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 Ponnamperuma (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 (ECc) of 4 dS m⁻¹ or more. ECc 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 ECc of 4 dS m⁻¹ or more and soils with ECc'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 ground water, 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 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 respond 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 phenolites, basic igneous rocks such as basalt, undifferentiated volcanic rocks, sandstones, alluvium and lagoon 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). Anthropic salinization occurs in arid and semi arid areas due to waterlogging brought about by improper irrigation (Ponnamperuma, 1984). Secondary salt affected soils can also be caused by human activities other than irrigation and include, but are not limited to the following:

(a) Deforestation: It is recognized as a major cause of salinization and alkalinization 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 (Domnies, 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 farmland 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 alkalinization (Bond, 1998).
(c) Contamination with chemicals: It often occurs in modern intensive agricultural systems, particularly in greenhouses 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 1dS m⁻¹ for sensitive crops. For moderately sensitive, the threshold is 1.8 dS m⁻¹; for moderately tolerant, 3.3 dS m⁻¹; and for tolerant crops, 5.8 dS m⁻¹. In each of these categories, water of higher salinity would lead to yield decline. Higher leaching fractions move the threshold value up, but by how much, depends on the circumstances (Rhoades and Loveday, 1990). 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 (EC < 1.5 dS m⁻¹) and should be 15% in case of moderately saline groundwater (EC = 5.0 dS m⁻¹) (Leffelaar et al., 1999).

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, 1989). 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
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 ‘Moneymaker’ did and, in this sense, it was considered more adaptable to salty conditions than ‘Moneymaker’ (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 increase 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 (Vasantha and Rajakshmi, 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; Kerépesi 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 maintains 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 1:** Variation in salinity levels in the world, in million hectares (Mha)

<table>
<thead>
<tr>
<th>Regions</th>
<th>Total area Mha</th>
<th>Saline soils</th>
<th>Sodic soils</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mha</td>
<td>%</td>
<td>Mha</td>
</tr>
<tr>
<td>Africa</td>
<td>1699</td>
<td>39</td>
<td>2.0</td>
</tr>
<tr>
<td>Asia, the Pacific &amp; Australia</td>
<td>3107</td>
<td>195</td>
<td>6.3</td>
</tr>
<tr>
<td>Europe</td>
<td>2011</td>
<td>07</td>
<td>0.3</td>
</tr>
<tr>
<td>Latin America</td>
<td>2039</td>
<td>61</td>
<td>3.0</td>
</tr>
<tr>
<td>Near East</td>
<td>1802</td>
<td>92</td>
<td>5.1</td>
</tr>
<tr>
<td>North America</td>
<td>1924</td>
<td>05</td>
<td>0.2</td>
</tr>
<tr>
<td>Total</td>
<td>12781</td>
<td>397</td>
<td>3.1%</td>
</tr>
</tbody>
</table>

Source: FAO Land and plant nutrition service, 2008
effect, some plants such as facultative halophyte therefore, to increase water use efficiency under salinity. To this due to the reduction in water potential. The aim of salt tolerance is, 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 (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 (Mesembryantheman 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. 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., 1979), 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-levulinate) probably are diverted either towards the biosynthesis of compatible osmolites for purpose of osmoregulation (as discussed before) or for growth regulators. In beans grown under saline conditions, older leaves showed higher C₄ concentrations than younger leaves (Greenway et al., 1979). 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

<table>
<thead>
<tr>
<th>Ion</th>
<th>Rainfall (local)</th>
<th>Sea water (global)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg kg⁻¹ (ppm)</td>
<td>µM (µmol l⁻¹)</td>
</tr>
<tr>
<td>Sodium (Na⁺)</td>
<td>2.0</td>
<td>86</td>
</tr>
<tr>
<td>Chloride (Cl⁻)</td>
<td>3.8</td>
<td>107</td>
</tr>
<tr>
<td>Sulfate (SO₄²⁻)</td>
<td>0.6</td>
<td>6</td>
</tr>
<tr>
<td>Magnesium (Mg²⁺)</td>
<td>0.3</td>
<td>11</td>
</tr>
<tr>
<td>Calcium (Ca²⁺)</td>
<td>0.1</td>
<td>2</td>
</tr>
<tr>
<td>Potassium (K⁺)</td>
<td>0.3</td>
<td>8</td>
</tr>
<tr>
<td>Total</td>
<td>7.0</td>
<td></td>
</tr>
</tbody>
</table>

Source: Encyclopaedia Britannica.

