LITERATURE REVIEW

A. Problem of Salinity and its Genesis :

India is encircled by sea on three sides, stretching around 5000 km, from extreme north of Gujarat on the west, to Calcutta of West Bengal in the east. Several rivers rave their course to sea making deltas which are often back washed by tidal waves or inundated during high tides. These lands or such lands are often called Khar lands in Maharashtra because of the high salinity in the soil which are often unsuitable for cultivation of many crops. However, varieties of other crops and halophytes are able to grow under moderate salinity conditions.

Yet another type of salinity is what is called upland salinity. It is rather amusing to know that salts occur naturally in all soils. Rains dissolve these salt which are then swept through streams and rivers to the sea, where rainfall is sparse or there is no route to the sea. Some of this water evaporates and the dissolved salt becomes more concentrated. In arid areas, this can result in the formation of salt lakes or in brakish ground water, salinized soil or salt deposits (saline Agriculture Report of a Panel of the B.S.T.T.D. Pb. National Academy Press, Washington W.C. 1990). According to the above report there are three possible domains for the use of salt tolerant plants in developing countries.

1) Farm lands salinized by poor irrigation practice,
2) Arid areas that overlie reservoirs of brakish water, and
3) Coastal deserts.

In developing regions, there are millions of hectares or salinized farmlands resulting from poor irrigation practices. The survey in this department tells that more than 50,000 ha. of sugarcane field in western Maharashtra alone has gone saline due to above reason and no crop grows there. This has mainly resulted due to the reasons listed above (Hegde 1989).

The report of B.S.T.I.D. of N.R.C. Saline Agriculture (1990) says that it is unfortunate since most of the earth's water sources are too salty to grow contemporary domestic and crop plants. According to the report following classification of potential crop damages from increasing salt level are seen.

Irrigation water	Salts, ppm	Crop problems
Fresh	125	None
Slightly saline	125-250	Rare
Moderately saline	150-50	Occasional
Saline	500-2500	Common
Highly saline	2500-5000	Severe

Saline soil is ranging 1.1 to 16 dS/m which is equivalent to 500 to 10,000 ppm of salt is very common (Hegde 1989).

B. Classification of Saline and Sodic Soils :

Among the major groups of soils, the saline and sodic soils belonging to intrazonal group i.e. to that group of soils whose special characteristics are affected by local specific factors rather than by the general climatic conditions.

Terminology regarding salt affected soils is not uniform and sometimes confusing while some investigators named all holomorphic soils "alkali soils" (Kelley, 1951), others tended to distinguish between saline (salt affected) and alkali soils (soils affected by high percentage of exchangeable sodium) (de Sigmond, 1927; Richards, 1954). As the term alkali seems to have many meanings and alkalinity may be caused by a multiplicity of factors, the use of "sodium" or "sodic soils" instead of alkali seems to be preferable (Dregne 1968).

Soils with excess salts - saline soils are also called white alkali (Hilgard, 1906) or solonchalk soils (a Russian term sol-salt). Kearney and Scofield (1936) and de Sigmond (1938) regard alkali soils, as those that contain salt above the 0.1% level. According to Stocker (1933), the critical level of salinity for plants is 0.5% of the dry soil weight. Saline soils are typical for arid regions in which soluble salts are accumulated primarily in the A horizen of profile.

Salts in saline soils are comprised of mixture of chloride, sulphate, sodium, magnesium and calcium ion, with sodium chloride being dominant gypsum may also comprise, in local sites a considerable part of soils, salt content. In arid regions, Gypsum concentrate near the soil surface or throughout soil profile. In humid regions, it is usually leacked into a certain depth below soil surface. In most cases, the profile of such soils is under-developed and vertical movement of salt is considerably greater than that of colloid particals, clay minerals, or seequloxides. Saline soils are low in organic matter because of their low carrying capacity and failure to support a dense stand of plants. Joffe (1949) distinguished three types of such saline soils:

1) Primary solanchak - Soils of arid and samiarid regions in which the development of soil profile is poor, and which are dificient in organic matter.
2) Secondary Solanchak - Soils with a developed profile which were affected by salinity only at late stage of their development. Secondary solanchak can be superimposed on any type of regional soil i.e. one can find laterite solonchak, podsol solanchak etc.
3) Hidden Solanchak - Soils of arid and semiarid regions in which layers of salt have accumulated in the subsoil forming a typical salt horizon in their profile, the upper horison of such soils are salt free.

In addition to the morphological sub divisions of saline soils, Solanchak such soils were also classified mostly by Russian scientists on the basis of their chemical composition. Thus solanchaks are subdivided also according to their dominant anions into chloride solanchak, sulphate solanchak etc. (de Sigmond, 1927).

According to Dan et.al.(1962) holomorphic soils can be divided into four subgroups : Organic solonchak, alluvial and eolian solonchak, marly solonchak, sterile solanchak. This is a classification which considers both substrate and source of salinity as well as plant cover under some conditions salts are washed out from holomorphic soils. When the water table is lowered, when in increase in rainfall occurs, or when soils are internationally leached by man, the saline soil solun., moves gradually down the soil profile and by so doing causes a replacement of a large part of the absorbed nutrient cations, potassium magnesium and calcium and sodium ions. Dissociation of absorbed sodium causes an increase in pH of the soil solution : more

CO_2 is dissolved, and finally sodium bicarbonate and carbonate are formed. Relative content of carbonate or of bicarbonate in the soil is pH dependent. Below pH 9 is carbonate ions predominate, above this pH carbonate also occur. A soln. which has a columnar structure in the horizon with over 15% of its cation exchange capacity saturated with sodium, and has a pH higher than 8.5 is called solonetz, alkali, or sodic soils. In cases where the soil still contains large amounts of soluble salts and its pH is thus lower, is defined as a saline alkali soil.

The presence of sodium carbonate is associated with high pH of the soil solution, under such conditions, the soils organic matter is decomposed and dissolved. As a result the soil obtains a typical black colour, and in certain cases was named black alkali. Under conditions of relatively high NaOH or Na_2CO_3 content certain clay minerals of the soil are also dissolved forming sodium aluminates, sodium silicates and silica-gel.

Disintegration of such clay minerals releases various substances into the soil some of them are nutritive (e.g. Potassium or Magnesium) and have a positive effect on plants, whereas other such as boron or aluminium are toxic.

Boron is mostly released from rock minerals where it comprises part of the mineral tourmaline. Boron concs. in the saturated soil extract of 0.7-1.5 ppm may already be toxic to some plants. Above a conc. of 1.5 ppm boron is toxic to some plants. Above a conc. of 1.5 ppm boron is toxic to most plants. At high soil pH, boron is adsorbed to a certain extent in the clay particals.

Soluble aluminate (AlO_2) as also toxic to plants under such soil conditions. However, preliminary experiments comparing halophytes and glycophytes reveal that halophyte such as *Aeluropus literalis* or *Sueda monoica* are much more tolerant to aluminate than many glycophytes.

Higher and exchangeable sodium percentage in the clay minerals of such soils tend to disperse and the A horizon becomes structurless. Permeability of water in sodic soil is low. Light rains are hardly absorbed and the downword drainage of water is impeded. Nevertheless, in due time the dissolved aluminates and silicates together with a colloid suspension of clay minerals, are gradually leached into B horizon where they are precipitated and form a impemeable hardpass. Horizon A of sodic soils may vary between 3-30 thickness. It is characterized by scarcity of organic matter and, in many cases, its upper layers are in laminated form. In some sodic soils which have a structureless and loose A horizon the upper layer is washed away. In such a case, the exposed compact layers of the B horizon form bare spots, known in North America as silk spots. Horizon B of sodic soils has generally a columnar structure. Some of such soil prisms have flat tops while others are cap-shaped.

Sodic soils are not uniform and five soil groups were defined by Kovda (1935). Such distinction was based on salt, carbonate, and gypsum content, on content of organic matter, and on location of the lime horizon in the profile.

Continuation of Leaching processes of sodic soils turn the surface layers eventually into a light gray acid horizon and the soil is named solod. This is the last stage in the genetic series of halogenic soils out of which the soluble salts are adsorbed sodium were exchanged and washed away. A solod soil profile very much resembles soils of podsol type, but differs from them in the state in which its silicates are precipitated, while in podsols silicates are crystalline and silica (quartz) is residual in the B horizon, in the soils of solod type silicates are precipitated in an amorphic form. The clay particlesof the B horizon in the solod type of soil break into prismatic columns with caplike tops. The acid leached horizon then extends downwards often like tongues, whereas saline and sodic soils are common, soils of the solod type are rare.

Usually saline, sodic and saline-sodic types of soils appear together in a salty spot, each occupying a niche in the topographically divergent site. Saline soils are also formed in the centers of terminal drainage basins while the various types of sodic soils are located more towards their periphery.

In addition to morphological pedological classification described previously, saline soils were also defined and classified by the staff of U.S. salinity laboratory, Riverside California, on the basis of their agricultural value (Richard, 1954). Accordingly a few types of salt affected soils were distinguished with their classification based on the conductivity and percentage of exchangeable sodium.

1. Saline soils : Nonalkali soils in which the soluble salt content is high enough to inhibit growth of most agricultural crops-electrical conductivity of the saturated extract of such a soil is above 4 mmhos/cm pH is below 8.5 and exchangeable sodium percentage is below 15.

