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## Review

## A critical review on halophytes: Salt tolerant plants

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Present work deals with the different mechanisms which are present in salt tolerant plants against high salt concentrations of the soil by combining information from different research papers to make a comprehensive account of halophytes. It covers all the aspects of halophytes regarding their classification, mechanisms against high salt concentrations (both at physiological and molecular level). Furthermore, the article discusses the importance of halophytes and some aspects regarding the transformation of non-salt tolerant plants to salt tolerant plants. ~400 million hectares land is affected by salinity and this area is increasing day by day due to excessive irrigation practices also the world population is tremendously increasing hence we need a large amount of food supply. The crops cannot be grown on a salt affected land but nature has provided us with a unique group of plants that is, halophytes. Owing to the consumption of fossil fuels we need the fuel that can be obtained from plants and halophytes can be a good approach in this respect. They can be grown on salt affected lands, by identifying the genes present in them functioning against salinity production of transgenic crops can be done.

**Key words:** Salt stress, stress genes, transgenic plants, molecular mechanisms, ion compartmentalization, halophytes.

### INTRODUCTION

One of the major abiotic stresses that affect the plant is soil salinity and this problem has been much enhanced due to agricultural practices (Zhu, 2001). Salt stress severely limits the plant growth and yield; in fact no toxic substance restricts the plant growth more than salt on world scale (Xiong and Zhu, 2002). Salinity is an escalating problem in coastal areas which are much vulnerable to salinity problem which are caused by natural and anthropogenic forces (Boesch et al., 1994; Rogers and McCarty, 2000) as well as it also effects agricultural regions where it has severely degraded the (Yeo, 1999). Most of the plants cannot tolerate high salt concentrations of the soil and cannot be grown on a salt affected land (Glenn and Brown, 1999). Such plants are known as non-salt tolerating plants, nonhalophytes or glycophytes (Xiong and Zhu, 2002). Some of the plants have the ability to grow under salinity due to the presence of different mechanisms in them for salt tolerance such plants are known as salt resisting plants, salt tolerating plants or halophytes (Flowers et al., 1986). Salt tolerating plants represent only 2% of terrestrial plant species but they represent a wide diversity of plant forms (Glenn and Brown, 1999). About half of the higher plant families consist of halophytes and they have a polyphyletic origin (Glenn and Brown, 1999).

The largest number of halophytes is included in Chenopodiaceae and it consists of about 550 halophyte species (Aronson, 1989). The other families that include halophytes are Poaceae, Fabeaceae and Asteraceae however less than 5% of the species in these families are halophytes (Aronson, 1989). One of the basic differences between halophyte and glycophytes is that halophytes have the ability to survive under a salt shock as for example due to tidal or rainfall events this capacity allows the halophytes to develop a metabolic steady state for growth in a saline environment as compare to glycophytes (Braun et al., 1986; Hassidim et al., 1990; Casas et al., 1991; Niu et al., 1993). Halophytes respond to salt stress at three levels i.e. cellular, tissue and whole plant level. It is important to study the mechanism

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operating at each level so as to develop complete understanding of the plant salt tolerance. Investigation of molecular mechanisms involved against different types of abiotic stresses (drought, salt and osmotic stress) has long been in progress in the recent years (Knight and Knight, 2001; Zhu 2001; Seki et al., 2003). Most of the halophytes utilize the basic mechanism of controlled accumulation and sequestration of inorganic ions which they utilize to adjust their internal osmotic balance to external salinity (Flowers and Yeo, 1986). However, the halophytes differ to a great extent to which they accumulate ions as well as their overall degree of salt tolerance (Glenn et al., 1996).

Today about 20% of the world cultivated lands and half of the irrigated lands are affected by salinity (Rhoades and Loveday, 1990). According to another report approximately 400 million/hectare of land is affected by salinity (Al-Sadi et al., 2010). If salt tolerance in plants is not improved, large areas of the world will be remaining uncultivated. However, engineering a salt tolerant plant may take many years. It is because of the fact that genes which are regulated under salt stress may be identified either through the analysis of RNA (Kawasaki et al., 2001) or proteins (Salekdeh et al., 2002) and finding a key gene for salinity tolerance is still farfetched. More than one mechanism is operating in salt tolerant plants against salinity, yet it is therefore important to study the mechanism operating at each level in full detail so as to develop a complete understanding of salt stress and utilizing this knowledge improvement of crops against salt stress. Halophytes can be very useful under such situations they can be used for industrial, ecological and agricultural purposes Figure 1 (Koyro et al., 2011).

Halophytic forage and seed products can be used for animal feeding salinity simultaneously effects several aspects of plant physiology such as reduction in the amount of water absorbed by the plants (Epstein, 1980), a rapid reduction in the growth rates as well as induction of several metabolic changes similar to those caused by water stress (Epstein, 1980). Halophytes are found in the areas where the concentration of the salt is relatively higher which indicate either a requirement for relatively high salt concentrations, a tolerance for the excess salt or a decrease a competitive ability with other plants in the environment which are less stressful (Ungar, 1991).

## **CLASSIFICATION OF HALOPHYTES**

Halophytes are classified in a variety of ways such as classification based on general ecological behavior and distribution, response of plant growth to salinity and quantity of salt intake etc (Waisel, 1972). Albert and Popp (1977) classified the halophytes grown along the salt marsh as physiotypes. Halophytes can also be classified on the basis of presence or absence of salt glands for example, black mangroves which have well developed

salt glands and red mangroves which do not have salt glands (Popp et al., 1993).

# Classification on the basis of internal salt content of the plant

Steiner (1934) classified the halophytes according to their response to internal salt content. According to him salt marsh halophytes can be divided into two main types that is, salt regulating types and salt accumulating types. Halophytes are also classified as excluders versus includers on the basis of internal salt contents of the plant (Ashraf et al., 2006).

## Classification on the basis of morphology

In this type of classification halophytes are often classified as excretive and succulents on the basis of their morphology.

#### **Excretives**

Such halophytes that are capable of excreting excess salt from the plant body are known as excretives. In such types of halophytes, the salt crystals may remain visible on the plant leaf surface; they have glandular cells that help to remove excess salt from the plant body (Marschner, 1995).

