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REVIEW

Salt tolerance mechanisms in mangroves: a review

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Abstract Mangroves are woody plants which form the dominant vegetation in tidal, saline wetlands along tropical and subtropical coasts. The current knowledge concerning the most striking feature of mangroves i.e., their unique ability to tolerate high salinity is summarized in the present review. In this review, we shall discuss recent studies that have focused on morphological, anatomical, physiological, biochemical, molecular and genetic attributes associated with the response to salinity, some of which presumably function to mediate salt tolerance in the mangroves. Here we shall also review the major advances recently made at both the genetic and the genomic levels in mangroves. Salinity tolerance in mangroves depends on a range of adaptations, including ion compartmentation, osmoregulation, selective transport and uptake of ions, maintenance of a balance between the supply of ions to the shoot, and capacity to accommodate the salt influx. The tolerance of mangroves to a high saline environment is also tightly linked to the regulation of gene expression. By integrating the information from mangroves and performing comparisons among species of mangroves and non-mangroves, we could give a general picture of salt tolerance mechanisms of mangroves, thus providing a new avenue for development of salt tolerance in crop plants through effective breeding strategies and genetic engineering techniques.

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Introduction

True mangroves and mangrove associates

Mangroves are constituent plants of tropical intertidal forest community. They include woody trees and shrubs, which flourish in the zone between land and sea along the tropical coastline of the globe. They fall into two groups according to their habitats in nature: true mangroves and mangrove associates. True mangroves occur only in mangrove habitat and their existence is rare elsewhere such as *Rhizophora*, *Kandelia*, *Ceriops*, *Bruguiera*, *Avicennia*, *Xylocarpus*, *Aegiceras*, *Sonneratia*, *Laguncularia*, *Lumnitzera*, *Nypha* etc. Mangrove associates are non-exclusive mangrove species occurring in the landward margin of mangal and often non-mangal habitats such as rainforest, salt marsh or lowland freshwater swamps (e.g. *Excoecaria*, *Camptostemon*, *Pemphis*, *Osbornia*, *Pelliciera*, *Aegialitis*, *Acrostichum*, *Scyphiphora*, *Heritiera* etc.). *Heritiera fomes* is a true mangrove with tolerance to high-saline conditions (Santisuk 1983; Naskar and Mandal 1999), but the status of *H. littoralis* as mangrove is controversial. The species *H. littoralis* has been described by most of the authors as fresh water loving back mangal or mangrove associate (Kartawinata et al. 1979; Mukherjee et al. 2003), whereas a few authors have described it as true mangrove (Das et al. 1994; Tam et al. 1997; Parani et al. 1998). Mangroves are taxonomically diverse. True mangroves include about 54 species in 20 genera belonging to 16 families (Hogarth 1999). Mangroves grow in the intertidal zone between land

and sea. They are frequently inundated by tide leading to waterlogging and fluctuation in salinity (Naidoo et al. 2002; Sengupta and Chaudhuri 2002; Paliyavuth et al. 2004; Jagtap and Nagle 2007). Like other marine organisms, they are exposed to the air and thus to the risk of desiccation and overheating; on the other hand they face waterlogging and salinity (Naidoo et al. 2002; Sengupta and Chaudhuri 2002; Paliyavuth et al. 2004; Jagtap and Nagle 2007). Under high temperature conditions in tropics the above problems become worse. Firstly, at low tide, overheating and desiccation is greater, and secondly, through evapotranspiration, any water that remains may become even more highly saline than that of the open sea. At high tide, the warmth of water lowers the oxygen in water (Hogarth 1999). High salinity makes it more difficult for mangroves to extract water from the soil, even though the soils on which mangroves grow are usually waterlogged. Consequently, many mangrove species have morphological characteristics and high water-use efficiencies characteristic of terrestrial xerophytes (Clough et al. 1982; Ball 1988a; Clough and Sim 1989).

Economic and ecological importance of mangroves

The mangrove forests have enormous economic potentiality and utilitarian value at the ecosystem as well as at the component levels (Robertson and Alongi 1992; UNEP-WCMC 2006). Mangroves have been playing a significant role in the economy of tropical societies for thousands of years, providing a wide variety of goods and services including wood production, support for commercial and subsistence fisheries, salt production and shoreline protection and coastal erosion control (Hamilton and Murphy 1988; Krauss et al. 2008). Mangrove trees are good sources of firewood for local communities; their wood makes a superior kind of charcoal and is a source of tannins, resins, medicines, etc. (Hamilton and Murphy 1988; Baconguis and Mauricio 1991). Many of the animals found within the mangal are harvested for food: fish, crabs and prawns in particular. Therefore, mangrove trees are very important for conserving and maintaining mangrove ecosystems. Mangrove ecosystems constitute a refuge, feeding ground and nursery for species of cyanobacteria, red algae, manglicolous fungi, invertebrates, fish and shrimp (Martosubroto and Naamin 1977; Sheridan 1991; Turner 1992; Sasekumar et al. 1992; Hyde and Lee 1995; De Graaf and Xuan 1999). Reptiles, including crocodiles, alligators, lizards, snakes and sea turtles also live in many mangroves. Mangroves provide important nesting sites for land birds, shorebirds and waterfowl, and they are home to a number of threatened species including spoonbills, large snowy egrets, scarlet ibis, fish hawks, royal terns, West Indian whistling-ducks, and Storm's Storks (Staus 1998). A variety of mammals make their homes in the mangal by association with the mangroves. Some of the noteworthy species present include dolphins, crab-eating monkeys, proboscis monkeys, fishing cats, mangrove monkeys and otters in India (Gopal and Krishnamurthy 1993), flying fox in northern Australia (Loughland 1998) and capuchin in Brazil (Fernandes 1991).

Exploitation of mangroves

Finally, mangroves are currently threatened by many different human activities. Exploitation is often taken beyond the level of natural replacement. Inland irrigation schemes divert river water from coastal regions and mangroves suffer from the resulting increase in salinity. Pollution takes its toll. Deliberate clearance for the development of aqua-culture takes place without consideration of what may be lost. Mangroves are likely to be one of the first ecosystems to be affected by global changes because of their location at the interface between land and sea. It has been predicted that as sea level rises, accompanying the rapid climate changes (Pernetta 1993; Field 1995; Ellison and Farnsworth 1997; Das et al. 2002; Kim et al. 2005; Jagtap and Nagle 2007; Gilman et al. 2008), mangroves tend to retreat landwards. And, of course, any significant rise in sea level resulting from global warming will mean encroachment on the relatively narrow zone within which mangroves flourish (Pernetta 1993; Das et al. 2002; Kim et al. 2005; Jagtap and Nagle 2007; Gilman et al. 2008). Destruction of mangrove habitats means a loss of the mangrove resource: as mangroves decline, so too do timber and charcoal production and fisheries, and the livelihood of the people who depend on them. This seems almost too obvious to need pointing out. The productivity and diversity of mangroves as well as their considerable social and economic values therefore make them of great interest to biologists and ecologists to understand their significance.

Mangroves and salt tolerance

Salt tolerance is the ability of plants to grow and complete their life cycle on a substrate that contains high concentrations of soluble salt. Plants that can survive on high concentrations of salt in the rhizosphere and grow well are called halophytes. Depending on their salt-tolerating capacity, halophytes are either obligate, and characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50% seawater or facultative and found in less saline habitats along the border between saline and non-saline upland and characterized by broader physiological diversity which enables them to cope with saline and non saline conditions. Mangroves are facultative halophytes tolerant to both high and fluctuating salinity. Some authors have also categorized mangroves under obligate halophytes (Downton 1982; Clough 1984). Several mangrove tree species reach an optimum growth at salinities of 5–25% of standard seawater (Downton 1982; Clough 1984; Ball 1988a; Burchett et al. 1989; Ball and Pidsley 1995). However, the range of salinity in which the plant is able to survive varies according to the species (Ball 1988a); in several species growth may be affected by either absence of or excess of NaCl in the substrate (Downton 1982; Clough 1984; Burchett et al. 1989; Pezeshki et al. 1990; Ball and Pidsley 1995). Because mangroves successfully live in high salinity environments it is advantageous to use them to study the mechanisms by which plants respond and adapt to these environments. Mangrove research has advanced considerably in the last few years, and the time seems right for an attempt to present our current understanding of the mechanisms of salt tolerance in mangroves. Although voluminous works are available on salt tolerance mechanism taking the model plant *Arabidopsis thaliana* (Apse et al. 1999; Nanjo et al. 1999; Quesada et al. 2000; Shi et al. 2000; Liu et al. 2000; Zhu 2000; Elphick et al. 2001), facultative model halophyte *Mesembryanthemum crystallinum* (Ratajczak et al. 1994; Low et al. 1996; Su et al. 2001; Golldack and Deitz 2001; Agarie et al. 2007), the information on morphological, anatomical, physiological, biochemical and molecular basis of salt tolerance mechanisms in mangroves which are facultative halophytes and potential stress adaptor (Downton 1982; Clough 1984) will throw new light and give a new dimension to salt stress research. Understanding the mechanisms of salt tolerance in mangroves and identification of salt tolerant genes from mangroves will lead to effective means to breed or genetically engineer salt tolerant crops.