2. Alkali sodic soils : Soils with enough absorbed sodium to inhibit growth of most agricultural crops. Usually, pH of those soils is above 1.5 and most commonly may reach values of 10 or higher. Two types of alkali soils were determined.

   a) Non-saline alkali soils : Soil in which conductivity of saturated extract is below 4 mmhos/cm but which have an exchangeable sodium percentage above 15%.

   b) Saline-alkali soils : Soils with an exchangeable sodium percentage of 15% or more, but which, in addition, have a high content of soluble salts. Electrical conductivity of saturated soil extract is above 4 mm /cm. Soils of this type frequently contain considerable amounts of gypsum.

Very little is known of the specific effects of various types of saline or sodic soils on growth and behaviour of halophytes. However, the scattered data available sugest that as a group, halophyte, do not respond only to salinity but also are more tolerant to entire complex of physical, chemical and biological modifications induced in the soil by salinity. Among such modifications, acration and microbiological activity seem to be most important.

C. Distribution of Saline Areas :

Maritime salt marshes, mangrove swamps and interior salt deserts are all available for reclamation for more food demand of nations. In Europe USA, Malaya some of the land has already been reclaimed. The mangrove forest is managed as a source of pulp (Bangladesh, Cutch and Charcoal (Malaysia) as well as local building Timber.

The soil in such areas is rich in nutrients, supply of nutrient occurs by Sea. And estuaries play important role in binding them and further deposition occur by rivers and from human settlements and cities (Arnon, 1972).

About 70% of the earths population live within coastal region which resulted in the development of port and industries. It led to misuse of the highly productive salt marshes and mangroves. The land reclaimed for agriculture has been reclaimed for industries. Between 1922 and 1954 one quarter of USA salt marshes were destroyed (Teal and Teal 1969) and between 1954 and 1964 a further 10% was destroyed.

It is difficult to determine the extents of the inland saline and alkali lands, because there is no accepted critierion as to when a soil is to be regarded as belonging to one category or the other.

In many cases salinity of inland area is related to high aridity plus a saline water table from rocks rich in sodium salts. There are low physiographic gradients so that the water accumulate rather than draining away (Flayward, 1954).

In India and Pakistan there are about 20 million acres of saline or salanized soils quite independent of all those maritime soils associated with coastal mangroves. Many are termed "reh" soils and contain salts of sodium brought to the surface by capillary action and evaporation saline mangrove soils are abundant around Karachi, Madras, Godavari and Krishna deltas and the deltas of Ganga and Brahmaputra. In Punjab area there are some 5 million acres of soil in which predominant salt are sodium carbonate and bicarbonate and sodium sulphate. Some 3 million acres have salanized as a result of irrigation and by 1960, 1.3 million acres have gone out of productivity because salt concentrations ever too high. In Maharashtra, the main salts are sulphates and chloride and there is less evidence of salanization due to irrigation.

In Africa vast saline areas lying along the north coast with extension into eastern mediterranean countries. In Egypt 3,00,000 acres have become saline as a result of irrigation.

40,000 acres in England and Scotland soil is saline, in Rumania there are 3 lac hectares, Hungary 5 lac hectares. In USA salt problem is mainly associated with the Great salt lake basin. In Central America saline soils with 90% exchangeable sodium in the base exchange complex occur in west coast.

D. Distribution of Maritime Salt Marsh Vegetation :

These marshes are wide spread especially in temperate parts of the world. Dominant vegetation is herb but some strubs occur. Algal vegetation also ocur. These are grouped as follows :

1) Aretic Groups :

Extend around aretic circle. Species are few, exists in extreme environment. The dominant species is grass *Puccinellia phryganodes* and two species of Carex *C. sabspathacea* and *C. maritima* being important at upperlevels.

2) North European Group :

This includes marshes from Spain northwards around the English channels and all north sea and Baltic Coasts and around shores of Great Britain. The sub-groups can be recognized which are related to soil differences Saprtina townsendii and S. anglica, Puccinella Salicarnia and Juncus occur as annual species. Clay and silt in the soil occur in this range and different varities occur. Spartina species are aggressive hence the character is changing.

3) Mediterranean Group :

Arthrocnemum & Limonium are the characteristic marshes, Sueda, Holocnemum, Petrosimonia, Anabasis and Kalidium capsicum also occur.

4) Western Atlantic Group : These marshes extend from the St. Lawrence to Florida here there is a transition to mangrove. They fall in three groups.

5) Pacific American Group :

These marshes extend from Southern Alaska to California with species not found elsewhere.

6) Sino-Japanese Group :

Limonium japonicum, Sweda, Puxciniella have character to this group, Some show transition to mangrove swamp.

7) Australian Group :

These are characterized by some specially southern homisphere species such as Salicarnia australis, Sueda Samolous repens.

8) South American Group :

Occur on both coast of S. America and compared with salt marshes. The local species of genera such as *Spartina*, *Distichlis*, *Heterosta.*

9) Tropical Group :

These generally occur at high levels behind mangrove swamps and flooded only by extreme tides. The typical species are *Sesuvium portulacastrum* and *Batis maritima*.

E. Distribution of Mangrove Vegetation :

In tropical and subtropical parts of the world maritime saltmarshes are replaced by mangrove swamps in which the dominant vegetation are trees, shrubs and few lianas. In the northern hemisphere Mangal (Mangrove communities) extends north to latitudes ranging between 24° and 32°N. The mangrove species occur in South Japan, Atlantic,Florida, Bermuda. In southern hemisphere these occur in Brazil to the tropic of capricorn but on the west coast they do not extend beyond 4°s it may be due to lack of physiographic conditions. Mangrove vegetation of the world falls naturally into two great groups - Old world and New world mangal. The old world contains large number of species about 60. In New world group only about 10 species occur (Chapman, 1944, 1970). The old world Indo-Malaysia area the greatest number of species are found. In Africa there is a sharp boundry species of two groups on east and west coast. The mangrove vegetation can be divided as follows :

1. New World group
2. East African group
3. Indian group
4. Indo-Malasian group
5. Australian group
6. Philippines, New Guinea & Oceasia group.

F. Distribution of Inland Marshes and Salt Deserts :

Inland salt marshes and salt deserts show a type of habitat where salinity problem is essentially related to ground waters and where salt of sodium other than sodium chloride are involved with salts of Magnesium. The dominant vegetation is shrubby. The division is based on floristic differences but there is no one centre of distribution as in mangrove vegetation, nor does the method of salt desert formation. Chapman (1972, 74) shown following groups.

1) Inland European Group :

These can be divided into sub-groups - northern and south-eastern sub-groups. Northern are European. The grass *Puccinella distans* is a characteristic species of this group. Others are eastern species such as *Crypis aculata*, *Aster tripolicum*, *Lepidium cartilaginum* etc.

2) Inland Asian Group :

These are not so well known as some of the others. Aralo-caspian subgroup exhibits some affinities with the south-eastern European group but there are species such as *Kalidicem foliatum*, *K. caspicum*, *Holostachys caspia* and *Holocnemum crassiflesa* that are typical of these salt deserts. *Sueda vermiculata*, *S. palestina* occur in the Iraq-Central Asian subgroup has some affinity with the north African subgroups. The third group East Asian and has species *Atriplex* and *Artemisia.*

3) African Group :

It is divided into northern-Eastern and Southern-eastern groups. The widespread community is dominated by *Salicornia fruticosa* and *Sphenopus diversicatus*. East group shares some species in common with North African subgroup- *Holoplelia Aeluropis*, *Scirpas robusta* and *S. spicatus* are common.

4) Inland North American Group :

Occur on Pacific and Atlantic coasts but there are others *Salicornia Allernafolia sposobolus*, *Puccinella*, *Tamaric pentandra*.

5) South American Group :

Species in inland saline areas are *Heterostachys ritterina*, *Spartina montevidensis*, *Salicornia glandichandina*.

6) Australian Inland Group :

Characterized by species of *Atriplex* and *Arthrocnemum holocncides*. Latter also occur on martime saltma.

Economic Uses :

Saline areas must have been familiar to man for a very long time, because so much glycophytic land was available. There has been no urge to utilize land that clearly was not favourable for plant growth. At some period in tropical areas local inhabitants must have found that the landcoast parts of mangrove swamps could be used for the growing of crops whilst timber could be used for house construction, fish ret poles and as a fence. Similarly at an early stage the use of *Rhizophora* bark as a source of tannin must have emerged.

The mangrove soils in tropical Africa are used for cultivation of sugar, rice, bananas, and rubber. In India mangrove soil is examined for rice culture (Sidhu, 1963). They have not so far used for agriculture.

Principal sources of tannin are the mangrove Swamps of East Africa, India, Indonesia and the Phillippines with other areas, although Chinese, Arabs used tannin from mangrove bark for a very long time.

In India soils are moderately saline and can be used for cultivation of rice by prolonged leaching. Heavily salinized soil can be economically reclaimed if cheap irrigation water is available for leaching out the salt. Sesbannia aculeata or S. aegypticca, Accacia arabica, Prosopis juliflora and commonly growing plants which are useful in reclamation of such land.

G. Salt Tolerance Mechanism :

Assessment of salt tolerant plants has been made by USDA Salinity Laboratory (California) and also Indian worker Kanwar (1939). Recently Hoftmann (1977) made an assessment of salt tolerance of 76 economically important species. It indicates that sugarbeet, barley, cotton, Datepalm, Bermuda grass, wheat grass are the most salt tolerant crops. While apple bean carrot, lemon, onion, are most salt sensitive crops. Species not only differ in salt tolerance but also verietal difference is noticed with respect to salt tolerance. Some of the mesophytes are evolved in such a way that they survive too high soil salt solution.