Table - 2: Approximate soil salinity classes

<table>
<thead>
<tr>
<th>Salinity rating</th>
<th>EC (dS m⁻¹)</th>
<th>Level of effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slightly saline</td>
<td>1.5-2</td>
<td>Salinity effects usually minimal</td>
</tr>
<tr>
<td>Moderately saline</td>
<td>2-6</td>
<td>Yield of salt sensitive plants restricted</td>
</tr>
<tr>
<td>Highly saline</td>
<td>6-15</td>
<td>Only salt tolerant plants yield satisfactorily</td>
</tr>
<tr>
<td>Extremely saline</td>
<td>&gt;15</td>
<td>Few salt tolerant plants yield satisfactorily</td>
</tr>
</tbody>
</table>

Source: FAO land and plant nutrition management service, 2008

Table - 3: Classification of salt water

<table>
<thead>
<tr>
<th>Water class</th>
<th>EC (dS m⁻¹)</th>
<th>TDS¹ (g l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-saline</td>
<td>&lt; 0.7</td>
<td>&lt; 0.5</td>
</tr>
<tr>
<td>Slightly saline</td>
<td>0.7-2.0</td>
<td>0.5-1.5</td>
</tr>
<tr>
<td>Moderately saline</td>
<td>2.0-10.0</td>
<td>1.5-7.0</td>
</tr>
<tr>
<td>Highly saline</td>
<td>10.0-20.5</td>
<td>7.0-15.0</td>
</tr>
<tr>
<td>Very highly saline</td>
<td>20.0-45.0</td>
<td>15.0-35.0</td>
</tr>
<tr>
<td>Brine</td>
<td>&gt; 45.0</td>
<td>&gt; 35.0</td>
</tr>
</tbody>
</table>

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

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

<table>
<thead>
<tr>
<th>Ion</th>
<th>Rainfall (local)</th>
<th>Sea water (global)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>µM (µmol l⁻¹)</td>
<td>µM (µmol l⁻¹)</td>
</tr>
<tr>
<td>Sodium (Na⁺)</td>
<td>2.0</td>
<td>86</td>
</tr>
<tr>
<td>Chloride (Cl⁻)</td>
<td>3.8</td>
<td>107</td>
</tr>
<tr>
<td>Sulfate (SO₄²⁻)</td>
<td>0.6</td>
<td>6</td>
</tr>
<tr>
<td>Magnesium (Mg²⁺)</td>
<td>0.3</td>
<td>11</td>
</tr>
<tr>
<td>Calcium (Ca²⁺)</td>
<td>0.1</td>
<td>2</td>
</tr>
<tr>
<td>Potassium (K⁺)</td>
<td>0.3</td>
<td>8</td>
</tr>
<tr>
<td>Total</td>
<td>7.0</td>
<td></td>
</tr>
</tbody>
</table>

Source: Encyclopaedia Britannica.
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 (Smirnoff, 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 (Spychalla 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 (Fadzila et al., 1997), wheat (Meneguzzo et al., 1999) and pea (Hernandez et al., 1999), but decreased in wheat roots (Meneguzzo and Navarilzzo, 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 Navarilzzo (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 Giraudet (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 mehylated 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 Rann 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 billion in rainfed land.

![Fig. 2: Division for classifying crop tolerance to salinity. Tanji and Neetje (2002).](image)
### Table 5: Relative tolerance level of some important economic crops