Mechanisms of salt tolerance in mangroves

The ecological success of the mangroves under harsh conditions is explained by several morphological, anatomical, physiological, biochemical and molecular features. Mangroves develop a plethora of mechanisms to cope with salt stress that are discussed under following headings.

Morphological and anatomical features

Mangroves grow in a soil that is more or less waterlogged and in water whose salinity fluctuates and may be as high as that of the open sea (Naidoo et al. 1997). Mangrove trees adapt to survive such uncompromising surroundings with several morphological features such as salt-excreting leaves, and viviparous water dispersed propagules. In response to salinity where water economy is stringent, leaves tend to be smaller and thicker in mangroves (Ball 1988a). A small leaf design enhances cooling as small leaves lose more heat by convection than do large ones. There are interspecific differences in salt tolerance among the mangroves (Ball and Pidsley 1995). Ball and Pidsley (1995) examined the effects of soil salinity on the growth of two closely related species, *Sonneratia alba* and *S. lanceolata* in relation to their differential distributions along naturally seasonal salinity gradients. They showed that there were interspecific differences in salt tolerance which were founded on the inherent growth characteristics of the two species. In fact, these species showed a neat trade-off between growth and salt tolerance with *S. lanceolata* growing in salinities of up to 50% that of seawater while *S. alba* can grow in 100% seawater. Both the species, however, showed optimal growth in culture at 5% seawater. Nevertheless, at optimal salinity the growth of more salt tolerant species *S. alba*, measured as biomass, height and leaf area, is less than half that of the less salt tolerant species *S. lanceolata*, indicating that *S. lanceolata* will be the successful competitor even at a salinity that is optimal for both the species. On the other hand, *S. lanceolata* could not grow or compete in high salinities. In this species pair, a species can apparently opt for salt tolerance, or for rapid growth and competitive ability under low salinity conditions, not both (Ball and Pidsley 1995). The root-to-shoot ratio becomes relatively high and increases with increasing concentration of salinity in *Avicennia* and *Aegiceras* (Ball 1988b; Saintilan 1997). In addition, vivipary is also a characteristic that might have some role to tolerate high salinity in mangroves (Zheng et al. 1999). Vivipary is the condition found in some species of mangroves in which the sexually produced embryo of the seed continues its development without dormancy into a seedling, while still attached to the mother plant (Elmqvist and Cox 1996). Vivipary is known in the four genera of mangroves such as *Bruguiera*, *Kandelia*, *Rhizophora* and *Ceriops* of Rhizophoraceae (Tomlinson 1986). The seedling develops without dormancy largely by elongation of the hypocotyl to produce a cigar-shaped seedling known as propagule, which remains conspicuously pendulous on the mother tree for several months (Tomlinson and Cox 2000). The viviparous condition is so strongly associated with mangroves that it is suggested to have adaptive significance in the intertidal environment (Tomlinson 1986). It was assumed that vivipary in mangroves may be an adaptive characteristic permitting avoidance of high salinity at germination (Henkel 1979). Some evidence has proved that developing viviparous propagules (i.e. hypocotyls) in Rhizophoraceae retain lower salt concentrations than in other organs of mother trees especially the leaves, but it increases gradually during the process of propagule maturation (Wang et al. 2002). This lowered salt concentration in developing propagules, whatever its origin, is interpreted as a mechanism to “protect” the embryo from the deleterious effects of high salt concentrations until maturity (Hogarth 1999). Nevertheless, a few authors have argued that the adaptation of developing propagules (hypocotyls) to salt originates when it is still attached to the mother tree by continuously absorbing salt from the mother tree (Lin 1988). After following the element concentrations on a dry weight basis, Zheng et al. (1999) concluded that the development of propagules was not a salt accumulation process, but a desalinating process, because salt concentration on a dry weight basis declined with propagule development. If it were truly a desalinating process, how can the propagule keep the osmotic balance and by what means can the propagule cope with the salt stress and osmotic stress after the propagule settles down in the hyposaline environment? Little research has dealt with the changes after a propagule leaves the mother plant (Tomlinson and Cox 2000). Wang et al. (2002) reported that no direct correlation was found between salt tolerance and vivipary. All features mentioned above reveal higher competence of salt tolerance of mangroves in terms of morphology.

Mangroves develop diverse mechanisms associated with anatomic characteristics in order to tolerate high salinity. Mangrove species usually have salt resistant-associated anatomic structures. Many species of mangrove possess salt glands in their leaves. All species in genus *Aegiceras*, *Avicennia*, *Acanthus* and *Aegialitis* have typical salt gland structures, and species in *Laguncularia* and *Conocarpus* have analogous structure to salt glands (Tomlinson 1986). In *L. racemosa* and *C. erectus* “tiny bumps” or “pimples” like structures are found on the petioles of the leaves that somewhat resemble salt glands (Tomlinson 1986). However, the salt secretory ability of these structures has not been precisely demonstrated. Biebl and Kinzel (1965) describe three morphologically different structures in the leaves of *L. racemosa*, the smallest of which sit in deep, irregular epidermal depressions and extrude chains of salt crystals. However, Kemis (1984) raised specimens of *Conocarpus* and observed them to secrete clear, sweet-tasting nectar. His observations and electron microscope studies led him to conclude that the “pimples” are, in fact, “extra floral nectarines (EFN)”. Kemis (1984) reported that these extra-floral nectaries (EFN) may serve an adaptive role and used mutualistically to attract ants to defend the tree from herbivorous pests. Kemis and Lersten (1984) follow up the study of *Conocarpus* with a similar electron microscope study of *Laguncularia* and conclude that, the pimples lack a salt excretory function, but the morphology is so different that there is “no evidence of an opening”. No evidence of an opening indicates that these pimples secrete neither salt nor nectar. They suggest a theory regarding the differences in the *L. racemosa* and *C. erectus* petiolar “pimples.” They suggest that the apparently non-functional nature of the pimples on *Laguncularia* is a consequence of a reversion from functionality to vestigiality. It is suspected that the mythical salt glands in *Conocarpus* are really the sugar glands become vestigial remnant in *Laguncularia*. Saenger (2002) pointed out that in *L. racemosa*, the formation of these salt glands analogous structures or pimples is found only in the presence of salt implying a secretory function (2002). Saenger (2002) reported that these salt glands analogous structures may be interpreted as hydathodes, salt glands or nectaries. Leaves of *Aegiceras* and *Avicennia* have deposits of salt crystals as a result of salt leak from the salt glands. The lower leaf surface of *Avicennia* is densely covered with hairs, which raise the secreted droplets of salt water away from the leaf surface, preventing the osmotic withdrawal of water from the leaf tissues (Osborne and Berjak 1997). In species *of Rhizophora*, *Sonneretia*, *Avicennia* and *Xylocarpus*, salt is also deposited in the bark of stem and roots (Scholander 1968). Another typical characteristic of mangrove is the induction of leaf succulence by thickening of leaves with increasing water content (Suarez and Sobrado 2000). For example, *Laguncularia racemosa* can increase leaf thickness and water content when stressed with high salinity (Sobrado 2005), by which absorbed salt was diluted and salt-induced damage was reduced to some extent. Under the condition of high salinity, there is increase of leaf thickness from the youngest to the oldest leaves along shoot in *L. racemosa* (Werner and Stelzer 1990). Salt-induced succulence can lower the resistance to CO_2 uptake and this increases the photosynthetic rate by increasing the internal leaf surface for gas exchange. The waxed epidermis in the leaves is also a protective trait in some mangroves, which contributes to low transpiration of mangrove species relative to that of other plants without this trait (Werner and Stelzer 1990). Several species deposit salt in senescent leaves, which are then shed (Zheng et al. 1999). This helps in removing salt from the metabolic tissues. There is also change in leaf anatomy i.e. development of kranz anatomy and dimorphism of chloroplast, reduction in number of stomata per leaf area and wide opening of stomata which is a typical feature of succulence (Werner and Stelzer 1990; Parida et al. 2004a).

