2. **REVIEW OF LITERATURE**

Although voluminous literature has been published during last 25 years on eco-physiological behaviour of halophytes with reference to edaphic and climatic conditions prevailing in saline habitats, limited information is available on accumulation of free amino acids, proteins, sugars and minerals in the same species at various growth stages. Similarly, physiologists have worked out various parameters to measure the degree of salt tolerance in halophytes (Hayward and Bernstein, 1958; Jennings, 1968; Waisel, 1972; Rains, 1972; Reimold and Queen, 1974; Joshi, 1975; Poljakoff - Mayber and Gale, 1975; Greenway and Munns, 1980; Neales and Sharkey, 1981; Genn and O'Leary, 1984). Poljakoff - Mayber (1975) stressed the need for studying the mechanism of salt tolerance at various growth stages of the same species. Furthermore, many investigations carried out in field conditions remained unconfirmed due to absence of experimental evidences. This fact is more applicable for halophytic plants growing on coastline of India. Attempts have been made in this chapter to review important eco-physiological aspects of plants growing in natural saline habitats as well as of those grown in laboratory conditions.

2.1 **GERMINATION**

The survival of halophytic plant species in nature depends upon its ability to reproduce under adverse salt stressed condition. Soil salinity also affects distribution and zonation of halophytes (Waisel, 1972; Reimold and Queen, 1974). Moreover, germination of halophyte seeds takes place when salinity of the
surface layers of the saline habitats is decreased by precipitation (Barbour, 1970; Macke and Ungar, 1971; Chapman, 1974; Ungar, 1978; Waisel, 1972). This is also strengthened by laboratory experiments, which showed that although seed germinate well under low osmotic potential, greater germination is recorded in distilled water or tap water (Seneca, 1969; Onnis and Bellettato, 1972; Waisel, 1972; Ungar, 1977; 1978; Dietert and Shorntz, 1978; Joshi and Iyengar, 1982).

The available information indicates that seeds of different halophytes are able to germinate in a wide range of salt concentrations. Similarly, the upper limit of salt tolerance of the seeds of the same species also varies considerably. For instance, Feekes (1936) observed greater germination of seeds of Salicornia herbacea in non-saline medium, whereas Walter (1968) recorded maximum germination of the same species in 50 per cent seawater. According to Ungar (1962), seeds of Suaeda depressa, Tamarix pentandra and Salicornia could germinate upto 4 per cent NaCl. Halophytes viz., Aster tripolium and Triglochin maritima showed low germination in seawater; whereas Plantago maritima germinated upto 75 per cent seawater and a few halophytes like Atriplex hastata, Beta maritima and Plantago coronopus germinated upto 50 per cent seawater. Malcolm (1964) reported that the seeds of Arthrocnemum halocnemoides germinated in 2 per cent NaCl solution. However, seeds of Aster tripolium did not germinate in salt concentration above that of seawater. Most of salt tolerant species studied so far, have shown their ability to tolerate salinity levels during seed germination beyond those tolerated by adult plants (Ungar, 1965; Pollak, 1967; Ovadia, 1969; Keren, 1970).
Salinity reduces and delays the process of seed germination in many salt tolerant plants (Waisel, 1972; Zid and Bourkhris, 1977; Breen et al., 1977; Ungar, 1982; Okusayan and Ungar, 1983). Recent studies on seed germination have revealed that this process was inhibited due to osmotic or toxic effects of salts (Ayers, 1952; Chatterton and McKell, 1969; Younis and Hatata, 1971; Ungar, 1978; Joshi, 1982; Joshi and Iyenger, 1985). 

So as to tide over the unfavourable edaphic conditions in nature the seeds of halophytes are endowed with a unique physiological character of retaining viability after a long exposure to high concentrations of salts. This is supported by high degree of recovery of seed germination in distilled or tap water of many halophytes like Atriplex halimus, Puccinellia nutalliana, Sporobolus virginicus, Crithmum maritimum (Zid and Bourkhris, 1977; Macke and Ungar, 1971; Breen et al., 1977 cited by Ungar, 1982). Similar results have also been recorded for halophytes growing in coastal areas (Waisel, 1972; Ungar, 1978; Joshi and Iyengar, 1982; 1985).

Studies on the effects of hormones in breaking the dormancy of seeds of plants growing under salt stressed condition suggested that GAs was more effective in increasing rate of germination than kinetin (Ungar and Boucaud, 1975; Ungar and Binet, 1975; Boucaud and Ungar, 1976; Ungar, 1978; 1982; Iyenger and Pandya, 1983).

Thus, the available information shows that the capacity of halophytes to withstand salt concentrations at germination stage varies from species to species and different kinds of factors such as, osmotic and toxic effects of salinity, temperature and
light impair the process of germination under saline environment. Likewise, information on effects of various salts on seed germination of the same species is scanty. This lacuna is still wider for halophytic species growing in India.

2.2 SALINITY AND EARLY GROWTH

Halophytes are endowed with a special mechanism, which helps them propagate, establish, grow and reproduce successfully in a high salt concentrations in growth media. It is now well established that growth of glycophytes is retarded by NaCl concentrations below 50 mM NaCl, while that of halophytes remain unaffected even by higher concentrations of salts. The available information further indicates that although the presence of salts in growth media increase the growth of salt tolerant species, their optimal concentrations vary from species to species (Montfort and Brandrup, 1928; Black, 1956; Hayward and Berstein, 1958; Waisel, 1972; Flowers et al., 1977; Greenway and Munns, 1980). Better growth of halophytes occurring in natural saline conditions as well as of those grown under salt stressed conditions than those of raised in non-saline condition has been observed by many investigators.

Plant physiologists have made efforts to correlate laboratory studies with growth of halophytes growing in natural conditions. Seedlings of halophytes were grown either in soils collected from the nature or in sand by adding various concentrations of salts along with nutrient solutions.

Batalin (1875, cited by Strogonov, 1964) grew Salicornia herbacea in sand by using seeds as a propagating medium. Till the emergence of cotyledons river water was used and later on
NaCl, MgSO₄ and 1:1 mixture of NaCl and MgSO₄ were added in growth media. River water treated plants were considered as control. This experiment was successfully carried out till the production of seeds by Batalian. Later on Stocker (1933) and Van Eijk (1939) found that the same species required 2 per cent NaCl for its growth. Montfort and Brandrup (1927) reported that *Salicornia europaea* could survive in 1 M NaCl. Pannier (1959) grew *Rhizophora mangle* in rain water and in salinities up to full strength of seawater. He observed that root growth was optimum at 50 per cent and shoot growth at 25 per cent seawater.

Terras (1906) raised five Scottish salt marsh species viz., *Spergularia marina*, *Plantago maritima*, *Glaux maritima*, *Suaeda maritima* and *Salicornia herbacea* in sand. Knop's solution containing 0.2 per cent salt and different dilutions of seawater were used for watering this species from the bottom for six months. Maximum growth of *Plantago maritima* and *Spergularia marina* was observed in non-saline condition while that of *Salicornia herbacea*, *Suaeda maritima* and *Glaux maritima* showed optimum growth in 1/3 seawater concentrations.