<table>
<thead>
<tr>
<th>Crop, Common name</th>
<th>Botanical name</th>
<th>Tolerance based on</th>
<th>Salt tolerance parameters</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artichoke, Jerusalem</td>
<td><em>Helianthus tuberosus</em> L.</td>
<td>Tuber yield</td>
<td>Threshold (EC&lt;sub&gt;e&lt;/sub&gt;) %</td>
<td>Newton et al., 1991</td>
</tr>
<tr>
<td>Barley*</td>
<td><em>Hordeum vulgare</em> L.</td>
<td>Grain yield</td>
<td>9.6</td>
<td>T</td>
</tr>
<tr>
<td>Canola or rapeseed</td>
<td><em>Brassica campestris</em> L.</td>
<td>Seed yield</td>
<td>14</td>
<td>T</td>
</tr>
<tr>
<td>Canola or rapeseed</td>
<td><em>B. napus</em> L.</td>
<td>Seed yield</td>
<td>13</td>
<td>T</td>
</tr>
<tr>
<td>Chickpea</td>
<td><em>Cicer arietinum</em> L.</td>
<td>Seed yield</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Corn</td>
<td><em>Zea mays</em> L.</td>
<td>Ear FW</td>
<td>12</td>
<td>MS</td>
</tr>
<tr>
<td>Cotton</td>
<td><em>Gossypium hirsutum</em> L.</td>
<td>Seed cotton yield</td>
<td>5.2</td>
<td>T</td>
</tr>
<tr>
<td>Flax</td>
<td><em>Linum usitatissimum</em> L.</td>
<td>Seed yield</td>
<td>12</td>
<td>MS</td>
</tr>
<tr>
<td>Millet, channel</td>
<td><em>Echinochloa tumerana</em> (Domin) J.M. Black</td>
<td>Grain yield</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Oats</td>
<td><em>Avena sativa</em> L.</td>
<td>Grain yield</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Peanut</td>
<td><em>Arachis hypogaea</em> L.</td>
<td>Seed yield</td>
<td>29</td>
<td>MS</td>
</tr>
<tr>
<td>Rice, paddy</td>
<td><em>Oryza sativa</em> L.</td>
<td>Grain yield</td>
<td>12</td>
<td>S</td>
</tr>
<tr>
<td>Rye</td>
<td><em>Secale cereale</em> L.</td>
<td>Grain yield</td>
<td>10.8</td>
<td>T</td>
</tr>
<tr>
<td>Safflower</td>
<td><em>Carthamus tinctorius</em> L.</td>
<td>Seed yield</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sorghum</td>
<td><em>Sorghum bicolor</em> (L.) Moench</td>
<td>Grain yield</td>
<td>16</td>
<td>MT</td>
</tr>
<tr>
<td>Soybean</td>
<td><em>Glycine max</em> (L.) Merrill</td>
<td>Seed yield</td>
<td>20</td>
<td>MT</td>
</tr>
<tr>
<td>Sugar beet</td>
<td><em>Beta vulgaris</em> L.</td>
<td>Storage root</td>
<td>5.9</td>
<td>T</td>
</tr>
<tr>
<td>Sugar cane</td>
<td><em>Saccharum officinarum</em> L.</td>
<td>Shoot DW</td>
<td>5.9</td>
<td>MS</td>
</tr>
<tr>
<td>Sunflower</td>
<td><em>Helianthus annuus</em> L.</td>
<td>Seed yield</td>
<td>5.0</td>
<td>MT</td>
</tr>
<tr>
<td>Triticale</td>
<td><em>Triticosecale Wittmack</em></td>
<td>Grain yield</td>
<td>2.5</td>
<td>T</td>
</tr>
<tr>
<td>Wheat</td>
<td><em>Triticum aestivum</em> L.</td>
<td>Grain yield</td>
<td>7.1</td>
<td>MT</td>
</tr>
<tr>
<td>Wheat (semi-dwarf)</td>
<td><em>T. aestivum</em> L.</td>
<td>Grain yield</td>
<td>3.0</td>
<td>T</td>
</tr>
<tr>
<td>Wheat, Durum</td>
<td><em>T. turgidum</em> L. var. <em>durum</em> Desf.</td>
<td>Grain yield</td>
<td>3.8</td>
<td>T</td>
</tr>
<tr>
<td>Alfalfa</td>
<td><em>Medicago sativa</em> L.</td>
<td>Shoot DW</td>
<td>7.3</td>
<td>MS</td>
</tr>
<tr>
<td>Bentgrass, creeping</td>
<td><em>Agrostis stolonifera</em> L.</td>
<td>Shoot DW</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bermudagrass</td>
<td><em>Cynodon dactylon</em> (L.) Pers.</td>
<td>Shoot DW</td>
<td>6.4</td>
<td>T</td>
</tr>
<tr>
<td>Broad bean</td>
<td><em>Vicia faba</em> L.</td>
<td>Shoot DW</td>
<td>9.6</td>
<td>MS</td>
</tr>
<tr>
<td>Gram, Black or Urd bean</td>
<td><em>Vigna mungo</em> (L.) Hepper</td>
<td>Shoot DW</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pigeon pea</td>
<td><em>Cajanus cajan</em> (L.) Huth</td>
<td>Shoot DW</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sesbania</td>
<td><em>Sesbania exaltata</em> (Raf.) V.L. Cory</td>
<td>Shoot DW</td>
<td>7.0</td>
<td>MS</td>
</tr>
<tr>
<td>Vegetable and fruit crops</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bean, common</td>
<td><em>Phaseolus vulgaris</em> L.</td>
<td>Seed yield</td>
<td>19</td>
<td>S</td>
</tr>
<tr>
<td>Crop</td>
<td>Species</td>
<td>Trait</td>
<td>Value 1</td>
<td>Value 2</td>
</tr>
<tr>
<td>-------------------------</td>
<td>--------------------------------</td>