In *Rhizophora mangle* salt-induced increase in succulence is predominantly based on the considerable expansion of the hyalinous hypodermal cells below the upper epidermis (Werner and Stelzer 1990). The high Na^+ and Cl^- concentrations in hypodermal and endodermal vacuoles of *Rhizophora* are the result of cellular metabolism. These vacuoles represent storage pools, supplied and/or unloaded by membrane activity. Apparently, the outer hypodermis and the endodermis represent ion regulating steps or two sheaths of the ultrafilter, respectively. The hypodermal cells layers of *Rhizophora* form a tight ring of cells with relatively long radial cell walls. Their vacuoles represent more than 40% of the total root volume and they contain relatively high Na^+ and Cl^- concentrations. The vacuoles of these cells act as salt traps, protecting the subsequent cell layers (Werner and Stelzer 1990). The processes of root elongation and suberization of cell walls are two possible other ways to avoid an invasion of these cells by salt. Root elongation maintains the capacity for accumulating ions by providing new cells (Stelzer et al. 1988); suberization seals the ion-invaded cells and blocks the apoplasmic pathway (Peterson 1988; Taura et al. 1988).

The mangrove species have several morphological and anatomical features which are quite similar to high water-use efficiency characteristics of terrestrial xerophytes (Clough et al. 1982; Ball 1988a; Clough and Sim 1989). These characteristics enable the mangroves to grow in a “physiologically” dry (or) saline environment without apparent adverse effects of severe water stress. The water conserving function of mangroves is very much similar to xerophytes (Ball 1988a). Most of the mangrove genera have thick-walled epidermis with waxy cuticle and sunken stomata. The waxy cuticles are covered by a tomentum of various shaped hairs, like tricellular peltale hairs in *Avicennia* sp., stellate hairs in *Hibiscus tiliaceous* and stellate scales in *Heritiera* sp. (Miller et al. 1975). This tomentum-like outgrowth reduced water loss via the stomata and the salt gland. Sunken stomata beneath the epidermis are prominent in *Avicennia* sp., *Bruguiera* spp., *Ceriops* spp., *Lumnitzera* spp. and *Rhizophora* spp. (Miller et al. 1975). Sclerenchymatous cells are distributed throughout the mangrove leaves including the epidermis (Sidhu 1975). The presence of large-celled water-storing hypodermis with strongly developed palisade mesophylls with small intercellular spaces in the mangrove leaves indicate their xerophytic characters (Sidhu 1975). The isobilateral leaves of *Aegialitis rotundifolia* have no hypodermal tissue and spongy mesophyll; on the other hand the isobilateral leaves of *Ceriops tagal* have enlarged spongy mesophyll cells both in upper and lower hypodermis (Saenger 1982). The isobilateral leaves of *Sonneratia caseolaris* and *Lumnitzera racemosa* also have enlarged water-storing hypodermal cells. The dorsiventral leaves of *Acanthus ilicifolius*, *B. gymnorrhiza*, *Excoecaria agallocha* and *xylocarpus* spp. have several layers of hypodermal cells (Saenger 1982). *Rhizophora* spp. also have marked differentiation of hypodermis with small tannin cells and large colorless water-storing cells. The leaves of most of the mangroves are succulent due to the well-developed large-celled water storing hypodermis and strongly developed palisade mesophyll tissues with small intercellular spaces (Saenger 1982). Several layered hypodermal aqueous tissues are present in most of the mangroves, e.g., *Avicennia* sp., *Hibiscus* spp., *Acrostichum* spp. and single-layered hypodermal cells have also been reported in *Bruguiera* spp., *Ceriops* spp., *Cynometra* spp., *Accanthus* spp. and *Excoecaria* spp. (Saenger 1982). Large undifferentiated mesophyll cells have formed a central aqueous tissue in *Sonneratia* sp. and *Lumnitzera* sp. (Saenger 1982). In *Aviccenia* spp., *Bruguiera* spp. and *Ceriops* spp., the ends of the vascular bundles are surrounded by irregular groups of tracheids (Saenger 1982). The walls of the tracheids bear spiral reticulated or pitted thickenings and the water storage function has been attributed to them (Saenger 1982). The stone cells and sclereides have been reported from *Avicennia* spp., *Rhizophora* spp., *Sonneratia* spp., *Bruguiera* spp., and *Xylocarpus* spp. (Saenger 1982). These cells give toughness and rigidity to leaves. The mucilaginous cells have been reported from *Sonneratia* spp. and *Rhizophora* spp. and these mucilaginous cells may be involved in reducing damages from wilting by conserving water (Ball 1988a). The water use efficiency of glycophytes is comparatively less than that of mangroves.

Physiological and biochemical mechanisms

Some of the most salt-tolerant mangrove species grow in an environment where tidal influence is minimized but evaporation of water from the soil surface is high. In these areas the concentration of salt in the soil rises to such an extent that it becomes hypersaline (more salty than seawater, Lovelock and Feller 2003). Seawater contain 35 g/l of salt (3.5%), 483 mM Na^+ and 558 mM Cl^-) with an osmotic potential of -2.5 MPa (Scholander 1968). Mangroves, therefore, have to maintain continuous water uptake, and regulate ion uptake and compartmentation against a strong external salt gradient (Ball 1996). To maintain water uptake, mangroves not only have to restrict water loss by means of conservative morphological and physiological adaptations such as thickening of leaves giving rise to greater retention times for leaf nitrogen and conservative water use efficiency (Ball 1996; Lovelock and Feller 2003) but also they need to maintain sufficiently low water potentials. Agricultural crops under well-saturated conditions generally have water potentials of approximately -1.0 MPa. However, as the osmotic potential of seawater is approximately -2.5 MPa (Sperry et al. 1988), mangrove leaf water potentials have to range between -2.5 and -6.0 MPa (Scholander et al. 1966; Aziz and Khan 2001a; Sobrado and Ewe 2006). Salinity stress causes low stomatal conductance, which decreases the rate of CO_2 accumulation and uptake, rate of transpiration and increase in xylem tension (Ball and Farquhar 1984; Aziz and Khan 2001a; Parida et al. 2004a). The low transpiration rates and slow water uptake are common features for all mangroves (Scholander et al. 1966). However, increase in transpiration in response to increase in salinity has also been reported in *B. gymnorrhiza* (Takemura et al. 2000) and in both *Avicennia alba* and *Rhizophora apiculata* (Becker et al. 1997). This is suggested to be the aim at increasing internal salt concentration and eventually balance the increased external salt concentration. As water salinity increases, some species of mangroves simply become increasingly conservative in their water use, thus achieving greater tolerance (Ball and Passioura 1995). Because mangrove roots exclude salts when they extract water from soil, soil salts could become very concentrated, creating strong osmotic gradients (Passioura et al. 1992). Zimmermann et al. (1994) reported that the xylem vessels of the roots and stems of mangrove (*Rhizophora mangle*) contain high molecular weight viscous, mucilage made up of acid polysaccharides (mucopolysaccharides). These mucopolysaccharides in the xylem sap are apparently involved in water transport in the xylem conduit of *R. mangle* (Zimmermann et al. 1994). Accumulation of mucilage in xylem vessels is an important strategy of mangrove trees to save water on its tortuous pathway to the uppermost crown (Zimmermann et al. 1994, 2002). The viscous, polymeric substances in the xylem sap limit flow rate and decrease transpiration (Zimmermann et al. 1994, 2002). This, combined with high water-use efficiency, slows the rate of water uptake and prevents salts from accumulating in the soil surrounding the roots. This helps the mangroves conserve water and regulate internal salt concentrations (Ball and Passioura 1995; Ball 1996).

Mangroves experience hypersaline conditions as a result of evaporation (which raises the salinity level) and fluctuation of salinity caused by tide (Lovelock and Feller 2003). High salinity and salinity variation pose a problem for mangroves (Lovelock and Feller 2003). To cope with this uncompromising situation, a number of physiological and biochemical mechanisms are adopted by mangroves, namely, salt excretion (Hanagata et al. 1999), salt accumulation (Popp 1984a, b; Kura-Hotta et al. 2001; Mimura et al. 2003), salt secretion (Sobrado and Greaves 2000), accumulation of compatible solutes (Ashihara et al. 1997) and induction of antioxidative enzymes (Takemura et al. 2000; Parida et al. 2004b) which are discussed under the following headings.