### Succulents

These types of halophytes have a salt bladder on their leaf surface. Succulents store large amount of water within their body to minimize salt toxicity (Weber, 2008). Almost all the halophytes found in deserts belong to this category.

### Classification based upon salt demand of halophytes

According to Sabovljevic and Sabovljevic (2007) depending upon their demands and tolerance for sodium salts halophytes can be classified as obligate and facultative. Eco-physiological aspects can also be used to differentiate between obligate, facultative halophytes and habitat-indifferent halophytes (Cushman, 2001).

### Obligate halophytes

Such types of halophytes need some salt for their growth and they are also known as true halophytes and they thrive when the water contain over 0.5 to 1% of the

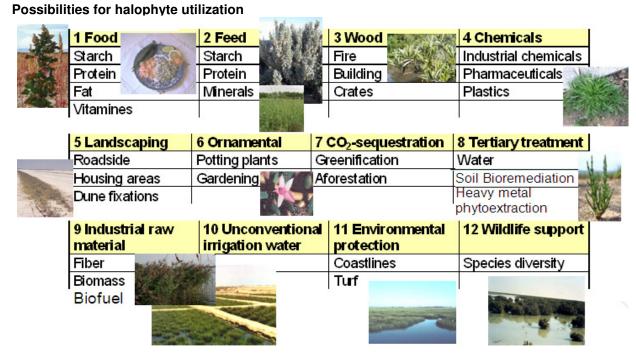


Figure 1. Uses of Halophytes (Hans-Werner et al., 2011): Utilizations of halophytes already existing and utilization purposes that are investigated.

sodium chloride (Ungar, 1978). Obligate halophytes show a clear optimization in their growth when the amount of salt is increased in their media. Members of the family Chenopodiaceae belongs to this category (Cushman, 2001).

### Facultative halophytes

They can be grown under saline stress but can grow well without salt or at least in an environment where the concentration of salt in the soil is quite low (Sabovljevic and Sabovljevic, 2007). Members of Graminae, Cypraceae and Juncaceae as well as large number of dicotyledons belong to this category (Sabovljevic and Sabovljevic, 2007).

### **Habitat-indifferent halophytes**

There are certain plants which are in-different to their habitat but they are able to cope with the salty soil in nature. Such plants usually prefer to live in a salt free soil but on the other hand can live on the salty soil as well and have the ability to compete with the salt sensitive species (Cushman, 2001). In such type of plants there may exist some sort of genetic difference between the plants which are living on salt free and the plants which are living on salt enriched soil, some examples are Festucarubra, Agrostisstolonifera and Juncusbufonius

(Sabovljevic and Sabovljevic, 2007).

### Classification of halophytes on the basis of habitat

Halophytes can be divided into two main types based on their geographical distribution or habitat (Youssef, 2009). These two types are as follow:

## **Hydro-halophytes**

These are the plants which can grow in aquatic soil or in wet conditions. Most of the mangroves and salt marsh species along costal lines are hydro-halophytes (Youssef, 2009).

## Xero-halophytes

They may grow in environment, where the soil is saline but the water content of the soil is less due to evaporation and many of them are succulents (Youssef, 2009).

# Effects of high salt concentrations of the soil on plants

Sodium ions and chloride ions when present in soil in higher concentrations are extremely toxic for plants

because of their effect on potassium ions nutrition, cytosolic enzyme activities, photosynthesis and cellular metabolism (Niu et al., 1995). Among the different effects of salt stress some are as follows:

### Stomatal closure

The salt stress may lead to the closure of stomata leading to the reduction in the availability of carbon dioxide in the leaves and inhibiting the carbon fixation (Prida and Das, 2005). It causes the exposure of chloroplast to excessive excitation energy which in turn could cause the generation of reactive oxygen species (ROS) causing oxidative stresses (Parvaiz and Satyawati, 2008).

## Hyper osmotic shock

The high salinity level of the soil may lead to oxidative stress as well as hyper osmotic shock for the plants leading to the loss of cell turgor (Borsani et al., 2001).

## Inhibiting cell division

Salt stress may affect the expression of cell cycle progression genes hence effecting cell division and cell expansion leading to growth inhibition (Burssens et al., 2000).

## Inhibiting photosynthesis

Salt stress may cause inhibition of photosynthesis due to several reasons for example effect of salt stress on the efficiency of translocation as well as assimilation of photosynthetic product and stomata closure (Xiong and Zhu, 2002).

#### **Nutrient imbalance**

The deleterious consequences of high salt concentrations of soil include ion toxicity and nutrient imbalance (Serrano et al., 1997). High Na+ ion concentrations of the soil reduces the amount of available K+, Mg++ and Ca++ (Epstein, 1972) hence, leading to nutrient imbalance.

## Osmotic effect

Excess salts in the soil may reduce the water absorption from the soil by the plant which may affect growth, flowering and fruiting of the plants. It happens because during salt stress plants must increase the energy that they expand to obtain water from the soil, under such conditions a plant eventually may die (Blaylock, 1994).

## **Toxicity**

Some of the elements (boron, sodium, chlorides and iron) may have great toxic effect on the plant and if the plants are sensitive to these elements they may be easily affected at relatively low levels of these ions in the soil (Blaylock, 1994). K<sup>+</sup> ion is used as a cofactor in various in various reactions Na+ ions interferes with the function of potassium hence causing a direct toxic effect on plant. In addition to this the other deleterious effects of Na+, however, seem to be related to the structural and functional integrity of membranes (Kurth et al., 1986).

## Effects of salinity on plant yield

The elongation process of new cell of a plant grown under high salt concentrations is adversely affected because the excess salt modifies the metabolic activities of the cell wall leading to the deposition of various materials which causes a reduction in the cell wall elasticity. Secondary cell wall sooner as a result of which cell wall becomes rigid hence causing a decrease in turgor pressure efficiency in cell wall enlargement (Ali et al., 2004).

The high salt concentrations of the soil also causes a shrinkage of the cell contents as well as reduction in the development and differentiation of the tissues unbalanced nutrition, damage of membrane and disturbed avoidance mechanism. All these factors contribute towards the reduction in plant yield (Ali et al., 2004).

