis and growth of plants under saline conditions is not well understood. Many changes take place in plants in order to enable them to tolerate saline conditions and maintain photosynthetic activity. An understanding of the mechanisms by which salinity affects photosynthesis would help in the improvement of growth conditions and crop yield and would provide useful tools for future genetic tailoring of plants.

(d) Ion levels and nutrient content: High salt (NaCl) uptake competes with the uptake of other nutrient ions, such as K⁺, Ca²⁺, N, P resulting in nutritional disorders and eventually, reduced yield and quality (Grattan and Grieve, 1999). Increased NaCl concentration has been reported to induce increases in Na⁺ and Cl⁻ and decreases in Ca²⁺, K⁺ and Mg²⁺ level in a number of plants (Perez-Afocea *et al.*, 1996; Khan *et al.*, 2000; Bayuelo-Jiménez *et al.*, 2003). Ghoulam *et al.* (2002) observed an increase in Na⁺ and Cl⁻ content in the leaves and roots of sugar beet with increasing NaCl concentration in the rooting medium. The K⁺ content of the leaves decreased in response to NaCl, but that of roots was not affected by the salt treatment. A significant increase in Na⁺ and Cl⁻ content in leaves, stem, and root of the mangrove (*B. parviflora*) has been reported without any significant alteration of the endogenous level of K⁺ and Fe²⁺ in leaves (Parida *et al.*, 2004). Decrease of Ca²⁺ and Mg²⁺ content of leaves have also been reported upon salt accumulation in this species.

Under salt stress conditions, the uptake of N by plants is generally affected. A number of studies have shown that salinity can reduce N accumulation in plants (Feigin *et al.*, 1991; Pardossi *et al.*, 1999; Silveira *et al.*, 2001). An increase in Cl⁻ uptake and accumulation has been observed to be accompanied by a decrease in shoot NO₃⁻ concentration as in eggplant (Savvas and Lenz, 1996) and sultana vines (Fisarakis *et al.*, 2001). Various authors have attributed this reduction to Cl⁻ antagonism of NO₃⁻ (Bar *et al.*, 1997) while others attributed the response to salinity's effect on reduced water uptake (Lea-Cox and Syvertsen, 1993). The nitrate influx rate or the interaction between NO₃⁻ and Cl⁻ has been reported to be related to the salt tolerance of the species under investigation. Kafkafi *et al.* (1992) found that the more salt-tolerant tomato and

melon cultivars had higher NO₃⁻ flux rates than the more sensitive cultivars.

The effect of salinity on P concentration has been reported by Grattan and Grieve (1999) to be highly dependent on plant species, plant developmental stage, composition and level of salinity, and the concentration of P in the substrate. In most cases, salinity decreased the concentration of P in plant tissue (Sonneveld and de Kreij, 1999; Kaya *et al.*, 2001), but the results of some studies indicate salinity either increased or had no effect on P uptake (Ansari, 1990). The reduction in P availability in saline soils was suggested by Sharkey *et al.* (1992) to be a result of ionic strength effects that reduce the activity of phosphate, the tight control of P concentrations by sorption processes and by the low solubility of Ca-P minerals.

Salinity stress has stimulatory as well as inhibitory effects on the uptake of some micronutrients by plants. For a detailed review on this subject refer to (Villora *et al.*, 1997; Grattan and Grieve, 1999). According to these authors nutrient imbalances may result from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant, or may be caused by physiological inactivation of a given nutrient resulting in an increase in the plant's internal requirement for that essential element.

