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Review article

Ecophysiology of mangroves

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> "What is the reason that seawater nourishes not trees? Is it not for the same reason that it nourishes not earthly animals?... Nor, though seawater be aliment to marine plants as to its fishes, will it therefore nourish earthly plants, since it can neither penetrate the roots, because of its grossness, nor ascend, by reason of its weight... Or is it because drought is a great enemy to trees?"
>
> Plutarch, 70 AD (translated by Bowman, 1917)

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Introduction

"Mangrove" is an ecological term referring to a taxonomically diverse association of woody trees and shrubs that form the dominant vegetation in tidal, saline wetlands along tropical and subtropical coasts. One striking feature of mangrove forests is the distribution of species in a marked zonation pattern normal to shore (e.g. Saenger et al. 1977; Semeniuk and Wurm 1987). These zonation patterns are generally well correlated with the frequency and duration of tidal immersion (Watson 1928; Chapman 1944; Macnae 1968). Such correlations between vegetation patterns and idal characteristics tend to be site-specific because the two factors are not directly related. Tidal characteristics exert their influence on vegetation through intermediate factors, which either directly affect growth or are resources required for growth. Such factors include the degree of soil saturation, the form and availability of nutrients and the salinity of surface and soil water. The present review considers the physiological bases of coping with two of the outstanding environmental features of mangrove swamps, waterlogging and salinity, and how these physiological attributes might contribute to the differential distribution of mangrove species along tidal gradients.

Waterlogging

Aerobic metabolism in anaerobic environments

Coping with waterlogged, or more correctly hypoxic, environments largely involves strategies of avoidance. The structure of mangrove roots, which are shallow and have numerous lenticels and extensive aerenchyma, increases the availability of oxygen to roots growing in oxygen deficient sediments (Tomlinson 1986). In addition, many species have aerial roots that vary widely in form (Tomlinson 1986) and include stilt roots (e.g. *Rhizophora stylosa*), knee roots (e.g. *Bruguiera exaristata*), pneumatophores (e.g. *Avicennia marina*) and plank roots (e.g. *Xylocarpus granatum*). The major feature of all these root systems is that the aerial roots are exposed to the atmosphere at least during periods of low tidal inundation. Such contact is essential because the diffusion of oxygen occurs 10,000 times more rapidly through air than through water, and aeration of the root system depends on the diffusion of oxygen down partial pressure gradients from the atmosphere to sites of respiration in the roots (Scholander et al. 1955). This is a highly efficient means of root ventilation in *A. marina*, in which the aerenchyma accounts for as much as 70% of the total root volume (Curran 1985). Indeed, leakage of oxygen from the roots of *A. germinans* causes the surrounding soil to be more oxidized than would be expected in anaerobic sediments (Nickerson and Thibodeau 1985; Thibodeau and Nickerson 1986). Thus, while the root systems may cope with temporary periods of anaerobiosis (McKee and Mendelssohn 1987), root functioning depends on the maintenance of aerobic conditions in tissues growing in an otherwise anaerobic environment.

Nutrient availability in relation to soil saturation

Recent studies have provided intriguing data linking tidal regimes and the nutritional status of coastal wetlands (Boto 1982; Valiela 1984). Tidal waters distribute both free and particulate-bound nutrients throughout the swamp systems, with the nutrient inputs being greatest in frequently flooded areas of sediment deposition. However, this is not the only effect of tidal flooding on the availability of nutrients along inundation gradients. The degree of soil saturation influences the redox status of the sediment which, in turn, affects both the form and availability of inorganic nutrients.

Boto and Wellington (1983, 1984) have found variations in the relative limitations of nitrogen and phosphorus to mangrove growth along a tidal inundation gradient. At one extreme of frequent tidal flooding, the saturated sediments are generally depleted of oxygen. In these reducing environments, the major form of combined inorganic nitrogen is ammonia. Ammonia is not easily leached from the sediments because it readily adsorbs onto organic particles. This can cause the levels of ammonia to be relatively high in highly organic sediments. However, the supply of phosphorus generally exceeds that of ammonia, causing nitrogen to be limiting to mangrove growth in flooded, anaerobic sediments at low tidal elevations (Boto and Wellington 1983, 1984).

At less frequently flooded elevations, drainage of flooded soils can cause them to become partially aerobic and hence more oxidized. Under these conditions, the major form of combined inorganic nitrogen is nitrate. The lower rate of input from flooding waters combined with the ease with which nitrate can be leached from the sediments would be expected to result in even greater nitrogen limitations to growth in oxidized soils at high tidal elevations than in reduced soils at low tidal elevations. However, mangrove growth in the more oxidized soils is apparently limited by the availability of phosphorus, which may become depleted by adsorption onto clay and precipitation with calcium, aluminium and iron (Boto and Wellington 1983, 1984).

There is also a pronounced interaction of salinity and waterlogging on nutrient availability, which is not well understood. For example, tolerance to increasing salinity is generally lowered by hypoxia, which apparently interferes with both salt exclusion and selectivity for K^+ over Na^+ (Kriedemann and Sands 1984; Drew and Dikumwin 1985). In *A. marina*, which has a high capacity for selective uptake of K^+, the K^+ levels in leaves decline with increasing salinity (Downton 1982; Ball and Farquhar 1984b; Clough 1984; Ball et al. 1987) and are lower in plants grown under waterlogged than under well-drained conditions (Naidoo 1985). Indeed, the levels found in field grown *A. marina* (Popp 1984a) are at or near the lowest K^+ level, which can be maintained without metabolic disorders (Ball et al. 1987).