Halket (1915) had grown halophytes like *Glyceria maritima*, *Suaeda maritima* and *Salicornia* in their natural sod by using various concentrations of salts. Observations on 15-week-old plants showed that growth of the first two species was decreased in response to increasing salt concentrations in growth media. But the maximum growth of *Salicornia* was observed up to 1 per cent salt. Furthermore, these three species showed capacity to grow up to 15 per cent salt concentrations in growth media but the maintenance of salinity was not uniform in this experiment (Barbour, 1970).
Keller's (1925) method of growing halophytes was similar to that of Terras (1906) except for the use of NaCl in place of seawater. He found that Salicornia showed poor growth below 0.4 and above 5 per cent NaCl concentrations, while better growth of Frankenia pulverulenta was observed up to 1 per cent NaCl.

Nine species of halophytes were grown for about 50-days by Taylor (1939), who had used sand and various concentrations of NaCl as growth media. The control plants, that were left in nature had shown vigorous growth at all NaCl concentrations than those of plants grown in laboratory condition. Five species showed optimum growth in tap water; best growth of three species was at moderate salinity concentrations; and Iva ovaria did not show any growth retardation up to 1.5 per cent NaCl. Oositng and Billings (1942) showed that the growth of Andropogon littoralis and Uniola paniculata was adversely affected by seawater salinity but such effect of seawater was not observed in case of Spartina patens. Barbour and Davis (1970) grew Californian salt marsh species in sand culture by using seawater and recorded maximum shoot length at 0.1 per cent salt.

Effect of seawater salinity on growth of Atriplex spongiosa and Suaeda monoica was studied by Storey and Wyn Jones (1979). Seeds of these halophytic species were germinated in moist vermiculite and seedlings were transferred to full strength Hoagland solution. Five-week-old seedlings were subjected to NaCl concentrations ranging from 0 to 750 mM NaCl by a daily increment of 50 mM. Treatments were continued up to 6 weeks. Both species showed maximum growth in low salinity. There was 300 per cent increase in fresh weight of S. monoica at 500 mol.m$^{-3}$ NaCl but growth was retarded in higher salinities.
However, root-length was not adversely affected by salinity in both the species. Similarly, increase in growth at moderate salinity in *A. spongiosa* and in *Distichlis spicata* were observed by Storey *et al.* (1983) and Warren and Gould (1982).

Yeo and Flowers (1980) germinated the seeds of *Suaeda maritima* in sand moistened with distilled water and 14-day-old seedlings were transplanted into the culture medium. These seedlings were exposed to NaCl salinity at the age of 21 days with daily increment of 0.33 mpa. They recorded better growth in increasing salinity with a maximum growth at 170 mol.m$^{-3}$ NaCl. The faster growth was observed in plants grown in saline conditions than raised in control condition.

Succulent halophytes namely, *Suaeda nudiflora* and *Salicornia brachiata* were grown in simulated condition using natural seawater and garden soil (Joshi, 1982). Seawater of known concentrations was added in soil to obtain the desired levels of electrical conductivity. Seeds of *S. nudiflora* and *S. brachiata* were germinated in pots having 10 to 20 dS.m$^{-1}$ salinity, which at an interval of 5 weeks were raised to 20, 30, 40 and 30, 40, 50 dS.m$^{-1}$ respectively. Few plants of *S. nudiflora* flowered during the experiment which lasted for 20 weeks, while all the plants of *S. brachiata* flowered at 50 dS.m$^{-1}$ salinity.

Konigshofer (1983) grew some halophytes as well as non-halophytic species of *Plantago* in quartz sand culture experiment. He found that growth of *P. maritima* was retarded but its succulence increased under NaCl treatments while non-halophytes exhibited chlorotic effect in saline concentrations.

Growth performance of some halophytes of dicot families was
studied by Glenn and O’Leary (1984). They reported that growth was stimulated at 180 mol.m⁻³ NaCl, but a few species showed the best growth in tap water. Moshe et al. (1984) also reported NaCl induced better growth in *Najas marina*.

The available literature, thus, clearly shows that researchers used different salt solutions to grow halophytes. However, the use of natural seawater rather than NaCl solution alone, appears to be ideal for growing halophytes in laboratory conditions. This is more important when laboratory results are to be compared with that of the field conditions, where fluctuations in salinity are mainly due to seawater.

### 2.3 PROTEINS

Because of the adequate proteins content, halophytes have been considered as good substitute for fodder. However, metabolism of proteins in salt tolerant plants is often adversely affected by salinity and as a result nitrogenous compounds accumulate in vegetative organs (Strogonov et al., 1970; Jefferies et al., 1979; Popp et al., 1984).

According to Malcolm (1982), salt tolerant species are useful in increasing forage and fuel production of saline wastelands. Chapman (1970) and Mudie (1974) had also stressed the need for assessing economic potential of halophytes. Altschul (1962) and Stahmann (1963) had discussed the possibility of supplementing the proteins supply for the ever increasing population of human beings and heads of animals by using the under exploited plant species.

Many researchers (Burkholder, 1956; Taschdjian, 1954; Yarlett, 1965; Hubbard and Ranwell, 1966; Ranwell, 1967; Udell
et al., 1969; Phleger, 1971) studied the proteins content in halophytic species of Spartina viz., S. alterniflora, S. cynosuroides, S. patens, S. townsendii and S. foliosa growing in coastal region of U.S.A. and British Isles. They found that young leaves contained more proteins than mature leaves. Many useful species growing in tropical and subtropical regions have been evaluated for their proteins content (Acharya and Patnaik, 1977; Franke and Lawrenz, 1980).

The Chenopods species yield good amounts of proteins (Lexander et al., 1970). For instance, five species of Atriplex and four species of Maireana accumulated 7 to 25 per cent crude proteins (Leigh, 1984; O'Leary, 1984). Similar concentrations of proteins were observed in Suaeda maritima collected from different salt marshes of Conway (Stewart et al., 1972).

Untawale et al. (1978) recorded 2.1 to 21.7 per cent proteins in leaves of seven mangrove species and they observed minimum proteins content in Rhizophora mucronata. From our laboratory Krishnakumar (1986) reported 3.3 to 22.4 per cent proteins in Salvadora persica growing on Gujarat coast and suggested that it was good forage for livestock. Similarly, Anjaiah (1987) examined proteins content in Atriplex griffithii and recorded that leaves of this species contained 17.5 to 24 per cent proteins.


Salt tolerant species accumulate high concentrations of
inorganic ions, which disturb the hydration shell surrounding the protein molecules (Klotz, 1958). Na⁺ and K⁺ are principal ions that alter the hydration of proteins (Kavanau, 1966). Moreover, the precipitation of proteins also takes place under salt stressed conditions (Waisel, 1972). According to Waisel and Vaadia (1967), low water potential enhance proteolysis which results into decreased protein content. In some species protein metabolism per se is adversely affected.

From what has been said above, it becomes clear that salt tolerant plants are good source of proteins and further research in this direction would be helpful in increasing productivity of saline wastelands.

2.4 FREE AMINO ACIDS

Many researchers have studied effects of salt stressed conditions on metabolism of free amino acids in plants. Bell (1980) reported that salinity induced accumulation of a large number of amino acids as their incorporation into protein metabolism was prohibited. According to Strogonov (1964), salinity brings about changes in metabolic activities of plants, which induce production of toxic products such as NH₃, urea, thiourea or amines in halophytes. Accumulation of compatible solutes like proline, pipelolique acid, amides and glycine betaine and their role in maintenance of osmotic potential in halophytes have been thoroughly discussed by Strogonov et al. (1970), Flowers et al. (1977), Wyn Jones et al. (1977) and Popp et al. (1984). Increased concentrations of proline, glycine betaine and sorbitols also prevent inactivation of enzymes and other essential structures (Borowitzka, 1981; Wyn Jones and
Storey, 1981; Gorham et al., 1981; Goas et al., 1982). Recently, Smirnoff and Stewart (1984) designated these compounds as "stress metabolites".