Salt secretion, salt exclusion and salt accumulation

Depending on their salt eliminating mechanism mangroves and their associates have been classified into three groups: (1) salt excluders, (2) salt secretors and (3) salt accumulators (Table 1). The salt-excluding mangrove species (e.g. *Rhizophora* spp., *Ceriops* spp., *Bruguiera* spp., *Lumnitzera* spp., *Excoecaria* spp.) eliminate excess salt by an ultrafiltration mechanism occurring at the root cell membranes of cortical cells (Scholander 1968; Zheng et al. 1999; Takemura et al. 2000; Aziz and Khan 2001a; Khan and Aziz 2001; Wang et al. 2002). Though the exact mechanism of ultrafiltration is not well characterized, it is understood that the process is a physical one. Negative hydrostatic pressure developed in plants by transpiration is enough to overcome negative osmotic pressure in the environment of the roots. Water is therefore drawn in, unwanted ions and other substances are excluded. *Rhizophora mangle* is not provided with salt glands, but it keeps the xylem sap essentially free of NaCl by ultrafiltration at the membranes of root cells (Scholander et al. 1966; Scholander 1968). The concentration of xylem sap is about one-tenth than that of seawater (Lawton et al. 1981). Furthermore, in *B. gymnorrhiza*, hypocotyls function as an additional filter to retain salt from the shoot (Lawton et al. 1981).They maintain ionic balance through K^+/Na^+ exchange at the xylem parenchyma cells in the basal part of

Table 1 Mechanism of salt adaptation and their known distribution in some mangrove species

Species	Exclude	Secrete	Accumulate	References
Acanthus		+		Hogarth (1999); Ye et al. (2005); Nguyen et al. (2007)
Aegialitis	+	+		Naidoo and von Willert (1995); Hogarth (1999)
Aegiceras	+	+		Naidoo and von Willert (1995); Mishra and Das (2003); Ye et al. (2005)
Avicennia	+	+	+	Sobrado (2002); Ye et al. (2005); Suarez and Medina (2006); Griffiths et al. (2008)
Bruguiera	+		+	Takemura et al. (2000); Kura-Hotta et al. (2001); Li et al. (2008); Miyama and Tada (2008)
Ceriops	+			Hogarth (1999); Zheng et al. (1999); Aziz and Khan (2001b)
Excoecaria	+			Tomlinson (1986); Hogarth (1999)
Laguncularia		+		Hogarth (1999); Sobrado (2004)
Osbornia	+		+	Tomlinson (1986); Hogarth (1999)
Rhizophora	+		+	Clough (1984); Werner and Stelzer (1990); Hogarth (1999)
Sonneratia	+	+	+	Tomlinson (1986); Hogarth (1999); Yasumoto et al. 1999
Xylocarpus			+	Hogarth (1999); Paliyavuth et al. (2004)

the plants and vacuolar K^+/Na^+ exchange in transpiring leaves and circulation of exchanged ions within the plants. The ultrafiltration process and K^+/Na^+ exchange contribute to keeping the xylem sap concentration of salt-treated plants low with mean rates of net ion transport into the shoot being even lower due to recirculation of exchanged ions (Mallery and Teas 1984; Werner and Stelzer 1990).

Salt secretors regulate internal salt levels by secreting excess salt through foliar glands and are represented by *Acanthus* spp., *Avicennia marina*, *Av. officinalis*, *Av. alba*, *Aegiceras corniculatum* and *Aegialitis* spp. (Meher-Homji 1988; Selvam 2003). Salt stimulation to secretion was a common feature in salt-secreting mangrove species (Ball 1988a; Drennan et al. 1992; Sobrado 2002). Salt secretion occurs through glands and it is facilitated by efficient leaf turnover for salt shedding (Aziz and Khan 2001b). Dschida et al. (1992) identified an energy-dependent process in salt excretion, achieved by plasma membrane H^+-ATPase in *Avicennia germinans*. The salt tolerance of three salt-secreting mangrove species, i.e. *Acanthus ilicifolius*, *Aegiceras corniculatum* and *A. marina* was compared by Ye et al. (2005). They reported that all of the three species exhibited increases in salt secretion with increases in salinity. The capacity to secrete salts at any given salinity was different between species, following an order of *A. marina* > *A. corniculatum* > *A. ilicifolius*, similar to the case of seedling growth. The salt tolerance of the three salt-secreting mangrove species was in the descending order of *A. marina* > *A. corniculatum* > *A. ilicifolius*. This indicated that salt secretion from leaves was related to salt tolerance (Ye et al. 2005). There are species, which can employ more than one mechanism to protect against adverse effects of salinity (Table 1). *Aegiceras* and *Avicennia*, which are provided with salt glands also, exclude 90–97% salt through the process of ultrafiltration (Ball 1988b). Salt-secreting ability is absent in glycophytes.

Salt accumulators accumulate high concentration of salts in their cells and tissues and avoid salt damage by efficient sequestering of ions to the vacuoles in the leaf, translocation outside the leaf, possible cuticular transpiration and efficient leaf turnover to salt shedding (Tomlinson 1986; Aziz and Khan 2001b). Species of *Lumnitzera* and *Excoecaria* accumulate salts in leaf vacuoles and become succulent. Salt concentrations in the sap may also be reduced by transferring the salts into senescent leaves or by storing them in the bark or roots (Tomascik et al. 1997; Perry et al. 2008). Regulation of K^+ uptake and/or prevention of Na^+ entry, efflux of Na^+ from the cell, and utilization of Na^+ for osmotic adjustment are strategies commonly used by plants to maintain desirable K^+/Na^+ ratios in the cytosol. Osmotic homeostasis is established either by Na^+ compartmentation into the vacuole or by biosynthesis and accumulation of compatible solutes. A high K^+/Na^+ ratio in the cytosol is essential for normal cellular function of plants. Na^+ competes with K uptake through Na^+–K^+ co-transporters, and may also block the K^+-specific transporters of root cells under salinity (Zhu 2003). This results in toxic levels of sodium as well as insufficient K^+ concentration for enzymatic reactions and osmotic adjustment. Under salinity, sodium gains entry into root cell cytosol through cation channels or transporters (selective and nonselective) or into the root xylem stream via an apoplastic pathway depending on the plant species (Chinnusamy et al. 2005). Silica deposition and polymerization of silicates in the endodermis and rhizodermis block Na^+ influx through the apoplastic pathway in the root (Yeo et al. 1999). Restriction of sodium influx either into the root cells or into the xylem stream is one way of maintaining the optimum cytosolic K^+/Na^+ ratio of plants under high salinity. In saline conditions, cellular potassium level can be maintained by activity or expression of potassium-specific transporters. In *Mesembryanthemum crystallinum* L., high affinity K^+ transporter-K^+ uptake genes are up-regulated under NaCl stress (Su et al. 2002). Sodium efflux from root cells prevents accumulation of toxic levels of Na^+ in the cytosol and transport of Na^+ to the shoot. Molecular genetic analysis in *Arabidopsis* have led to the identification of a plasma membrane Na^+/H^+ antiporter, SOS1 (Salt Overly Sensitive 1), which plays a crucial role in sodium extrusion from root epidermal cells under salinity (Chinnusamy et al. 2005). Sodium efflux by SOS1 is also vital for salt tolerance of meristem cells such as growing root-tips and shoot apex as these cells do not have large vacuoles for sodium compartmentation (Shi et al. 2002). The expression of SOS1 is ubiquitous, but stronger in epidermal cells surrounding the root-tip, as well as parenchyma cells bordering the xylem. Thus, SOS1 functions as a Na^+/H^+ antiporter on the plasma membrane and plays a crucial role in sodium efflux from root cells and the long distance Na^+ transport from root to shoot (Shi et al. 2002). Sodium efflux through SOS1 under salinity is regulated by SOS3–SOS2 kinase complex (Chinnusamy et al. 2005).