The cost(s) of waterlogging tolerance

The carbon costs of tolerating waterlogged soils are difficult to assess. There are, perhaps, greater carbon costs of root functioning in waterlogged than in well-drained soils in that carbon invested in structures for root ventilation might otherwise be invested in structures for absorption of water and nutrients. Curiously, the rates of water uptake are lower in waterlogged than in well-drained soils (Naidoo 1983, 1985), such that the supply of water to the shoot is lower in environments with an infinite supply of water. As carbon cannot be gained without the expenditure of water, a limitation in the supply of water is also a limitation to growth. Interspecific differences in the ability to cope with waterlogged conditions, including effects of hypoxia on the uptake of water and nutrients, may well contribute to the characteristic segregation of species along tidal inundation gradients.

Salinity

Halophytes and the physiological continuum of salinity tolerance

Mangroves are halophytes, plants which naturally complete their life cycles under saline conditions (Flowers et al. 1986). Salinity in the mangrove environment is due largely to NaCl and varies in time and space from freshwater to hypersaline conditions. The salt concentration in seawater is approximately 35 g/l, which in solution includes 483 $mM\,Na^+$ and 558 $mM\,Cl^-$ (Harvey 1966).

Assessment of the salinity tolerance of a species is complicated by the variation in sensitivity to salinity with the developmental status of the plant. For example, *A. marina* is viviparous, in that germination and subsequent development into a juvenile seedling or propagule occur on the mother tree. Following release of the propagules, further growth and development into an established seedling are maximal in 50% seawater (Connor 1969; Clarke and Hannon 1970; Ball 1981). However, effects of salinity on growth of propagules are confounded by effects of salinity on redistribution of cotyledonary reserves (Ball 1981). Once the seedlings are mature and no longer dependent on reserves, the optimal salinity for growth is substantially lower, ranging from 10%–25% seawater (Downton 1982; Burchett et al. 1984; Clough 1984; Naidoo 1987; Ball 1988). Similar results have been found in other species in which reserves apparently enable seedling establishment under conditions which are otherwise unsuitable for growth (Ball and Pidsley 1988).

The mangrove species exhibit a broad spectrum of growth responses to salinity, as shown in a recent study of 16 mangrove species (Ball and Pidsley 1988). At one salinity extreme, growth of *Sonneratia lanceolata* is maximal in salinities ranging from freshwater to 5% seawater, and declines to minimal values in 50% seawater. Most mangrove species also grow in freshwater, but growth is stimulated by saline conditions, with the optimal salinities for growth ranging from 5% to 50% seawater. In some cases, e.g. *Ceriops decandra* and *S. alba*, extremely poor growth and time-dependent decline in vigour indicate that the plants are not likely to grow to maturity under freshwater conditions. In this ecological sense, these species could be considered obligate halophytes. Long-term growth studies may identify other obligate halophytes, as the presence of high salt concentrations in seed and propagule reserves may enable temporary growth in freshwater habitats but not sustain growth to maturity. Finally, some species may be obligate halophytes in the physiological sense that they require saline conditions for growth. Propagules of two species, *Bruguiera parviflora* and *C. tagal* var. *australis*, failed to grow in freshwater. The addition of as little as 5% seawater to the culture solutions was sufficient to produce vigorous specimens of all four apparently obligate halophytes. The physiological basis of either growth stimulation or the apparent requirements for saline conditions are unknown (Flowers et al. 1986). Thus, the growth responses of mangroves to salinity are as varied as the environments in which they are found and reflect a physiological continuum of salinity tolerance ranging from the responses of a moderately salt tolerant glycophyte to those of highly salt tolerant and apparently obligate halophytes (Ball and Pidsley 1988).

Physiological bases of salt tolerance

Mangroves have frequently been classified according to three strategies of salt tolerance: salt exclusion, salt accumulation and salt secretion. This classification scheme is misleading as none of these so-called strategies are means of salt tolerance in themselves. All of the mangroves exclude salt at the roots, with those possessing salt secretion glands apparently being the least effective at salt exclusion (Scholander et al. 1962, 1966; Atkinson et al. 1967; Scholander 1968; Clough 1984). All of the mangroves accumulate ions for osmoregulation (Popp 1984a, b; Popp et al. 1984), although they presumably differ in the extent to which ions can be accumulated without metabolic dysfunction. A few species have salt secretion glands, which may allow more flexibility in coping with fluctuations in the salt influx to the shoot, but do not free the plant from the rigors of coping with saline environments: osmoregulation, ion compartmentation, selective ion uptake, and maintenance of a balance between the supply of ions to the shoot and the capacity to accommodate the salt influx.

Osmoregulation and ion compartmentation

Naturally, there are interspecific differences in the capacity to maintain favourable water relations along gradients of increasing salinity. Such gradients are notoriously difficult to quantify, not only because of spatial and temporal variation, but because the sources of water actually used by a plant may not reflect the prevailing salinities of surface waters. For example, freshwater seepage can be an important determinant of the distribution of mangroves in hypersaline habitats (Semeniuk 1983). Sternberg and Swart (1987) have devised an elegant method to determine the sources of water used by mangroves. The method is based on comparison of the hydrogen and oxygen isotope composition of stem water with the isotope compositions characteristic of freshwater and seawater. In general, the isotopic ratios of stem water indicated a spectrum of water usage, ranging from freshwater to seawater in mangroves growing along a tidal inundation gradient from the inland to the seaward margins of a swamp, respectively (Sternberg and Swart 1987). They also found that some species whose surface roots were bathed in seawater were primarily obtaining water from a lens of brackish to freshwater salinity. These studies underscore the enormous importance of stable isotopes in understanding physiological responses to environmental factors.

A positive water balance can only be maintained if tissue water potentials are lower than the osmotic potentials of the substrate in which the plants are growing (Clough et al. 1982). For example, leaf water potentials in mangroves growing in seawater, which has an osmotic potential of approximately −2.5 MPa, range from −2.7 to −5.7 MPa (Scholander et al. 1964; Scholander 1968). The water potential of a plant cell is determined by the hydrostatic pressure and osmotic potential of the cell sap, with the latter being the major component. The osmotic potential is generated by dissolved solutes in the cell sap. Thus, the intracellular concentrations of such solutes must increase with increasing salinity if cellular osmotic potentials are to be maintained at levels lower than those in the root environment.