Ter-Karapetyan and Akopyan (1957) reported that Goebelia alopecuroides, a facultative sulphate halophyte, accumulated high concentrations of serine, valine, tyrosine and leucine and less amounts of arginine, aspartic acid, glutamic acid, proline and tryptophan. On the other hand, heavy accumulation of aspartic acid and glutamic acid was observed in mangroves growing at Bombay (Bharucha and Rangnekar, 1957). Massive accumulation of alanine, aspartic acid, glutamic acid, proline in succulent halophytes was reported by Joshi and Iyengar (1984). High accumulation of alanine, aspartic acid, glutamic acid, proline and of some other amino acids has been observed in many halophytes (Popp and Albert, 1980; 1981; Popp et al., 1984).

Attempts have also been made to examine relationship between concentrations of proline and salt stressed conditions in order to assess its osmoregulatory function in salt tolerant species (Stewart and Lee, 1974; Larher, 1971; 1977; Ahmad et al., 1979; 1981; Gorham et al., 1980; Popp and Albert, 1981; Aspinall and Paleg, 1981). Such correlation in Aster tripolium was observed by Goas (1967). Similar observations were made by Stewart and Lee (1974) for Suaeda macrocarpa and Limonium vulgare. These and some other investigations showed increased accumulation of proline in halophytes with response to increasing levels of salinity in growth medium (Goas, 1971; Goas et al., 1970; Palfi and Juhasz, 1970; Treichel, 1975). According to Cavalieri and Huang (1979), proline was species specific and
it was less important to succulent halophytes growing in saline environment. Furthermore, they had observed greater accumulation of proline in C_4 grasses than C_3 plants under saline conditions. Gorham et al. (1980) reported high concentrations of proline in Puccinellia maritima, Spergularia media, Triglochin maritima, Zostera marina and in other species. It was also suggested that proline acted as a protective substance (Strogonov et al., 1970) while Bar-Nun and Poljakoff – Mayber (1977) found its stimulatory effects on seed germination.

The report from our laboratory (Joshi and Iyengar, 1984) showed heavy accumulation of some amino acids such as alanine, aspartic acid, phenylalanine and proline in Suaeda nudiflora, a succulent halophyte. Similar observations were made for Juncus maritimus and Salvadora persica, with exception for proline in the last halophytic shrub species (Khairatkar, 1986; Krishnakumar, 1986).

Although extensive studies on accumulation of proline has helped understanding its physiological role in halophytes, further research is needed to understand metabolic as well as osmotic role of other amino acids, which occur in high concentrations and whose concentrations in vegetative organs of halophytes positively increase in response to salinity in culture media.

2.5 SUGARS

The accumulation of sugars in plants subjected to salinity has remained topic of controversy because various workers have made conflicting reports on sugars content in halophytes. Carbohydrates are important organic metabolite since they are
primary source of energy for most of the living organisms and act as compatible solutes in salt tolerant species.

One of the earliest reports (Steiner, 1935) suggested that reducing sugars, sucrose, Na\textsuperscript{+} and Cl\textsuperscript{-} contributed to the osmotic adjustments in glycophytes as well as in halophytes. Later on, the study on accumulation of sugars in different groups of plants by Iljin (1957) indicated their variations not only within each group of plants but also in a single species. Similarly, Langlois (1971) observed that plants of *Salicornia* growing in area inundated twice a day accumulated less sugars as compared to those growing in uninundated area.

Maximum accumulation of sugars in plants growing under salt stressed condition was observed by Raheja (1966). Caldwell (1974) reported increased amounts of total sugars as well as change in the types of sugars during winter season in halophytes growing in northern coastal areas of Europe. Observations on seasonal changes in total and reducing sugars in halophytes viz., *Juncus maritimus* and *Salvadora persica* growing on the West coast of India were made by Khairatkar (1986) and Krishnakumar (1986). They reported greater amounts of sugars in these halophytes during summer than winter and monsoon. Furthermore, roots of *J. maritimus* contained maximum sugars.

Jefferies et al. (1979) studied effects of salts on accumulation of reducing sugars in, *Triglochin maritima*, *Limonium vulgare* and *Halimione portulacoides* and they found increase in reducing sugars in these halophytes in response to salinity stress. On the other hand, increasing salinity had little effects on the sugars content in *Plantago maritima* (Jefferies et al., 1979; Ahmad et al., 1979). Albert and Popp
(1978) reported that there was a quantitative difference in sugar accumulation in dicotyledonous (2 to 16 per cent) and in monocotyledonous (25 to 36 per cent) halophytes. Rozema (1976) observed varying response of species of _Juncus_ to salt stressed conditions. The soluble sugars in _J. maritimus_ and _J. bufonius_ increased at high NaCl concentrations of 150 mol.m⁻³; the reverse trend was noted for _J. alpinoparticulatus_; and concentrations of sugars was not affected in _J. gerardii_.

According to Albert and Popp (1978), accumulation of sugars played a major role in the mechanism of salt tolerance in halophytes. Similar observations were made by many researchers (Bhosale, 1974; Gorham, 1981; Briens and Larher, 1982; Kotmire, 1983; Jefferies and Rudmik, 1984). Likewise, possible role of reducing sugars in osmotic adjustment in plants growing under salt stressed conditions has been discussed by many physiologists (Flowers et al., 1977; Jefferies, 1981; Gorham et al., 1981; Popp, 1984).

Thus, from the available information it can be inferred that salinity causes varying effects on carbohydrate synthesis in salt tolerant plants. Furthermore, it is necessary to generalise this phenomenon as existing literature presents a good deal of conflicting reports.

2.6 MINERAL IONS

Unlike glycophytes, halophytes grow successfully in an environment of low osmotic potential developed due to dominance of sodium (Na⁺) and chloride (Cl⁻). Halophytic plants also possess special adaptations, which enable them to absorb water from physiologically dry environment. In doing so, plants have
to maintain high internal osmotic pressure as compared to external medium (Waisel, 1972; Reimold and Queen, 1974; Flowers et al., 1977; Sen and Rajpurohit, 1982; Flowers, 1985) and as a result halophytes accumulate excessive quantity of salts in their organs. Nevertheless, various metabolism go on without much hinderance, inspite of conglomeration of toxic ions in the cells of salt tolerant species.

Extensive research work has been carried out in the last 50 years on special mechanisms like accumulation, exclusion, excretion and sequestration of salts in the vacuole, which help salt tolerant plants survive successfully in highly saline conditions (Dodd and Coupland, 1966; Waisel, 1972; Levitt, 1972; Reimold and Queen, 1974; Flowers, 1975; Hellebust, 1976; Flowers et al., 1977; Flowers, 1985).