H. Mechanism of Adaptation :

Mechanism of adaptation is right from seeds and their germination. Seeds have air in seedcoat and they float on sea-water without injury. Hibiscus and Tiliaceous seed float upto 120 days. Seeds tolerate salinity upto 100 mm to 500 mm and germinate. In Mangrove plant seeds germinate on mother plant what is called vivipary. Fully developed seedlings are dropped in muddy regions to establish vegetative propagation by stolon. Mechanism of dissemination of fruit and seeds also exists. So far growth is concerned in such plants it is unaffected or even stimulated by salinity.

E.g. Salicornia shows optimal growth at 2% NaCl. Most halophytes show rapid root growth by having apical cambial activity even in saline conditions. Some halophytes like Sueda, Salicarnia, Atriplex show growth retardation in Na deficient soil.

(i) Osmotic Adaptation : Osmotic potential of soil solution is high where halophytes grow. This increases water retaining capacity of soil solution and limits availability of water to the plants. It is now well known that when O.P. of soil solution increases the O.P. of plant tissue also increases considerably. Such osmatic adjustment in plant tissue occurs due to osmotically active substances like sugars, organic acids, amino acid, polyols and proteins. In glycophytes partial osmotic adjustment occurs while in halophytes complete or over osmotic adjustment takes place. Chapman (1960) based on the mechanism of osmotic adjustment divided plants into two classes:

Euhalophytes -	Those which accumulate salts for effecting osmotic adjustment.
Glycophytes -	Those which accumulate organic solutes rather than salts in effecting osmotic adjustment.

Euhalophytes have ions such as Ca^{2+}, Na^{+}, Cl^{-}, K^{+}, SO_4^{2-} increase osmotic pressure of the cell sap whereas in saline grasses accumulation organic acid such as oxalic acid is known e.g. Atriplex. Moreover in grasses large amount of soluble sugars, several aminoacids such as proline level are higher and one more compound known as quarternary ammonium compound called glycine betaine is also known to occur - Halophytes accumulate more Na, Cl, K and less SO_4.

(ii) Ion uptake : There are following mechanism known :
Salt exculsion, Salt excretion, Salt accumulation and Shedding of salt loaded parts. Scholander (1968) recognised ultrafilteration mechanism. Succulance is induced by salt.

(iii) Salt excretion : Following plants have established salt excretion mechanisms : Aeluropus tamarix, Avecinia acanthes.

(a) The excretion of sodium (Sodium pump) :

It is well known fact that living cells of plants as well as animal display a characteristic cation distribution with respect to their milieu. Potassium concentration in the cell is always much higher than the external concentration, whereas the converse is true with sodium distribution. Hence even at high external sodium concentration the internal potassium concentration is often higher than that of sodium. As a rule sum of the sodium and potassium concentration tend to be constant for any particular type of cell.

The ability for maintaining this characteristic ionic distribution will be lost under the influence of a great variety of factors, the common effect of which is a tendency to lower the metabolic activities of the cells and tissues involved. At first sight it may be seen that these effects might be explained in terms of selective permeability of cytoplasmic membranes, specific binding capacity for K of some cell constituents etc. In fact for many years physiologists have been discussing the problem along these lines. However during the past 15 years careful quantitative analysis of the movements of the monovalent cation has affected a profound change in attitude with respect to interpretation of these ionic distributions. It is now realized that, although alterations in selective permeability may have bearing in physiological processes of limited duration, and ultimate ionic distribution representing steady state conditions can never be explained by them, but should be considered as being the result of active processes by which the ions move either inward or outward. Moreover, as with most cells and tissues, the distribution of K^+ seem to be in accordance with Donnan-equilibrium. Attention has also moved from the 'active' potassium uptake to the extrusion of sodium.

Dean (1941) was the first to mention the possibility of socalled sodium pump being present in musde cells as a result of which low internal sodium level, and consequently a high potassium level is effected. The significance of this modern trend in physiology is perhaps best realized by considering that such an active excretion mechanism is also assumed to be present in such a structure as the human Erythrocyte.

Regulation of salt content of shoot :

(1) Salt transported into plant shoots via. transpiration stream.

(2) Secretion of ions by special salt glands is the best known mechanism for regulation mineral content of plant shoot.

(3) Salt released through cutical or in the guttation fluid. They are retransported via the phloem back to roots and soil or get concentrated in leaf hairs (Stenlid, 1956).

Salt glands were known and described in the middle of the nineteenth century - described as Chalk glands as special hydathode as early as in 1988. Marloth (1888) described salt glands as Tamaricacea for the first time. Schtscherback (1910) and Ruhland (1915) gave structure function and ecological significance of the salt glands in plumbagenaceae. Transport of substances out of plants was divided by Frey Wyssling (1935) into the following three categories.

Exeretion : Removal outward of metabolic end products.

Secretion : The transport outward of metabolic products that function outside the organ or plant.

Recretion : The transport outward of substances taken up by plant but not assimilated.

Out of these three categories only recretion can be used for salt secretion. However, the term 'secretion' has been so commonly used for ion transport out of plant tissues. Salt secretion is a common phenomenon in various halophytic plant genera. It is found in the terrestrial halophytes. Following is the brief account of it :

Convolvulaceae - *Cressa*, *Frankeniaceae* - *Frankenia* *Gramineae* - *Spartina*, *Chloris*, *Aeluropus* *sinedon*, Plumbaginaceae - *Glaux* Tamaricaceae-*Tamarix*, *Reaumuria*. It is also found in the mangrove species. Acanthaceae *Acanthus* Aviceniaceae - *Avicenia*, Combretaceae - *Laninucularia*, Myrsinaceae *Aegiceros*, Plumbaginaceae - *Aegialitis*, Rhizophoraceae - *Ceriops*, *Brugeria*, Sommeratiaceae - *Sonneratia*.

However, inspite of large choice of plants, the process of salt secretion was extensively studied in only a few genera of plumbaginaceae (*Aegiatitis*, *Limonium*, *Statice*) in *Tamarix* *aphylla* and in *Avicenia* *marina*. Investigations were both physiological (Ruhland, 1915; Arisz et.al. 1955, Helder 1956, Waisel 1961, Scholander et.al. 1962, Atkinson et al. 1967, Berry and Thomson 1967, Pollak and Waisel, 1970) as well as anatomical and ultrastructural (Ruthland, Walter & Steiner 1976, Ziegler and Luttge 1966, 1967, Atkinson et al. 1967, Thomson and Liu 1967, Shimony and Fahn 1968, Thomson et al. 1960). Data obtained from the above investigations posed a few hypothesis as to the mechanism of salt secretion. Three fundamental features determine the effectiveness of salt glands in removing salt excesses (a) their structure location and abundance, (b) their mechanism, and (c) their physiological and ecological significance.

Structure of salt glands in various plant species :

Salt glands are common in several families of plants. Most species with salt glands are able to tolerate a high salinity and as a rule their distribution is limited to salines of various types. Salt is secreted from well defined salt glands located on or sunken into the epidermis. Although the structure of the salt glands varies greatly in different plants, it is similar in plants of the same genus or within one family.

The simplest two celled hairlike gland found in Spartina or in Aeluropus A three celled gland is found in Chloris gayana. InAviceniaceae, glands are composed of indefinite number of cells (usually five to nine) arranged in a group of four or more cells located on top of one stalk and two four collecting cells. A similar gland is found in Acanthus illicifolius. A Tamaricaceae have a more complicated gland composed of eight cells arranged in four pairs. A multicellular glands comprised of sixteen cells are found in the plumbaginaceae. In some species of this family (on the stem of Statice pruinosa) the glands are located on the top of special structure. According to Ruhland (1915) the number of glands in Statice greneline is about one-tenth the number of stomata.

In all cases investigated the glands have been investigated at an early stage in the development of the leaf, and their differentiation was completed much earlier than the development of various other leaf tissues. Cells of salt glands differ in many respects from surrounding epidermal cells. Cells lack central vacuole and number of mitochondria and other organ cells is extremely high. This suggests that gland cells do not act primarily as accumulating organ, but rather as transit cells. Salts are transported outward by specific mechanisms, which consume energy originating on mitochandrial surface but concentration of ions in gland cells may be high in comparison with surrounding cells (Ziegler and Luttage, 1966).

There is much similarity between active transport processes operating in salt glands acid transport process in other tissues and organs. Similarity is specially striking between salt secretion on one hand and secretion of nectar in nectaries, acid secretion of ions into xylem elements of roots on the other hand. There are also similarities in structural and ultrastructural features.

Structures that control free transport and are analogous to the casparican strips of the endodermis are found as salt secreting glands. Some of the gland cells are characterised by cutinised and suberised cell walls, especially the wells bordering normal paranchyma cells. In certain cases the cytoplasm is tightly connected to the strips exactly, as in the cesperian strips. Thus ions can be transported into the gland cells only through the symplast. Although this is true for water absorbing hairs (e.g. hairs of leaf bases of Tillandsia) and nectaries (e.g. in flowers of Syringe) it is especially clear in salt glands. Thus, the basal cells of the salt gland in Avicenia, the culticularised layers in the glands of Aegialitis, Limonium and Tamarix as well as the stalk cells of the salt accumulating hairs in Artiplex might be compared to the endodermal cells to their caspariam strips. The impermeable walls of the endodermal cells as well as the impermiable cuticular layers in salt glands would serve in this case as a barrier to leakage of secreted salt solution back to the tissue.