Vacuolar sequestration of Na^+ is an important and cost-effective strategy for osmotic adjustment that also reduces the Na^+ concentration in the cytosol. Na^+ sequestration into the vacuole depends on expression and activity of Na^+/H^+ antiporters as well as V-type H^+- ATPase and H^+-PPase. These phosphatases generate the necessary proton gradient required for activity of Na^+/H^+ antiporters. Salt accumulation in mangroves occurs with the sequestration of Na^+ and Cl^- into the vacuoles of the hypodermal storage tissue of the leaves (Werner and Stelzer 1990; Aziz and Khan 2001a; Kura-Hotta et al. 2001; Mimura et al. 2003). Cram et al. (2002) reported two subsequent phases of salt accumulation in leaves of *Bruguiera cylindrica*, *Avicennia rumphiana* and *A. marina*. The first phase is the rapid increase in leaf salt concentration, as it grows from bud to maturity followed by a slower but continuous change in salt content via changes in ion concentration and/or in increased leaf thickness. Increased accumulation of Na^+ is generally coupled with reduced Ca^{++} and Mg^{++} uptake (Greenway and Munns 1980; Delphine et al. 1998) and sometimes with decline in carbon assimilation (Parida et al. 2004a). It was reported that Na^+ and Cl^- ion levels increase in root and shoot tissues of *Kandelia candel* and *B. gymnorrhiza* with increasing NaCl stress but, *B. gymnorrhiza* shows a rapid Na^+ accumulation upon the initiation of salt stress and leaves contain 90% more Na^+ and 40% more Cl^- than *K. candel* (Li et al. 2008). The X-ray microanalysis of leaf mesophyll cells shows evidence of distinct vacuolar compartmentation of Na^+ in *K. candel* but Cl^- in *B. gymnorrhiza* seedlings subjected to 100 mM NaCl. Moreover, Na^+ within cell wall, cytoplasm, vacuole and chloroplast remains 23–72% lower in stressed *B. gymnorrhiza* as compared to *K. candel*. It was concluded that *B. gymnorrhiza* exhibit effective salt exclusion from chloroplasts although increasing salt stress causes a rapid and higher build up of Na^+ and Cl^- in the leaves (Li et al. 2008). Net photosynthetic rate (P_N) declines with increasing salinity in both the species, and the most marked reduction occurred after exposure of mangrove seedlings to a severe salinity, 400 mM NaCl. However, the inhibitory effects of severe stress varied with species: P_N decreased by 80% in *K. candel* whereas in *B. gymnorrhiza* the decline was 60%. The lesser reduction in photosynthesis in *B. gymnorrhiza* could be a consequence of salt exclusion from mesophyll chloroplasts (Li et al. 2008). Compartmentalizing NaCl into the vacuole is likely to depend on Na^+/H^+ antiporter systems (Garbarino and DuPont 1988; Tanaka et al. 2000; Fu et al. 2005), H^+-coupled Cl^- antiport (Schumaker and Sze 1987) or ion channels (Pantoja et al. 1989; Maathuis and Prins 1990). Ion compartmentation in the vacuole would limit excessive salt accumulation in the symplast, thus protecting salt-sensitive enzymes in the cytoplasm and chloroplasts. Hence, the ability to maintain lower Na^+ and Cl^- in the symplast may be an underlying determinant of the tolerance of mangroves (Li et al. 2008).

Accumulation of compatible solutes and osmolytes

One of the important biochemical mechanisms by which mangroves counter the high osmolarity of salt is accumulation of compatible solutes (Takemura et al. 2000; Parida et al. 2004c). To accommodate the ionic balance in the vacuoles, cytoplasm accumulates low-molecular-mass compounds termed compatible solutes because they do not interfere with normal biochemical reactions; rather they replace water in biochemical reaction (Hasegawa et al. 2000; Ashihara et al. 2003). With accumulation proportional to the change of external osmolarity within species-specific limits, protection of structures and osmotic balance supporting continued water influx (or reduced efflux) are accepted functions of compatible solutes (Parida et al. 2005). Hibino et al. (2001) reported that three mangroves, *B. gymnorrhiza*, *K. candel*, and *R. stylosa*, accumulate exclusively pinitol as compatible solute. Mannitol is the compatible solute for intact plants of *Sonneratia alba* under salinity (Yasumoto et al. 1999). Although, pinitol and mannitol are the most common compatible solutes of a number of mangrove species, proline (in *Xylocarpus* species), methylated quaternary ammonium compounds (in *Avicennia eucalyptifolia*, *A. marina*, *Acanthus ilicifolius*, *Heritiera littoralis* and *Hibiscus tiliaceus*), and carbohydrates (in *Acanthus ilicifolius*, *Heritiera littoralis* and *Hibiscus tiliaceus*) are found to be dominant osmoregulating compounds (Popp et al. 1985). Glycinebetaine, the most common compatible solute, which offers protection to photosynthetic machinery, is found in some mangroves like *A. marina* (Ashihara et al. 1997; Hibino et al. 2001). Although glycinebetaine accumulates as compatible solute in mangroves and many species of non-mangrove halophytes such as *Suaeda maritima*, *Atriplex nummularia* and *Salicornia europoea* but is absent from many crop species (e.g. rice) and the model species in plant transformation, tobacco (Flowers and Colmer 2008). There has therefore been considerable work on engineering the production of glycinebetaine in crop species that do not produce it naturally. Compatible solutes of *Rhizophora stylosa* and *B. gymnorrhiza* are *O*-methylmucoinositol (Ashihara et al. 2003). Mannitol is a compatible solute in *Sonneratia alba* and *Lumnitzera racemosa* (Ashihara et al. 2003). Many mangrove species e.g. *Sonneratia alba*, *A. marina* also accumulate inorganic ions and use them as osmolytes to maintain osmotic and water potential (Yasumoto et al. 1999; Suarez and Medina 2006). Salt tolerance of *B. gymnorrhiza* might be attributed to their ability to accumulate high concentrations of Na^+ and Cl^- (Miyama and Tada 2008). The uptake of additional Na^+ and Cl^- by this mangrove is used as osmolytes and to maintain K^+ homeostasis under salt stress (Miyama and Tada 2008). A summary of specific compatible solutes in mangrove species is given in Table 2. The increased synthesis of compatible solutes is achieved by modulating genes encoding enzymes of the osmolyte biosynthetic pathway. For instance, upregulation of pyrroline-5-carboxylate synthetase (*P5CS*) gene that is involved in proline biosynthesis leads proline accumulation during salt stress in *A. marina* (Mehta et al. 2005). A significant upregulation of *AcP5CS* gene was also observed in *A. corniculatum* during salinity stress. The upregulation of Betaine-aldehyde

Table 2 Compatible solutes in mangroves and mangrove associates

Compatible solutes	Mangrove species	References
Pinitol	*Kandelia candel*, *Rhizophora stylosa*, *Bruguiera gymnorrhiza*, *Avicennia marina*	Hibino et al. (2001)
	Ceriops tagal	Popp et al. (1985)
Mannitol	*Kandelia candel*, *Rhizophora stylosa*, *Bruguiera gymnorrhiza*	Hibino et al. (2001)
	Sonneratia alba	Yasumoto et al. (1999); Ashihara et al. (2003)
	Lumnitzera racemosa	Ashihara et al. (2003)
Proline	*Kandelia candel*, *Rhizophora stylosa*, *Bruguiera gymnorrhiza*	Hibino et al. (2001)
	Bruguiera parviflora	Parida et al. (2002)
	Aegiceras corniculatum	Fu et al. (2005)
	Bruguiera sexangula, *Avicennia alba*, *Xylocarpus granatum*	Datta and Ghosh (2003)
	Acanthus ilicifolius, *Hibiscus tiliaceus*	Datta and Ghosh (2003)
	Avicennia marina	Datta and Ghosh (2003); Hibino et al. (2001)
	Ceriops roxburghiana	Rajesh et al. (1999)
	Ceriops tagal	Aziz and Khan (2001b)
Glycinebetaine	*Avicennia marina*	Hibino et al. (2001); Ashihara et al. (1997); Popp et al. (1985)
	Ceriops roxburghiana	Rajesh et al. (1999)
	Hibiscus tiliaceus	Popp et al. (1985)
O-methylmucoinositol	*Rhizophora stylosa*, *Bruguiera gymnorrhiza*	Ashihara et al. (2003)
Starch/polysaccharide	*Aegiceras corniculatum*	Parida et al. (2004c)
Aspartic acid	*Aegiceras corniculatum*, *Acanthus ilicifolius*	Datta and Ghosh (2003)
Sterol	*Ceriops roxburghiana*	Suarez and Medina (2006)

dehydrogenase (*BADH*) gene that is involved in glycinebetaine synthesis results in the accumulation of glycinebetaine in *A. marina* under salt stress (Hibino et al. 2001). Waditee et al. (2002) reported that under high salinity conditions, the betaine/proline transporters (AmT1, -2, and -3) also involved in the accumulation of betaine by increasing the mRNA levels as well as post-translational activation in *A. marina*.