Na\(^+\) and Cl\(^-\) are principal inorganic ions which accumulate in vegetative organs of plants growing in saline environment. Now it is known that some halophytes requires Na\(^+\) as an essential element (Brownell and Wood, 1957; Brownell, 1965; 1968). Epstein (1972) reported that Na\(^+\) helps plants decrease wilting in hot climate. Similarly, Broyer et al. (1954) had observed high amounts of chlorides in higher plants and suggested its necessity for their growth. Earlier studies of Steiner (1935) and Arnold (1955) showed that Cl\(^-\) together with cations could account for about 35 to 95 per cent of osmotic potential in plants growing in saline environment. At present, it is widely accepted that the heavy accumulation of inorganic ions viz., Na\(^+\) and Cl\(^-\) play a major role in osmoregulation in halophytes (Scholander et al., 1966; Brownell, 1965; 1968; Waisel, 1972; Flowers et al., 1977; Flowers, 1985).
Growth and accumulation of mineral ions in *Disphyma australis*, an Australian halophyte, under salt stressed condition was studied by Neales and Sharkey (1981). They found that concentrations of Na\(^+\) and Cl\(^-\) increased with increase in salinity in growth media. Similar observations were recorded for halophytes and mangroves by other researchers (Downton, 1982; Stewart and Ahmad, 1983; Popp, 1984).

The reports from our laboratory (Joshi, 1979) showed increased levels of salinity accompanied by an increase in Na\(^+\) and Cl\(^-\) accumulation in *Suaeda nudiflora*, a succulent halophyte. Krishnakumar (1986), Bhoite (1987) and Misra (1990) also recorded similar observations for *Salvadora persica*, *Aeluropus lagopoides* and *Sporobolus madraspatanus*.

A key role of Na\(^+\) and Cl\(^-\) in osmotic adjustments in salt tolerant plants has been accepted beyond any doubts in recent years (Black, 1960; Flowers, 1985).

Halophytes and mangroves, which grow in highly saline conditions are able to accumulate adequate amounts of K\(^+\) (Waisel, 1972). The uptake of K\(^+\) from NaCl rich environment and its accumulation in vegetative organs of halophytes and mangroves has been investigated in detail in recent years (Christian and Waltho, 1962; Larsen, 1962; Chirputkar, 1969).

The reports from our laboratory also showed adequate uptake of K\(^+\) from Na\(^+\) rich environment by *Sporobolus madraspatanus* (Misra, 1990), a halophytic grass species. Sagar Kumar (1987) and Anjaiah (1987) also made similar observations on *Avicennia marina* and *Atriplex griffithii*, growing on the West coast of India. Potassium (K\(^+\)) also plays a vital role in the salt tolerance mechanism of plants growing under salinity stress.
(Joshi, 1975). Similar observations were made on monocotyledonous halophytes by Albert and Kinzel (1973), Albert and Popp (1977), Gorham et al. (1980) and Flowers (1985).

The concept of "dual carrier mechanism" initially proposed by Epstein and Hagen (1952) and Epstein et al. (1963) explains the uptake of K\(^+\) from Na\(^+\) rich environment and its role in the physiology of salt tolerant plants. The work of Larsen (1967) further strengthened such role of K\(^+\) in salt tolerance mechanism of halophytes.

The concept operates through two systems though significant functional differences occur between them. System I operates below 1mM NaCl while system II operates over a concentrations of 1mM to 50 mM. The former mechanism shows high specificity and greater affinity for the selection of K\(^+\) than the latter one (Epstein et al., 1963; Rains and Epstein, 1967; Rains, 1972). Na\(^+\) is absorbed through system II.

This concept has been strengthened by observations on number of halophytes, mangroves and glycophytes (Elzam et al., 1964; Elzam and Epstein, 1965; Osmond, 1966; Luttge and Laties, 1966; Torii and Laties, 1966; Rains and Epstein, 1967; EL-Sheikh et al., 1967; Osmond and Laties, 1968; Poole, 1979; Amonkar, 1977; Flowers et al., 1977; Neales and Sharkey, 1981). Rains and Epstein (1967) further suggested that at lower concentration (system I) Cl\(^-\) and SO\(_4^{2-}\) had less influence on K\(^+\) uptake than at higher concentrations (system II).

Divalent cations viz., Ca\(^{2+}\) and Mg\(^{2+}\) occupy next position to Na\(^+\) and Cl\(^-\) as major elements of seawater, barren saline soils, halophytes and mangroves. Furthermore, they have ameliorating effects on growth of plants growing under salt
stressed conditions (Hyder and Greenway, 1965; Epstein, 1972; Poljakoff - Mayber and Gale, 1975). LaHaye and Epstein (1969; 1970) reported that salt induced retarded growth could be accelerated by the addition of CaSO₄ in the growth media. In contrast, Greenway (1968) observed that Ca²⁺ causes inhibitory effects on the growth of some halophytes. For instance, growth of Atriplex nummularia was not much affected at 300 meq.l⁻¹ NaCl, KCl and MgCl₂ but it was remarkably retarded by CaCl₂.

Necessity of adequate amounts of Mg²⁺ for leaf initiation and during leaf expansion was suggested by Ford (1968). It is also an important constituent of chlorophyll, acts as an activator of certain enzymes and plays a role in osmotic adjustment (Sutcliffe, 1962). Studies on accumulation of Mg²⁺ showed that halophytes and mangroves contained less Mg²⁺ (Pradhan, 1957; Warick, 1960; Shetty, 1971; Hegde and Joshi, 1974). Similarly, accumulation of Mg²⁺ was adversely affected under saline conditions (Joshi, 1976). However, Albert and Popp (1977) found greater amounts of Mg²⁺ than K⁺ in halophytes growing under saline conditions. Such findings are supported by series of investigations on salt tolerant species growing on West coast of India (Joshi and Iyengar, 1984; Joshi, 1986; Anjaiah, 1986).

It is apparent from the literature reviewed that the information on mineral ions of salt tolerant species during different seasons and growth stages is insufficient and fragmentary. However, much remains to be done on their collective role in a particular halophyte at different growth stages. Furthermore, comparision between field data and laboratory findings would help to elucidate the osmoregulatory
role of inorganic ions in halophytes.

2.7 TRACE ELEMENTS

Though voluminous information is available on accumulation of major inorganic ions and their role in osmoregulation in plants grown in saline conditions (Waisel, 1972; Reimold and Queen, 1974; Sen and Rajpurohit, 1982), limited attempts have been made to study the trace elemental composition in halophytes and mangroves (Morton, 1965; Walsh, 1974). Baumeister and Ernst (1970), Mutsch (1980), Rozema and Bloom (1977), Rozema et al. (1985) have reported accumulation of trace elements in halophytes growing in estuarine sediments. While working on trace elements in leaves and stems of Salsola tetrandra, S. tetragona, Juncus rigidus and Halocnemon strobilaceum growing in the United states EL-Ghonemy (1982) reported that accumulation of Zn\(^{2+}\) was not affected by climatic changes. Succulent halophytes also accumulate high amounts of heavy metals such as Fe\(^{3+}\), Mn\(^{2+}\), Cu\(^{2+}\) and Zn\(^{2+}\) (Baumeister and Ernst, 1979; Mutsch, 1980; Beeftink et al., 1982; Rozema et al., 1985 a; b; Singer and Havila, 1985). Similar observations on accumulation of Fe\(^{3+}\), Cu\(^{2+}\) and Zn\(^{2+}\) in Salicornia brachiata and Atriplex griffithii succulent halophytes collected from West coast of India were made by Joshi et al. (1987).

