REVIEW ARTICLE

COPING WITH EXCESS SALT IN THEIR GROWTH ENVI-RONMENTS: OSMOREGULATION AND OTHER SURVIVAL STRATEGIES DEPLOYED BY THE MANGROVES.

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INTRODUCTION

Mangroves are defined here as a collection of woody plants and the associated fauna and flora that use a coastal depositional environment. Mangrove forests consist of plant communities that belong to many different genera and families that are not always related phylogenetically. However, they share some common characteristics based upon physiological, reproductive and morphological adaptations that enable them to grow in a broad range of coastal environments in the tropical and subtropical areas of the world. By this definition, they occupy the interface between the land and the sea (Walsh, 1974). Throughout the world, approximately 54 species of plants belonging to about 20 genera in 16 families have been recognized as belonging to the mangroves (Tomlinson, 1986). The mangrove forests of Pakistan consist of 8 species in the Indus River delta region and 5 species along the Makran Coast. However, the species of the genus *Avicennia* are the dominant members in both these areas and represent 90-95% of the total mangrove vegetation (Snedaker, 1984).

Jennings and Bird (1967) have described the six most important geomorphological characteristics that affect estuaries, and they are: (1) aridity, (2) wave energy, (3) tidal conditions, (4) sedimentation, (5) mineralogy and (6) neotectonic effects. All of these directly or indirectly affect the establishment of mangroves. Walsh (1974) and Chapman (1975, 1977) have described in all seven characteristics that may be considered as essential requisites for mangroves on a world-wide basis; (1) air temperature (within a restricted range), (2) mud substrate, (3) protection, (4) salt water, (5) tidal range, (6) ocean currents, and (7) shallow shores.

Successful establishment of mangroves in the coastal environments necessitates dealing with such factors as flooding, salt stress, tidal abrasion and deposition, nutritional ion imbalance, oxygen deficiencies, reducing environments, specific ion toxicities and low water potentials. The variable nature of these factors requires physiological, morphological and phenological adaptations in the generally stressful and harsh coastal environments. Thus the productivity and distribution of plants which are found growing in saline environments are closely related to soil edaphic conditions. While no halophytic species have developed all of the successful adaptation stratgegies, some of those listed below are regarded as necessary for survival in saline environments: osmotic adjustment at the cellular level, ion compartmentation, succulence, salt glands, salt hairs, ionic exclusion at the root, tolerance to the dominant specific

ions as well as tolerance to heavy metals, poorly aerated soils, reducing environments and low nitrogen availability (Ungar, 1991).

In this paper I will primarily focus on the effects of fresh and salt water on the growth and propagation and the long term survival of mangrove species. It should be pointed out that most mangroves are not obligate halophytes, although a number of them exhibit their optimal growth in the presence of some amount of sodium chloride (Stern and Voigt 1959, Connor 1969, Sidhu 1975 a,b). Both Walsh (1974) and Chapman (1975, 1977) have argued that the real role played by salt is in the limitation or elimination of competition by the faster growing glycophytes since mangroves, being slow growing, cannot successfully compete against them. Therefore, I will elaborate upon the specific mechanisms utilized by the mangroves in maintaining a suitable osmatic balance for proper physiological functioning.

In this discussion, I draw upon the knowledge which has been previously acquired from studies of other species which also may have to cope with high salt concentrations. Often, such studies have been more thoroughly carried out with unicellular prokaryotic and eukaryotic organisms than in higher plants, mainly because of the ease with which growth and physiological studies in such organisms can be performed under a variety of controlled environmental conditions. Finally, the process of osmoregulation will be closely examined. This process is universal in that virtually all living organisms may have to contend with it during some part of their life cycle but which is more highly evolved in organisms which must grow in saline and stressful environments. Therefore, this process will be examined with concerted attention.

MECHANISMS OF OSMOTIC ADJUSTMENT AND OSMOREGULATION IN CYANOBACTERIA:

Cyanobacteria (blue-green algae) live in different environments that can differ gratly in their salinities. Therefore, many studies using cyanobacteria focus on the elucidation of the mechanisms of halotolerance. For definition purposes, it should be mentioned here that when the external salt concentration is diluted it results in the development of hypo-osmotic conditions and an increase in this concentration results in hyper-osmotic conditions.

MacKay et al. (1983, 1984) studied the formation of osmoregulatory solutes in 36 cyanobacteria from a wide range of habitats. Cyanobacteria from all habitats and taxonomic groups were found to accumulate organic osmoregulatory solutes. The chemical class of the solute correlated with the salt-tolerance and habitat of the strain. Predominantly freshwater strains only accumulated simple saccharides, mainly sucrose and trehalose, while marine strains accumulated the heteroside 2-O-a-D-glucopyranosyl-(1-2)-glycerol, and hypersaline strains accumulated sucrose and/or trehalose with glycine betaine or the novel solute L-glutamate betaine (N-trimethyl-L-glutamate), or they accumulated glycine betaine alone. These authors have suggested that an examination of osmoregulatory solutes may be useful in the numerical taxonomy of cyanobacteria.