(e) Plant growth: Salinity causes reduction in plant growth e.g. in tomato (Romero-Aranda *et al.*, 2001), cotton (Meloni *et al.*, 2001) and sugarbeet (Ghoulam *et al.*, 2002). However, there are differences in tolerance to salinity among species and cultivars as well as among the different plant growth parameters, recorded. For instance, Aziz and Khan (2001) found that the optimum growth of *Rhizophora mucronata* plants was obtained at 50% seawater and declined with further increases in salinity while in *Alhagi pseudoalhagi* (a leguminous plant), total plant weight increased at Ca-salinity (50 mM NaCl) but decreased at high salinity (100 and 200 mM NaCl) (Kurban *et al.*, 1999). Application of NaCl (ECc 4.0 mS cm⁻¹) resulted in about 52, 50 and 55 % reduction in total nitrogen contents in mung-bean leaf, root and nodule, respectively (Chakrabarti and Mukherji, 2003). In sugar beet, leaf area, fresh and dry mass of leaves and roots were dramatically reduced at 200 mM NaCl, but leaf number was less affected (Ghoulam *et al.*, 2002). Fisarakis *et al.* (2001) working with sultana vines recorded a larger decrease in accumulation of dry matter in shoots than in roots, particularly at high NaCl concentration, indicating partitioning of photo-assimilates in favour of roots. They proposed that the results may be due to a greater ability for osmotic adjustment under stress by roots.

(f) Salt sensitivity and yield of crop plants: By plotting the relative yield as a continuous function of soil salinity the salt tolerance of a crop can be best described. A sigmoidal curve is obtained as a response function for most of the crops except for those that may die before the seed or fruit yields declines to zero. (therefore, the curve vanishes at their bottom). It was proposed that a two line segments could represent this response curve: one, a tolerance plateau with a zero slope, and the other, a concentration-dependent line whose

slope indicates the yield reduction per unit increase in salinity (Maas and Hoffman, 1977). The point at which the two lines intersect designates the threshold, *i.e.* the maximum soil salinity that does not reduce yield below that obtained under non-saline conditions. This two-piece linear response function provides a reasonably good fit for commercially acceptable yields plotted against the electrical conductivity of the saturated paste (EC_e). EC_e is the traditional soil salinity measurement with units of deci siemens per metre ($1 \text{ dS m}^{-1} = 1 \text{ mmho cm}^{-1}$). For soil salinities exceeding the threshold of any given crop, relative yield (Y_r) can be estimated with the following equation:

$$Y_r = 100 - b(EC_e - a) \quad (1)$$

where a = the salinity threshold expressed in dS m^{-1} ; b = the slope expressed in percent per dS m^{-1} ; and EC_e = the mean electrical conductivity of a saturated paste taken from the root zone.

The greatest value in providing general salt tolerance guidelines for crop management decisions was translated by the threshold and slope concept. It would be better to know the soil salinity levels that begin to reduce yield (-threshold) and the extent of yield will be reduced at levels above the threshold. For the crop simulation modeling, however, more precise plant response functions would be advantageous. Several non-linear models that describe the sigmoidal growth response of plants more accurately against salinity have been described (Van Genuchten and Hoffman, 1984). Furthermore, computer programs for these models were also developed and documented (Van Genuchten, 1983).

The revised version of Irrigation and Drainage paper no. 29 was published in FAO (1989). This publication contained an extensive list of crop salt tolerance data. An updated list of salt tolerance data have also been published by Maas and Grattan (1999). Table appended enlists threshold and slope values some crops in terms of EC_e . Most of the data were obtained where crops were grown under conditions simulating recommended cultural and management practices for commercial production. Consequently, the data indicate relative tolerances (T= tolerant, MT= moderately tolerant, MS= moderately sensitive and S= sensitive) of different crops grown under different conditions and not under a standardized set of conditions. Furthermore, the data apply only where crops are exposed to fairly uniform salinities from the late seedling stage to maturity where crops have particularly sensitive stages (Table 5).

(g) Cultivation under saline conditions: Many plant species that tolerate high levels of salinity have been identified over and have been proposed as alternative crops for cultivation in saline conditions (Aronson, 1989; NAS, 1990; Yensen, 1999). Some practical approaches for saline agriculture and afforestation have also been discussed (Ahmad and Malik, 2002) *e.g.* biotechnology, to describe examples of cultivating salt tolerant/halophytic plants for instance wheat, rice, millet, halophytes and mangroves. Suitable crops include a wide range of types of plants includes the species of food, forage, timber, ornamental with salinity tolerances up to and