While working on mangroves of south India Ramadas et al. (1975) suggested that Mo\(^{2+}\) and Mn\(^{2+}\) had stimulatory effects on primary production of the mangrove ecosystem. Bhosale (1979), who studied distribution of Co\(^{2+}\), Mn\(^{2+}\), Mo\(^{2+}\), Cu\(^{2+}\) and Zn\(^{2+}\) in leaves of nine mangrove species growing at coastal area of Ganptipule in India, suggested that range of variations in the
concentrations of trace elements was more because of specificity of the species for a particular element rather than the response of the plants to edaphic factors. Later on, Untawale et al. (1980) also reported high concentrations of Fe$^{3+}$, Mn$^{2+}$, Pb$^{2+}$ and Cu$^{2+}$ in Indian mangrove species.

Accumulation of trace elements in vegetative organs of the same species also differs considerably. According to Joshi et al. (1987), roots of *Juncus maritimus* contained greater amounts of heavy metals than leaves and stems. It was further strengthened by Rozema et al. (1985 a), Baumeister and Ernst (1978). However, excretion of metals through salt glands in salt tolerant plants has been reported (Liphschitz and Waisel, 1982).

Furthermore, a few efforts have been made to examine effects of various salts on accumulation of trace elements in halophytes. Wallace et al. (1982), who had grown two species of *Atriplex* viz., *A. canescences* and *A. polycarpa* in different concentrations of NaCl and Na$_2$SO$_4$, suggested that these salts did not affect accumulation of Fe$^{3+}$, Cu$^{2+}$ and Zn$^{2+}$ in these species. Similar observations were made by Soufi and Wallace (1982), while working on effects of Na salts on accumulation of trace elements in *Atriplex hymenelytra*; but a decline in concentrations of Fe$^{3+}$, Zn$^{2+}$, Mn$^{2+}$ and Cu$^{2+}$ in leaves of *A. hymenelytra* at high concentration of salts was noticed.

Thus, it is evident that the available information on accumulation of trace elements in halophytic species; their relative concentrations in vegetative organs of the same species; effects of edaphic and environmental conditions on their accumulation and on experimental evidences showing effects of various salts on their accumulation in salt tolerant plants is
scanty. These facts stress the need for research in this area.

2.8 MISCELLANEOUS ASPECTS OF SALT TOLERANCE

Many researchers have studied the effects of salinity on ecological, physiological and biochemical processes in salt tolerant species during the second half of this century. These studies collectively explain how halophytes adapt to adverse conditions of saline environment.

2.8.1 Compartmentalization of ions

As mentioned in earlier sections, halophytes absorb huge amounts of inorganic ions, which are required to maintain internal osmotic pressure. But high accumulation of inorganic ions like Na+ and Cl− will be deleterious to salt sensitive enzymes in halophytic cells. Surprisingly, the enzymatic machinery remains unaffected in the presence of toxic ions and thereby indicates that the latter are not in direct contact with the enzymes.

Adriani (1958), Chapman (1960), Jennings (1968; 1976), Diana et al. (1976) and Osmond et al. (1980) suggested that the amounts of Na+ and Cl− get accumulated in the vacuoles in halophytes to keep them away from the enzymatic machinery. Waisel and Eshel (1971) studied the distribution of Na+, Cl−, K+ and phosphorus in Suaeda monoica. Existence of two compartments for Cl− ion viz., the cytoplasm and vacuoles in plants growing in saline condition was suggested by Hodges and Vaadia (1964). Similar observations on compartmentalization of Cl− in halophytes were made by Arnold (1955).

Arnold (1955) and Jennings (1968) suggested that most of
the accumulated Na\(^+\) in halphytic cells may be pumped into vacuoles through the pump located at the tonoplast. Webber et al. (1977), who carried the electroprobe analysis in succulent halophyte *Salicornia pacifica* found greater accumulation of Na\(^+\), K\(^+\) and Cl\(^-\) in spongy tissue than palisade tissue in young plants.

According to Diana et al. (1976), maximum concentration of Cl\(^-\) was in vacuoles as compared to cytoplasm, chloroplast, cell wall and intercellular spaces in *Suaeda maritima*, but the plants that were depleted with salt showed more Cl\(^-\) in chloroplasts. Others also believe that accumulation of Cl\(^-\) could be in the vacuole, in chloroplast, cell wall, plasmodesmata or cytoplasm (Ziegler and Luttge, 1967; Van Stevenick et al., 1973; Hess et al., 1975; Campbell and Thompson, 1975). Ramati et al. (1976) observed that *Sporobolus arenarius* accumulated huge amounts of various mineral ions in the cell wall as compared to cytoplasm. Preferential accumulation of Na\(^+\) in vacuoles of root cells in *Hordeum* was reported by Jesckhe and Stelter (1976) and Storey and Wyn Jones (1979).

In the light of above facts Flowers et al. (1977) suggested that accumulated evidence supports the existence of a high vacuolar ionic concentration than that of cytoplasm and that cytoplasmic NaCl concentration was 1/2 to 1/3 of the vacuolar concentrations.

Yeo (1981) suggested maximum accumulation of ions in the vacuoles as compared to cytoplasm in *Suaeda maritima* under saline conditions. This was further confirmed by results of steriiological analysis of mesophyll, vascular bundles and central parenchymatous cells of *Suaeda maritima* raised in saline
conditions (Hajibagheri et al., 1984). According to them, 94.3 per cent of Na\(^+\) in the mesophyll cells of salt treated plants was in vacuole; 3 per cent in the cytoplasm and quite less amount in the chloroplast and cell wall. With the help of X-ray microanalysis of cells and cellular compartments in *Atriplex spongiosa* grown in hydroponic cultures of various NaCl concentrations, Storey et al. (1983) also suggested that the ions were compartmentalized in the vacuole.

The above findings obviously suggest that cells of salt tolerant plants possess compartments for necessary ions in vacuoles for osmoregulation and to decrease their concentration at functional sites of enzymes.

### 2.8.2 Photosynthesis

Accumulation of carbohydrates is closely related with photosynthesis and role of such metabolites in lowering osmotic potential of cells in halophytes and mangroves has been discussed by Waisel (1972).

Montfort (1927) observed that salt stressed condition severely affected photosynthesis rate and the starch content in glycophytes, while these parameters in halophytes were slightly affected. Increased rate of photosynthesis activity was reported in terrestrial halophytes like *Frankenia*, *Tamarix* and *Phragmites* growing in saline media by Stocker (1954). Nevertheless, Arnold (1955) and Adriani (1958) noted a decrease in carbohydrate metabolism in succulent halophytes such as, *Salicornia* and *Arthrocnemum* growing under salt stressed conditions. Recently Kuramoto and Brest (1979) observed that the decreasing osmotic potential of the medium caused a decline in photosynthetic
activity in halophytes like Salicornia europaea, Batis maritima, Spartina foliosa and Distichlis spicata; the effect was more pronounced at an osmotic potential of -25.4 atmosphere; and the process was more severely affected in monocot species. Similar observations were made for Ruppia rostellata at 1.8 M NaCl (Waisel, 1972).