OSMOTIC ADAPTATIONS IN BACTERIA AND IN EUKARYOTIC ALGAE:

A common mechanism of osmotic stress adaptation in bacteria is the rapid intracellular accumulation of organic compounds (osmolytes) which results in the restoration

of turgor (Yancey *et al.*, 1982). The halophile *Ectothiorhodospira halochloris* synthesizes and accumulates glycine betaine in the cytosol, presumably to protect the cell against its highly saline environment (Galinski and Truper, 1982). Recently Smith *et al.* (1990) studied the osmoregulation properties in *Agrobacterium tumefaciens*, a soil phytopathogen and found that the accumulation of a novel disaccharide (mannosucrose) is controlled by osmotic strength and glycine betaine. Thus osmoregulation of *A. tumefaciens* may play a potential role in the transformation of plants.

The unicellular marine algae *Phaodacytlum tricornutum* and a number of other species synthesize and accumulate glycine betaine and proline in response to increasing NaCl concentrations (150 to 1000 mol m-3 NaCl) in the growth medium. Also K^+ concentrations in the algae are found to be 3-6 fold greater than the Na^+ concentration (Dickson and Krist, 1987 a,b). From these studies it can be concluded that marine unicellular algae achieve and maintain osmotic equilibrium primarily by the synthesis of organic compounds, uptake and accumulation of K^+, and partial exclusion of Na^+. Such results concur with the conclusions drawn upon by Wyn Jones and Gorham (1983) for the mechanisms of cytoplasmic osmoregulation in higher plants.

MECHANISMS OF INDUCTION OF SMALL MOLECULAR WEIGHT ORGANIC COMPOUNDS AND THEIR ROLE IN PHYSIOLOGICAL PROTECTION:

One of the most intensively studied systems is the production of isofloridoside as a response to increased external ion concentration in *Poteriochromonas malhamensis*, a freshwater flagellate (Kauss, 1979). In this organism it has been observed that activity of a key enzyme, i.e. isofloridoside synthase increases when these cells are subjected to hyperosmotic conditions. This activation proceeds in many steps in a cascade-like manner such that a very fine regulation of this system is possible. The trigger step is located in the plasmalemma. Through a Ca^{++} calmodulin-complex, an endogenous protease is found to be activated which in turn stimulates the increase in isofloridoside-synthase activity (Kauss and Thompson, 1982).

Although osmotic regulation appears to be quite complex and not all steps are understood in full detail, certain generalizations can be made:

(a) Small fluctuations in salinity (ranging from 50-150 mosmol kg -1) can be countered through the changes in internal ion concentrations. However, greater osmotic pressure is usually encountered through the synthesis of organic solutes in order to maintain cell integrity through maintenance of a constant turgor pressure resulting in constant cell volume.

(b) Depending on the milieu in the external environment i.e. whether hyper or hypo-osmotic conditions exist, different mechanisms may be invoked, resulting in either activation of ion uptake or changes in permeability, synthesis or decomposition of organic solutes.

(c) For at least the two major cell compartments i.e. cytoplasm and the vacuoles, the ions and organic compounds play different roles as osmotic and "compatible solutes".

Recent studies (Gabbay-Azaria *et al.*, 1988) also indicates that the organic solutes prevent the decrease in solubility and inactivation of enzymes which are caused by high concentrations of inorganic ions. In barley, glycinebetaine protected the enzyme malate dehydrogenase against inhibition by 0.5 M NaCl which in cyanobacteria restored the G6PDH (glucose 6-phosphate dehydrogenase) activity inhibited by 0.4 M

KCl, prevented the dissociation of ribulose-biphosphate carboxylase caused by 0.25 M KCl, and reversed the inhibition of glutamine synthetase by up to 2 M NaCl (Incharoensakdi *et al.* 1986, Hawkins *et al.* 1987, Pavlicek and Yopp, 1983). In the halotolerant cyanobacteria, *Spirulina subsalsa*, which in its natural habitat is exposed to extreme changes in the external salt concentations due to tidal and seasonal variation, a major survival strategy for this organism is to provide adequate protection of salt-sensitive metabolic activities parallel with the accumulation of osmolites. Thus the synthesis of glycinebetaine in this organism is hypothesized to serve three major functions: (1) osmotic regulation, (2) counteraction of non-specific salt effects such as decreases of solubilty and activity of enzymes, and (3) reversal of specific inhibition by NaCl at the binding site for G6P.

SALT REGULATION AND OSMOTIC COMPENSATION REACTIONS IN HIGHER PLANTS:

Compared to most glycophytic (freshwater) plants, halophytic mangroves are slow growing and thus cannot compete with them on equal terms in the absence of salt. The abundance of salt is thus regarded as the single most important factor for growth of mangroves. Seawater which contains about 35 g of dissolved salts per litre has an osmotic potential of about -2.5 MPa, and the water of the soil (porewater) often possesses an even lower (more negative) potential. Clearly, the fact that mangroves are able to grow in highly saline substrates indicates that they possess mechanisms which allow them to control the intake of salt and maintain a water balance which is physiologically acceptable.

Mangroves deal with the excess salt in their environment essentially through three mechanisms (Jennings, 1968): (1) take up very saline water and subsequently secrete salt (extrusion mechanism), (2) take up water but prevent the entry of salt (exclusion mechanism), and (3) develop tolerance to high salt loads and allow salt to accumulate in tissues (accumulation mechanism).