<td>------------------------</td>
<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>Bean, lima</td>
<td><em>P. lunatus</em></td>
<td>Seed yield</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bean, mung</td>
<td><em>V. radiata</em></td>
<td>Seed yield</td>
<td>1.8</td>
<td>20.7</td>
</tr>
<tr>
<td>Beet, red</td>
<td><em>Beta vulgaris</em></td>
<td>Storage root</td>
<td>4.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Broccoli</td>
<td><em>Brassica oleracea</em> (L.)</td>
<td>Shoot FW</td>
<td>2.8</td>
<td>9.2</td>
</tr>
<tr>
<td>Cabbage</td>
<td><em>B. oleracea</em> (Capitata Group)</td>
<td>Head FW</td>
<td>1.8</td>
<td>9.7</td>
</tr>
<tr>
<td>Carrot</td>
<td><em>Daucus carota</em> L.</td>
<td>Storage root</td>
<td>1.0</td>
<td>14</td>
</tr>
<tr>
<td>Cauliflower</td>
<td><em>Brassica oleracea</em> (L.)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Corn, sweet</td>
<td><em>Zea mays</em></td>
<td>Ear FW</td>
<td>1.7</td>
<td>12</td>
</tr>
<tr>
<td>Cowpea</td>
<td><em>V. unguiculata</em> (L.) Walp.</td>
<td>Seed yield</td>
<td>4.9</td>
<td>12</td>
</tr>
<tr>
<td>Cucumber</td>
<td><em>Cucumis sativus</em> L.</td>
<td>Fruit yield</td>
<td>2.5</td>
<td>13</td>
</tr>
<tr>
<td>Eggplant</td>
<td><em>Solanum melongena</em> var</td>
<td>Fruit yield</td>
<td>1.1</td>
<td>6.9</td>
</tr>
<tr>
<td>Garlic</td>
<td><em>Allium sativum</em> L.</td>
<td>Bulb yield</td>
<td>3.9</td>
<td>14.3</td>
</tr>
<tr>
<td>Gram, black or</td>
<td><em>V. mungo</em> (L.) Hepper</td>
<td>Shoot DW</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Urd bean</td>
<td>[syn. <em>Phaseolus mungo</em> L.]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lettuce</td>
<td><em>Lactuca sativa</em> L.</td>
<td>Top FW</td>
<td>1.3</td>
<td>13</td>
</tr>
<tr>
<td>Muskemelon</td>
<td><em>Cucumis melo</em> L.</td>
<td>Fruit yield</td>
<td>1.0</td>
<td>8.4</td>
</tr>
<tr>
<td>Okra</td>
<td><em>Abelmoschus esculentus</em> (L.)</td>
<td>Pod yield</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Onion (bulb)</td>
<td><em>Allium cepa</em> L.</td>
<td>Bulb yield</td>
<td>1.2</td>
<td>16</td>
</tr>
<tr>
<td>Onion (seed)</td>
<td></td>
<td>Seed yield</td>
<td>1.0</td>
<td>8.0</td>
</tr>
<tr>
<td>Pea</td>
<td><em>Pisum sativum</em> L.</td>
<td>Seed FW</td>
<td>3.4</td>
<td>10.6</td>
</tr>
<tr>
<td>Pepper</td>
<td><em>Capsicum annuum</em> L.</td>
<td>Fruit yield</td>
<td>1.5</td>
<td>14</td>
</tr>
<tr>
<td>Pigeon pea</td>
<td><em>Cajanus cajan</em> (L.) Huth [syn. <em>C. indicus</em> (K.) Spreng.]</td>
<td>Shoot DW</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Potato</td>
<td><em>Solanum tuberosum</em> L.</td>
<td>Tuber yield</td>
<td>1.7</td>
<td>12</td>
</tr>
<tr>
<td>Pumpkin</td>
<td><em>Cucurbita pepo</em> L. var <em>Pepo</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Radish</td>
<td><em>Raphanus sativus</em> L.</td>
<td>Storage root</td>
<td>1.2</td>
<td>13</td>
</tr>
<tr>
<td>Spinach</td>
<td><em>Spinacia oleracea</em> L.</td>
<td>Top FW</td>
<td>2.0</td>
<td>7.6</td>
</tr>
<tr>
<td>Squash, scallop</td>
<td><em>Cucurbita pepo</em> L. var <em>melopeo</em> (L.) Ales.</td>
<td>Fruit yield</td>
<td>3.2</td>
<td>16</td>
</tr>
<tr>
<td>Squash, zucchini</td>
<td><em>C. pepo</em> L. var <em>melopeo</em> (L.) Ales.</td>
<td>Fruit yield</td>
<td>4.9</td>
<td>10.5</td>
</tr>
<tr>
<td>Strawberry</td>
<td><em>Fragaria x Ananassa</em> Duch.</td>
<td>Fruit yield</td>
<td>1.0</td>
<td>33</td>
</tr>
<tr>
<td>Sweet potato</td>
<td><em>Ipomoea batatas</em> (L.) Lam.</td>
<td>Fleshy root</td>
<td>1.5</td>
<td>11</td>
</tr>
<tr>
<td>Tepary bean</td>
<td><em>Phaseolus acutifolius</em> Gray</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tomato</td>
<td><em>Lycopersicon lycopersicum</em> (L.) Karst. ex Farw. [syn. <em>Lycopersicon esculentum</em> Mill.]</td>
<td>Fruit yield</td>
<td>2.5</td>
<td>9.9</td>
</tr>
<tr>
<td>Tumpip (greens)</td>
<td><em>Brassica rapa</em> L. (Rapifera Group)</td>
<td>Storage root</td>
<td>0.9 3.3</td>
<td>9.0 4.3</td>
</tr>
<tr>
<td>Watermelon</td>
<td><em>Citrullus lanatus</em> (Thunb.) Matsum. and Nakai</td>
<td>Fruit yield</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