Mangroves, like most other salt tolerant plants (Flowers et al. 1986), accumulate high concentrations of inorganic ions that function in the osmoregulation of leaves and other tissues (Popp 1984a). For example, the salt concentrations in leaves of *A. marina* increase from 300–600 m*M* NaCl with increase in salinity from 50–500 m*M* NaCl, respectively (Downton 1982; Ball and Farquhar 1984b; Clough 1984). The vacuole is the major site of ion accumulation, with the concentrations of ions in other intracellular compartments probably differing little from those in salt sensitive species, except perhaps during salinity stress. Osmotic adjustment in chloroplasts (Hanson et al. 1985), cytoplasm and presumably other metabolic compartments is apparently achieved by synthesis of compatible solutes, low-molecular-weight organic compounds that do not interfere with metabolism (Popp 1984a, b; Popp et al. 1984). In this manner, intracellular compartmentation of ions protects biochemical processes that are just as sensitive to high concentrations of NaCl in vitro as those isolated from glycophytes.

The importance of ionic compartmentation to physiological functioning is exemplified by the ionic relations of chloroplasts, in which inorganic ions play a major role in the regulation of photosynthetic processes (Barber 1976). To date, there is no convincing evidence of fundamental differences in the properties of either enzymes or photosynthetic membranes that would identify chloroplasts as a site of adaptation to the high internal salt concentrations typical of leaves of salt tolerant plants (see review: Ball 1986). These similarities in the photosynthetic machinery are consistent with similarities in the ionic composition of chloroplasts isolated from salt sensitive and salt tolerant species. For example, chloroplasts isolated from the pea, *Pisum sativum*, contain 100 m*M* Cl^- (Robinson and Downton 1984). Similar concentrations of Cl^- also occur in chloroplasts of the salt tolerant species, *Suaeda maritima* (Harvey et al. 1981), *Beta vulgaris* (Robinson and Downton 1984), *Spinacia oleracea* (Kaiser et al. 1983; Robinson et al. 1983; Robinson and Downton 1984), and *Suaeda australis* (Robinson and Downton 1985). Potassium is the major monovalent cation, but the Na^+/K^+ ratios in chloroplasts of salt tolerant species are much higher than those found in salt sensitive species (Harvey et al. 1981; Kaiser et al. 1983; Robinson et al. 1983; Robinson and Downton 1984, 1985). This difference in the composition of cations raises questions about the extent to which Na^+ may substitute for K^+ in chloroplasts of salt tolerant plants.

Failure to maintain the ionic composition of the chloroplast as high concentrations of ions accumulate within the leaf could have disastrous consequences for photosynthetic metabolism. High concentrations of NaCl would interfere with enzymatic reactions (Greenway and Osmond 1972) as well as cause disorganization of photosystem II through release of electrostatically bound polypeptides of the oxygen-evolving complex (Andersson et al. 1984). Such damage to photosystem II would result in loss of photochemical capacity and in vulnerability to photoinhibition (Ball and Anderson 1986). Thus, accumulation of NaCl in chloroplasts, even those of highly salt tolerant mangroves, would result in rapid loss of photosynthetic activity, particularly in the light.

Variation in salinity also affects the foliar concentrations of K^+, a nutrient required in relatively high concentrations for photosynthesis and other metabolic processes (Huber 1985). Studies of photosynthetic properties in relation to the ionic composition of leaves have shown that the decrease in photosynthetic capacity in *A. marina* with increase in salinity from 50 to 500 m*M* NaCl is due to salinity-induced K^+ deficiency rather than to toxic effects of NaCl accumulation (Ball 1981; Ball and Farquhar 1984b; Ball et al. 1987). With increase in salinity from 50 to 500 m*M* NaCl, the concentration of Cl^- increased from 352 to 628 m*M*; sodium concentrations also increased, but decline in the K^+ concentration from 157 to 98 m*M* caused the Na^+/K^+ ratio to increase from 1.53 to 5.68 (Ball and Farquhar 1984b). The photosynthetic capacity in these leaves decreased 50%

with increase in salinity from 50 to 500 mM NaCl. In contrast, the photosynthetic capacity of *A. marina* was unaffected by the same range of salinity and NaCl accumulation in leaves when the plants were grown such that the K^+ concentration in leaves remained relatively constant (Ball 1981). It appeared from these experiments that loss of photosynthetic capacity with increasing salinity was related to metabolic requirements for K^+ and a decreasing capacity to satisfy those needs with increasing salinity (Ball et al. 1987).

Selective ion uptake by the roots

There have been few studies of the structure and function of roots in mangroves, and most recent research has concentrated on roots of *A. marina.* This is one of the most salt tolerant species, frequently occurring in environments that are at least seasonally hypersaline, with salinities ranging from 2 to 3 times that of seawater. In an elegant study, Moon et al. (1986) found that most of the root system in *A. marina* is isolated from the external solution by a barrier to apoplastic transport in the periderm and exodermis. Access of the external solution to the symplasm is restricted to the distal 17 mm of third- and fourth-order roots. Moon et al. (1986) noted that the location of an apoplastic barrier at the root periphery has two major consequences for root functioning in saline environments. First, it prevents the cortex from experiencing salt concentrations equal to those of the external solution. Second, the NaCl concentrations in the cortical apoplast could increase to deleterious levels if ion exclusion from the stele were to occur only at the endodermal Casparian band.