Induction of antioxidative enzymes

Mangroves inhabiting the intertidal zones suffer from diverse stresses such as high salinity, hypoxia, ultraviolet radiation, nutrition deficiency and so on. These primary stresses may lead to secondary oxidative stress, resulting in accumulation of reactive oxygen species (ROS) such as superoxide (O_2^{-}), hydrogen peroxide (H_2O_2), hydroxyl radical and singlet oxygen ($^1O_2$) (Parida et al. 2004b). These cytotoxic reactive oxygen species can seriously disrupt normal metabolism through oxidative damage to lipids, protein and nucleic acids (Parida et al. 2004b). Mangroves with high levels of antioxidants, either constitutive or induced, have been reported to have greater resistance to this oxidative damage (Cheeseman et al. 1997; Takemura et al. 2000; Parida et al. 2004b; Jithesh et al. 2006). The activities of the antioxidative enzymes such as catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (POD), glutathione reductase (GR), and superoxide dismutase increase under high salinity and a correlation of these enzyme levels and salt tolerance exists in mangroves (Parida et al. 2004b; Takemura et al. 2000). There are several reports of upregulation of antioxidative enzymes and their corresponding genes in mangroves under salinity. In *B. gymnorrhiza*, the activities of the antioxidant enzymes, superoxide dismutase (SOD) and catalase, show an immediate increase after the plants are transferred from water to high salinity (Takemura et al. 2000). In *B. parviflora*, salt treatment preferentially enhances the content of H_2O_2 as well as the activity of ascorbate peroxidase (APX), guaiacol peroxidase (GPX), glutathione reductase (GR), and superoxide dismutase (SOD), whereas it induces the decrease of catalase (CAT) activity (Parida et al. 2004b). It has also been reported that in the salt-secreting mangrove *Aegiceras corniculatum*, there is a linear increase of salt secretion of leaf with increase in period of salt treatment and a concomitant decrease in antioxidative enzymes such as catalase, ascorbate peroxidase and guaiacol peroxidase (Mishra and Das 2003).

Molecular mechanism of salt tolerance in mangroves

The mechanism of salt tolerance of mangroves can be partially explained by morphological, anatomical, physiological and biochemical studies. However, these are insufficient to clarify the salt tolerance mechanism. Recently, some progress has been achieved in understanding the mechanism of salt tolerance in mangroves at a molecular level. Several salt stress-associated genes from mangroves have been evaluated for their contribution to salt tolerance in laboratory studies (Table 3). Table 4 also lists some relevant studies in mangroves at the genomic levels. These results indicated that the tolerance of mangroves to a high-saline environment is indeed tightly linked to the regulation of gene expression. Some molecular biological studies of mangroves are discussed below in order to illustrate this point.

A molecular biological study of salt tolerance was first reported in a mangrove *B. gymnorrhiza* by Sugihara et al. (2000) and they suggested that an oxygen evolving enhancer protein 1 (OEE1) has an important role in the salt tolerance of this mangrove. They reported that when young plants of *B. gymnorrhiza* are transferred from freshwater to a medium with a seawater salt level (500 mM NaCl), the intensity of a 33 kDa protein with p*I* 5.2 increases in the leaf extract as observed in 2-D gel electrophoresis. The N-terminal amino acids sequence of this protein has a significant homology with the mature region of the oxygen evolving enhancer protein 1 (OEE1) precursor. The deduced amino acid sequence consists of 322 amino acids and is 87% identical to that of *Nicotiana tobacum*. The expression of OEE1 was analyzed together with other OEE subunits (OEE2 and OEE3) and D1 protein of photosystem II. The transcript levels of all the three OEEs were enhanced by NaCl treatment, but the significant increase of D1 protein was not observed in *B. gymnorrhiza*. Sugihara et al. (2000) suggested that not only the OEE1 but also the OEE2 and OEE3 play an important role in the maintenance of PSII activity under NaCl stress conditions. In particular, OEE1 is essential for oxygen evolving activity and PSII stability. The expression of OEE1 is also considered to be the rate-limiting step in the assembly of the PSII subunit (Mizobuchi and Yamamoto 1989). Therefore, it is considered that the recovery or turnover of OEE1 is one of the mechanisms to maintain the capacity of PSII under NaCl stress.

Currently there are also ongoing genomic studies of *B. gymonorrhiza*. The first *B. gymonorrhiza* expressed sequence tag (EST) library, which collected 14,842 ESTs from leaves and roots after high salinity or hormone treatments were established by Miyama et al. (2006). Clustering and assembling of these sequences resulted in 6,943 unique genes. The EST collection of *B. gymonorrhiza* includes genes that share significant similarities with salt stress inducible genes. These genes can be categorized into five major categories such as (1) osmolyte biosynthesis, (2) reactive oxygen scavenger, (3) chaperones, (4) transporters and (5) signaling components. The unique gene collections obtained from the assembly of those ESTs were later used in microarray experiments to monitor transcript profiling in leaves and roots of salt-stressed *B. gymonorrhiza* (Miyama and Hanagata 2007). Totally, 228 genes displayed transcript levels fivefold higher than in controls, while 61 genes were downregulated to one-fifth of control levels. Among these remarkably differentially expressed genes, only 32.5% upregulated and 3.3% downregulated genes were co-regulated in upper and lower leaves, as well as in roots (Miyama and Hanagata 2007). The rest showed tissue-specific expression patterns (Miyama and Hanagata 2007). Differing from EST analysis, differentially expressed genes in microarray analysis fell into six categories of gene expression patterns (Miyama and Hanagata 2007).

The transcriptional response of *B. gymnorrhiza* to high salinity (500 mM NaCl) and hyperosmotic stress (1 M sorbitol) was investigated by microarray analysis (Miyama and Tada 2008). Statistical analysis of microarray revealed that 865 of 11,997 genes showed significant differential expression under salt and osmotic stress. Comparison of gene ontology (GO) categories of differentially expressed genes under the stress conditions revealed that the adaptation of *B. gymnorrhiza* to salt stress was accompanied by the upregulation of genes categorized for cell communication, signal transduction, lipid metabolic process, photosynthesis, multicellular organismal development and transport, and by downregulation of genes categorized for catabolic process. Hierarchical clustering of the 865 genes showed that expression profiles under salt stress were distinctly different from those under osmotic stress. *B. gymnorrhiza* maintains its leaf water potential and recovered from its photosynthesis rate that declined temporarily under salt stress, but not under osmotic stress. These results demonstrated a fundamental difference between the responses to salt and osmotic stress (Miyama and Tada 2008). The salt-responding genes that showed no sequence similarity to the public database entries were also detected in *B. gymnorrhiza* (Miyama and Tada 2008). Therefore, it is possible that these unknown salt-responding genes may contribute to the salt adaptation of *B. gymnorrhiza* in a unique and specific manner.

The differential display method was applied to transcripts extracted from leaves of *B. gymnorrhiza* treated with 500 mM NaCl for 0, 6 h, 3 and 28 days to identify genes that are differentially expressed in response to salt stress (Banzai et al. 2002). The expression of 12 transcripts, whose corresponding cDNA fragments differentially