SALT SECRETION:

Salt secretion occurs by means of salt glands in the leaves of *Avicennia, Sonneratia, Aegiceras, Aegialitis, Acanthus* and *Laguncularia*. Glycinebetaine, an organic solute involved in balancing total leaf osmotic potential has been detected in the leaves of *Avicennia marina* (Wyn Jones and Storey, 1981). Similar osmolytes have also been reported from other mangroves with salt glands.

In *Avicennia*, salt glands are formed only under saline conditions (Mcnae, 1968) whereas in *Aegiceras* they appear to be formed regardless of whether salt is present in the medium. Joshi *et al.*, 1975 concluded that among salt-secreting species *Avicennia* is the most efficient and therefore, it is able to grow in highly saline conditions, whereas the less efficient *Acanthus* and *Aegiceras* are restricted to less salty habitats.

SALT EXCLUSION:

On the other hand, salt excluders are endowed with an effective mechanism, possibly an ultra-filter in the roots (Scholander, 1968) through which water is allowed in, but salt is mostly excluded. Species able to exclude salt are *Ceriops, Sonneratia, Rhizophora, Avicennia, Osbornia, Bruguiera, Excoecaria, Aegiceras,* and *Aegialitis*. It is

interesting to note that the salt secreting species exclude about 80-90% of the salt in seawater (Scholander, 1968) although the physiological mechanism involved in such dual functional capacities are poorly understood (Field, 1984).

SALT ACCUMULATION:

Mangrove species that accumulate salt e.g. *Avicennia, Osbornia, Rhizophora, Sonneratia,* and *Xylocarpus* are known to deposit sodium and chloride in the bark of stems and roots and in older leaves (Joshi *et al.,* 1975; Clough and Attiwill 1975). Joshi *et al.,* (1975) have shown that in certain species of mangroves, before leaf fall, sodium and chloride are deposited in senescent leaves which may be a mechanism for removal of excess salt from metabolic tissues. Downton (1982) has reported that seedlings taken from *A. marina* growing on tidal mudflats had osmotic potentials more negative than seawater, yet contained little sodium or chloride. This is accomplished by their ability to control Na^+ and Cl^- uptake and adjust osmotically by the accumulation of organic rather than inorganic solutes. After the fall of seed, salt content may increase rapidly until their root system becomes functional for ultra-filtration of seawater.

EFFECT OF HIGH SALT CONCENTRATION ON ENZYME SYSTEMS:

In considering the deleterious effects of salt on enzyme activity of mangroves and salt marsh plants, one is struck by the observation that they do not differ markedly from those of other plants. Therefore, one is confronted with the next logical question--how are such enzymes protected from the inhibitory effects of salt? This is accomplished primarily in halophytic plants by locating most of the salt in vacuoles, whereas enzymes are located in the cytoplasm where much lower salt concentrations prevail. It is obvious that if partitioning of salt in the vacuole is to take place, other solutes must be synthesized and located in the cytoplasm which are not detrimental to enzymatic structure and function and are at a sufficient concentration to achieve water potential equal to the vacuole. This is where the role of "compatible solutes" and osmoregulators such as proline, mannitol and glycinebetaine becomes of significant importance (Wyn Jones and Storey, 1981). Downton (1982) has reported that if such a osmoregulatory solute occupied a cytoplasmic volume of approximately 5-10% of the cell, this would be sufficient to balance total leaf osmotic potential.

Other compounds which have been reported as osmoregulants in various halophytes are : choline-O-sulfate, choline-O-phosphate, the amino acid proline and the sugar alcohol sorbitol. In *Avicennia germinans* and *Rhizophora mangle* (Mizrachi *et al.,* 1980) proline may be a key osmoregulatory substance. It should also be noted that certain halophytes such as *A. germinans* may preferentially accumulate some chloride in chloroplasts because this ion is needed for maximum production of oxygen during photosynthesis.

WHY IS FRESHWATER SUCH A PRECIOUS COMMODITY FOR MANY MANGROVE PLANTS?

The mangrove ecosystem and the mangrove habitat is often referred to as "physiologically dry" or "physiologically arid" which on the surface appears to be a direct contradiction of the fact that the inhabitants of such an environment often are surrounded by an adequate supply of water. However, it should be realized that the

water surrounding the mangroves is saline when compared with the internal sap concentration of mangroves and must therefore, be taken up against an osmotic gradient. Such a process is associated with an energy cost and this metabolic energy expenditure becomes part of the condition for growth and development in such an environemnt. Under such circumstances, waste of this high cost desalinated water is minimized by the development of xeromorphic features of mangroves which often resemble some of the characteristics displayed by plants of the arid environments. Conservation of water is maximized by structural development of specialized features such as thick-walled epidermis, low transpiration rates (Lugo *et al.*, 1975; Moore *et al.*, 1973) and higher respiration rates, by growing in bursts when freshwater is available and very slowly or not at all, at other times. Despite these strategies, the salinity of a given environment may be such a major metabolic burden on specimens of a given species that most of the energy is spent in maintaining proper conditions for solute transport and little remains for net growth and hence, dwarfing or stunting may result. Dwarfed mangrove systems are acknowledged to use a large portion of their energy supply for respiration and low loss recycling processes and a correspondingly smaller portion for growth and development (Lugo *et al.*, 1975).