beyond the equivalent of seawater (Glenn *et al.*, 1998). Seawater agriculture is defined as growing salt-tolerant crops on land using water pumped from the ocean for irrigation. The system appears to work well in the sandy soils of desert areas, but requires larger water applications than irrigation with low salinity water (Glenn *et al.*, 1998). Research into identifying suitable crop species has focused either on breeding salt tolerance into conventional crops or the domestication of halophytes. The more productive species are *Salicornia*, *Suaeda* and *Atriplex* (family: *Chenopodiaceae*). Other high producers were *Distichlis* (salt grass -*Poaceae*), and *Batis* (*Batidaceae*). Goats and sheep fed on a diet where hay was replaced with *Salicornia*, *Suaeda* and *Atriplex*, gained as much weight as when hay was used. The animals' meat was unaffected by the halophyte rich diet, but the feed conversion ratio was 10% lower than that of animals eating a traditional diet (Glenn *et al.*, 1998). The special grain and fodder crops such as pearl millet, barley, fodder beet and buffel grass (*Cenchrus ciliaris*) as well as other grasses (*Spirobolus*, *Distichlis* and *Paspalum*), shrubs (*Atriplex*) and trees (*Acacia ampliceps*) for amenity uses, that can grow well even when watered with saline water with an electrical conductivity in excess of 15 dS m^{-1} could be developed (ICBA, 2004). The communities of poor farmers would directly benefit from greater availability of fodder, especially as winter feed. The latter is important as in several of these countries the demand for winter forage, *i.e.* from perennials that continue to produce at low temperatures, is far greater than the domestic supply.

Salinity tolerance: Salinity tolerance may be defined as the ability of a plant to grow and complete its life cycle under stressful salt conditions like NaCl or with association of other salts.

(a) Morphological basis of salt tolerance: Two things are very important for the adaptation of a species under saline environment, one is control of water loss another is improved ionic balance. In many dicots and chenopods halophytes that succulence is increased in response of salinity stress during adaptation. This succulence and enlargement of parenchyma cells are correlated as observed in *Atriplex species* (Greenway *et al.*, 1966). Plants under salt stress show succulence and xero-morphism *e.g.* NaCl presence caused succulence in cotton, tomato and *Salicornia* (Blits and Gallagher, 1991). It causes many structural changes as smaller leaves with reduction in number, fewer stomata, thickening of leaf cuticles and earlier lignifications of roots. These adaptations may play important role in maintaining tissue water contents or succulence but depend on the plant species and type and extent of salinity stress (Poljakoff-Mayber, 1975).

The leaf water contents in wheat are not affected by salinity but in case of radish and sunflower, salinity significantly decreases the leaf water contents (Heikal, 1977). It has also been observed in many crop species that succulence is correlated with increase in total leaf volume (Jennings, 1976). This may happen by increasing the cell size, and in this way there is more accumulation of Na and Cl in vacuole and finally vacuole-cytoplasm ratio is increased (Gorham *et al.*, 1985).

In some halophytes, special structures can be observed such as salt glands and bladders or trichomes, in these structures, excessive salt is accumulated which restricts the growing cells to exposure to the salts (Flowers *et al.*, 1977; Greenway and Munns, 1980). Ion selection for NaCl via these special structures is highly selective (Luttge, 1975). Salt glands have been found in wild rice (*Oryza coarctata* Roxb) (Bal and Dutt, 1986).

(b) Physiological basis of salt tolerance: Salts decrease water potential and create water deficit problem for plant growth. In such circumstances, plants must decrease inner water potential so that it may uptake water continuously. All plant species, whether halophytes or glycophytes, face two main problems when grown in saline soils, one is ion toxicity and the other is water deficit. The salt tolerance ability varies in different crop species. It is actually based on the type of species and the extent of stress. On the basis of tolerance level species have been divided into halophytes and glycophytes, former can tolerate high concentrations of salt while the latter are susceptible (Maas and Nieman, 1978). Halophytes have the ability to tolerate high concentrations of Na⁺ and Cl⁻ by excluding toxic ions (Greenway and Munns, 1980; Jeschke, 1984; Lauchli, 1984). While in glycophytes, ions are present in the roots and do not move but halophytes move these ions towards shoot and this is the way, they tolerate the toxicity of ions (Flowers *et al.*, 1977).