The gland of Limonium is made up of a complex of sixteen cells. There are four secreting cells arranged in circle each occupying one quarter. Each cell is accompanied at its outer side by a smaller adjoining cell. Both the secretary cells and adjoining cells are surrounded by two cup-shaped cell layers, each comprised of four flat cells arranged similar to secretary cells (Ruhland 1915, de fraine 1916, Ziegler & Luttge 1966). The upper side of the glands and the neighbouring epidermal cells are covered by a thick cuticle the outer walls of the outermost cup-shaped layer of gland cells are also strongly cutinised, thus partially isolating the gland. This process of cutinisation is not restricted to these walls only but also extends to a slight degree, to the adjacent contiguous walls. In this way a rigid structure is formed below the leaf epidermis in which the gland is firmly inserted (Ruthland 1915, Helder 1956).

The walls of gland cells are pitted in a few places. One single small pore 1 um diameter is found in the cuticle, covering top of each secretary cell. The total amount of secreting fluid produced by the gland thus passes through these four small pores. The presence of such pores does not mean that the cytoplasme of the secretary cells is directly exposed to the open atmosphere, because it is still protected by the cell wall. In fact the chemical composition of cellulose near the pore is different from that of bulk of cellulose. Large pits are also found in the walls of gland cells adjacent to the assimilating tissue of the leaves. Through these pits contact is provided with four extraglandular large cells, called collecting cells. Each of these collecting cells has usually contacts with a few normal mesophyll cells. The main function of these cells is to transport ion from mesophyll into the glands.

Gland cells differ from normal mesophyll cells in shape and arrangement. They possess a characteristic dark granular cytoplasm with large nucleus and thin membranes. Instead of central vacuole large number of small vacuoles and organeles may be observed. This applies to four secretary cells; nuclei are often found near pits. Chloroplast are lacking in both secretary and collecting cells. In this respect they may be similar to epidermal cells and easily distinguished from ground tissues.

Glands of other members of plumbaginace are extremely similar (De Bary 1877, Volkens 1884). It is worthile to mention that salt glands located on stem of statice Pruinosa are not sunken into epidermice. Rather those glands are located individually with each one on the top of a special elevated cortical structure.

It is interesting to note that the salt glands of Limonium do not serve solely as transport organs but also accumulate large quantities of chloride ions (Luttage 1960, Ziegler & Luttage 1967). Since these cells lack central vacuole the accumulated ions seem to be evenly dispersed over the entire cell volume. Salt glands of Spartina are epidermal structures very close to, or have contacts with the assimilating tissue, but not with the bundles. They are very much simpler in structure than those of Statice (Skelding & Winter Bothom 1939, Helder 1956). Instead of 16 cell complex, there are only two typical cells, a large cell and cell sap. Cell whose wall is cutinized and not pitted. The basal cell is connected by pits to surrounding cells. On one side it is connected to cells of assimilating tissue and on other side to the four epidermal cells which are well like opening of gland. The walls of epidermal cells are perforated by numerous pits. Hence salt solutions are believed to be forced from the basal gland cell through adjacent epidermal cells outward to the well like dip in epidermis.

The structure of salt gland is similar to salt accumulating hours of *Atriplex* (Osmond et.al 1969). In both cases, the basal stalk cell seems to be the functioning one while in *Spartina* salt is forced outward and it remains trapped in bladder cells of *Atriplex*.

Glands of *Atriplex* are simple two celled type, large based cell and small cutinised cap cell. Gland is not sunken, resembles a hair, each cell is unknown.

The salt gland of *Chloris gayana* consists of three cells, a large collecting cell, a stalk cell and an upper cell which function as secretary cell. Salt glands of genus *Tamar aphylla* have been frequently described (Brunner 1909, Decker 1961, Cambell & Strong 1969, Thomson & Liu 1967, Waisel et.al. 1966, Shimony & Fabn 1968). The gland consists of two highly vacuolated extraglandular collecting cells and six small secretary cells with dense protoplasm. The secretary cells are coated with a sheath of cuticle except for few patches on the walls serving as connections with the collecting cells. Many plasmodesmata pass through these patches and connect the protoplast of the two groups of cells. Large number of mitochondria and protoplast are observed in all the secretary cells but in the upper two pairs.

(b) Sites of Salt Pumps :

Site of chloride accumulation within gland cell and the pathway of chloride transport through leaves and salt glands of Limonium valgare were investigated by Ziegler & Luttge (1967). According to this investigation, chloride in the leaf was transported both through symplast as well as through free space of cell walls. Using autoradiographical and precipitation methods they showed that chloride accumulates mostly in protoplasm of epidermal or mesophyll cells, The concentration of chloride in cytoplasm of gland and paranchryma cells of mesophyll did not differ. Therefore, the relatively higher activity of ^{36}Cl seen in microautoradiographs of the gland cells was linked primarily to a higher concentration of Cl^- in cytoplasm (Luttge 969). A high concentration of chloride was also reported to be inside chloroplast and nulei of mesophyll cells.

Much of the transport of ions through leaf tissues was found to occur through free space. On the other hand, transport through symplast has a great advantage, because of its selectivity and independence of ion transport from the rate and direction of the transpiration stream. Plasmodesmata thus seem to play role in transport of ions both into gland cells as well as within gland between peripheral and central secreting cells. Inspite of precise structural and ultrastructural descriptions available for most salt glands, very little is known of the connections between their structure and function. Only in very few glands is the exact site of secretion known. Practically in no one of these do we know about the role played by each of the gland cells.

(c) Secretion Mechanism :

The need for oxygen, the anhibitary effect of various metabolic inhibitors, and the effects of low temperature on the secretion mechanism suggest that as a whole, this mechanism is an active one, i.e. a mechanism that depends on an undisturbed metabolism for normal operation. It alsoseems that the secretion mechanism must be located inside the salt gland itself because brine secretion occurs not only in intact plants but also in detached leaves and even leaf disks with nearly isolated glands. Of course, this does not exclude the possible contribution of metabolic energy from other tissue as well for control of secretion.

(d) Concentration Effect :

Salt glands are assumed to transport ions against concentration gradient. This capability was shown by Scholander et.al. (1962) who found that NaCl concentration in the secreted solution collected from various mangrove (*Aegialitis*, *Aegiaceros* and *Avicennia*) exceeded the NaCl concentration in the root medium. A similar case was also reported for *Aeluropus litoralis* (Pollak and Waisel 970), where the concentration of secreted fluid (upto 1 M NaCl) were always higher than the concentration of the treatment solutions. On the other hand according to Ruhland (1915), leaf disks of *Statice gmelini* floated over a salt solution, secreted out of their salt gland a fluid of the same concentration of salts. For *Liminium latifolium* the concentration of secreted fluid exceeded that of external salt solution only at lower values of latter.

concentration of secreted salts is often so high that under dry atmospheric conditions, salt crystallizes and cover the plants with either salty scales or whiskers (Aeluropus, Tamarix, Limonium spartria). This is noticeable in plants growing in highly saline habitats or in detached leaves that are exposed to salty solutions. The fine texture and cylindrical shape of salt crystals indicate that salts are added in minute quantities at the base of each Whisker (Decker 1961). Growth of whisker is not constant, secreted brine is viscous and concentrated. They can be dissolved and recrystallized into large salt cubes. Ability to secrete ions against a concentration gradient is not unique to halophytes. Tissue segments of Nephrolepis may transport chloride against a concentration gradient one hundred times higher than their own. The addition of even minute quantities of NaCl e.g. 5 mM into growth medium resulted in a marked increase in volume and amount of Na secreted.

Attempts of assessing the influence of the osmatic constituents of the salt solution on the secretion process were reported by Ariz et al.(1955). In these investigations Limonium leaf disks were exposed to salt solutions with a constant chloride concentration but with varying osmatic potential which mainly affected the amount of liquid secreted and resulted in higher chloride concentrations. Exposure to higher osmatic potentials (-10 to -20 bars) reduced both the volume and concentration of chloride secreted. Increase in NaCl concentration in irrigation showed correlation between concentration of secreted brine and concentration of salt in leaves. Media with high NaCl secretion from Aeluropus leaves is about three to five times higher than its retention by the leaves. Evidently most of the Na absorbed is transported to shoot and the leaves for secretion.

Similar results were obtained for Cl^- secretion from Limonium leaf disk exposed to solutions of various NaCl concentrations. High concentration of NaCl increased the rate of secretion and concentration in the secreted fluid. However, increase in concentration of external solution above a certain level reduced Cl content of leaf as well as the amount of secretion. Despite such inhibition secretion continued at low rate and a highly concentration fluid was produced (Arisz et.al. 1955, Helder 1956).