### Mechanism of salt resistance in halophytes

Salt resistance is a reaction between an organism and the salt stress (Yeo, 1983). Plants generally respond against salinity at two levels that is, physiological level or molecular level (Munns and Tester, 2008). The physiological mechanisms that are involved in providing resistance against salinity and drought stress are similar, as the concentrations of salt in the soil is increased the availability of water in the soil is decreased causing reduction of the water potential leading to the shortage of water available to the plants (Hasegawa et al., 2000).

The adaptations to the stresses can either be done by the pre-existing or either by induced defenses (Pastori and Foyer, 2002). According to Sabovljevic and Sabovljevic (2007), the mechanisms for the salt resistance in halophytes generally fall into two main categories that is, salt tolerance and salt avoidance. Another aspect against salinity of the soil includes the

modifications at cellular level which involves certain mechanisms operating at molecular level and germination reponses in case of young seedlings.

#### Salt tolerance

Such type of strategy may involve certain physiological or biochemical adaptations in the plants, which help the plant to maintain protoplasmic viability as the ions accumulate inside the cells (Sabovljevic and Sabovljevic, 2007). Salt tolerance can be achieved either by salt exclusion or salt inclusion; salt tolerant organisms utilize the energy for the exclusion of excess salt from them so as to protect themselves from toxic effects of high salt content of the soil as for example protein aggregation etc (Ashraf et al., 2006).

### Aspects of salt tolerance

To achieve the salt tolerance, three interconnected aspects of plant activity are important. This employs to both types of the plants either with or without salt glands (Zhu, 2001). These aspects are:

Detoxification: Salt stress cause the generation of reactive oxygen species (ROS) which may cause severe damage to the cellular components of the cells. The plants exposed to salt stress get rid of themselves from these reactive oxygen species by the production of stress proteins and compatible osmolytes, many of the enzymes and proteins with unknown function are believed to scavange the ROS (Zhu et al., 1997). Various examples of osmolytes include proline, glycine, betaine etc.

**Homeostasis:** Another strategy in plants against high salt concentration of the soil is the restoration of homeostasis. One of the toxic effects of sodium ions in higher concentrations is the inhibition of enzymatic activity, it is therefore important that the concentrations of sodium ions within the plant cell cytoplasm and organelles should remain low (Zhu et al., 1997).

Several non-selective ionic channels are present in the cells that may be responsible to mediate sodium ion entry in the plant cell (Amtmann and Sanders, 1998). Plants accumulate various compatible osmolytes in the cytosol, thus lowering the osmotic potential to sustain water absorption from saline soil solutions (Zhu et al., 1997). Some water channel proteins are present across the cellular membranes which may also involve in controlling water flux across membrane (Chrispeels et al., 1999). Growth regulation: During stress, most of the plants slow down their growth rate as it allows plants to relay on multiple resources to combat the stress (Zhu, 2001). One cause of the reduction in the growth rate during stress is inadequate photosynthesis which occurs due to the stomata closure leading to the limited carbon dioxide

uptake (Xiong and Zhu, 2002). CBF1, DREB1A (Liu et al., 1998) and ATHB7 (Soderman et al., 1996) are the genes which are expressed during stress only, the proteins produced by them affect cell division and expansion machinery, leading to growth regulation under stress (Zhu, 2001).

#### Salt avoidance

Avoidance is a phenomenon in which plant tries to keep away the salt ions from those parts of the plants where they may be toxic or harmful (Allen et al., 1994). Salt avoidance may involve certain physiological and structural adaptations so as to minimize the salt concentrations of the cell or physiological exclusion by root membranes. This may involve passive exclusion of ions by means of a permeable membrane, the active expelling of ions by means of a pump or dilution of ions in the tissues of the plants (Allen et al., 1994). There are four main methods of salt avoidance in halophytes. These are as follow:

**Exclusion:** The most common means of surviving in high salt concentrations in halophytes is the salt exclusion (Waisel et al., 1986). In case of mangroves, 99% of the salts are excluded through the roots (Tomlinson, 1986). Exclusion of salt at whole plant level occurs at the roots and the casparian strips may play role in salt exclusion from the inner tissues (Flowers et al., 1986).

**Secretion:** Some of the halophytes specialized salt glands present, are responsible for the secretion of excess salt from the plant (Weber, 2008). The water evaporates through these salt glands and the salt remains on the leaf surface in the form of crystals, these crystals are then blown away through wind or by rain (Liphschitz et al., 1974). Salt secretion is also known as excretion and it is one of the common ways of salt avoidance (Waisel et al., 1986).

Salt can be released either through the salt glands or through the cuticle or guttation fluid. It can then be retransported to the plant via the phloem or become concentrated in the salt hairs (Stenlid, 1956). Saltglands are found either on the epidermis or may be found as depressed into it, they are more concentrated in leaves but are found on every aerial part of the plant, these glands are rich in mitochondria and other organelles but lack a central vacuole so they are the transit cells not storage cells (Waisel, 1972).

**Shedding:** According to Albert (1975) in some of the plants, the shedding of the old leaves of the plants which are grown under high salt concentrations is a strategy to avoid the toxic effects of excess sodium salts, which are accumulated in leaves. Some of the halophytes release excess of salt through the discard of salt saturated

organs (Chapman, 1968).

Succulence: The term succulence stand for a plant condition that involve increase in cell size, decrease in the growth extension, a decrease in surface area per tissue volume as well a higher water content per tissue volume (Flowers and Yeo, 1986). According to Drennan and Pammenter (1982), the leaves of succulent plants are very thick, their mesophyll cells are increased in size and they have smaller intercellular spaces as compared to the plants without succulence. Such leaves have more mitochondria and are relatively larger showing that some extra energy is needed in these plants for the salt compartmentalization and excretion (Siew and Klein, 1969). Succulence causes an increase in cell size, decrease in extension of growth, decrease in surface area per tissue volume leading to higher water content per unit surface area and helps the plant to cope with salinity stress (Weber, 2008). During salinity some of halophytes (mostly halophytes of the deserts) undergo succulence and this characteristic is of adaptive value for survival under stress (Waisel, 1972).