MT = Moderately tolerant, MS = Moderately sensitive, S = Sensitive, T = Tolerant, *= Estimated ratings, FW = Fresh weight, DW = Dry Weight, - = Not Estimated
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 Troughton, 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 sugar beet 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 Brugueira 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 CO₂. 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 NO₂⁻ uptake by the roots. Fisarakis et al. (2001) found that NO₂⁻N was significantly reduced in salt-stressed sultana vines and this reduction was correlated with photosynthetic reduction. The reduced NO₂⁻N uptake combined with osmotic stress may explain the inhibitory effect of salinity on photosynthesis.

(3) Reduction of CO₂ supply because of the closure of stomata: The reduction in stomatal conductance results in restricting the availability of CO₂ 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 CO₂ 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 CO₂ 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 in 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 nutrients, 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 has 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 pseudalhagi (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 (EC=4.0 mM 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 dS m$^{-1}$ = 1 mmho cm$^{-1}$). For soil salinities exceeding the threshold of any given crop, relative yield ($Y_r$) can be estimated with the following equation:

$$Y_r = 100 - b(EC_e - a)$$ (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 salinity and salinity 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 (Batidaeaceae). 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 (Cenches ciliaris) as well as other grasses (Spirobolus, Distichlis and Paspalum), shrubs (Atriplex) and trees (Acacia amplexica) 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 exposal to the salts (Flowers et al., 1977; Greenway and Munns, 1980). Ions selection for NaCl via these special structures is highly selective (Lutte, 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 Ca\(^+\) 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 loose 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 semi-arid 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’.

Acknowledgements
The authors are thankful to the anonymous reviewers for their valuable suggestions. Ms. S. Yadav is thankful to the CSIR, New Delhi, India for the award of CSIR - SRF [09/112 (0447) - 2K 10 - EMR - 1].


US Salinity Laboratory Staff: Reclamation and improvement of saline and sodic soils. USDA Handbook 60, Riverside, California (1954).


Journal of Environmental Biology  September 2011 ©}