Table 3 Salt inducible genes reported in mangroves

Mangrove species	Genes	Characteristic feature(s)	References
Aegiceras corniculatum	*P5CS*	Delta 1-pyrroline-5-carboxylate synthetase, a key enzyme of proline synthesis pathway Accumulation of transcript of this gene under high salinity tended to accompany recruitment of proline in *Aegiceras corniculatum*	Fu et al. (2005)
	PIP1	PIP1 aquaporin—This gene was upregulated by salt stress	Fu et al. (2005)
	PIP2	PIP2 aquaporin—This gene was upregulated by salt stress	Fu et al. (2005)
	NHA	Na^+/H^+ antiporter—This gene was upregulated by salt stress	Fu et al. (2005)
	BADH	Betaine-2-aldehyde dehydrogenase—High salinity induced increase of transcript level and such an increase was accompanied by accumulation of betaine. Although activity of this enzyme decreased with an increase in salinity, the extent of decrease is less than its homologue in *E. coli* and spinach	Hibino et al. (2001)
Avicennia marina	*Sod1*	Cytosolic Cu/Zn superoxide dismutase—Overexpression of this gene in *indica* Rice var Pusa Basmati-1 confers abiotic stress tolerance	Prashanth et al. (2008)
	Sod1	Cu/Zn superoxide dismutase—High salinity did not lead to transcriptional change but osmotic stress decreased transcript level of this gene. Under oxidative stress, its transcription was transiently upregulated	Jithesh et al. (2006)
	Cat1	Catalase—It was upregulated by saline or oxidative stress but downregulated by osmotic stress	Jithesh et al. (2006)
	Fer1	Ferritin 1—It was transcriptionally Upregulated by saline or oxidative stress but didn't change under osmotic stress	Jithesh et al. (2006)
	AmT1; *AmT2*	Betaine/Proline transporter—Transgenic *E. coli* with such genes could accumulate	Waditee et al. (2002)
	AmT3 [partial]	Betaine under salt stress; In *Avicennia marina*, salt stress induced transcription of such genes in root and leaf	
Bruguiera gymnorrhiza	*OEE1*	OEE1 is one component of PS II and high salinity induced accumulation of its transcript and protein	Sugihara et al. (2000)
	DLDH	Dihydrolipoamide dehydrogenase—Upregulated when treated with 500 mM NaCl for 1 day	Banzai et al. (2002)
	LAS	Lipoic acid synthase—Being upregulated when treated with 500 mM NaCl for 1 day	Banzai et al. (2002)
	Unnamed gene	Fructose-6-phosphate, 2-kinase/fructose-2, 6-bisphophatase—Transcription of this gene increased after 6 h of salt stress. It was supposed to act in osmotic regulation process by controlling the content of Fru-2, $6\text{-}P_2$	Banzai et al. (2002, 2003)
	Cytosolic	Cytosolic Cu/Zn superoxide dismutase—High salinity, mannitol and ABA induced accumulation	Takemura et al. (2002)
	Cu/Zn SOD	Of its transcripts in leaves; Transcript was induced by high salinity in young and mature leaves rather than in old leaves	
	Cytosolic *CAT* (partial)	Catalase——No significant change occurred in the expression of this gene during the treatment with NaCl, mannitol and ABA, but CEPA (2-chloroethylphosphonic acid) can increase its transcript level	Takemura et al. (2002)
Bruguiera sexangula	*CCTα*	*CCTα* α subunit of CCT complex——Transgenic *E. coli* with one domain of this subunit displayed enhanced tolerance to high salinity	Yamada et al. (2002a)
	Mangrin	Partially homologous to gene encoding Allene Oxide Cyclase (AOC)——It was upregulated by high salinity and its overexpression enhanced salt tolerance of transgenic yeast and tobacco cell	Yamada et al. (2002b)
Kandelia candel	*SIGKC1; SIGKC2*	Cytosolic low molecular mass heat shock protein (sHSPs)—sHSPs act as molecular chaperones to prevent thermal aggregation of proteins by binding non-native intermediates	Huang et al. (2003)
	SIGKC3	ADP-ribosylation factor (ARF)—a ubiquitous, highly conserved 21 kDa GTP-binding protein; The ARF proteins are thought to function as regulators of membrane traffic	Huang et al. (2003)
	SIGKC4; SIGKC5	Unknown function	Huang et al. (2003)

The names of various genes have been by and large reproduced here as per the original publications of the authors

Table 4 Genomic studies in mangroves

Mangrove species	Description	References
Aegiceras corniculatum	A leaf SSH library was constructed. By sequencing the whole SSH library 577 ESTs were found that are up-regulated by high salinity. Fourteen catagories were assigned for this EST collection and those categories of "protein synthesis", "defense", "transport", "ion homeostasis", "protein destination" and "signal transduction" were remarkable	Fu et al. (2005)
Avicennia marina	A leaf cDNA library was constructed from 500 mM NaCl-treated seedlings. Random sequencing generated 1602 ESTs which were grouped into 13 categories; Among these, 7% were homologous with stress-responsive genes	Mehta et al. (2005)
Bruguiera gymnorrhiza	Large-scale sequencing of ESTs collected from high salinity or hormone treated leaves and roots. Assembly of 14,842 high quality sequences generated 6,943 unique genes and 62.5% of such EST collection matched known proteins in Blast searching. Totally 129 statistically-confident genes were grouped into 4 clusters depending on their EST frequency and each group has specific pattern of transcript profiling under high salinity	Miyama et al. (2006)
	Salt-responsive transcript profilings of 7,029 unique genes in leaf and root tissues were monitored using microarray technique. Clustering generated at least six categories of transcript accumulating under saline condition; Some genes displayed similar salt-responsive patterns to those in other plants, indicating shared mechanisms in *Bruguiera gymnorrhiza* and other glycophytes. Distinct expression patterns of other genes suggested existence of specific mechanisms in this species	Miyama and Hanagata (2007)
	Differentially expressed candidates genes were identified through differentially display technique from leaves stressed with 500 mM NaCl for 0 h, 6 h, 3 days, and 28 days. Totally 89 clones were identified as differentially expressed candidates; nine out of these candidates were verified by Northern Blot and classed into three groups depending on their salt-induced patterns of transcript accumulation	Banzai et al. (2002)
Bruguiera cylindrica	126 salt tolerant cDNAs were identified and isolated from the root using suppression subtractive hybridization (SSH) and bacterial functional screening. Sequencing of 51 subtracted cDNA clones that were differentially expressed in the root of *B. cylindrica* exposed to 342 mM NaCl revealed 10 tentative unique genes (TUGs) with putative functions in protein synthesis, storage and destination, metabolism, intracellular trafficking and other functions; and nine unknown proteins. The 75 cDNA sequences of *B. cylindrica* that conferred salinity tolerance to Escherichia coli consisted of 29 TUGs with putative functions in transportation, metabolism and other functions; and 33 with unknown functions. Both approaches yielded 42 unique sequences that have not been reported elsewhere to be stress related	Wong et al. (2007)
Acanthus ebracteatus	A leaf cDNA library was constructed from seawater-growing seedlings. Random sequencing generated 521 readable sequences and 67% of them matched function-known genes by homolog searching; among which, 18% were predicted to function in stress response, 23.9% in metabolism, 7.3% in regulation of transcription and 2.7% in others	Nguyen et al. (2006)
Sesuvium portulacastrum	In an attempt to isolate and identify the target genes relevant to salt tolerance in the mangrove associate (*Sesuvium portulacastrum* L.), a subtracted cDNA library was constructed via suppressive subtractive hybridization (SSH). Screening of this subtracted cDNA library revealed five clones involved in salt-tolerance pathways. Among the clones isolated, P66, P175, and P233 are novel because no significant similarity was obtained upon alignment with the GenBank database. Clone P89 demonstrated high homology with NADPH of *Arabidopsis thaliana*, whereas clone P152 was highly homologous with the gene encoding late embryogenesis abundant (LEA) protein of *A. thaliana*	Zeng et al. (2006)

appeared on differential display, was then analyzed by Northern hybridization. Nine of them were affirmed to be upregulated or induced by salt treatment. The nine transcripts were divided into three groups based on their expression patterns. RNA transcripts to BG7, BG50, BG51, BG55 and BG67, whose levels were temporarily raised at 6 h, were assigned to Group I. Transcripts to BG60 and BG70, whose levels increased at 6 h, and remained at a high level for at least 28 days were assigned to Group II. Transcripts to BG56 and BG64 were assigned to Group III as their levels increased at 3 days, but then decreased (Banzai et al. 2002). By screening a cDNA library, five full-length cDNAs were cloned and putative protein products were identified for three of them by homology with known protein. The RNA transcript *bg51* encodes a protein with homology to fructose-6-phosphate, 2-kinase/fructose-2,6-bisphophatase (F6P, 2-K/F26BPase), the bifunctional enzyme catalyzing both synthesis and degradation of fructose-2,6-bisphosphate (Fru-2,6-P2) which is an important regulator in the carbohydrate metabolism. The protein encoded by *bg55* has homology with a protein of *A. thaliana* whose function is unknown. Transcripts *bg56* and *bg64* are encoded by proteins having very significant homology with dihydrolipoamide dehydrogenase (DLDH) and lipoic acid synthase (LAS), respectively. The results suggest that these RNA transcripts and their respective encoding proteins have some role in salt tolerance in *B. gymnorrhiza* (Banzai et al. 2002). The protein encoded by *bg70*, Group II transcript, is a novel protein with no homology with any proteins registered in the databases so far (Banzai et al. 2002). Further analysis of such Group II genes will reveal how *B. gymnorrhiza* adapts to high salinity.