Stomatal response: Glycophytes stomatal function is damaged by sodium ions, and this disruption can be seen as a mechanism of their lack of survival in saline conditions (Robinson et al., 1997). There are two stomatal response of plant to salinity either the guard cells can utilize potassium to achieve their normal turgor regulation in place of sodium or the guard cells may use potassium to limit their intake of sodium (Robinson et al., 1997), this type of mechanism is more important in those halophytes that lack glands.

### Cellular adaptations of the plants against salt stress

# Synthesis of compatible solutes (Osmolyte production)

Osmolytes are the organic compounds they affect osmosis and play role in maintaining fluid balance as well as cell volume for example a cell may burst as a result of external osmotic pressure under this situation certain osmotic channels, may get open which allow the efflux of certain omolytes through them as they move outside they carry water with themselves preventing the cell from bursting out. Sugars, alcohols, amino acids, polyols, tertiary and quaternary ammonium and sulphonium compounds are different examples of osmolytes (Rhodes and Hanson, 1993). Due to the increase of salt contents of the soil, the flow of water towards the roots of the plants is decreased causing a decrease of the cell membrane permeability (Waisel, 1972). Under such a situation, osmotic adjustment of the plant cells is required. Plants carry out this adjustment by the synthesis of compatible solutes called osmolytes, which play role in the reduction of oxidative damage that may

occur due to the production of ROS under salinity stress as well as they protect sub-cellular structures (Hare et al., 1998). Some omolytes and their roles in stress are given subsequently:

## **Proline analogues**

Naidu (2003) reported that some of the halophytes are able to cope with the high salinity of the soil due to the production of proline analogue as it happens in Australian. Melanleuca species as for example *Melanleuca bracteata* which accumulate the proline analogue 4-hydroxy-N-methyl proline (MHP). Such proline analogues increase the ability of plants to survive during salinity stress due to their ability to cause regulation, compartmentalization, and production outlay (Bohnert and Shen, 1998).

## Aquaporin

Another type of osmolyte is named as aquaporin, which believed to be involved in intracellular compartmentalization of the water (Maurel, 1997). These pore forming proteins in halophytes conduct the water molecules. It indicates that the gating of water channels could have an impact on inter compartmental movement of water (Maurel, 1997). Such aquaporins are believed to play some role in salt toleranceby maintaining osmotic homeostasis and turgor of the plant cells under salt stress.

Glycine betaine (GB): GB is basically a quaternary ammonium compound which acts as an osmo-protectant and can offset the high salinity concentration in the vacuole (Wyn and Storey, 1981). It is a stabilizing osmolyte and has the role of protection of macromolecule of the plant under dehydration stresses (Yancey, 1994). GB is not found to accumulate in crops during stress but is generally found in halophytic members of Poaceae and Chenopodiaceae (Flowers et al., 1986).

### Protection of cell wall integrity

In order to maintain the cell growth during salt stress, the maintenance of cell wall properties such as permeability is required, which is important for salt tolerance (Iraki et al., 1989). TPX2 is cell wall peroxides found in tomato, it's over expression increases the germination rate under salt stress. This fact indicates that the protection of cell wall integrity during stress helps the plant cell to retain water which protects the cell under stress (Amaya et al., 1999).

## Ion compartmentalization and selective transport and uptake of ions at the plasma membrane

When the salt concentrations of outside medium is more as compared to the inside of the cell, more amount of salt move inside the plant body and if this condition persists it may lead to high amount of salt depositions inside the shoot therefore halophytes must have the ability to keep the salt concentrations within their body low (Borsani et al., 2003). Plant cells respond to high salt concentrations of the soil by increasing sodium efflux at the plasma membrane and by the accumulation of sodium in the vacuole (Zhu, 2000).

However, the compartmentalization of sodium and chloride in the vacuole can be attained only if sodium and the chloride ions are transported actively in the vacuole and if the tonoplast permeability to these ions is relatively low so that an ion concentration gradient can be sustained at an energy cost that can then be prolonged for months (Maathius et al., 1992).

Halophyte tonoplast channels must therefore be modified either to be increasingly discriminating against sodium and chloride, or the channels remain closed for the greater part of time, or to have a decreased number of channels per cell. Halophytes generally utilize the control accumulation and sequestration of inorganic ions for the adjustment of osmotic potential of their internal tissues to the external salinity (Flowers and Yeo, 1986; Cheeseman, 1988).

However, the extent to which halophytes accumulate ions and the degree of salt tolerance is widely different among halophytes (Glenn and O'Leary, 1984; Glenn et al., 1996). Cells are able to increase salt levels in the vacuoles by intracellular compartmentalization of ions hence preventing the high levels of salts in the cytoplasm (Gorham, 1995).

Molecular mechanisms involved in providing resistance against salinity in plants: According to Xiong and Zhu (2002), one of the important strategies against high salt concentrations is to regulate the expression of certain genes. Genes that may be regulated by salt stress may belong to different groups based on their function. These genes encode:

- 1. LEA protein (late embryogenesis abundant proteins),
- 2. Enzymes (involved in biosynthesis of osmolytes, hormones, detoxification, and general metabolism).
- 3. Transporters (ions transporters, ABC that is, ATP-binding cassette transporters, and aquaporins),
- 4. Regulatory molecules such as protein kinases and phosphotases.

The most common and the most important stress regulated genes are LEA-like genes or LEAs. LEA genes encode LEA proteins or late embryogenesis abundant proteins (Baker et al., 1988). Although, these genes have a wide occurrence but the function of this group of genes

are still not well defined except in some cases where the over expression of individual LEA genes resulted in some degree of stress protection (Xuet al., 1996).

The expression of transcription factor that regulate the expression of LEA-like genes has been enhanced under stress in transgenic plants, it indicates that these proteins do have protective affect against abiotic stress (Liu et al., 1998). However, the fact that these genes are not expressed under normal growth but they are only expressed during stress (salt drought or low temperature stress) suggest that their products have some role in protecting the cellular structure during stress. One major hypothesis is that these genes product may act as chaperon hence protecting the denaturation of some key proteins of the cell (Xiong and Zhu, 2002).