MANGROVE ROOT SYSTEMS:

Before examining the specific effects of salinity changes in mangroves, two major problems confronting mangrove growth in the field should be fully appreciated: (1) mangroves often grow in water-logged soils that are low in oxygen (anaerobic), and (2) they grow in a semi-fluid substrate that often provides little mechanical support. For these reasons, mangrove plants have developed adaptations that help them overcome such problems. These adaptations include the development of pneumatophores, knee roots and stilt, buttress, and aerial roots. Such roots are part of an adaptation system to provide aeration for subterranean root systems as well as provide anchorage and support.

WATER AND IONIC RELATIONS OF PLANT CELLS:

Within a plant cell there are two major membranes: the plasmalemma (the outer membrane of the cell) and the tonoplast. The tonoplast separates the cytoplasm from the central vacuole.

In terrestrial environments, water is transported from the soil through the roots and up the xylem to the leaves where it evaporates into the air. In order to maintain transpiration flow, the water potential in the leaves must be less (more negative) than that of the soil. The water relations of mangroves can be described in terms of the water potential (ψ) of the plant tissues and of the environment. The water potential is the sum of the pressure potential and the osmotic potential, i.e($\psi = \psi_p + \psi_\pi$).In plant cells the water potential is determined by the osmotic potential of the cell sap and the turgor pressure of the cytoplasmic membranes against the cell wall. Accordingly, a plant which is growing in seawater must generate an extra hydrostatic pressure of about 25 bars (the negative water potential of seawater) as compared with a plant growing in fresh water. Mangroves also raise water against a hydrostatic gradient to variable heights. Water loss is controlled by stomatal closure (see Tomlinson, 1986). Scholander *et al.*, (1965) found very low hydrostatic pressure values for mangroves (-30 to -60 bars) but these values always exceeded the negative water potential of

normal seawater. However, in progressively more saline water (when for seawater becomes increasingly more negative) the ability of mangroves to absorb water decreases. The upper limit appears to be reached at a value of about 90 ppt NaCl when even the most efficient mangroves lose their ability to absorb water. As we shall examine in the next paper, this factor is an important determinant of the distribution and speciation of mangroves in highly saline environments such as those currently encountered in Pakistan.

SPECIFIC OSMOTIC ADJUSTMENT MECHANISMS IN PLANT CELLS:

Sodium chloride, the predominant salt is present in seawater at a concentration of approximately 0.5 M. However, depending on a number of important variables (such as frequency of tidal inundation, precipitation, evapotranspiration), hypo (<0.5 M NaCl) or hypersaline (>0.5 M NaCl) conditions may exist in the porewaters of the soil. In order to transport water and nutrients, halophytes accumulate solutes and thus lower their osmotic potential. If roots are flushed with seawater, the internal osmotic potential of the root cells will likely be less than -30 bars, corresponding to an internal salt concentration of about 700 mM. Halophytes are distinct from glycophytes in possessing the ability to accumulate large amounts of ions in their cells. Glycophytes are seldom known to possess internal salt concentrations greater than 150 mM. Furthermore, halophytes also show selectivity in the types of ions which are accumulated (Rains, 1972). It should also be noted that a vacuole may occupy about 90% of the cell volume of most mature cells. However, the solute concentrations in protoplast and vacuole are maintained in such a way that an equilibrium is maintained between these two compartments. Since the concentration of salt in vacuoles may reach 700 mM or more and a similar salt concentration would greatly affect the enzymic functional integrity of protoplasts and thus disrupt metabolic processes, organic solutes serve as compatible solutes within the protoplasts. These soluble organics are low molecular weight compounds which unlike inorganic ions, do not interfere with activity of soluble enzymes. In this respect, eukaryotic cells are distinctly different in that they must compartmentalize their orgnanic and inorganic solutes at high concentrations compared with the prokaryotic halophytic bacteria in which enzymes are active and stable in solutions of high ionic strength. In halophytic plants, a number of enzymes are actually stimulated by solutions of monospecific ions, but up to a concentration of 150 mM and at higher concentrations the rate of enzymic activity significantly decreases (Wyn Jones et al., 1979; Brown, 1976, Lanyi, 1974, Jefferies, 1980). Organic compounds which serve as compatible solutes may be of different types e.g. polyols (mannitol, glycerol and sorbitol), amino acids (e.g. proline, aspartic acid) methylated quarternary ammonium compounds (e.g. glycine betaine, alanine betaine) and reducing sugars e.g. glucose (Hellebust, 1976, Jefferies, 1980). The amount and type of the organic solutes present are usually a function of the stress and the respondent species involved. However, in most halophytic plant cells it has been noted that even in the absence of salt in the environment, a residual amount of organic solutes may still be synthesized. Under many circumstances the need for organic osmotic solutes in the cytoplasm may be exceeded and some of it may also be located in the vacuole in order to maintain an osmotic equilibrium. Thus it is clear from a comparative study of glycophytes and halophytes that the asymmetry in ion distribu-

tion is nearly absent in glycophytes while halophytic cells expend considerable metabolic energy in maintaining such ionic asymmetry. In halophyte cells for example, the concentration of sodium, potassium, and chloride ions in vacuoles are approximately 800, 1100, and 900 mM respectively, whereas in the protoplast, corresponding concentration may be only 100, 100, and 150 mM. Even these mechanisms may not be fully sufficient to combat the very high soil salinities of some of the halophytic plants. For example, in mangroves additional salt exclusion and excretion mechanisms may be simultaneously elicited (e.g. exclusion of salt, pumping of salt through salt glands on the leaves and dislocation of excess sodium and chloride ions in senescing leaves).