The mechanism(s) of salt exclusion are unknown. It has been argued that the apoplastic uptake of from 1% to 5% of the external salt solution would be sufficient to account for the rates of salt transport to the shoot (Pitman 1977). However, several lines of evidence indicate minimal apoplastic uptake of water and ions in *A. marina.* Using a fluorescent tracer dye which is confined to the apoplast, Moon et al. (1986) found that the concentration of dye in xylem fluid expressed from *A. marina* was less than 0.17% of that in the solution bathing the roots. Further, the concentrations of ions in the xylem would be expected to remain nearly constant with variation in the volume flux if apoplastic uptake were the major source of ions in the transpiration stream. However, the xylem Cl^- concentrations in *Aegiceras corniculatum* and *Avicennia marina* are inversely related to the transpiration rates such that the salt flux to the leaves does not increase with increase in rates of water loss at a given salinity (Ball 1988). Similarly, the concentrations of Na^+, K^+ and Cl^- in the xylem of *A. marina* were minimal during periods of maximal evaporation under field conditions (Waisel et al. 1986). All of these results imply that the major means of ion entry into the transpiration stream is via symplastic pathways, consistent with studies on root functioning in another halophyte, *Suaeda maritima* (Yeo and Flowers 1986).

Clearly, the structural and functional attributes of roots in *A. marina* are admirably suited to coping with highly saline environments. The extent to which similar characteristics occur in other mangrove species is unknown. It seems likely that interspecific differences in the relative contributions of apoplastic and symplastic pathways to ion uptake and in the ability of the symplasm to regulate ion uptake with increasing external salinity may be major factors affecting differences in salt tolerance.

Coping with the salt influx to the shoot

Salt tolerance depends on balancing the transport of ions to the shoot with the requirements or capacities of the shoot to accommodate the salt influx. Once supplied to the leaf, the ions must either remain in the apoplast, be taken up by the leaf cells or be re-exported from the leaf (Flowers et al. 1986; Flowers and Yeo 1986). The apoplast occupies only 1.9% to 3.3% of the mesophyll cell volume and hence has a small ion storage capacity (Flowers and Yeo 1986). An imbalance between the supply of ions to the apoplast and their removal either by cellular uptake or re-export would lead to excessive ion levels in the apoplast and dehydration of the mesophyll (Oertli 1968). Of the cellular compartments, the cytoplasm occupies only 5% to 10% of the mesophyll cell volume and must maintain relatively low concentrations of ions in order to protect sensitive metabolic processes from ion stress. Thus the vacuole, which occupies at least 80% of the cell volume, is the only significant ion storage site within the leaf. An imbalance between the uptake of ions by the symplasm and the capacity for storage in the vacuole would lead to the toxic accumulation of ions in the cytoplasm and metabolic dysfunction.

Species in the genera *Acanthus, Aegialitis, Aegiceras,* and *Avicennia* possess salt secretion glands in the leaves (Scholander et al. 1962; Atkinson et al. 1967; Cardale and Field 1971; Fara-

Table 1. Salt balance in shoots of *Aegiceras corniculatum* and *Avicennia marina* in relation to salinity (after Ball 1988)

Parameter	*A. corniculatum*			*A. marina*		
Growth salinity (m*M* NaCl)	50	250	500	50	250	500
Net water use efficiency (mg dw mol^{-1} water)	73.8	45.0	41.4	81.0	79.2	91.8
Net Cl^- uptake (μmol Cl^{-1} mol^{-1} water)						
Accumulation:						
Roots	15.6	25.1	19.2	44.0	35.1	112.9
Stems	20.8	7.7	2.2	10.5	17.0	28.3
Leaves	26.1	26.0	16.9	34.2	34.6	47.3
Total	62.5	58.8	38.3	88.7	86.7	188.5
Secretion	28.7	85.6	157.0	13.4	64.2	94.8
Total Uptake	91.2	144.4	195.3	102.1	150.9	283.3
Shoot salt balance						
Cl^- uptake to shoot per unit shoot growth (mmol g^{-1} dw)	1.2	3.5	8.5	1.1	2.3	3.0
Cl^- accumulation (% shoot uptake)	62.0	28.2	10.8	76.9	44.6	44.4
Cl^- secretion (% shoot uptake)	38.0	71.8	89.2	23.1	55.4	55.6

dw, dry weight

day and Thomson 1986). In these salt-secreting species, some of the salt borne in the transpiration stream to the leaves is absorbed for osmoregulation of growing tissues, with the ion concentrations maintained within physiologically acceptable levels by salt secretion (Atkinson et al. 1967; Ball 1988). Ions apparently diffuse down concentration gradients in the apoplast and symplast (depending on the flow of solution through the leaf) to the salt secretion glands (Shimony et al. 1973). These glands are non-specific. *A. marina*, for example, naturally secretes a variety of ions, but primarily Na^+ and Cl^- (Leshem and Levison 1972; Boon and Allaway 1986). The composition of the secretion can be varied by changing the supply of cations to the leaf (Boon and Allaway 1986). Curiously, the capacity for ion secretion in *A. marina*, as determined by supplying the transpiration stream of excised leaves with 1 *M* NaCl (Boon and Allaway 1986), greatly exceeds the rates measured in leaves of intact plants (Scholander et al. 1962, 1968; Boon and Allaway 1982; Drennan and Pammenter 1982; Ball 1988). Such an excessive capacity for secretion may be advantageous when structural damage to root systems allows the uncontrolled entry of external salt solution into the transpiration stream.

Salt secretion becomes increasingly important to the maintenance of favourable ion levels in the shoots of *Aegiceras corniculatum* and *Avicennia marina* with increasing salinity as shown in Table 1 (Ball 1988). Salt exclusion at the roots increased from 90% to 97% with increase in salinity from 50 to 500 m*M* NaCl in both species. Some of the salt was retained in the roots and the remainder was borne to the leaves in the transpiration stream. Although the flux of salt to the leaves was similar in both species, the transport of Cl^- to the shoot per unit of shoot growth was greater in *Aegiceras corniculatum* than in *Avicennia marina* because the net water use efficiencies were lower in the former species. As both species accumulate similar concentrations of Cl^- per unit growth, the amount of salt secreted per mole water transpired (and hence also per mole cabon gained) increased more with increasing salinity in *Aegiceras corniculatum* than in *Avicennia marina*. It is apparent that the leaves would be overwhelmed by the salt influx in the absence of salt secretion.