A large number of enzymes are believed to be involved in providing tolerance against high salt concentrations in the halophytes. Such enzymes are found to be sensitive against sodium chloride. It has been observed in Suaedamaritima, when the concentration of sodium chloride is increased, the activity of various enzymes is inhibited. It also includes those enzymes that are involved in protein synthesis. It happens at 200 to 400 mMNaCl concentrations (Munns et al., 1983). There is particularly very little evidence that an inherent difference exists between the enzymes isolated from halophytes and nonhalophytes. ROS species is produced under salt stress conditions in plants. These ROSs have the ability to interact with the cell membrane and other cellular components of the cell leading to the damage to these cellular components. Plants contain variety of antioxidants and antioxidant enzymes which are responsible for maintaining the level of ROSs relatively low (Gaoet al., 2008). In plants enzymes like superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) may be responsible in protecting the cell from oxidative damage (Mittler, 2002). In various reports the role of CAT, POD, SOD have been reported in providing resistance during salt stress by preventing oxidative damages to the cell (Rahnama and Ebrahimzadeh, 2005). On the basis of these findings it can be suggested that the presence of antioxidant enzymes can be the most important strategy of plants grown under high salinity levels. The role of some of the antioxidant enzymes is given below:

- 1. SOD can easily repair the damage that is caused by ROS. SOD is one of the important enzymes responsible for the maintenance of normal physiological conditions of the plants and hence coping with the stress (Mittler, 2002). A large number of studies have been carried out which highlight the positive correlation between the salt stress and level of SOD (Badawiet al., 2004; Shalata and Tal. 2002; Al Scher et al., 2002).
- 2. POD has wide distributions among the families of higher plants. POD plays various roles in the plants like lignifications, oxidative metabolism, salt tolerance and heavy metal stress (Passardi et al., 2005). The increased

POD activity is believed to be responsible in providing an antioxidant mechanism during the conditions of salt stress (Gao et al., 2008).

3. CAT is the most active enzyme in providing resistance against oxidative damage in the plant. This enzyme basically brings out the degradation of hydrogen peroxide into water and oxygen (Mittler, 2002). The CAT activity may depend upon the species as well as the developmental and metabolic state of the plant as well as duration and stress intensity and hence varies (Chaparzadeh et al., 2004).

## Whole plant level adaptations of halophytes against salinity

### **Germination responses**

According to Pollack and Waisel (1972) if a seed is sown in the soil when the salinity level of the soil is high, then the young seedling may face one of the following two dangers:

- 1. High osmotic potential of the surrounding medium may prevent the embryo from taking up of water.
- 2. The toxic effects of some of the ions may cause poisoning of the embryo.

Both halophyte and glycophyte behave similarly when grown under high salinity level in the soil. Both of them may cause delay in the germination as well as reduction in the seed number (Ungar, 1996). It has been found that NaCl inhibits the germination of many plants and even some halophytes.

Laboratory investigations indicate that seeds of most halophytic species reach maximum germination in distilled water (Ungar, 1982). Seed germination in saline environments usually occurs during the spring or in a season with high precipitation, when soil salinity levels are usually reduced (Ungar, 1982). Halophytes germinate better under saline conditions but the definite mechanism at germination stage needs investigation if this exact mechanism is being defined that will be extremely beneficial in improving the crops resistance against salinity.

## Genetic modification of plants to make them salt resistant

Plants can be modified genetically to make them more salt tolerant. In tomato transgene have been inserted into its genome successfully, the main target was that tomato plant should be able to survive under salt stress while the taste must not be affected, however not much success in this regard has yet been achieved (Winicov and Bastola, 1997). Classical breeding for salt tolerance has been

tried but that was also not much successful. Now a days, the alternate strategy is to produce the salt tolerant plants through genetic engineering is under consideration and genes which are important for salt tolerance are under investigation (Borsani et al., 2003).

Grass has been made salt tolerant by transforming it with ricevacuolar membrane Na<sup>+</sup>/H<sup>+</sup> anti porter gene via the *Agrobacterium*-mediated transformation. The resultant plant species has a better salt stress tolerance (Wu et al., 2005). The transgenic salt tolerant plants have the advantage that they also have resistance against other type of stresses for example chilling, freezing, heat and drought (Zhu, 2001).

### CONCLUSION

Halophytes represent versatile group of plants which can be grown on such salt affected lands where glycophytes cannot survive. The biochemical mechanisms leading to salt tolerance in halophytes are regulated in a way that gives them a competitive advantage over other plants that is glycophytes (Hasegawa et al., 2000). Majority of the halophytes can be grown under fresh water however, glycophytes growth rates are found to be higher under such conditions. Halophytes are therefore at a competitive disadvantage which is great enough to eliminate them from favorable fresh water site (Hasegawa et al., 2000).

Halophytes face a twofold problem: first is they must have the ability to tolerate high salt concentrations of the soil and second is they have to absorb water from a soil solution where the water potential is low. Hence, halophytes must maintain a water potential that is more negative than that existing in the soil solution. In order to overcome such problems a number of mechanisms are found operating n halophytes. However, it has been found that individual plants will vary in the traits that they possess and to the extent of which they are utilized.

The areas of the world affected by salinity are increasing day by day due to the degradation of the irrigation system, addition of waste salts to our environment as well as increasing contamination of underground water sources (Ashraf, 1999). It is due to this reason that increasing salt resistance of many crops will become essential in near future (Flowers and Yeo, 1995). The approaches leading to the production of transgenic salt tolerant are possible and so far the results obtained with many genes are promising. However, in order to have great success in this respect it is required that identification of uncovered tolerance traits and stress inducible promoters must be further explored. Owing to the day by day increasing population of the world it seems reasonable that changing the salt tolerance of the crops will be an important aspect of plant breeding in the future, if global food production is to be maintained. Hence, it is much important to carry out vast research in

this field because the future generations will be depending on the halophytic resources to large extent.

## What hypothesis or questions does this work address?

This work is basically a review article on halophytes which are the salt tolerant plants. This work deals with the different mechanisms which are present in salt tolerant plants against high alt concentrations of the soil. This review article combines the information from different research paper to make a comprehensive account of halophytes. So far the review articles published on salt tolerant plants discuss few aspects of halophytes but in this review all the aspects of halophytes regarding their classification their mechanisms against high salt concentrations have been summed up.