ENERGETIC REQUIREMENTS OF HALOPHYTES:

It is clear that with the ability to survive in a saline environment, there is a significant associated energy cost because processes concerned with growth, reproduction and maintenance all compete for limited resources. Dainty (1979) has shown that it is more difficult for the halophyte cell than the glycophyte cell to keep the concentration of inorganic ions low in the cytoplasm compared to that in the vacuole. Under changing external salinity conditions, an additional burden is introduced on the cell metabolic process to cope with transient conditions. Thus halophytes may have to utilze a greater proportion of their metabolic energy in the maintenance of ion pumps than has been previously appreciated.

From an assessment of the metabolic costs of maintaining large quantities of organic solutes in cytoplasm, it is clear that many of the compatible solutes utilized are nitrogen compounds (e.g. proline and glycinebetaine) and in coastal environemnts which do not receive adequate land runoff, nitrogen is likely to be limiting (see also Valiela and Teal, 1979). Although equimolal solutions of a number of these different organic solutes have approximately the same osmotic potential (-2.5 MPa), the amounts of carbon and nitrogen in different solutes are quite different. Therefore, in plants where carbon or nitrogen is limiting, certain solutes may be selected in order to exert the least pressure on a limited resource. Furthermore, the organic compounds used in osmoregulation may play a significant role also in the overall economy of carbon and nitrogen compounds during gorwth and development. Proline for example, can act not only as an osmolyte but also as a nitrogen storage compound. Since it is structurally related to glutamate, it can be easily converted to other amino acids and TCA cycle intermediates. Thus proline may sometimes be sotred in vacuoles and yet a rapid decrease in internal osmotic potential can be achieved simply by transporting proline into the cytoplasm from the vacuole and a concomitant increase in the concertration of the vacuolar fluid (Jefferies, 1980, 1981). In this way the organic solutes serve a dual role of acting as osmolytes and compatible solutes as well as storing carbon and nitrogenous compounds that are not wasted, but can be recycled under appropriate conditions for growth and development.

DIRECT SALT EFFECTS OBSERVED ON MANGROVE PLANTS:

Ball and Farquhar (1984b) have carried out studies on the photosynthetic and stomatal response of the grey mangrove, A. marina to transient salinity conditions. Their study attempted to examine changes in gas exchange characteristic of hydroponically grown plants to short term salinity variation over the range of 10 to 100%

seawater, a condition that simulates changes that may be brought about by tidal cycles or rainfall. It was found that rapid and reversible changes in the photosynthetic capacity of $A.$ $marina$ were induced by short-term variation in salinity. The CO_2 assimilation rate, stomatal conductance, intracellular CO_2 concentration and evaporation rate decreased at salinities above 250 mM NaCl (50% of the strength of seawater) and recovered substantially upon return to the original salinity. It should also be noted that the overall assimilation rate is coordinately limited by sotmatal conductance and photosynthetic capacity. It should also be mentioned that Ball earlier (1981) had made similar observations with another mangrove species $Aegiceras$ $corniculatum$. Ball and Farquhar (1984a) also examined photosynthetic and stomatal respones in $A.$ $corniculatum$ and $A.$ $marina$ to long term salinity and humidity conditions. Growth of $A.$ $corniculatum$ is more sensitive to salinity than that of a sympatric species, $A.$ $marina$. The photosynthetic capacity decreased with increase in salinity from 50 to 500 mM NaCl, as indicated by a decline in both the initial linear slope and the plateau of the chloride curve with $A.$ $corniculatum$ being the more sensitive species. Stomatal conductance and photosynthetic capacity coordinately limited the assimilation rate which declined with increasing salinity and decreasing humidity. Thus it is apparent that when challenged with either transient or long-term salinity changes, the stomata remain coordinated with the metabolic response.

RESPONSE OF THE MANGROVES TO SALINITIES IN TWO DIFFERENT GEOMORPHIC HABITATS:

Cintron et $al.$ (1978) have reported that for Puerto Rico and adjacent islands, tree height is negatively correlated with salinity. Ball (1981) demonstrated that an increase in salinity caused by the construction of dikes during an urban development project affected secondary succession in mangroves. However, Thom (1982) has suggested that substratum, ground-water level, soil drainage and salinity were dependent on the geomorphic variables, pointing to tight relationship between height, diameter at chest height, and cover of three mangrove species i.e. $A.$ $germinans$, $R.$ $mangle$ and $Laguncularia$ $racemosa$ along a compound gradient represented by salinity and variation in the geomorphic habitat (geoform) (see also Lopez-Portillo and Ezcurra 1989). Their results indicated salinity as well as geoform (an indicator contrasting environmental condition), played an imortant role in mangrove distribution and abundance. The two geoforms (mudflats and interdistrubutary basins) have different salinities and water regimes. Soil texture may also exercise a salinity buffering effect (which may be higher in the interdistributary basin) since fine particles and organic matter act as chelators during cation exchange. The study led to the conclusion that although what is observed is very much influenced by past history (e.g. species colonization and competition in different habitats, rising water level, sediment deposition and soil subsidance and compaction), interspecific interactions change with salinity and position within geoforms and therefore, influence the actual aspect of the mangrove communities. Mizrachi et $al.$, (1980) in their assessment of salt resistance mechanisms, have also regarded it as a determinant physioecological parameter of zonal distribution of mangrove species.