On the other hand, the net photosynthesis in many halophytes like Tamarix ramosissima, Atriplex confertifolia, A. halimus, Salicornia rubra, S. herbacea, Aster tripolium, Suaeda maritima and Mesembryanthemum nodiflorum was not much affected over a wide range of NaCl levels in the growth media (Baumeister and Schimidt, 1967; Gale and Poljakoff - Mayber, 1970; Winter, 1974; Kleinkopf and Wallace, 1974; Kleinkopf et al., 1975; Tiku, 1976). Thus, the available literature suggest that salinity may have favourable, adverse or no effects on photosynthesis in salt tolerant species.

In the middle of this centuary many researchers concentrated on CO₂ fixation in plants and the discovery of C₄ pathway by Kortschak et al. (1965) and Hatch and Slack (1966) have opened a new vistas in this direction.

According to Winter (1979), some halophytes from dry inland saline habitats belong to \( \text{C}_4 \) plants, while coastal halophytes follow \( \text{C}_3 \) pathway. Beer and Robert (1982) showed that Zostera marina, Thalassia testudium, Syringodium filiforme and Halodule wrightii growing in the Gulf of Mexico followed \( \text{C}_3 \) mode of \( \text{CO}_2 \) fixation. They suggested that out of eleven sea grass species tested, only one exhibited \( \text{C}_4 \) metabolism, while remaining ten belonged to \( \text{C}_3 \) type. According to Amonkar (1979), \textit{Salvadora} is a \( \text{C}_4 \) plant. The 40 per cent of \textit{Atriplex} species follow \( \text{C}_3 \) pathway and 60 per cent fix \( \text{CO}_2 \) via \( \text{C}_4 \) pathway (Osmond et al., 1980). Baskin and Carol (1981) studied photosynthetic pathway in leaves of fourteen annual species including \textit{Sporobolus vaginiflorus} and found that eight species followed \( \text{C}_3 \) pathway. While working on mangrove, \textit{Aegiceras corniculatum} and halophyte, \textit{Sesuvium portulacastrum} Bhosale and Shinde (1983) observed that both these species did not follow Hatch and Slack mode of \( \text{CO}_2 \) fixation. Similarly, shifting of \( \text{C}_3 \) pathway to \( \text{C}_4 \) in \textit{Aeluropus littoralis} under saline conditions was observed by Shomer - Ilan and Waisel (1975). Bhosale (1981) reported \textit{Bruquiera gymnorrhiza} as \( \text{C}_3-\text{C}_4 \) intermediate species.

Crassulacean Acid Metabolism (CAM) has a special significance in those halophytes, which have succulent habits. The CAM enables plants to consolidate their water and carbon balance in arid environment and thereby help them conquer ecological niches, where there is insufficient water (Kluge, 1982).

Salinity induces a CAM mode of carbon fixation in some halophytes. For instance, \textit{Aptenia cordifolia}, a salt tolerant species, fixed 80 per cent of carbon in malate during dark
period in saline conditions (Treichel, 1975). Similarly, it was observed that prolonged exposure to high salt concentration resulted in the shifting of the C₃ pathway in *Mesembryanthemum crystallinum*, *M. nodiflorum* and *Carobrotus edulis* to CAM (Winter and Von Willert, 1972; Winter et al., 1974; Treichel and Bauer, 1974; Van Willert and Schwobel, 1978). However, recent ¹⁴CO₂ studies by Neales et al. (1983) suggested that salinity could not apparently induce CAM in *Disphyma*.

Hence, the available information is not enough for arriving at any definite conclusion regarding effects of salinity on C₃ and C₄ pathway in salt tolerant plants. Furthermore, it is clear that salt tolerant plants are not confined to one specific mode of CO₂ fixation. They follow C₃, C₄, combined C₃ and C₄ or CAM pathway for CO₂ fixation.

**2.8.3 Respiration**

Persuasive of literature shows that limited information is available on effects of salinity on rate of respiration in salt tolerant plants. The experimental evidences of Kuramato and Brest (1979) suggested that the rate of respiration in *Salicornia europaea*, *Batis maritima* and grass species declined with decreasing osmotic potential in the culture media. Similar observations were made for *Suaeda maritima* by Flowers, (1972).

On the other hand, an increase in respiration in 5-day and 11-day-old seedlings of *Suaeda nudiflora* and *Salicornia brachiata* was observed at increased salt concentrations at temperatures varying between 10 to 30 °C by Joshi and Iyengar (1980). An increase in the rate of respiration in response to increase in salinity had been reported for *Plantago coronopus*. 
and *Phragmites communis* (Takaoki, 1957) and other halophytes (Van Eijk, 1939). Poljakoff-Mayber and Meiri (1969) observed an increase in RQ from 1 to 2 in roots of *Tamarix tetragyna* when plants were transferred from non-saline condition to -15 bars condition. Similar observation was made for salt tolerant species like *Tamarix ramosissima* (Keleinkoff and Wallace, 1974).

Seedlings of *Avicennia marina* contained high amounts of anaerobic components (Chapman, 1962). Bharucha and Shirke (1947) studied respiration rate in seedlings of *Avicennia officinalis* and noticed less respiration rate in submerged parts and an increase in respiration with increase in age. Von Willert (1970) noticed maximum rate of respiration in 2-week-old seedlings of *Salicornia europaea*, *Aster tripolium* and *Plantago maritima* as compared to glycophytes.

Because of limited and contradictory experimental evidences it is difficult to generalize the effects of salinity on rate of respiration in plants subjected to salt stressed condition.

**2.8.4 Enzymes**

Physiologists have made efforts to examine activity of some enzymes in salt tolerant plants with reference to salinity. It is of interest to note that most of enzymes in microorganisms like halobacteria tolerate high salinity (Holmes and Halverson, 1965; Bayley and Mortan, 1978). According to Larsen (1967), halophytic bacteria required high salt concentration for optimal enzymatic activity.

Queen (1974) and Popp (1974) suggested that malic dehydrogenase (MDH) in *Spartina alterniflora*, *Salicornia*
virginica and *S. pacifica* was highly salt tolerant. Cavalieri and Huang (1977) noticed that malic dehydrogenase (MDH) in the leaf and root tissue of *Spartina alterniflora*, *S. patens*, *Distichlis spicata*, *Juncus roemerianus* and *Salicornia virginica* exhibited normal function at low NaCl concentrations. Further studies on two species of *Spartina* showed a decreased activity of MDH under addition of NaCl (Gettys et al., 1980). On the other hand, Cavalieri and Huang (1977) reported that *Borrichia frutescens* contained a salt tolerance MDH that do not loose its normal function at a high NaCl concentration. Amonkar (1977) observed that the MDH in *Salvadora persica* from saline habitats showed greater salt tolerance capacity than plants growing in non-saline habitats. In *Halimione portulacoides* the activity of MDH was inhibited at a concentration of above 0.5 M NaCl, though low NaCl concentration showed stimulatory effects on MDH activity (Kalir and Poljakoff-Mayber, 1981).

Phosphoenol pyruvate carboxylase (PEP-case) from various halophytes showed a higher rate of activity (Shomer-Ilan and Waisel, 1975; Treichel et al., 1974; Amonkar, 1977; Waghmode and Joshi, 1981) but Osmond and Greenway (1972) and Ting and Osmond (1972) observed a inhibition in optimum activity of PEP-case by addition of NaCl in the culture medium. Similarly, 30 per cent high rate of PEP-case activity in plants of *Cakile maritima* grown in 100 mM NaCl as compared to raised in control condition was reported by Beer et al. (1975). The ATP-ase activity in leaves of *Avicennia* was stimulated by addition of Na⁺ and K⁺ (Kylin and Gee, 1970). Lerner et al. (1983) found a stimulated broad peak of ATPase activity between 150-300 mol.m⁻² of NaCl or KCl in roots of *Atriplex numularia*. Horovitz and Waisel (1970
observed inhibitory effects of NaCl on activity of ATP-ase in *Suaeda monoica* and *Atriplex halimus*.