A concentration rise of the external solution to 0.3 M NaCl still increased the sodium concentration in secreted fluid of Aeluropus but no increase in amount of solution secreted was observed. Such results point out the possibility that two separate mechanisms are involved in secretion of fluid from glands (1) an osmotic mechanism which is involved in secretion of fluid from gland and (2) an ion transport mechanism which affects salt contents and composition of fluid. Both mechanism we apparently effected differently by concentration of external salt solution (Pollak and Waisel,1970) Similar conclusion may be drawn from the data collected by Arisz et.al.1955) for chloride secretion. They showed that fluid secreted by leaves, but not its composition, was unaffected by high or by low salt levels of leaf. Such assumptions of existence of two different mechanism were further supported by data of Pollak and Waisel (1970) which showed a higher Na secretion from plants treated with 0.1 M KCl or 0.05 M CCl_2 than from controlled plants given the basic nutrient solution alone. It seems that fluid secretion mechanism must be achieved by a critical ionic strength of the outer solution, and that such activation is relatively independent of ionic composition of the activating external solution.

Apart from the positive correlation between concentration of external solution and amount of Na^+ secreted, a correlation was found between concentration of medium and Na^+ content of leaf. However, amount of Na^+ in the leaves are much lower than the amounts of sodium secreted. It may be assumed that transport of Na^+ from the roots via the stems and out of leaves to the secreted solution is very fast. Pulse labelling roots of Aeluropus litoralis plants reveals that the time elapsed between uptake of Na and its secretion does not exceed one hour. The amount of sodium secreted daily (u moles gm^{-1} $dory^{-1}$) almost equal the sodium content of the leaves. Thus, it is apparent that most of Na ions reaching the leaves of Aeluropus through the roots secreted and rate of accumulation in leaves are low. Two interpretations for this phenomenon are feasible, first that there are two successive mechanism operating. Under this hypothesis accumulation of Na^+ in leaf cells constitutes an intermediate stage between uptake and secretion. While the period during which sodium is retained in the leaf cells is very short. The second interpretation based on the existence of two parallel mechanisms an accumulation mechanism in the leaf mesophyll and an independent secretary mechanism. Latter usually shows a higher efficiency for the uptake of Na^+ from xylem sap reaching the leaves.

1) Effects of Temperature :

(a) Investigated in Limonium (Arisz et.al. 1955) and Aeluropus (Pollak and Waisel 1970). Increasing temperature from 5^oC to 25^oC acelerated rate of salt secretion by eight times but Cl^+ content remain constant. Change in volume was observed.

(b) High salt leaves show little difference under 10^o or 20^oC. When leaves show low in salt little secretion was at 20^o to 30^o.

2) Effect of Metabolic Inhibitors :

Toxic or narcotic substances may either stimulate or inhibit secretion process (Ruhland 1915). Arisz et.al. (1955) showed that Cl^- secretion was highly stimulated at low concentration of various inhibitors including potassium cyaride, sodium azide, sodium fluoride and arsenite, whereas marked inhibition of the secretion occured at concentration above $5 \times 10^{-3}M$. Dinitro phenol had similar effect.

Carbonylcyanide - 3 chlorophenylhydrazide greatly inhibited the secretion process in Aegilitis - after 2 hours Atkinsemetal effect of oxygen pressure.

Ecological Significance of Salt Removal :

Active secretion of toxic ions as well as their passive loss out of live or dead tissues is apparently a major contribution for plant adaptation to saline environments. For example, salt secretion is an efficient mechanism which prevent accumulation of large quantities of sodium and chloride inside tissues, while having little effect on the balance of potassium, calcium nitrate and phosphate. It is of adaptive characteristic of nonsucculent halophytes growing in saline habits. Sacculents release accumulated salts by shedding leaves or rather flashy tissues.

Secretion of salts out of glands of various salt secreting species differ both quantitatively and qualititatively. When growing on non-saline sand dumes, plants such as Tamarix aphyela and Limonium latifolium secrete mainly $CaCO_3$, which is an important constituent of such sands. Nevertheless under saline conditions, those plants were found to secrete large quantities of sodium as well as of chloride. Thus, such mechanisms enable plants to keep a low concentration of those ions inside their tissues.

In other plants e.g. Aeluropus the secretion mechanism seems to exhibit higher preference towards NaCl. When NaCl is present in the medium Aeluropus plants secrete droplets containing high concentration of both sodium and chloride ions. The efficiency of secretion mechanism was demonstrated in Limonium plants. In leaves of this species chloride contents decreased even then leaf disks were placed in dilute salt solutions. And despite a concurrent chloride uptake values of 1 ml mm^{-2} hr^{-1} of liquid secretion and 0.05 mg NaCl mm^{-2} hr^{-1} were reported for Limonium (Ruhland 1915). Even higher values of chloride secretion by mangroves were reported by Atkinson et al. (1967). Because of such a high efficiency, chloride conc. of the secreting leaves evidently remains only slightly higher than its conc. in the external medium. The same is also true also for sodium. In all examined cases the amount of Na secreted from leaves of Aeluropus during 3 or 5 days period was higher than the sodium content of the same leaves.

Despite these findings the secretion mechanism seems to be limited in their capacity. For Tamarix aphylla it was noted that secretion was positively correlated with concentration of external medium. However, when NaCl, concentration reached 0.4 M, the secretion of sodium and chloride was reduced. Apparently, in this range of concentration flow of xylem sap from the roots to the shoots may be reduced by the high osmotic potential of the root environment and consequently, NaCl supply of the leaf salt glands could be lowered. It is also possible that under such conditions the secretion mechanism per se is affected. Thus inspite of higher salt enflux under highly saline conditions, only little can be secreted, and such conditions consitute the upper limit where the secretion mechanism is of ecological significance.

Inspite of higher capacity of salt removal via the salt glands most salt secreting species possess a second safety mechanism in their roots for the secretion of toxic ions and for slowing down their penetration inward. A dual selection mechanism i.e. in the root and in the shoot, was reported for the transport of ions into the guttation of fluid, as well as into the secreted fluid of the salt secreting species *Aeluropus litoralis.*

Accumulation of chloride in bladders seems also to be considerable and high accumulation at high external NaCl concentration was reported. However, inspite of ecological significance that are many try to attach to such an accumulation that the total mass of bladders seem to be too small to remove appreciable amounts of salts from the mesophyll of *Atriplex* leaves throughout the plant life span.

Inspite of the series of mechanisms found in different plants for regulation of salts in shoots, it seems that each of the mechanisms is limited in its capacity. Evidently the results are a limitation of plant distribution in saline habitats.

Effect of Oxygen Pressure :

Since the secretion mechanism seems to be an active one, anaerotic conditions have considerable effect and inhibited secretion process altogether (Arizs et al. 1955).

Effect of Light :

Arisz et al. (1955) first reported that salt secretion in *Limonium* leaves was light dependent. Transferring leaf disks from light to the dark resulted in a shear decrease in rate of secretion. It occurs only under specific conditions. Positive response to light (Pollak & Waisel 1970) of detached leaves gave result effect is dual. A direct effect may couple light induced electron transport to ion transport. Light may also affect secretion indirectly by changing transpiration rates and rate of flow of xylerm sap.

II. Adaptations of Flooding with Fresh Water :

Plant may adapt metabolically to tolerate anoxia (truly anoxia tolerant) adapt morphologically and physiologically to avoid anoxia (apparently anoxia tolerant) or may not adopt and succumb very quickly to anoxia (anoxia intolerant) (Vartapetian 1978).

A few plant species that tolerate prolonged soil flooding exhibit both metabolic and avoidance traits (Hook et.al. 1971, John & Greenway 1976, Vartapetian et.al., 1978, Hook & Scholens 1978, Davies 1980, Kozlowaski 1982) which suggest that flood tolerance is not conveyed by a single adaptation but rather by a combination of adaptations. Hook and Brown (1973) showed for pine hardwood tree species that relative flood tolerance was a function of a number of degree of refinement of adaptations the species exhibited. Although classifying species into three tolerance types may be helpful for sorting out the basic mechanisms of flood tolerance, they have limited practical value for segregating species on the basis of relative flood tolerance. For instance, Vardapetian et.al. (1978) showed that nitochondria of roots of cotton (Gossypium hirsutum relatively tolerant of flooding) maintained their ultrastructure longer under anoxia than those of rice (Oryza sativa very tolerant to flooding) hence former appears to be the most flood tolerant. Apparently the tolerance of rice to flooding is strongly related to its capacity to transport oxygen to the rhizosphere; that is avoid anoxia (Van Roalte 1940, Armstrong 1969, Karan 1974). The adaptations that enable plants to tolerate or avoid anoxia are fairly common among vascular plants. This suggest that there are few morphological, physiological and biochemical solutions to the problem of plant life in a periodically flooded habitat.

A. Seed germination :

It has long been known that seeds of land plants will not germinate under water and that they lose their vitality quickly under such conditions (Crocker & Davis 1914). Germination of seed under water may be beneficial or hazardous, depending on the depth and duration of inundation (Kramer & Kozlowaski 1979). Seeds of rice and some other lowland species germinate under water and if the water is shallow enough for the shoot (coleoptile in rice) to extend above water surface, root growth will be initiated (Nagai 1916, Sasaki 1930, Edwaris 1933). If the duration is not sufficient to cause injury to the germinating seedling it may be an advantageous position over competing vegetation whose seeds germinate only after the water level recedes. However, where flooding is deep and prolonged as in the swamps of United States, seed germination under water is hazardous because few species can withstand prolonged submergence of the foliage. Seeds of species that dominate these swamps do not germinate under water. Natural regeneration in swamps is usually limited to drought periods when the soil surface is exposed. This occurs only under prolonged droughts. Swamp tree-species typically grow rapidly in height in the first year or two. The rapid juvenile growth is believed to be an inherent trait of such species. In that it enables them to extend their foliage as high as possible before the normal flood level returns (De Bell and Nayler 1972, Hook et al., 1983). A number of bottomland hardwood species may germinate under water (Du Barry 1963). The flooding regime on such sites is usually shorter and shallower than in swamps. Hence germination under water may have some ecological significance.