Most mangrove species lack salt secretion glands and must accommodate the salt influx to the shoot by growth, increasing succulence, and re-export from the leaves. The leaves of non-secreting species characteristically maintain relatively constant concentrations of Na^+ and Cl^- on a bulk-leaf water basis, although the concentrations of ions per unit dry weight increase with leaf age (Atkinson et al. 1967). This contrasts with salt sensitive species in which the concentration of ions in leaves increases with time (Flowers et al. 1986). The demand for ions is presumably greatest during leaf area expansion as ions play an important role in the water relations of developing tissues (Kriedemann 1986). As leaf area expansion ceases, the leaves may increase in succulence (i.e. water content per unit leaf area), which apparently maintains leaf ion concentrations at relatively constant levels (Flowers et al. 1986). In mangroves, the increase in succulence is due largely to development of hypodermal tissue

(Tomlinson 1986). Naturally, there are limits in the extent to which ions can be accumulated in the leaf cells and this may affect leaf longevity. For example, the longevity of leaves of *Rhizophora apiculata, R. stylosa*, and several other mangrove species under investigation declines with increasing salinity, presumably as a result of increased salt transport to the leaves (Ball and Pidsley, unpublished results).

Any re-export of ions from these leaves must take place via the phloem. There is no convincing evidence that excess ions are transported via the phloem to scenescing leaves for disposal. However, growing tissues receive ions from the phloem. The ionic composition of these and other phloem fed tissues reflects that of the phloem, with relatively low Na^+ concentrations and much lower Na^+/K^+ ratios than occur in the xylem (Flowers and Yeo 1986). Indeed, the Na^+ concentration in phloem is lower the greater the salt tolerance of the species (Lessani and Marschner 1978; Munns et al. 1986). Finally, the rates of salt re-export to growing tissues are not sufficient to balance the rates of salt influx to the leaves because salt accumulates in the leaves with time (Atkinson et al. 1967). However, re-export of as little as 10% of the salt influx could lead to a 10% increase in the productive life span of the leaves. This could be significant to the carbon balance of many species such as those in the Rhizophoraceae whose leaves live for 6–18 months, depending on the environmental conditions (Tomlinson 1986). However, none of the above observations are consistent with a major role for the phloem in maintaining the salt balance of leaves. It appears that balancing the salt influx with the capacity for salt storage remains the major means of maintaining the internal ion concentrations within physiologically acceptable levels in non-secreting species.

In summary, the uptake and distribution of ions must be controlled so as to maintain turgor and yet protect sensitive metabolic sites from ion stress. The problem arises because even highly salt-tolerant species only partially exclude salt from entry into the transpiration stream. The mechanisms by which mangroves achieve salt balances are poorly known. While salt-secreting species can (within limits) expel excess salt from the leaves, growth must keep pace with the rates of salt uptake in the non-secreting species (Atkinson et al. 1967). Hence, the balance between carbon gain and the expenditure of water with its associated salt uptake may be critical to growth under saline conditions. The implication is that differences in salt exclusion at the roots, coupled with differences in water use and water-use efficiency at the leaves, may play major roles in interspecific differences in salt tolerance.

Carbon gain in relation to water loss

The photosynthetic characteristics of mangroves are clearly those of plants utilising C_3 photosynthetic biochemistry. The CO_2 compensation point at 25° C and saturating light intensity ranges from 45 to 60 $\mu l\ l^{-1}$ and increases with increasing leaf temperature (Moore et al. 1972; Ball 1981; Andrews et al. 1984) consistent with the photorespiratory activity typical of C_3 photosynthesis. The photosynthetic rates are maximal at leaf temperatures less than 35° C (Moore et al. 1972, 1973; Ball 1981; Andrews et al. 1984; Ball et al. 1988) and generally become light saturated at quantum flux densities ranging from 30% to 50% sunlight (Moore et al. 1972, 1973; Attiwill and Clough 1980; Ball 1981; Ball and Critchley 1982; Andrews et al. 1984). The quantum yield of healthy leaves averages 0.106 mol O_2 evolved per mole quanta absorbed in leaves grown under field (Bjorkman and Demmig 1987) or laboratory conditions (Ball et al. 1987), consistent with the bioenergetic demands of C_3 photosynthesis (Ehleringer and Bjorkman 1977). The carbon isotope composition of mangrove foliage ranges from $\delta^{13}C$ values of −24.6 to −32.2‰ (Farquhar et al. 1982; Andrews et al. 1984), which are well within the range reported for C_3 plants (Smith and Epstein 1971). Finally, there is no convincing evidence in mangroves of environmentally induced shifts from C_3 to C_4 or CAM photosynthetic biochemistry (Clough et al. 1982).

There is, however, an unusual feature of the gas exchange characteristics of mangroves. Despite growing in environments with an infinite supply of water, the rates of water loss and the water-use efficiencies are unusually conservative for C_3 species (Ball 1986). The amount of water spent in gaining carbon varies between species as well as between environmental conditions. However, it appears that the water-use characteristics become increasingly conservative with increase in the salinity tolerance of both salt-secreting (Ball and Farquhar 1984b; Ball 1988) and non-secreting species (Ball et al. 1988).