MANGROVE METABOLIC RESPONSE TO ALTERATIONS OF NATURAL FRESHWATER DRAINAGE TO SOUTHWESTERN FLORIDA ESTUARIES:

In southwestern Florida, seasonal overland sheet flow of freshwater infuses minerals and nutrients into coastal mangrove communities along a broad front. Drainage canals which have been built recently shore-circuit this sheet-flow of water thus diverting water-borne minerals and nutrients directly to estuarine bays and the Gulf of Mexico. Hicks and Burns (1974) have studied the metabolic responses of mature mangrove trees to differential freshwater inputs to the forest. Mangrove metabolism responds to a freshwater concentration gradient that ranged from a minimum of 4.7 ppt to a maximum of 16 ppt chloride. Gross productivity of red mangroves, *R. mangle*, decreased with increasing concentrations of chlorides; an opposite trend in metabolic response was found for black and white mangroves (*A. germinans* and *L. racemosa*). The metabolism of the tree community in response to a decreasing gradient of freshwater concentration exhibited an increase in gross productivity and respiration but the net productivity decreased. Bowman (1971) had shown earlier that *Rhizophora, Avicennia* and *Laguncularia* are all capable of growing for at least 2-3 years in salt-free water or soil. In natural environments mangroves may be exposed to a range of salinities, from nearly zero to hypersaline conditions without apparent damage; however, a brackish condition appears to be most favorable for the optimum growth of mangroves. Thus Hicks and Burns (1974) concluded that availability of brackish water for injection into the soil system increases forest productivity and decreases salt stress and inhibition of production. The salt content of soil water determines the osmotic pressure gradient between the soil water and the plant's vascular system, which partially controls the rate at which water can be made available to the leaves to support tranpirational water losses. Therefore, when water supply is deficient, stomata close to reduce the rate of water loss concomitant with reduction in CO_2 uptake from the air reduced productivity. Furthermore, glandular excretion of excess salts from mangrove leaves requires expenditure of metabolic energy, otherwise available for tissue growth.

MANGROVES OF THE INDUS RIVER DELTA IN PAKISTAN:

Although as many as 8 species of mangrove plants have been observed in the Indus Delta in recent past (Snedaker, 1984) for all practical purposes, the vast majority of the mangrove stands consist almost exclusively of *A. marina*. These monospecific mangrove forests consits of *A. marina* because this is the species with the highest reported salt tolerance among the mangroves. As mentioned earlier in this paper, as the salinity of water reaches about 90 ppt, at this level even the most adaptable species such as *Avicennia* reach their limit of water transport capability. We have already measured mangrove porewater salinities of as much as 70 ppt in the soil of Indus River Delta mangroves and this points to how stressful the current growth conditions for mangroves already are. And many mangrove stands are clearly stunted, a manifestation of this stress. In the next paper an attempt will be made to evaluate the status and prospects of the Pakistani mangroves forests and what effective measures can be taken to restore and preserve them.

ACKNOWLEDGEMENTS

REFERENCES

Ball, M.C. 1981. *Physiology of photosynthesis in two mangrove species: responses to salinity and other enviro-nemntal factors.* Australian National University, Canberra, Ph.D. Thesis.

Ball, M.C. and G.D. Farquhar. 1984a. Photosynthetic and stomatal responses of two mangrove species, *Aegicera corniculatum* and *Avicennia marina,* to long term salinity and humidity conditions. *Plant Physiology* 74:1-6.

Ball, M.C. and G.D. Farquhar. 1984b. Photosynthetic and stomatal responses of the grey mangrove, *Avicennia marina,* to transient salinity conditions. *Plant Physiology* 74: 7-11.

Bowman, H.H.M. 1971. Ecology and physiology of the red mangrove. *American Philosophical Society Proceedings* 56: 589-672.

Brown, A.D. 1976. Microbial water stress. *Bacterial Review* 40: 803-846.

Chapman, V.J. 1975. Mangrove Biogeograpy. In: *Proceedings of the International Symposium on Biology and Management of Mangroves,* Vol.1, (Eds. G.E. Walsh, S.C. Snedaker and H.J. Teas), Gainsville: University of Florida, Pp.3-22.

Chapman, V.J. 1977. Introduction, In: *Ecosystem of the World. I. Wet Coastal Ecosystem,* Amsterdam, Elsevier. Pp.1-29.

Cintron, G., A.E. Lugo, D.J.Pool and G. Morris. 1978. Mangroves of arid environemnts in Puerto Rico and adjacent islands. *Biotropica* 10: 110-121.

Clough, B.F., and P.M. Attiwill. 1975. Nutrient cycling in a community of *Avicennia marina* in a temperate reigon of Australia. In: *Proceedings of the International Symposium on Biology and Management of Mangroves* Vol.1 (Eds. G.E. Walsh, S.C. Snedaker and H.J. Teas), Gainesville: University of Florida, Pp.137-146.