Indian mangrove species such as *Sonneratia acida*, *Aegiceras majus* and *Avicennia officinalis* exhibited more activity of PEP-case than that of RUDP-case in response to salinity (Joshi, 1976).

Inhibitory effects of NaCl on other enzymes in halophytes was also reported. Recently Kalir and Poljakoff – Mayber (1976; 1981) and Billard and Boucaud (1982) reported that accumulation of glutamine dehydrogenase, acetolactate synthetase decreased with increase in salinity in growth media. Similar observations were made in case of glucose-6-phosphate dehydrogenase activity (Flowers, 1972). The optimal function of NADP specific malic enzyme and alanine aminotransferase in *G. persica* showed decline in activity at 50 and 100 mM NaCl concentrations respectively; whereas the in vitro activity of leucine amino peptidase and peroxidase in *Spartina* species was inhibited either 0.25 of 0.5 M NaCl (Amonkar, 1977; Gettys et al., 1980).

It is evident from the above information that pumping of salts from cytoplasm into vacuoles or its accumulation in cell organelles or excretion from the halophytes create favourable condition for compartmentation of salt sensitive enzymes. Thus, these enzymes are protected from high concentrations of salts through cellular compartmentalization in salt tolerant plants.

### 2.9 SALT TOLERANT PLANTS, SALINE SOILS AND FORAGE PRODUCTION

Mangroves and halophytes, which constitute the major group of salt tolerant plants and which grow in highly saline conditions have been considered as a sustainable source of
forage production during last 20 years (Hollaender et al., 1977; Mudie, 1974). Only because these species are well adapted to salt stressed conditions, they can successfully be used for increasing productivity of saline wastelands.

The existence of mangrove species *Rhizophora* and *Avicennia* was reported by Nearchus and Theophrastus as early as 300 years B.C. Thereafter, the distribution of mangroves in different parts of world (cf. Chapman, 1976) had been described by Pliny (77 A.D.), Arrian (136 A.D.), Oviedo (1556), Peter Martyar (1597), Clusius (1600), Tertre (1667), Ray (1693), Sloane (1695). Dodoens (1563) was the first to identify *Plantago maritima* as halophyte and in the beginning of nineteenth century the term ‘halophyte’ was coined by Pallas (cf. Uphof, 1941).

Similarly, maritime salt marshes, which support the coastal flora are widely distributed in all continents (Chapman, 1976). The latter have been divided into ‘nine’ major groups, each having its own distinct type of vegetation due to physiographic differences. The list of 550 species belonging to 220 genera and 75 families and which have high economic potential as forage, fuel etc. was presented by Mudie (1974).

India has 5,700 km - long coastline and saline wasteland spread in 8 million hectares (Abrol, 1984). According to Sidhu (1963), mangroves and halophytes occupies about 7 lakh ha in our country but Blasco et al. (1975) put this area as 3.6 lakh ha. and 30 mangrove species and equal number of halophytes grow along the Indian coast. Chapman (1960; 1974) suggested that the tropical salt marshes were characterized by plants *Salicornia* sp., *Batis maritima*, *Sesuvium portulacastrum* and mangrove
species. It should be noted here that due to most favourable climatic and edaphic conditions, maximum number of mangrove species grow in India. Navalkar (1973), Blasco (1975), Joshi (1976) and Joshi and Shinde (1978) have presented recent reviews on Indian mangroves and their economic importance.

In Gujarat saline soils spread in about 1.2 million hectares along 1600-km-long coastline and two third of this area falls in Saurashtra region. Similarly, fifteen salt tolerant species, which have high economic potential, grow in this area. Sidhu (1963) suggested that coastal vegetation occupied about 52,000 hectares while Blasco et al. (1975) reported this area 20,000 hectares for this region.

The halophytic vegetation of Saurashtra coast is mainly represented by the following groups of mangroves and halophytes:

(i) mangroves - Avicennia and Rhizophora
(ii) succulent halophytes - Salicornia, Suaeda, Arthrocnemum and Sesuvium
(iii) monocots - Aeluropus, Sporobolus, Heleochloa and Juncus
(iv) Others - Salvadora, Atriplex and Cressa.

Although huge area is occupied by coastal vegetation in Saurashtra, limited information is available on physico-chemical characteristics of such soils (Rao and Aggrawal, 1964; 1966; Rao et al., 1966; Rao and Mukharjee, 1967; Rao and Shanware, 1967; Joshi and Iyengar, 1982). A few studies have been carried out by Indian researchers to examine variations in salinity, pH and mineral composition of coastal soils, which supports mangroves and halophytes. The available information shows that this salt tolerant group of plants and even the same species grow on soils
having a wide range of salt concentrations.

Efforts were made by Bolen (1964), Ungar (1965), Ungar et al. (1969) and Rajpurohit and Sen (1977) to study the effects of salinity on growth and distribution of salt tolerant plants. They suggested that salinity affected the growth and distribution of halophytes and mangroves. Misra (1990) reported that halophytic grass species viz., Sporobolus madraspatanus grew on soils having salinity range between 5.7 to 94.4 dS.m⁻¹. Joshi (1982), who studied physico-chemical characteristics of soils supporting succulent halophytes such as, Suaeda nudiflora and Salicornia brachiata, recorded soil salinity reaching upto 216 dS.m⁻¹.

Salinity of soils supporting A. marina and A. lagopoides varied between 15 to 31 and 10 to 24 dS.m⁻¹ respectively (Sagar Kumar, 1987; Bhoite, 1987). Similar range of salinity was observed by Rao and Aggarwal (1964) and Kassas and Zahran (1967) for habitats of these plant communities. Nevertheless, 14 percent of total dissolved salts recorded by the last authors for habitats of Arthrocnemum glaucum was five times less than salinity of soils supporting Arthrocnemum indicum (Sagar Kumar, 1987).

Salinity of soils supporting Salvadora persica, Juncus maritimus and Aeluropus lagopoides varied between 1.3 to 36.2 dS.m⁻¹, 7.6 to 18.4 dS.m⁻¹, 10.1 to 24.0 dS.m⁻¹ respectively (Krishnakumar, 1986; Khairatkar, 1986; Bhoite, 1987). This suggests that these halophytes grow in habitats with a wide range of salinity. According to Ungar (1974) and Joshi (1976), other halophytes and mangroves also grew on soils with similar salinity levels. While working on different groups of barren
soils from semi-arid zones, Gundalia and Patel (1982) observed salinity levels varying between 23 to 283 dS.m⁻¹.

Various authors (Dodd et al., 1964; Hadley and Buccos, 1967; Ungar, 1969; Ungar, 1970) reported that salinity of habitats of Salicornia community ranged between 24.3 to 39 dS.m⁻¹. Flowers (1934) recorded a broad salinity range between 0.5 to 6 per cent salts in habitats of the same genus. However, another succulent halophyte, Suaeda depressa grew on soils having salinity range between 0.2 to 4 per cent (Keith, 1958; Kearney et al., 1914; Weaver and Clements, 1938; Flowers, 1934).