Such conservative water use has implications for leaf functioning under natural field conditions. Although salinity varies both temporally and spatially in a mangrove swamp, the soil salinity changes much more slowly at the roots than the microclimatic conditions, which affect the di-

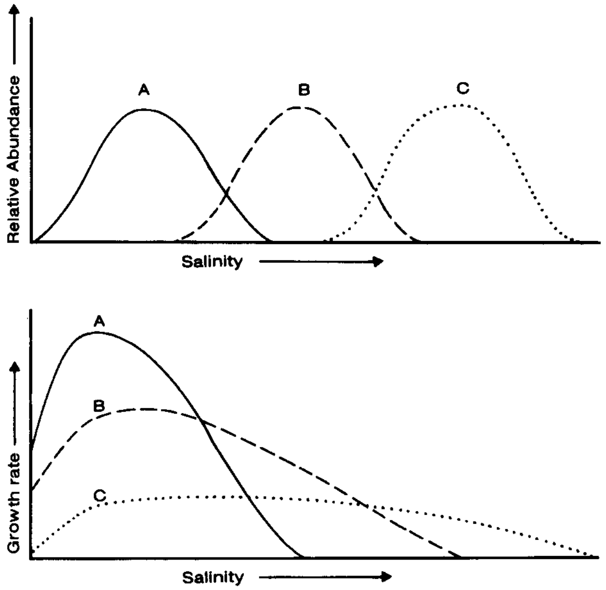
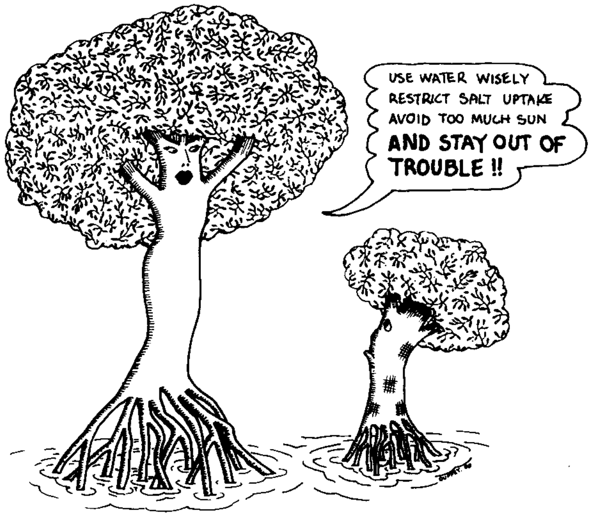


Fig. 1. Schematic diagram of the ecological and physiological responses of three hypothetical mangrove species to variation in salinity. The *top figure* shows the distribution of three species (*A*, *B*, *C*) along a natural salinity gradient. Each species is dominant over a different range of salinities. The *bottom figure* shows the physiological responses of the same species to the salinity gradient. Species *A* is dominant in salinities optimal for its growth, whereas species *B* and *C* are dominant in salinities which are sub-optimal for their growth but which prevent or limit the growth of other species

urnal expenditure of water in relation to carbon gain in the leaves. The evaporation rates depend on both the leaf conductance to water vapour and the vapour pressure gradient between the leaf and air (vpd). Diurnal variation in the latter is due mainly to variation in leaf temperature because the ambient vapour pressure changes little during the course of a day. The closer leaf temperature stays to air temperature, the closer the evaporative demand of the leaf will reflect the saturation vapour deficit of the air.

Leaves that operate with high evaporation rates can take advantage of the high irradiances required to maintain high photosynthetic rates with minimal increase in leaf temperature over air temperature. In contrast, leaves with more conservative expenditures of water must avoid high irradiances if leaf temperatures are to be maintained within physiologically acceptable ranges. In such leaves, avoidance of high light intensities during midday, when the heat load on the leaf is greatest, could allow the leaves to sustain relatively constant, albeit lower assimilation rates throughout the photoperiod. This would result in a greater net gain of carbon than would occur if the leaves were horizontal and subject to temperature-dependent inhibition of photosynthesis for extended periods during the day (Cowan 1982). Thus, maximizing carbon gain for a fixed total expenditure of water involves a complex balance between stomatal behaviour in relation to photosynthesis and variation in leaf properties in relation to light interception and evaporative demand (Cowan and Farquhar 1977; Cowan 1986).



In mangroves, as in other C_3 species (Farquhar and Sharkey 1982), the relationship between stomatal conductance and photosynthetic capacity is such that the leaf expends an amount of water consistent with maintenance of the assimilation rates at or very near the photosynthetic capacity except under extreme conditions when such coordination may be lost (Ball 1981; Ball and Farquhar 1984a, b). Both assimilation rate and stomatal conductance are maximal at leaf temperatures ranging from 25° to 30° C, and decline precipitously with increase in leaf temperature above 35° C (Moore et al. 1972, 1973; Andrews et al. 1984; Andrews and Muller 1985; Ball et al. 1988). The decline in stomatal conductance at high leaf temperatures is not sufficient to reduce the evaporation rate, which increases with temperature-induced increase in vpd. This causes the water cost of carbon gain to increase with increase in leaf temperature above optimal levels. Nevertheless, the positive correlation between stomatal conductance and assimilation rate with variation in irradiance, temperature and vpd has been shown in simulations (Farquhar 1979) to be consistent with minimizing water loss relative to carbon gain even as water-use efficiency varies (Cowan and Farquhar 1977).

Interspecific differences in water-use characteristics in the Rhizophoraceae are manifest in

Table 2. Variation in gas exchange characteristics and in the display and properties of sun leaves in relation to salinity tolerance in the Rhizophoraceae

Species	A/g (µmol/mmol)	Rosette area (cm^2)		Individual leaf area (cm^2)		Specific leaf weight (g dw m^{-2})	Succulence (g water m^{-2})
		Total	Projected	Total	Projected		
Bruguiera gymnorrhiza	0.072	635	356	58	32	133.1	262.5
Rhizophora apiculata	0.096	553	196	69	25	148.8	348.4
Rhizophora stylosa	0.101*	419	126	44	13	169.3	387.9
Ceriops tagal	0.113	102	39	8	3	189.2	463.2

Species are listed in order of increasing salinity tolerance, with *Bruguiera gymnorrhiza* being the least salt tolerant. Values for A/g are slopes obtained by linear regression of the assimilation rate (µmol CO_2 $m^{-2}s^{-1}$) as a function of stomatal conductance to water vapour (mmol $m^{-2}s^{-1}$) with variation in irradiance, leaf temperature and leaf-to-air vapour pressure difference over a range naturally experienced by the leaves under tropical field conditions. All data from Ball et al. (1988) except * from Andrews and Muller (1985)
dw, dry weight

differences in the slope of stomatal conductance as a function of the assimilation rate with variation in leaf temperature, irradiance and vpd (Table 2). The slope increases as water use becomes more conservative with increasing salinity tolerance of the species. Thus, for a wide range of environmental factors affecting photosynthesis during the course of a day, the assimilation rate at a given stomatal conductance is greater (and water use is more conservative) the greater the salinity tolerance of the species (Ball et al. 1988).