Most of the halophytes respond to salinity through ion exclusion. In case of excessive NaCl, K⁺ and Ca²⁺ ions are decreased (Lauchli, 1990; Cramer *et al.*, 1991). There are many mechanisms by which plants limit the Na⁺ and Cl⁻ to reach the shoot. High K⁺/Na⁺ ratio in shoot is one of the mechanisms plants use to survive (Gorham *et al.*, 1985; Greenway and Munns, 1980; Aslam *et al.*, 1993; Gorham, 1994). Pearson *et al.* (1976) concluded that most of the Na⁺ absorbed is retained in roots and lower part of the stem. Greenway (1973) called the exclusion an avoidance mechanism where roots remained impermeable to salts to some extent but, after attaining the threshold level, roots lose this ability and the existing salts burst and damage the shoot which leads to the death of plant. Under salt stress conditions, accumulation of salt in the plant is a must. Therefore, plants adapt different mechanisms to get rid of it may be through glands (Flowers *et al.*, 1977) or via pumps at the plasma membrane of root cells (Jeschke, 1984). There are some plants which cope with the deleterious effects of salts by having more water to dilute the cell sap (Yeo and Flowers, 1984), while other plants distribute higher quantity of the salts in older leaves than in younger leaves (Yeo and Flowers, 1982). The intake of ions in older leaves is based on xylem transport while the export is through phloem. In case of younger leaves intake is through both xylem and phloem that is why, in younger leaves the load of ions is lesser as compared to older leaves (Flowers *et al.*, 1977; Greenway and Munns, 1980).

The problem of increasing downhill gradient of water potential from soil to leaf in glycophytes, wherein falls the major economic crops, with the increasing irrigational depositions of salts, particularly in arid and semiarid crops, gradually hinders the plant

growth and development. The successive accumulation of salts reaches up to the extent that it renders the plants to escape the consequences of physiological desiccation and injuries due to specific ion effects. However, still plants do try to respond to this increasing catastrophe regulating their metabolism aided by growth regulators (ABA, JA and ethylene etc.) to shift the flux of concerned biochemical pathways and activating related enzymes and molecules including those related with preventive strategies (osmolytes, polyamines, LEA proteins and antioxidant system). However, possibly plants may not be able to keep pace particularly when such condition are superimposed by additive adversity of environment. Assuming genetic engineering for production of salt tolerant transgenic crops will be successful in the near future on a broad scale, it will provide crop plants superior productivity on salt-affected soils in comparison with existing varieties and cultivars. The production of transgenic lines and tailoring of metabolic pathways e.g. Shikimic acid pathway, SOS pathway, phenylpropanoid pathway and others definitely improved the cultivars lines in this regard. The predisposition of agriculturally desired varieties with effective dose of potential growth regulators emerged as feasible and applicably more accessible strategy to farmers.

Salinity management is required in most irrigated areas in the semi-arid regions of the world in order to sustain agricultural production. Drainage networks also facilitate the reuse of saline drainage water. The large parts of the irrigated lands of the Indo-Gangetic Plains are without adequate drainage systems. Optimization of the leaching fraction is especially relevant in areas with saline and rising groundwater. The aim of optimizing the leaching fraction is to maintain an acceptable low salinity level in the root zone and also to prevent further rise of the watertable. Whether a leaching fraction would lead to a rising watertable depends on the site-specific hydrological conditions and soil characteristics. Crop cultural practices to mitigate the effects of salinity have also been devised (Pasternak, 1987) and are widely applied. With the arising need farmers tend to move from salinity sensitive to salinity tolerant crops within and even outside their acceptable range. Advice from extensive services may help in the adoption of new crops.

Upcoming years in future may incorporate the integrated efforts considering planning of soil and site specific requirements of deploying strategies discussed above enhance the yield considering sustainable agriculture incorporating resistant varieties within the reach of farmers. Attempts have sought and being sought to look for future food security at physiological, biochemical and molecular levels. However, an integrative and feasible management still required to meet with presently available plant preventive strategies for 'salt amalgamated with stress hindered production'.

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