An average salinity of 1.9 per cent for thirty five soil samples collected from A. occidentalis habitat was recorded by Marks (1950); while soils supporting a succulent halophyte, Suaeda nudiflora in the same area had only 0.56 per cent total salts. Ungar et al. (1969) reported Distichlis stricta growing in soils with salinity ranging from 0.03 to 5.6 per cent. Keith, (1958), Hadley and Buccos, (1967), Ungar, (1967a), Ungar et al. (1969) and Ungar (1970) observed that electrical conductivity in soil extracts of Distichlis community varied between 5 to 23 dS.m⁻¹.

While working on 22 soil samples supporting Puccinellia nutalliana Dodd et al. (1964) recorded mean electrical conductivity of 28.1 mmhos.cm⁻¹. However, soil salinity in Puccinellia-Distichlis habitat was 23.1 mmhos.cm⁻¹. Ungar (1970), who studied physical and chemical properties of soils from Dakota supporting the same species recorded 18 mmhos.cm⁻¹ salinity in 1:1 soils extracts. Sloan (1970) reported Scirpus paludosus growing in soils with salinity varying between 0.3 to 3.5 per cent; while 1.5 per cent salinity was noted for habitat
of the same species by Ungar (1968) and Kaushik (1963).

A few research workers have emphasized the importance of pH in deciding the plant distribution in saline environment. For instance, Keith (1958) suggested that the pH played an important role in plant distribution after a certain level of salinity. On the contrary, Evan (1953), Kruz and Wagner (1957), Bolen (1964) and Ungar (1974) did not find any correlation between distribution of salt tolerant plants and pH of soils. Similar observations were made by Joshi (1982), Joshi and Sagar Kumar (1985), Khairatkar (1986) and Krishnakumar (1986) while working on physico-chemical characteristics of soils supporting halophytes. Kassas and Zahran (1967) reported 8.9 pH for A. marina soils while less pH in habitats of Juncus and Arthrocnemum was observed by Catling and Mckay (1980). Rao and Aggarwal (1966; 1971) had reported Sporobolus tremulus growing on coastal soils of Gujarat having pH 8, whereas two other species of same genus viz., S. virginicus and S. glaciflora grew on soils with slightly greater pH (Rao and Meher-Homji, 1985). Similarly, Bolen (1964) and Vogl and McHargue (1966), reported pH range between 6.5 to 10 for soils supporting S. airoides. Khairatkar (1986), Krishnakumar (1986) and Bhoite (1987) observed that halophytes such as J. maritimus, S. persica and A. lagopoides grew on saline soils with pH range between 7 to 8.3.

Flowers (1934), Dodd et al. (1964), Ungar (1965a), Ungar (1969) and Ungar (1970) found that soils occupied by Salicornia community had pH range between 7.5 to 8.8. Baalman (1965), Ungar (1965a; 1968a) reported pH 8.1 for habitats of Sesuvium verrucosum at Great Salt plains. Flowers (1934) and Keith (1958) observed that S. depressa grew in soils with pH range between
8.4 to 9.8 and between 7.1 to 8.2 respectively. Kearney et al. (1914) observed that *Allenrofexa* community grew on soils having pH range between 6.5 to 8.2.

Flowers (1934), Keith (1958), Ungar (1967a), Ungar (1968a), Ungar et al. (1969) and Ungar (1970a) reported *Distichlis stricta* growing on soils having pH range between 7.6 to 8.6. Dodd et al. (1964) observed a median pH 8.3 in soils by *Puccinellia nutalliana*. Later on Ungar (1970) reported that soils pH for these two communities varied between 8 to 8.6. Thus, it appears that soils pH has little effect on distribution of the salt tolerant plants.

Ungar (1969) and Flowers (1934) found less concentration of Na\(^+\) (0.6 per cent) than that of Cl\(^-\) (0.7 per cent) in soils supporting *Salicornia*. Similar observations were made for *Triglochin* and *Hordeum* habitats respectively by Ungar (1971, unpublished data) and Ungar et al. (1969). On the other hand, Dodd et al. (1964) had reported greater amount of Na\(^+\) (0.4 per cent) than that of Cl\(^-\) (0.1 per cent) in habitats of *Salicornia*. This trend was also noticed for *Distichlis* and *Hordeum* by Hunt (1966) and Ungar (1970).

Ungar (1967a) recorded 0.2 per cent Cl\(^-\) in soils supporting *Hordeum* but Ungar (1968a) noticed 0.1 per cent Cl\(^-\) in another habitats of same species. Soils supporting *Puccinellia nutalliana* and *Sesuvium* sp., had 2.8 and 1.1 per cent Cl\(^-\) respectively (Baalman, 1965; Ungar 1965a; 1968a). Kassas and Zaharan (1967) had reported 59.2 meq.g\(^{-100}\) Cl\(^-\) in soils supporting *Aeluropus*; 35 meq.g\(^{-100}\) Cl\(^-\) in those supporting in *Arthrocnemum*; and 14.1 to 49.4 meq.g\(^{-100}\) Cl\(^-\) in that of *A. marina*. Mangrove soils on Indian coast contained Na\(^+\) between
19.6 to 32.2 meq.g\(^{-1}\) and Cl\(^-\) between 22 to 45 meq.g\(^{-1}\) (Joshi, 1976; Kotmire, 1983). Similar ranges for Na\(^+\) and Cl\(^-\) were observed by Khairatkar (1986) and Krishnakumar (1986), who studied physico-chemical characteristics of soils supporting Juncus maritimus and Salvador a persica.

Reports on habitats occupied by A. marina, A. indicum and Heliochloa setulosa showed greater concentration of Mg\(^{2+}\) (0.4 to 10.4 meq.g\(^{-1}\)) than that of Ca\(^{2+}\) (0.3 to 4.6 meq.g\(^{-1}\)). Similar observations were made by Chittar (1971), Amonkar (1977), Siddhanti (1977), Khairatkar (1986) and Krishnakumar (1986), while working on soils supporting halophytes. In contrast, mangrove soils contained greater amount of Mg\(^{2+}\) (4.9 to 23.4 meq.g\(^{-1}\)) than that of Ca\(^{2+}\) (1.45 to 2.99 meq.g\(^{-1}\)) (Bhosale, 1974; Joshi, 1975; Kotmire and Bhosale, 1980).

The concentration of K\(^+\) in the soils supporting to S. madraspatanus was low (Misra, 1990). Joshi (1976) and Joshi and Iyengar (1982) showed the halophytes grew in soils with low K\(^+\) levels. Similar observations were made for habitats of halophytes viz., Juncus maritimus, Aeluropus lagopoides, Atriplex griffithii, Salvador a persica respectively by Khairatkar (1986), Bhoite (1987), Anjaiah (1986) and Krishnakumar (1986). A low concentration of K\(^+\) was also noticed in habitats of H. setulosa, A. indicum and A. marina (Sagar Kumar, 1986).

It is evident from what has been said in preceding pages that many economically useful species can withstand high degree of salinity. If barren saline wastelands, whose physico-chemical characteristics vary within the range of tolerance of the said plant species, the latter can be introduced on such soils. This
can be done provided that specific data is available on salt
tolerance limit of the concern species and physico-chemical
characteristics of wastelands.