Connor, D.J. 1969. Growth of grey mangrove (*Avicennia marina*) in nutrient culture. *Biotropica* 1: 36-40.

Csonka, L.N. 1989. Physiological and genetic responses of bacteria to osmotic stress. *Microbiologyical Reviews* 53: 121-147.

Dainty, J. 1979. The ionic and water relations of plants which adjust to a fluctuating saline environment. In: *Ecological Processes in Coastal Environements.* (Eds. R.L. Jefferies and A.J. Davy) Blackwell Scientific Publications, Oxford.

Dickson, D.M.J. and G.O. Krist. 1987a. Osmotic adjustment in marine eukaryotic algae: The role of inorganic ions, quaternary ammonium, tertiary sulphonium and carbohydrate solutes. I. Diatoms and a Rhodophyte. *New Phytology* 106: 645-655.

Dickson, D.M.J. and G.O. Krist. 1987b. Osmotic adjustment in marine eukaryotic algae: The role of inorganic ions, quaternary ammonium, tertiary sulphonium and carbohydrate solutes. II. Parsino-phytes and haptophytes. *New Phytology* 106:657-666.

Downton, W.J.S. 1982. Growth and osmotic relations of the mangrove *Avicennia marina* as influenced by salinity. *Australian Journal of Plant Physiology.*

Field, C.D. 1984. Ions in Mangroves. In: *Tasks for Vegetation Science* Vol.9. (Ed. H.J. Teas) The Hague: Dr. W. Junk, Pp.43-48.

Gabbay-Azaria, R.,E. Tel-Or and M. Schonfeld. 1988. Glycinebetaine as an osmoregulant and compatible solute in the marine *Cyanobacterium Spirulina subsala. Archives of Biochemistry and Biophysics* 264:333-339.

Galinski, E.A., and H.G. Truper. 1982. Betaine, a compatible solute in the extremely halophilic photo-trophic bacterium *Ectothiorhodospira halochloris. FEMS Letter* 13:357-360.

Hawkins, L., D. Ritter and J.H. Yopp. 1987. Proposed additional role for glycinebetaine in the adaptatio of halophilic cyanobacteria to hypersalinity: protection against pH-induced loss of enzymatic activity. *Plant Physiology* 83:S-85.

Hellebust, J.A. 1976. Osmoregulation. *Annual Review of Plant Physiology* 27:485-505.

Hicks, D.B. and L.A. Burns. 1974. Mangrove metabolic response to alterations of natural freshwater drainage to southwestern Florida estuaries. In: *Proceedings of the International Symposium on Biology and Management of Mangroves.* (Eds. G. Walsh, S. Snedaker and H. Teas), Honolulu, Hawaii. Pp.238-255.

Incharoensakdi, A., T. Takabe and T. Akazawa, 1986. Effect of betaine on enzyme activity and subunit interaction of ribulose -1, 5-biphosphate carboxylase-oxygenase from *Aphanothece halophytica. Plant Physiology.* 81: 1044-1050.

Jefferies, R.L. 1980. The role of organic solutes in osmoregulation in halophytic higher plants. pp.135-154. In: *Genetic Engineering of Osmoregulation: Impact on Plant Productivity for Food, Chemicals and Energy.* (Eds. A. Hollaender, D.W. Raijins and R.C. Valentine). Plenum Press, New York.

Jefferies, R.L. 1981. Osmotic adjustment and the response of halophytic plants to salinity. *Bioscience* 31: 42-46.

Jennings, D.H. 1968. Halophytes, succulence and sodium in plants--a unified theory. *New Phytologist* 67: 899-911.

Jennings, J.N. and E.C.F. Bird. 1967. Regional geomorphological characteristics of some Australian estuaries. In: *Estuaries* (Ed. G.H. Lauft), A.A.A.S., Washington. Pp.121-128.

Joshi, G.V., L.Bhosale, B.B. Jamale and B.A. Karadge. 1975. Photosynthetic carbon metabolism in plants. In: *Proc. Int'l Symp. Biol. & Management of Mangroves.* Vol.II, (Eds. G.E. Walsh and H.J. Teas), University of Florida, Gainesville. Pp.595-607.

Kauss, H. 1979. Biochemistry of osmotic regulaion in *Poteriochromonas melhamensis. Bericht der Deutschen Botanischen Gesellschaft* 92: 11-22.

Kauss, H., K.S.Thompson. 1982. In: *Plasmalemma & Tonoplast: Their Function in the Plant Cell.* (Eds. D. Marme, e. Marre and R. Hertel). Amsterdam: Elsevier Biomedical Press.

Lanyi, J.K. 1974. Salt-dependent properties of proteins from extremely halophytic bacteria. *Bacteriologial Review* 38:272-290.

LeRudulier, D., A.R.Strom, A.M. Dandekar, L.T. Smith, and R.C. Valentine. 1984. Molecular biology of osmoregulation. *Science* 224: 1064-1068.

Lopez-Portillo, J. and E. Ezcurra. 1989. Response of three mangroves to salinity in two geogroms. *Functional Ecology* 3: 355-361.

Lugo, A.E., G. Evink, M.M. Brinson, A. Broce and S.C. Snedaker. 1975. Diurnal rates of photosynthesis, respiration and transpiration in mangrove forests in South Florida. In:*Ecological Studies. II. Tropical Ecological Systems* (Eds. F.B. Golley and E. Medina) New York. Pp.335-350.