# How this work does advances our current understanding of plant science?

This work discusses in detail various aspects of halophytes. Prior to this work, so many review articles have been published on halophytes but none of the paper describes all the aspects of halophytes. The main theme of this review was to write down such an article which covers up all the aspects of halophytes so that once a reader goes through it, he/she may develop a good understanding of the halophytes. This article discusses halophytes classification, their mechanisms against salt (both at physiological and molecular level). Furthermore, the article discusses the importance of halophytes and some aspects regarding the transformation of non salt tolerant plants to salt tolerant plants. In this way article is very useful in improving our understanding of plant science.

## Why is this work important and timely?

The main objective of the present work is to discuss the importance of halophytes. Now a days a major of the world (400 million hectares) is affected by salinity and this area is increasing day by day due to excessive irrigation practices also the world population is tremendously increasing hence we need a large amount of food supply. Now the crops cannot be grown on a salt affected land but nature has provided us with a unique group of plants, that is, halophytes which can be grown on such land. Hence, the need of the time is to study the mechanisms operating in halophytes against high salt concentrations of the soil and also to make use of the fact that how halophytes can be utilized as crops, animal fooder, medicines and many more Figure 1.

Owing to the consumption of fossil fuels we, need the

fuel that can be obtained from plants and halophytes can be a good approach in this respect. They can be grown on salt affected lands and by identifying the genes present in them functioning against salinity production of transgenic crops can be done. In this way the present review is important and the need of the time.

#### **REFERENCES**

- Allen JA, Cambers JL, Stine M (1994). Prospects for increasing salt tolerance of forest trees: a review. Tree Physiol., 14: 843-853.
- Al scher RG, Erturk N, Heath L (2002). Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. J. Exp. Bot., 53: 1331-1341.
- Al-Sadi AM, Al-Masoudi RS, Al-Habsi N, Al-Said FA, Al-Rawahy SA, Ahmed M, Deadman ML (2010). Effect of salinity on Pythium damping-off of cucumber and on the tolerance of *Pythium aphanidermatum*. Plant Pathol., 59: 112-120.
- Amaya I, Botella MA, De La Calle M, Medina MI, Heredia A, Bressan RA, Hasegawa PM, Quesada MA, Valpuesta V (1999). Improved germination under osmotic stress of tobacco plants over expressing a cell wall peroxidase. FEBS Lett., 457: 80-84.
- Amtmann A, Sanders D (1998). Mechanisms of Na<sup>+</sup> uptake by plant cell. Adv. Bot. Res., 29: 75-112.
- Aronson J (1989). Haloph. A database of salt tolerant plant of the world. Office of Arid Lands Studies, Univ. Arizona Tucson, Arizona.
- Aronson JA (1985). Economic halophytes-A global review. In: G. E. Wickens, J. R. Goodin., D.V. Field (eds). Plants for arid lands. George Allen and Unwin, London, pp. 177-188.
- Ashraf M, Hameed M, Arshad M, Ashraf Y, Akhtar K (2006). Salt tolerance of some potential forage grasses from Cholistan desert of Pakistan In: M. A. Khan and D.J. Weber (eds.). Ecophysiol. high salinity tolerance plants. Springer, Netherlands, pp. 31-54.
- Ashraf M (1999). Breeding for salinity tolerance proteins in plants. Crit. Rev. Plant Sci., 13: 17-42.
- Badawi GH, Yamauchi Y, Shimada E, Sasaki R, Kawano N, Tanaka K (2004). Enhanced tolerance to salt stress and water deficit by over expressing superoxide dismutase in tobacco (*Nicotianatabacum*) chloroplasts. J. Plant Sci., 166: 919-928.
- Baker J, Steele C, Dure L (1988). Sequence and characterization of 6 LEA proteins and their genes from cotton. Plant Mol. Biol., 11: 277-291
- Blaylock AD (1994). Soil salinity, salt tolerance, andgrowth potential of horticultural and landscape plants. Cooperative Extension Service. University of Wyoming. Department of Plant, Soil, and Insect Sciences, Coll. Agric., Laramie, Wyoming.
- Boesch DF, Josselyn MN, Mehta AJ, Morris JT, Nuttle WK, Simenstad CA, Swift DJP (1994). Scientific assessment of coastal wetland loss, restoration and management in Louisiana. J. Coastal Res., 20: 11-103
- Bohnert HJ, Shen B (1998). Transformation and compatible solutes. J. Hortic. Sci. Biotechnol., 191: 41-46.
- Borsani O, Diaz P, Botella J (2003). Developing salt tolerant plants in a new century: a molecular biology approach. Plant Cell Tiss. Organ Cult., 73: 101-115.
- Borsani O, Valpuesta V, Botella MA (2001). Evidence for a role of salicylic acid in the oxidative damage generated by NaCl and osmotic stress in Arabidopsis seedlings. Plant Physiol., 126: 1024-1030.
- BraunY, Hassidim M, Lerner HR, Reinhold L (1986). Studies on H-Translocating ATPases in plants of varying resistance to salinity: I. Salinity during growth modulates the proton pump in the alophyte *Atriplex nummularia*. Plant Physiol., 81: 1050-1056.
- Burssens S, Himanen K, Van de Cotte B, Beeckman T, Van Montagu M, Inze D, Verbruggen N (2000). Expression of cell cycle regulatory genes and morphological alterations in response to salt stress in *Arabidopsis thaliana*. Planta, 211: 632-640.
- Casas AM, Bressan RA, Hasegawa PM (1991). Cell growth and water relation of the halophyte *Atriplexnummulria* L., in response to NaCl. Plant Cell Rep., 10: 81-84.