As in other mangroves, the optimal leaf temperatures for photosynthesis in the Rhizophoraceae are very close to the average air temperatures in the tropical (Andrews et al. 1984; Andrews and Muller 1985; Ball et al. 1988) and sub-tropical (Moore et al. 1972, 1973) environments in which the plants are grown. However, the rates of transpiration in all of the species examined are not sufficient to prevent heating of the leaves above ambient air temperatures during periods of intense insolation. For example, when exposed canopy leaves of *Rhizophora apiculata* were constrained in a horizontal position, the leaf temperatures increased from 4° to 11° C above ambient air temperatures of approximately 30° C, with increase in incident irradiation from 1430 to 2585 $\mu E\ m^{-2}\ s^{-1}$, respectively. In contrast, leaves left in their natural, almost vertical orientation avoided the maximum heat load during midday when irradiance and air temperatures are greatest. During midday, these leaves received only 20% of available sunlight and were approximately 10° C cooler than than they would have been if fully exposed to the sun. Earlier and later in the day, the leaves received about 1000 $\mu E\ m^{-2}\ s^{-1}$ and leaf temperatures were 30° C, conditions nearly optimal for photosynthesis (Ball et al. 1988). Thus the increase in leaf angle is a compromise between the requirements for illumination and for maintenance of favourable leaf temperatures with minimal evaporative cooling. Indeed, Andrews and Muller (1985) found that similar avoidance behaviour in a stand of *R. stylosa* leading to maintenance of leaf temperature close to air temperature is critical to maximizing the total integrated gain of carbon for a minimum expenditure of water during a day.

Variation in the display and properties of foliage reflect the increasingly conservative water-use characteristics associated with increasing salinity tolerance. In particular, there are interspecific differences in three major characteristics of leaves that relate to maintenance of favourable leaf temperatures with minimal evaporative cooling. Leaf angle (i.e. the inclination to the horizontal) affects the radiant heat loading on the leaf. Leaf angle increased with increasing exposure to the sun among members of the Rhizophoraceae growing together in a mixed community in North Queensland. The angle was greater, and hence the proportion of projected leaf area was smaller the greater the salinity tolerance of the species (Table 2). Apparently, the species which are more conservative in water use are those that tend most to avoid intense radiation (Ball et al. 1988).

Leaf temperatures are also influenced by leaf size. Heat convection between a leaf and its environment depends on resistance to transfer imposed by a boundary layer, the characteristics of which are a function of leaf geometry and wind speed. Decrease in leaf size enhances boundary layer conductance and results in the temperature of the leaf being closer to ambient air temperature without putting the leaf at a disadvantage in terms of light interception. In the Rhizophoraceae, leaf size decreases with increasing exposure (Ball et al. 1988) and is smallest in the most salt-tolerant species (Table 2). Similarly, leaves of mangrove species that dominate hypersaline environments along the arid coasts of Northern Australia (i.e. *Avicennia marina, Ceriops tagal* var. *australis, Excoecaria ovalis, Lumnitzera racemosa* and *Osbornia octodonta*) are much smaller than those of species dominating humid, low salinity wetlands (e.g. *Bruguiera gymnorrhiza* and *R. apiculata*). Thus, mangrove leaves are smallest under conditions in which, due to intense radiation and/or limitations to evaporative cooling, they sustain the greatest heat load (Ball et al. 1988).

A third leaf property influencing leaf temperature is that of heat capacity per unit area, which increases with increase in the dry weight and water content per unit area. Among the Rhizophoraceae, specific leaf weight and succulence, and hence also the heat capacity, increase with salinity (Camilleri and Ribi 1983), exposure (Ball et al. 1988) and with increase in the salinity tolerance of the species (Table 2). The heat capacities of the leaves in Table 2 range from 1.1 to 2.2×10^3 J m^{-2} C^{-1} in *Bruguiera gymnorrhiza* and *Ceriops tagal* var. *australis*, respectively. Leaf temperatures of both species would increase during a lull in air movement because of reduction in boundary layer conductance. However, the rate of temperature increase would be slower in the leaf with a greater heat capacity, thereby damping fluctuations in leaf temperature due to transient variations in leaf microclimate. For example, the period of a fluctuation in environment on a typical day in North Queensland such that the amplitude of fluctuation in leaf temperature is halved would be 1.8 min in *Bruguiera gymnorrhiza* and 3.6 min in *Ceriops tagal*. Thus, although succulence may be primarily involved in the maintenance of favourable internal ion concentrations (Flowers et al. 1986), there is a tendency for mangrove leaves to be more succulent under conditions in which, due to intense irradiation and/or limitations to evaporative cooling, they are most vulnerable to rapid fluctuations in leaf temperature (Ball et al. 1988).