B. Growth and Dormancy :

It has been recognised for some time that dormant plants are not susceptible to flooding damage (Broadroot and Williston 1973). In the Mississippi Delta of U.S. some tree species such as overcup oak (Quercus lyrata) green-ash (Fraximus penisylvania) and water hickory (Carya aquatica) do not leaf out until almost a month later than the other hardwoods in the surroiunding uplant areas and thereby avoid growth during prolonged flooding. These delayed emergence typically occur in areas of backwater flooding (areas subjected to flood water that is backed into an area by a rising river and that may be retained in the area for an extended period).

Some marsh plants such as Typha species may exhibit a response opposite to that of tree species. They tend to emerge very early in the spring and complete most of their growth before the soil temperature rises and the soil becomes highly reduced.

C. Morphological Characteristics :

A stem hypertrophy : Hypertrophy is observed in some herbaceous species such as tomato and sunflower and on several tree species such as tomato and sunflower and on several tree species (Bala appress, pond cypress swamp tapelo, Eucalyptus globulus, red maple, green ash, Fraxinum penisylvania, white ash (*F. americana*) to lesser degrees but it has not been clearly substained as an adaptation. However, it appears that stem hypertrophy in conjunction with knees and exposed roots is important in faciliating internal acration of the roots of swamp tree species, the wood of swollen buttresses does not have aerenchyma but it does have lower density, larger cells more parenchyma than noninundated wood of the trunk (Penfound 1934). The changes in anatomy probably increase intercellular species and make them more pervious to gas. In sunflower and most herbaceous species, stem hypertrophy is associated with enlargement of cortical layer (Kawase 1981). Enlargement of lower stem appears to increase the surface area of previous tissue near the flood line and therefore, increases the surface area over which O_2 may readily diffuse into them.

Stem hypertrophy that occurs in association with flooding appears to be caused by an interaction of ethelene and auxins that is more or less controlled by the flooding or water effect (Wample and Reid 1979). Although ethylene was transported through root to stem in tomato plans, only a small quantity of amount artifically applied was transported. In addition Ethylene rapidly escapes from the stem through lenticells (Chirkova and Gutman, 1972 Zeroni et.al. 1977). Bradford and Yang 1981) hypothesised that insufficient ethylene would be transported to the shoot to account for epinasty in flooded plants. They concluded that anaerobiosis inhibits ethylene production, hence little ethylene is produced in flooded roots. On the other hand they found that Ethylene precursor, 1, Amirocyclopropane-1, carboxylic acid, carboxylic acid (ACC) was stimulated under anaerobiosis and was readily transported in the xylem sap. The precursor, ACC, in the presence of an enzyme that is constitutive in many plant tissues, is converted to ethylene in presence of O_2. Therefore, they proposed that under flooding conditions and anaerobiosis in roots, ACC is produced and transported upward in the xylm sap. On exposure to O_2, ACC is converted to ethylene in quantities sufficient to cause epinasty and other physiological effects. Their theory perhaps explains stem hypertrophy. It is known that flooding causes IAA to accumulate in flooded tissue in sunflower (Phillips 1964, Wample & Reid 1979) and that IAA and ethylene in conjunction stimulate hypertrophy (Wample & Reid 1979). Hence it appears that the signal that Wample and Reid (1978,1979) suggested is transported from the root probably is ACC. When ACC reaches the acrated position of the stem, ethylene is produced and causes IAA to accumulate. The two hormones working in conjunction could contribute to development of stem hypertrophy. Unfortunately data for this process in woody species are lacking.

(i) Knee and Pneumatophores :

Knees primarily occur on bald aypress and pond cypress and are the result of meristematic growth on the arched upper (adaxial) side of the root. Because knees primarily occur on sites where the water table fluctuate (not in lakes or dry land). It appears that the tissue is stimulated to grow by repeated cycles of anaerobioss and acration (Penfound 1934, Whitford 1956). Although no data exists to varify it, such growth may be a direct response to ACC accumulating on the adaxial site during the anaerobiosis and conversion of ACC to Ethylene during the aerobic phase.

The role that knees play on trees in flooded habitats is not clear. They do not occur on cypress trees growing in lakes, where the need would be greatest for acration. Kramer et.al. (1952) concluded that knees did not aid in aerating the remainder of the tree, on the other hand, it is known that gas exchange occurs freely through knee (Kramer 1969, Clowes 1975). It seems probable that knees are beneficial if they occur but are not necessary for survival.

Pneumatophores on black mangrove (A. nitiada) provide O_2 to submerged roots in relation to tide cycle (Scholander et.al. 1955) hence they are beneficial in acrating the root system of the tree in its natural environment, primarily in the intertidal zone.

(ii) Roots :

Several distinct forms of roots regenerate in flooded plants. Failure to distinguish between these has led to a misunderstanding the function of different root types in relation to flooding. The most common type of root regeneration is in the development of adventitions roots on the stem above the soil usually within flooded zone. They are initiated directly on the stem, and are designated adventitious water roots.

(iii) Water Roots :

The second type of root regeneration occurs in the soil. This type of development is less common, or less frequently reported, for only a few researches have reported their findings such that these distinctions can be made and they usually have dealt with rice or woody species (Hosner and Boyce 1962, Yu et.al., 1969, Hook et.al. 1971, Couts and Philipson 1978a-b, Keeley 1979, Alya et.al.,1980). The typical sequence is observed that on flooding, the original roots die back to major secondary roots or the primary roots and new roots are initiated from these points, Heek et.al. 1971, Coutis and Philipson 1978a-b). These are designated as soil water roots.

The third type of root produced in response to flooding differs micrologically from the original roots. For example in swet gum (Liquidamber styraciflua) the new roots are more succulent and almost clear in appearance as compared to the original roots (Hook and Brown 1973) the new roots are designated altered soil roots.

Still another response to flooding involves death of all or most of the root system without production of new roots. Obviously plants exhibiting such response are intolerent to waterlogging and die if flooded condition persists. Most agronomic plants exhibit this response as do some tree species namely yellow poplar- Ciriodendron tulipifera (Hook and Brown 1973) and to a lesser extent, Silka sprice Picea sitchensis (Coults & Philipson 1978a,b). The rooting traits of Neatlhland species are so complex, specialized and dependant on habitat that no attempt is made to include them here.

Adventitious water roots have been observed on many species, Tomato, Sunflower, corn which develop adventitious water roots, tolerate flooding or recover from flooding damage more quickly and completely than when such roots are experimentally removed. Epinasty was less pronounced and shoot growth was retarded less where adventitious water roots were left intact than when they were removed (Jackson 1955, Drewetal 1979, Wenkert et.al. 1981). However, Wample and Reid (1978) found no apparent contribution of adventitious water roots to survival of flooded sunflower plants. Similarly, experiments on woody species have led to conflicting results. Gill (1975) found that removing adventitious water roots from flooded Alnus glutinosa had no significant effect on shoot growth, lateral shoot number, leaf dry weight and bud number. That treatment appeared to reduce leaf number. However, Senagoules and Kozlowski (1980) found that Faxinums pennrylvania seedlings with adventitious water roots had higher water absorbing efficiency than seedlings without advantitious water roots, and there was a correlation between adventitious water root and stomatal reopening.

For highly flood tolerant species, the soil water roots probably became the primary root system and enable the flooded trees to flourish (Hook et.al. 1971, Keeley 1979, Alvaetal 1980). Soil water roots on rice penetrated 30-40 cm into a flooded soil (Yu et.al. 1969). In lodgpole pine (Pinus coronata) the roots penetrated upto 16.7 cm into a waterlogged peat soil at $10^{o}C$ but at $20^{o}C$ penetration was greatly reduced (Coutis and Philipson 1978a-b). It appears that the tendency of Wetland species to develop soil water roots may account for their capacity to withstand the alternating flooding and drying of the Wetland site. Apparently roots harden off during dry periods and lose the capacity to oxidize their shizosphere (i.e., the roots grown under well-aerated conditiona do not allow to oxidize their shizospheres (Hook et.al. 1971). Presumably on reflooding, initial roots die back and soil water roots develop that oxidize their shizosphere. Keeley (1979) found that the soil water roots of swamp. Tupelo also tended to harden off within one year after flooding, and there was a net increase in O_2 diffusion rate from 1 month to 1 year age. Responses of mature swamp Tupelo and bald cypress trees in the field substantiated that soil water roots developed where the flood level substantially increased (Harms et al. 1980). Pinus sylvestris trees also oxidize their shizosphere (Armstrong & Reid 1972). Mostly woody species that develop soil water roots also have adventitious water roots.

In semi controlled experiment Hook et.al. (1970b) found that many adventitious water roots formed on swamp and water tupelos that were flooded with moving water, but few or none developed after flooding with stagnant water. Also, in pondsites (stagnant water) Atlantic coastal plain swamp tupelo trees seldum developed adventitious water roots but do so profusely in head water and slough swamps, where the flood water is usually moving (Hook 1968). Hummocks do not develop in ponds around the swamp tupelo trees but they do in headwater swamp. Apparently the adventitious water roots are not only stimulated by moving water but are functional in trapping debris and soil from moving water and thereby overtime build hunmock around the base of the tree. This process permits a position of the roots to remain above the general food level.