- Chaparzadeh N, Amico ML, Nejad RK, Izzo R, Izzo FN (2004). Antioxidative responses of *Calendula officinalis*under salinity conditions. Plant Physiol. Biochem., 42: 695-701.
- Chapman M (1968). Vegetation under saline conditions. In: H. Buyko (ed.). Saline irrigation for agriculture and forestry. Dr. W. Junk publishers, The Hague, 210-216.
- Chrispeels MJ, Holigue L, Latorrer R, Lunas S, Orellana A, Pena-Cortes H, Raikhel NV, Ronald PC, Trewavas A (1999). Signal transduction networks and the biology of plant cells. Biol. Res., 32: 35-60.
- Cushman JC (2001). Osmoregulation in plants: Implications for agiculture. Am. Zool., 414: 758-769.
- Drennan P, Pammenter NW (1982). Physiology of salt excretion in mangroves, Avicennia marina (Forsk.) Vierh. New Phytol., 91: 597-606.
- Epstein E (1980). Responses of plants to saline environments. In: Genetic engineering of osmoregulation. Eds. D.W. Rains, R.C. Valentine and A. Hollaender. New York: Plenum Press, 7-21.
- FAO (2000). Extent and Causes of Salt-affected Soils in Participating Countries. http://www.fao.org/ag/agl/agll/spush/topic2.htm.
- Flowers TJ, Colmer TD (2008). Salinity tolerance in halophytes. New Phytol., 179: 945-963.
- Flowers TJ, Hajibagheri MA, Clipson NJW (1986). Halophytes. Q. Rev. Biol., 6: 313-337.
- Flowers TJ, Yeo A (1995). Breeding for salinity resistance in crops. Where next? Austr. J. Plant Physiol., 22: 875-884.
- Flowers TJ, Yeo AR (1986). Ion relations of plants under drought and salinity. Austr. J. Plant Physiol., 13: 75-91.
- Gao S, Ouyang C, Wang S, Xu Y, Tang L, Chen F (2008). Effects of salt stress on growth, antioxidant enzyme and phenylalanine ammonia-lyaseactivitie in *Jatrophacurcas*L. seedling. Plant Soil Environ., 54: 374-381.
- Glenn EP, Brown JJ (1999). Salt tolerance and crop potential of halophytes. Crit. Rev. Plant Sci., 18: 227-255.
- Glenn EP, Poster R, Brown JJ, Thompson TL, O'Leary JW (1996). Na and K accumulation and salt tolerance of Atriplexcanescens (Chenopodiaceae) genotypes. Am. J. Bot., 83: 997-1005.
- Hare PD, Cress WA, Van-staden J (1998). Dissecting the roles of Osmolyte accumulation during stress. Plant Cell Environ., 21: 535-554
- Hasegawa PM, Bressan RA, Zhu J-K, Bohnert HJ (2000). Plant cellular and molecular responses to high salinity. Ann. Rev. Plant Physiol. Plant Mol. Biol., 51: 463-499.
- Hassidim M, Braun Y, Lene H and Reinhold L (1990). Na<sup>+</sup>/H<sup>+</sup>antiport in root membrane vesicles isolated from the halophyte *Atriplex*and the glycophyte Cotton. Plant Phsiol., 94: 1795-1801.
- Iraki NM, Bressan RA, Hasegawa PM, Carpita NC (1989). Alteration of physical and chemical structure of the primary cell wall of growth-limited plant cells adapted to osmotic stress. Plant Physiol., 91: 39-47.
- Kawasaki S, Borchert C, Deyholos M, Wang H, Brazille S, Kawai K, Galbraithand D, Bohnert HJ (2001). Gene expression profiles during the initial phase of salt stress in rice. Plant Cell, 13: 889-905.
- Knight H, Knight MR (2001). Abiotic stress signalling pathways: specificity and cross-talk. Trends Plant Sci., 6: 262-267.
- Lipscshitz N, Shomer-Ilan A, Eshel A, Waisel Y (1974). Salt glands on leaves of Rhodes grass (*Chlorisgayana*Kth). Ann. Bot., 38: 459-462.
- Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, Yamaguchi-Shinozaki K, Shinozaki K (1998). Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low temperature-responsive gene expression, respectively, in *Arabidopsis*. Plant Cell, 10: 1391-1406.
- Maathius FJM, Flowers TJ, Yeo AR (1992). Sodium chloride compartmentation in leaf vacuoles of the halophytes *Suaedamaritima* (L.) Dum. and its relation to tonoplast permeability. J. Exp. Bot., 43: 1219-1223.
- Marschner H (1995). Mineral nutrition of plants. 2 Ed., Academic press. Boston.
- Maurel P (1997). Aquaporins and water permeability of plant membranes. Ann. Rev. Plant Physiol. Plant Mol. Biol., 48: 399-429.
- Mittler R (2002). Oxidative stress, antioxidants and stress tolerance.