On the cost(s) of salt tolerance

Salinity regimes under natural field conditions vary in time and space, with the time scale and magnitude of fluctuations dependent on the climate and hydrological characteristics of the coastal environment. Naturally, the extent to which a species can cope with fluctuations in salinity will be an important determinant of the distribution and relative importance of that species along salinity gradients. Mangroves generally exhibit maximum growth under relatively low salinity conditions, but differ in the range of salinities over which high growth rates are sustained (Fig. 1). Apparently, natural selection has favoured the extension of ranges of salinity tolerance rather than major shifts in the salinity optima for growth. The ability to sustain growth over a wide range of salinities is clearly advantageous in fluctuating environments. However, the increase in salinity tolerance is not without costs to the species. In general, the broader the range of salinity tolerance of a species, the slower is its growth rate under optimal conditions (Ball 1988; Ball and Pidsley, unpublished results).

Recent studies have identified two major trade-offs between salt tolerance and growth. First, salt exclusion during water uptake appears to entail considerable carbon costs to the plant. For example, maintenance of a particular shoot evaporation rate, say 1 mmol m^{-2} s^{-1}, in *Aegiceras corniculatum* with increase in salinity from 50 to 500 m*M* NaCl was associated with an increase in the root mass/leaf area ratio from 38 to 79 g m^{-2} and a decrease in the rates of water uptake from 26.3 to 12.7 μmol g^{-1} s^{-1}, respectively (Ball 1988). *Avicennia marina*, a more salt-tolerant species, took up water at half the rate of *Aegiceras corniculatum*, and hence the cost of water gain in the former species was twice that in the latter (Ball 1988). These results are consistent with previous studies showing that the hydraulic conductances of roots of *Avicennia marina*, even those grown in freshwater, are as much as two orders of magnitude lower than those of salt-sensitive plants and decrease with increase in salinity (Field 1984). It may be that restricting the rate of water uptake is involved in salt exclusion and maintenance of specificity for uptake of K^+ over Na^+. Thus, if the rates of water uptake were to decline with increasing salinity and/or with the effectiveness of ion exclusion, then a greater root mass might be required to supply a given quantity of water at a given tolerable salt concentration. However, preferential distribution of carbon to roots is at the expense of canopy development and hence also growth.

Second, conservative water use may also entail considerable carbon costs to the plant. Conservative water use may be a consequence of the high carbon costs of water uptake and may also contribute to the maintenance of favourable carbon/salt/water balances (Ball 1988). However, restriction of the rates of water efflux also restricts the rates of CO_2 influx, causing the leaf to operate at low internal CO_2 concentrations, but with a high water-use efficiency (Cowan 1977). Thus, conservative water use within the constraints of C_3 photosynthetic metabolism is at the expense of the assimilation rate (Cowan and Farquhar 1977) and hence also the growth rate.

Conservative water use also incurs costs to the plant in terms of the variation in display and properties of leaves required for maintenance of favourable leaf temperatures with minimal evaporative cooling. First, increasing the angle of inclination reduces heat loading on a leaf, but is at the expense of the amount of the light available to support photosynthesis. Second, decrease in leaf size enhances the heat transfer rates, but this requires greater investment in supportive and conductive tissue per unit of exposed leaf area than large leaves. Finally, increase in leaf succulence, or more correctly in heat capacity, buffers against rapid changes in temperature, but at the expense of leaf carbon which might otherwise be invested in expansion of leaf area. Thus, maintenance of favourable leaf temperatures with minimal evaporative cooling is at the expense of the assimilative capacity of the plant, with the expense increasing as water use becomes more conservative (Ball et al. 1988).

In summary, there are many attributes associated with increasing salt tolerance, but two in particular have major implications for interspecific differences in physiognomy and growth. First, the carbon cost of water uptake increases with increasing salinity and is greater in the more salt tolerant species (Ball 1988). This is manifest in the field by increase in root biomass along gradients of increasing soil salinity. Indeed, the root biomass of tropical mangrove forests is generally greater than that measured in other forest systems (Komiyama et al. 1987). Second, water use becomes increasingly conservative with increasing salinity and with increase in the salinity tolerance of the species (Ball and Farquhar 1984a, b; Ball 1988; Ball et al. 1988). This is manifest in the field by the decreasing degree of canopy coverage along gradients of increasing salinity. Enhancement of these two attributes is at the expense of the growth rate, such that species tolerant of broad ranges of salinity tend to grow more slowly than less tolerant species even under optimal conditions (Fig. 1).

Ecological implications

Differences in water-use characteristics in association with interspecific differences in salinity tolerance have implications for the organization of mangrove forests along salinity gradients (Ball et al. 1988; Ball 1988). Species tolerant of lower ranges of salinity, such as *Bruguiera gymnorrhiza*, operate with lower water-use efficiencies and hence can maintain larger leaves with greater projected leaf areas than those with greater salt tolerance. Under low salinity conditions, stands of this species have dense canopies that allow little transmission of light to the forest floor. In contrast, species that are highly salt tolerant, such as *Ceriops tagal* var. *australis*, operate with very high water-use efficiencies and hence maintain small leaves with a low proportion of projected leaf area. This slowly growing species characteristically forms stands with open canopies, which under low salinity conditions could not exclude the more rapidly growing, densely canopied species characteristic of low salinity environments. Thus, despite growing maximally under low salinity conditions, the attributes that enable species such as *C. tagal* to tolerate highly saline conditions appear to exclude it from being an effective competitor under low salinity conditions. Indeed, vigorous individuals of *C. tagal* occasionally occur in low salinity environments, but the species is limited largely to highly saline habitats where competition from other species is reduced or absent.

Conclusion

Mangrove forests are of major ecological and commercial importance, yet the future of these resources is threatened by pollution, development and over-exploitation. There is an urgent need to develop sound management practices based on a functional understanding of the physical and biological processes underlying mangrove ecosystem dynamics. Such biological processes include dispersal (Rabinowitz 1978), herbivory (Smith 1987) and the physiological bases of species interactions and responses to environmental factors. Understanding these processes is essential for the development of more comprehensive and predictive modelling of mangrove ecosystem dynamics than has previously been possible.

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