In herbaceous and woody species, adventitious water roots may reduce flooding damage, but data substaning such effects are somewhat conflicting circumstancial evidence from field observation indicates that they help build hummocks around some tree and thereby may become permanent roots of the tree. On the other hand soil water roots appears to be a major part of root system in rice and some tree species that are extremely toleranct to flooding and therefore may be of utmost importance to survival and growth of such species in wetland habitats. Their rate in other species is not known. In Zea mays the original roots died back and new roots did not develop in the soil, but adventitious water roots penetrated the flooded soil and the plants survived upto 13 days of flooding (Wenkert et.al. 1981). The function or value of altered soil roots is not known. The only species that has been reported to exhibit this type of root response (sweet gum) will tolerate relatively long periods of flooding but its growth is severely reduced.

Explanations of development of adventitious water roots are similar but differ slightly from that of stemhypertrophy in regard to which hormones are most important. Wample and Reid (1975, 1979) hypothesized that the higher Ethylene concentrations in stems of plants with flooded roots cause auxins to accumulate, in conjunction with other factors coming from leaves (such as carbohydrates) that cause adventitious water roots to develop on sunflowers. They attributed the major rooting signal to auxin and other leaf factors. Jackson et.al., (1981) and Drew et.al. (1979) reported that Ethylene stimulated adventitious water rooting of maize, but they could not exclude the possibility that Ethylene interacted with other growth hormones to stimulate rooting.

D. Anatomical Characteristics :

Considerable evidence shows that plants that tolerate prolonged soil flooding transport O_2 to the shizosphere more readily than plants that are not tolerant to water logging (Van Realte 1940, Berber et. al. 1962, Armstrong 1968, 1969, Hook et. al. 1971, Coults and Armstrong 1976, Keeley 1979). For O_2 transport to occur, there must be continuity in intercellular space between atmosphere and shizophere and the intercellular space must be sufficient in volume to account for the gas movement. Although mass flow of gases apparently occurs in the floating water lily (Nupharluteum macrophylla and N. lentersu-Variegatum) (Decay 1981, Decay & Klug 1982). The majority of vascular plants are acrated by static gas phase diffusion (Armstrong 1978, 1979). The site of entry and pathway of O_2 diffusion varies considerably among species. In woody species O_2 appears to enter the plant primarily through the lentice (Armstrong 1968, Hook et.al. 1971) although

Chirkova (1968) reported that leaves and lenticels are a source of O_2 entry into rooted cuttings of willow (Salix alba) and poplar (Populus petro Waskiana). In nonwoody plants the point of entry is more obscure, but in general the leaves appears to be more important as a site of entry than is the case in woody plants (Sifton 1945, Soldatenkov and Hsiun-Teran 1961, Chirkova & Soldatenkov 1965, Greenwood 1967). The coleospitile of rice serves as the entry for O_2 to the germinating rice seed whether it germinates under water or in air (Kordan 1976). The difference in size of woody and nonwoody plants may be a factor as to which entry point is most important.

(i) Stomata

Stomata are the gas exchange ports of leaves and are an entry point for O_2 and other gases. Stomatal closure and reduced leaf growth in herbaceous species may be most rapid external plant responses to flooding (Pereira & Kozlowski 1977, Werkertl et. al. 1981). Hence stomatal closure could be especially important in species that depend on internal acration entirely through the leaf and possibly in young tree seedlings. Pericra and Kozlowski (1977) found considerable variation among woody species in how quickly stomata closed and reopened. Similar variability may exists in nonwoody plants also.

(ii) Lenticels

Lenticels become hypertrophic on stems within and just above flood zone (Devaux 1900, Templeton 1926 after Sifton 1945 and Hook et.al. 1970a). The hypertrophic lenticel is composed primarily of complementary cells having one or more closing layers at varying distances from the phellogen. The closing layers all have large breaks and provide little or no resistance to gas diffusion. Also, the phellogen appears to be previous to gas diffusion, in swamp and water tupelo for the active cells are Spherical in shape and have columner arrangement (Hook et.al. 1970a). This would provide the largest amount of intercellular space per unit cell size (Kawase 1981). These changes in the anatomical structure of balicels in relation to flooding increase the size of cutical appreciably and the amount of intercellular space, therefore, they would appear to enhance internal acration.

(iii) Intercellular Space :

Internal acration arises through lysigenous/schizogenous processes (Mc Pherson 1939, Siphton 1945, de Wit 1978, Kawase 1981). Generally intercellular space is more evident in cortical tissue than in xylem tissue, but it does not occur in xylem tissue in some woody plants. Development of intercellular space in the cortex of roots of Barley (Hordecum vulgare), (Bryant 1934), Corn (Zea mays) (Mc Pherson, 1930) and Pinus sylvestris (Armstrong & Reid 1972) is assumed to provide pathway for O_2 diffusion in these species but development of large intercellular spaces in the stele of roots of lodgepole pine (Coults & Philipson 1978b) and Lololly pine (Pinus taeda) (M.R.Mckevlin and D.D.Hook unpublished) apparently provide for limited gas diffusion in these species. Numerous herbaceous crop plants (Mc Pherson 1939 Greenwood 1967), Marsh plants (Bergman 1920, Coults and Wallance 1958, Armstrong & Boatman 1967) and woody plants (Armstrong 1969, Hook et.al. 1971, Chirkava & Gutman 1972, Armstrong & Reid 1972, Philipson & Coults 1980) transport O_2 to their roots. In addition flooding causes root porosity to increase in many species (Mc Pherson 1939, Schramm 1960, Yu et.al.1969) as well as lentical formation and stem hypertrophy, as discussed previously.

Based on evidence of O_2 diffusion from shoot to root and increased porosity of cortical and some steler tissues, large number of species of vascular plants appear to have well developed internal acrating system.

The stimulus for intercellular space development appears to be associated with increased ethylene concentrations and increased cellulase activity in the tissue. Kawase (1981) presented a partial explanation of how flooding stimulates acrenchyma (intercellular space) to develop. Cellulase may play a role in cell softening but not in cell extension (Kawase 1981). It seems probable that because IAA also tend to accumulate in tissue under an aero biosis, it may be involved with ethylene and cellulase activity in intercellular space development. However, Kawase (1981) noted that there is a different response among cortical cells to cellulase activity, and as yet there is no suitable explanation why under this scheme some cells become stronger and increase in size while others become weaker and die.

E. Oxidation of Rhizosphere :

For the wetland plants, oxidation of rhizosphere is important even if not crucial to its survival (Armstrong 1978, 1979, Coalts and Philipson 1978b, Hook & Scholtens 1978) Plants of wetland live with their roots in highly reduced soils that contain numerous gas compounds, organic, inorganic phytotoxic compounds. Hence, in large part their survival depends on their capacity to transform soil-borne toxins to less harmful products. Such transformations are usually oxidative and thereby related to internal acration and oxidative capacity of roots (Armstrong 1979). Permeability of roots in wet land species to O_2 decrease rapidly with increasing distance from the root apex (Armstrong 1964) and O_2 diffusion may cease 2 cm distal from root apex (Armstrong 1979). Such decreasing permeability distally from root apex is important, otherwise aerobic pollutions of organisms could build up overtime along the oxidized zone and exceed the capacity of roots to supply O_2 radically from the root. As a consequence the radially oxidized zone could collapse and permit an influx of phytotoxins. Because only growing tip oxidizes its surroundings. Microbial population do not have the opportunity to overpower it as it moves through the soil (Armstrong 1979).

Rhizosphere oxidation occurs only when internal respiration demands are exceeded and root tissues are permeable to radial diffusion of O_2. This process is migrated by increased porosity of roots, which not only reduces the amount of respiring tissue per unit area but also decreases resistance to the longitudinal and radial diffusion. The radias of oxidation zone aroung the root also depends on soil reduction rate and O_2 demand.

Root respiration rates is greater at root tip and decreases distally to the apex until it stabilizes about 3-5 cm distal to the apex (Armstrong and Gaynard 1976). Hence the internal O_2 loss to respiration is minimized along most of the O_2 diffusion pathway. This tends to provide for diffusion of a higher O_2 concentration to the root apical region.

Using equations developed from Fick's laws of diffusion, Armstrong (1979) illustrated the effect of porosity of plant tissues and O_2 consumption on the length of O_2 diffusion pathway in plants when an effective porosity of 60% and plant O_2 consumption of 1 mg cm^{-3} of tissue per second, the maximum diffusion path would be 250 cm. Such extremely high porosity and very low O_2 consumption probably would occur only in the roots of hydrophytic species such as rice, Eriophorum angustifolium and swamp tree species. The stem or trunk of wood species would likely to have a much lower porosity. Coults and Armstrong (1976) proposed that gas filled vessels and Tracheids may be important in longitudinal diffusion in woody species. Couts & Philipson (1978a,b) demonstrated with excised mature roots of lodgepole pine that O_2 would diffuse through the xylem tissue of root but would diffuse further if the bark were kept on the roots. Hook and Brown (1972) showed that air could be pulled through xylen element of species nontolerant of water logging at lower tensions than through the lenticels. This indicated that there was less resistence to the longitudinal flow in the xylem of non tolerant species than cambium. However, oxidation of the shizosphere of Nyssa aquatica (a flood tolerant species) was less pronounced and occurred more slowly when the stem was girdled, forcing O_2 diffusion through only the combium xylen pathway. In non girdled stems O_2 was free to diffuse through the Cortex and combium-xylem pathways (Hook and Brown 1972).