MacKay, M.A., R.S. Norton and L.J. Borowitzka. 1983. Marine blue green algae have a unique osmoregulatory system. *Marine Biology* 73: 301-307.

MacKay, M.A., R.S. Norton and L.J. Borowitzka. 1984. Organic osmoregulatorysolutes in cyanobacteria. *Journal of General Microbiology* 130: 2177-2191.

Macnae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Advances in Marine Biology* 6: 73-270.

Mizrachi, D, R. Pannier and F. Pannier. 1980. Assessment of salt resistnace mechanisms as determinant physio-ecological parameters of zonal distributions of mangrove species. I. Effect of salinity stress or nitrogen metabolism balance and protein synthesis in the mangrove species *R. mangle* and *A. nitida*. *Botanica Marina* 23: 289-296.

Moore, R.T., P.C. Miller, J.Ehleringer and W. Lawrence. 1973. Seasonal trends in gas exchange characteristics of three mangrove species. *Photosynthetica* 7: 387-394.

Morrow, L. and N.H. Nickerson. 1973. Salt concentration in ground waters beneath *Rhizophora mangle* and *Avicennia germinans*. *Rhodophora*. 75: 102-106.

Pavelicek, K.A., and J.H. Yopp. 1983. Variation in counteracting effects of glycine betaine on salt inhibition of glucose 6 phosphate dehydrogenase from halo-tolerant microorganisms. *Plant Physiology* 72:5-136.

Pool, D.J., S.C. Snedaker and A.E. Lugo. 1977. Structure of angrove forests in Florida, Puerto Rico, Mexico and Costa Rica. *Biotropica*. 9: 195-212.

Rains, D.W. 1972. Salt transport by plants in relatio to salinity. *Annual Reviews of plant physiology* 23: 367-388.

Scholander, P.F. 1968. How mangroves desalinate seawater. *Physiol Plantarum* 21: 251-261.

Scholander, P.F., H.T. Hammel, E.D. Bradstreet and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148: 339-346.

Sidhu, S.S. 1975a. Culture and growth of some mangrove species. In: *Proceedings of the International Symposium on Biology and Management of Mangroves* Vol.1 (Eds. G.E. Walsh, S.C. Snedaker, and H.J. Teas). Gainseville: University of Florida. Pp.394-401.

Sidhu, S.S. 1975b. Structure of epidermis and stomatal apparatus of some mangrove species. In: *Proc. of the Int'l Symp. Biol. and Mangement of Mangroves* (Eds. G.E. Walsh and H.J. Teas) Gainesville, Universtiy of Florida. Pp.569-575.

Smith, L.T., G.M. Smith and M.A. Madkour. 1990. Osmoregulation in *Agrobacterium tumfaciens*: Accumulation of a novel disaccharide is controlled by osmotic strength and glycine betaine. *Journal of Bacteriology* 172: 6849-6855.

Snedaker, S.C. 1984. Mangroves: A summary of knowledge with emphasis on Pakistan In: *Marine Geology and Oceanography of Arbian Sea and Costal Pakistan* (Eds. B.U. Haq and J.D. Milliman), Van Nostrand Reinhold Company, New York. Pp.255-262.

Stern, W.J., and G.K. Voigt. 1959. Effect of salt concentration on growth of red mangrove in culture. *Botanical Gazette* 121: 36-39.

Thom, B.G. 1982. Mangrove ecology--a geomorphological perspective. In: *Mangrove Ecosystems in Australia. Structure, Function and Management* (Ed. B.F. Clough) Australian National University Press, Australia. Pp.3-17.

Tomlinson, P.B. 1986. *The botany of mangroves*. Cambridge University Press, Cambridge, U.S.A. Pp.1-413.

Ungar, I. 1991. *Ecophysiology of Vascular Halophytes*. CRC Press, Boca Raton, Florida. Pp.1-209.

Valiala, I. and J.M. Teal. 1979. The nitrogen budget of a salt marsh ecosystem. *Nature* 280: 652-656.

Walsh, G.E. 1974. Mangroves: A review. In: *Ecology of halophytes* (Eds. R.J. Reinhold and W.H. Queen), Academic Press. New York. Pp.51-174.

Wyn Jones, R.G., C.J. Brad, and J. Speirs. 1979. Ionic and osmotic relations in plant cells. pp.63-104. In:
    Recent Advances in the Biochemistyr of cereals (Eds. D.L. Laidman and R.G. Wyn Jones) Academic
    Press, New York.

Wyn Jones, R.G., and J.Gorham. 1983. Osmoregulation. In: *Encyclopedia of Plant Physiology,* New Series,
    Vol.12c (Eds. O.L. Large, P.S. Nobel, C.B. Osmond and H. Zeigler), Springer Verlag, Berlin. Pp.35-
    38.

Wyn Jones, R.G., and R. Storey, 1981. Betains. In: *Physiology and Biochemistry of Drought Resistance in
    Plants.* (Eds. L.G. Paleg and D. Aspinall), Academic Press, Sydney. Pp.171-204.

Yancey, P.H., M.E., Clark, S.C. Hand, R.D. Bowlus, and G.N. Somero. 1982. Living with water stress:
    evolution of osmolyte systems. *Science* 217: 1214-1222.