- Trends Plant Sci., 7: 405-410.
- Munns R, Greenway H, Kirst GO (1983). Halotolerant Eukaryotes. In: O. L. Large, P. S. Nobel., C. B. Osmond and H. Zeiger (eds.). Encyclopedia of Plant Physiology. Springer-Verlag, Berlin, Heidelberg, New York. 12C.
- Munns R, Tester M (2008). Mechanisms of salinity tolerance. Ann. Rev. Plant Biol., 59: 651-681.
- Naidu BP (2003). Production of betaine from Australian Melaleuca spp for use in agriculture to reduce plant stress. Austr. J. Exp. Agric., 43: 1163-1170.
- Niu X, Bressan RA, Hasegawa PM, Pardo JM (1995). Ion homeostasis in NaCl stress environments. Plant Physiol., 109: 735-742.
- Niu X, Narasimhan ML, Salzman RA, Bressan RA, Hasegaw PM (1993). NaCl vegetation of plasma membrane (H<sup>+</sup>)-Atpase gene expression in a glcophyte and engineering of salt and drought tolerance with yeast regulatory genes. J. Hortic. Sci. Biotechnol., 78: 261-269.
- Parvaiz A, Satyawati S (2008). Salt stress and Phytobiochemical responses of plants. Plant Soil Environ., 54: 89-99.
- Passardi F, Cosio C, Penel C, Dunand C (2005). Peroxidases have more functions than a Swiss army knife. Plant Cell Rep., 24: 255-265.
- Pastori GM, Foyer CH (2002). Common components, networks and pathways of cross tolerance to stress. The central role of 'redox' and abscisic-acid-mediated controls. Plant Physiol., 129: 460-468.
- Pollack G, Waisel Y (1972). Salt secretion in *A. Litoralis* (Gramineae). Physiol. Plant., 47: 177-184.
- Popp M, Polania J, Weiper M (1993). Physiological adaptations to different salinity levels in mangrove. In: Lieth, H. and A. Masoom (eds.). Towards the Rational Use of HighSalinity Tolerant Plants. Kluwer, Dordrecht, 1: 217-224.
- Rahnama H, Ebrahimzadeh H (2005). The effect of NaCl on antioxidant enzyme activities in potato seedlings. J. Plant Biol., 49: 93-97.
- Reamon-Buttner SM, Jung C (2000). AFLP-derived STS markers for the identification of sex in *Aspargusofficinalis* L. Theor. Appl. Genetics, 100: 432-438.
- Rhoades JD, Loveday J (1990). Salinity in irrigated agriculture. In: B. A. Steward and D. R. Neilsen. (eds.). Irrigation of agricultural crops. 108 Agron. Monogr. 30. ASA, CSSA, and SSSA, Madison, WI. 1089-1142.
- Rhodes D, Hanson AD (1993). Quarternary ammonium and tertiary sulphonium compounds of higher plants. Ann. Rev. Plant Physiol. Plant Mol. Biol., 44: 357-384.
- Richards LA (1954). Diagnosis and improvement of Saline and Alkali Soils. – Agric. Handbook 60. U. S. Dept. Agric. Washington, D.C., 160.
- Robinson MF, Very AA, Sanders D, Mansfield TA (1997). How can stomata contribute to salt tolerance? Ann. Bot., 80: 387-393.
- Rogers CE, McCarty JP (2000). Climate change and ecosystems of the Mid-Atlantic Region. Clim. Res., 14: 235-244.
- Rohlf FJ (2000). Numerical taxonomy and multivariate analysis system. Version 2.1., Department of Ecology and Evolution, New York state University.
- Sabovljevic M, Sabovljevic A (2007). Contribution to the coastal bryophytes of the Northern Mediterranean: Are there halophytes among bryophytes? Phytol. Balcanica, 13: 131-135.
- Salekdeh GH, Siopongco J, Wade LJ, Ghareyazie B, Bennett J (2002). Aproteomic approach to analyzing drought and salt responsiveness in rice. Field Crops Res., 76: 199-219.
- Serrano R, Marquez JA, Rios G (1997). Crucial factors in salt stress tolerance. In: Yeast Stress Responses. Hohmann, S. and W. H Mager (eds.). R. G. Lande Company, Austin, TX., pp. 147-169.
- Shalata A, Tal M (2002). The effect of salt stress on lipid peroxidation and antioxidants in the leaf of the cultivated tomato and its wild salttolerant relative *Lycopersicon pennelli*. Physiol. Plant., 104: 169-174.
- Siew P, Klein CR (1969). The effect of NaCl on some metabolic and fine structural changes during the greening of etiolated leaves. J. cell Biol., 37: 590-596.
- Soderman E, Mattsson J, Engstrom P (1996). The Arabidopsis homeobox gene ATHB-7 is induced by water deficit and by abscisic acid. Plant J., 10: 375-381.
- Steiner M (1934). To the ecology of the salt march of the Nordostlichen united countries of Nordamerika. Jahrb. Know. Offered, 81: 94.

- Stenlid G (1956). Salt losses and redistribution of salts in higher plants. Encycl. Plant Physiol., 4: 615-637.
- Tomlinson PB (1986). The Botany of Mangroves. Cambridge University Press. Cambridge, London, 21: 413.
- Ungar IA (1978). Halophyte seed germination. Bot. Rev., 44: 233-364.
- Ungar IA (1991). Ecophysiology of vascular halophytes. Boca Raton: CRC press.
- Ungar IA (1996). Effect of salinity on seed germination, growth and ion accumulation of *Atriplexpatula* (Chenopodiaceae). Am. J. Bot., 83: 604-607.
- Ungar IA (1982). Germination ecology of halophytes. In: D.N. Sen and K. S. Rajpurohit (eds.). Tasks for Vegetation science. Dr. W. Junk Publishers, 2, The Hague.
- Waisel Y, Eshel A, Agami M (1986). Salt balance of leaves of the mangrove Avicennia marina. Physiol. Plant., 67: 67-72.
- Waisel Y (1972). Biology of halophytes. Academic press, New York and London.
- Weber DJ (2008). Adaptive mechanisms of halophytes in desert regions. In: Salinity and water stress. Springer Netherlands, Netehrlands, 44: 179-185.
- Winicov I, Bastola DR (1997). Salt tolerance in crop plants: New approaches through tissue culture and gene regulation. Acta Physiol. Plant., 19: 435-449.
- Wu Yu-Ye, Chen QJ, Chen M, Chen J, Wang XC (2005). Salt-tolerant transgenic perennial ryegrass (*Loliumperenne* L.) obtained by *Agrobacterium tumefaciens*-mediated transformation of the vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter gene. Plant Sci., 169: 65-73.

- Xiong L, Zhu JK (2002). Molecular and genetic aspects of plant responses to osmotic stress. Plant Cell Environ., 25: 131-139.
- Xu DP, Duan XL, Wang BY, Hong BM, Ho THD, Wu R (1996). Expression of a late embryogenesis abundant protein gene, HVA1, from barley confers tolerance to water deficit and salt stress in transgenic rice. Plant Physiol., 110: 249-257.
- Yancey PH (1994). Compatible and counteracting solutes. In: K. Strange and B. Raton (eds.). Cellular and molecular physiology of cell volume regulation. CRC Press, Boka Raton, pp. 82-109.
- Yeo AR (1999). Predicting the interaction between the effects of salinity and climate change on crop plants. Sci. Hortic., 78: 159-174.
- Yeo A (1983). Salinity tolerance: Physiologies and prices. Phsiologia Plantarum, 58: 214-222.
- Youssef AM (2009). Salt Tolerance Mechanisms in Some Halophytes from Saudi Arabia and Egypt. Res. J. Agric. Biol. Sci., 5: 191-206.
- Zhu JK (2000). Genetic analysis of plant salt tolerance using Arabidopsis. Plant Physiol., 124: 941-948.
- Zhu JK (2001). Plant salt tolerance. Trends Plant Sci., 6: 66-71.