Oxygen diffusion from the shoot through the root appears to account for root penetration of rice upto 35 cm in flooded soils (Voloras and Letey 1966) and theoretically upto 250 cm in woody species (Armstrong 1979) yet even these distance are inadequate to acrate the lateral roots of mature trees and probably, some herbaceous species under all water logged conditions.

For adequate lateral root acration, entry of O_2 from source other than the stem would appear to be beneficial. It is in this context that the porous knees of bald cypressand the exposed roots of tapelos (Penfound 1934) appear to perform beneficial function. One can theorize that their removal would not kill the tree, as O_2 diffusion through the stem would be adequate for survival. The presence of knees at varying distances from the trunk would greatly aid in acrating lateral roots that may be 5-10 m or more from the trunk. However, these structures would fail to provide adequate acration under deep and prolonged flooding (1-2 m) deep which occur fairly regularly in some swamps. Hypoxia or anoxia in the root environment appears to set off a chain reaction of enzymatic and hormonal responses in the roots in which some compounds may be quickly transported to the shoot. These signals from the root may quickly reduce growth and transpiration. If the species genetic capabilities are lacking these compounds seem to be generated in quantities or qualities that spell immediate death to the roots and eventually, to the entire plant. If the genetic capabilities are present compounds such as ethylene or its precursor ACC, abscisic acid, cellulase, IAA and carbohydrate seem to work in various combinations to stimulate immediate development of adventitious water roots and or soil water roots acrenchyma or intercellular space lenticels and stem hypertrophy, which thereby increase the capacity of plants to transport O_2 from the shoot to the root. In the process, aerobic respiration is usually accelerated or stabilized at some metabolic level that provides the root with an energy source to carry on nutrient uptake. Because less tissue is synthesized under flooded conditions, less energy is required. However, if flooding persists, the internal acration must develop such that through some aerobic respiration needs of the root are met and sufficient nutrient O_2 diffuses into the surrounding reduced soil to oxidize, reduce nutrients and transform toxic to less harmful products.

F. Metabolic Adaptations :

Metabolism

The presence of well developed acration systems such as those in tupelos, rice and Spartina alterniflora are not sufficient to avoid anoxia in roots under all field conditions when stomata close/and or the soil becomes highly reduced about - 200 mV redox potential (En), anaerobic metabolism of roots increases substantially (John and Gireaway 1976, Mendelssolm et.al. 1881). In the intertidal salt marshes species Spartna alterniflora alcohol dehydrogenase (ADH) activity was much higher in plank growing in soils with an Eh ofabout - 200 mV than in those closer of tidal streams where the En was 200-300 mV energy charge was also closely correlated with En soil and ADH activity of roots (Mendess Ohn et.al. 1981). Root anaerobisosis is probably even more pronounced in swamp tree species, as mentioned previously, when deep seasonal flooding of 1-2 m covers the lower trunk and all knees and exposed roots for a few days to a few weeks.

The root apices of many species contain end products of anaerobic respiration even when grown in well acrated conditions, apparently the result of compact structure of cells in meristematic regions (Armstrong 1978 Crawford 1978), Smith and Rees (1979), Varlapetian (1978) pointed out aptly that aerobic respiration succeeded anacralic respiration in the process of evolution but did not suppress it. Aerobic respiration is built as a super structure on the anaerobic foundation and in the absence of O_2 switched off. If an organism retained the appropriate enzymes, the anaerobic process (glycolysis) will continue to function, albeit at a lower efficiency per unit of carbohydrate metabolized.

Considering anaerobic respiration a beneficial mechanism for adoptation to a flooded habitat has been criticized because of the inefficiency of anaerobic metabolism (Yields only 2 ATP per glucose molecule verser 38 ATP under aerobic conditions) and because some products of anaerobic respiration are presumed to be phytotoxins. The chemistry of metabolic adaptation has been reviewed in depth (Ganford 1978, Davies 1980). Therefore, this section concentrates primarily on general mechanism of mechanical adaptation.

Several theories have been advanced to explain the mode of metabolic adaptations of plants to flooding (Crowford 1966, 1967, Crawford and Mc Manmon 1968, Crawford & Tayer 1969) but have been modified byCrawford (1978) into two basic explanations. The response observed depends on the degree of flooding stress the plant is capable of substaining. The first type of adaptation consists of plants that tolerate limited seasonal flooding and adopt metabolically to hypoxia or short term anoxia by accumulating malate as major and product of anaerobic respiration and by controlling the rate of glycolysis ethanol toxicity is reduced, but malate production via glycolysis does not result in yield of ATP, energy yild is reduced per unit of carbohydrate metabolized also. Hence this type of adaptation is only valuable for short term periods of flooding.

In the second type of adaptation, it is proposed that plants during growing season, adopt by stimulating glycolysis, ethanal production and ATP synthesis. The toxicity is avoided by loss of ethanal through the root and malate is not accumulated to a significant degree. This scheme known to fit the known responses of plants better than previous ones, but it still has some flaws, swamp tupelo, a highly flood tolerant tree species, loses about 55% of ethanol from its roots, whereas Loblolly pine (moderately tolerant) loses about 85% of the ethanol. Also both species accumulate ethanol and malate, although ethanol appears to be the primary end product (Hook et al

1983) as it is in rice (Avadhani et al 1978, Smith and Rees 1979, Mocquot et.al. 1981).

It is also argued that malate production is beneficial because it is less toxic than ethanol and it may function in transferring O_2 deficit from roots to shoots by its upward transport in xylem sap. Crawford (1978) and Avadhani et.al. (1978) reported that the malate present in rice seedlings was not rapidly consumed when they were exposed to air, which raises some doubt as to the efficiency of this process. In contrast, ethanol is rapidly metabolized on exposure to acrated conditions (Rouse 1966, Effer & Ranson 1967). Keeley (1979) suggested that malate may accumulate in response to anionic imbalance resulting from flooding, but Avadhani et al.(1981) found that the maximum amount of malate produced in rice could not account for more than 40% of the electrical balance of Kin rice coleoptiles. But in support of Crawfords strategy Avadhani et al (1981) found that rice cells accumulated more malate at low O_2 tensions than in air or nitrogen.

Amino acid compositions of roots and plant sap are significantly altered by anerobiosis in roots. In pumpkins (<u>Cucurbita</u> sps.), Tomato (<u>Lycopersicon</u> sps.) and Willow (<u>Salixcinera</u>) root anaerobiosis resulted in increases of glutamic acid amino butyric acid and alamine and decreases in glutamine relative to the amount in acrated roots (Subinina 1961). Glutamin synthesis and increased alkanine synthesis under hypoxia have been reported in other species and were attributed to a low energy charge and high pyruvate concentrations (Kohl et al. 1978). Also CO_2 concentration which accompanies ethanol fermentation favours synthesis of Yaminobilyric acid via alfa-keto-glutaric acid and glutamate (Zemlianukhin & Ivanov 1978).

The persistant concern over the toxicity of ethanol to plants seems to be largely unfounded. Because ethanol is not localized, it is readily eliminated from cells (Davies 1980). Furthermore, anaerobiosis appears to increase membrane permeability thereby faciliating the elimination of metabolites (Cransford 1978, Smith apRees 1979, Hook et al. 1983). In addition, the tissues of species tolerant to waterlogging appears to withstand high concentrations of ethanol with little adverse effect (Chirkova 1978). The mechanism for this increased tolerance, that exists is not well understood but may be related to interaction between enzymes that regulate the cell pH (Pradet and Bonsel 1978, Zalmlianettchin and Ivanov 1978) and or induction of quasi-dormancy in tissue (Rowe 1966). Drew and Lynch (1980) concluded that as yet ethanol has not been identified as factor in waterlogging injury to roots or shoots.

Accumulation of organic acids occurs under anaerobiosis and potentially could induce toxicity. However, this is apparently prevented by pH state in the cells. For instance, if the malic enzyme and PEP carboxylase are present with malate dehydrogenase, they interact to control pH. If the pH rises the carboxylating system is stimulated and decarboxylation is reduced and the reverse occurs if the pH falls (Davies 1980).

G. Energy Charge and Regulating Mechanisms :

Pradet and Bomsel (1978) pointed out that adaptation of plants or other organisms to changing environmental conditions involves both coarse and fine control mechanisms. The coarse control occurs at the gene level and requires a long time to become effective. But the find control mechanisms, which involve reactions between enzymes and substrate already present in the cell, respond almost instantaneously.

The energy charge of cell seems to function as a fine control mechanism and appears to have some implications in measuring adaptation to environmental changes. However, there is some controversy among researchers as to whether concentrations or ratios and mole fraction of adenine nucleotides is more important (Davies 1980). The energy charge is defined as the concentration of various adenine nucleotides.

Spartina alterniflora showed reduced growth and metabolic adaptations along a transect perpendicular to a tide stream in a Louisiana salt marsh, apparently in response to increased hypoxia (Mendelssohn et al. 1981). Growth was best near the stream where soil Eh was 300 mV, root energy charge height (0.8) and ADH activity and malate concentration in roots low. About 8 m from the stream, growth was slightly reduced Eh was about 100 mV, malate concentration was higher, and energy charge was near zero.