In order to identify key genes in the regulation of salt tolerance in the mangrove plant *B. gymnorrhiza*, cDNA expression libraries were constructed from salt-treated roots and leaves using the host organism *Agrobacterium tumefaciens* (Ezawa and Tada 2009). Functional screening of the *Agrobacterium* libraries identified 44 putative salt tolerance genes in *B. gymnorrhiza*. A cDNA clone which is homologous to an unknown cDNA from the mangrove plant *K. candel* and the *cyc02* gene from *Catharanthus roseus* conferred the highest level of salt tolerance to *A. tumefaciens*, which indicates that it plays a major role in the regulation of salt tolerance in mangrove plants. Several of the genes that were identified have not previously been implicated in plant salt tolerance (Ezawa and Tada 2009). Transgenic *Arabidopsis* plants expressing *Bg70* and *cyc02* homolog exhibited increased tolerance to NaCl. These results demonstrate that *Agrobacterium* functional screening is an effective supplemental method to pre-screen genes involved in salt tolerance (Ezawa and Tada 2009).

Screening for salinity tolerant genes was done in the root of the mangrove plant *Bruguiera cylindrica* by using suppression subtractive hybridization (SSH) and bacterial functional screening (Wong et al. 2007). One hundred twenty-six salinity tolerant cDNAs were identified and isolated from the root of *B. cylindrica* by both approaches (Wong et al. 2007). Sequencing of 51 subtracted cDNA clones that were differentially expressed in the root of *B. cylindrica* exposed to 342 mM NaCl revealed 10 tentative unique genes (TUGs) with putative functions in protein synthesis, storage and destination, metabolism, intracellular trafficking and other functions; and 9 unknown proteins. Bacterial functional screening revealed that the 75 cDNA sequences of *B. cylindrica* that conferred salinity tolerance to *Escherichia coli* consisted of 29 TUGs with putative functions in transportation, metabolism and other functions; and 33 with unknown functions. Both approaches yielded 42 unique sequences that have not been reported elsewhere to be stress related might have some role in salt tolerance in *B. cylindrical* (Wong et al. 2007). These unique genes may be valuable gene candidates for further analyses to unravel the mystery of salinity tolerance in mangrove plants.

In order to reveal the molecular mechanism of salt tolerance in mangroves gene expression pattern was identified in *Kandelia candel* (Huang et al. 2003). Ten cDNAs of genes were isolated and identified from *K. candel* by representational difference analysis of cDNA (cDNA RDA) under different NaCI concentrations (Huang et al. 2003). Of five genes expressed preferentially under salt condition, two were unknown; three were two kinds of cytosolic low-molecular mass heat-shock proteins (sHSPs) and ADP-ribosylation factor (ARF), respectively. The upregulation of sHSPs and ARF has some role in osmotic equilibrium by which the *K. candel* plant can resist salt damage. The expressions of other five genes were repressed under NaCI stress, two encoded cyclophilins; three were tonoplast intrinsic protein, early light-induced protein and 60S ribosomal protein, respectively.

Betaine-aldehyde dehydrogenase (*BADH*) gene that is involved in glycinebetaine synthesis in *A. marina* was first identified and cloned by Hibino et al. (2001). *BADH* was upregulated under salt stress, and this tendency was consistent with the accumulation of glycinebetaine in *A. marina*. Three other genes that encode *A. marina* betaine and/or proline transporters 1 (*AmT1*), 2 (*AmT2*) and 3 (*AmT3*), respectively, were also isolated by Waditee et al. (2002). The mRNA levels of the three transporters were measured, and it was observed that the levels of mRNAs for AmT1, AmT2 and AmT3, were constitutively low and almost the same in both leaf and root when *A. marina* was grown without salt stress. Upon the salt stress (400 mM NaCl), the levels of mRNAs in all three transporters, AmT1, -2 and -3, increased in both leaf and root. However, the increases in leaf were more pronounced than those in root for all three transporters. Salt stress induced the highest level of mRNA for AmT1 followed by AmT2 and AmT3, respectively. The accumulation levels of mRNA for AmT1, -2 and -3 increased with increasing concentration of NaCl, especially in leaves (Waditee et al. 2002). Since betaine synthesis occurs in chloroplasts upon the salt stress, it is reasonable that the synthesis of betaine transporters is also induced upon the salt stress because the synthesized betaine must be transported to the other plant organs where betaine synthesis activity is low (Takabe et al. 1997). Therefore, under high-salinity conditions, the betaine/proline transporters (AmT1, -2 and -3) appear to be involved in the accumulation of betaine by increasing the mRNA levels as well as post-translational activation in betaine-accumulating *A. marina* (Waditee et al. 2002).

In order to characterize the genes that contribute to combating salinity stress, the cDNA library of *A. marina* genes was constructed by Mehta et al. (2005). Random EST sequencing of 1,841 clones produced 1,602 quality reads. These clones were classified into functional categories, and BLAST comparisons revealed that 113 clones were homologous to genes earlier implicated in stress responses. Of the ESTs analyzed, 30% showed homology to previously uncharacterized genes in the public plant databases. Of this 30%, 52 clones were selected for reverse Northern analysis: 26 were shown to be upregulated and 5 shown to be downregulated under NaCl stress (Mehta et al.

2005). Expression patterns for the ‘unknown’ genes provide a starting point for the isolation of salt tolerance candidate genes, and further functional analysis will elucidate their role in salt tolerance. ESTs showing homology to stress-tolerant genes reported in literature represent the sixth most abundant category. Dehydrins (34 clones/12 genes) predominate in this class and include late-embryogenesis-related proteins and desiccation or drought-induced proteins. Other stress-induced genes present in this category include heat shock proteins, thioredoxin, osmotin and genes for osmolyte production such as *BADH* and pyrroline-5-carboxylate synthase. The analyzed EST pool contained transcripts coding for enzymes involved in the oxidative stress response such as catalase, superoxide dismutase, peroxidases, glutathione S-transferase and epoxide hydrolase. In addition, genes reported to be induced by heavy metal stress, such as metallothioneins, aluminum-induced protein(s), truncated copper-binding protein CUTA and divalent cation-tolerant gene, and those induced by anaerobic stress, such as alcohol dehydrogenases and submergence-induced genes, were also found in the ESTs sequenced. Transcripts coding for proteins involved in membrane transport and processing play an integral role in the response to water deficit such as that imposed by salt stress and include aquaporins, proline/glycine betaine transporter and Na^+/H^+ antiporter. In addition, protein factors involved in the regulation of signal transduction events, such as receptors, protein and lipid kinases, calmodulins and protein phosphatases, which may have a role in stress signaling pathways, have been categorized separately. Genes for a variety of transcription factors that contain typical DNA binding motifs, such as MYB, bZIP, ERF/AP2, have been demonstrated to be stress-inducible (Zhu 2002). Transcription factors containing similar domains are present in the *A. marina* ESTs and may have a role in regulating the response to salt stress (Mehta et al. 2005). At the genomic level, a large number of ESTs have been collected from NaCl stressed seedlings of *A. marina* through techniques of differential display or random sequencing of cDNA library clones (Mehta et al. 2005). Some genes in such EST collections, e.g., those coding for dehydrin and polypeptide hormone phytosulphokine, were continuously upregulated after 48 h of salt-stress (Mehta et al. 2005). Their transcript abundance returned to the normal level if salt stress was prolonged to 12–24 weeks, indicating adaptation of *A. marina* after long-term stress (Mehta et al. 2005).

Jithesh et al. (2006) studied the expression of antioxidant genes such as Cu–Zn SOD (*Sod1*), catalase (*Cat1*) and ferritin (*Fer1*) in response to salt, iron, hydrogen peroxide, mannitol and light stress by mRNA expression analysis in *A. marina.* In response to NaCl stress *Cat1*, *Fer1* showed short-term induction while *Sod1* transcript was found to be unaltered. *Sod1*, *Cat1* and *Fer1* mRNA levels were induced by iron, light stress and by direct H_2O_2 stress treatment, thus confirming their role in oxidative stress response.

Transcripts that showed enhanced expression during salt stress was cloned in the leaves of a salt-tolerant mangrove species, *Aegiceras corniculatum* using suppressive subtractive hybridization (SSH, Fu et al. 2005). cDNAs of freshwater germinated and irrigated seedling were used as driver and cDNAs of 6 h salt-stress seedling were used as tester. By sequencing the whole SSH library, 577 ESTs were found. Among which, 30 had no significant homology to any previously identified genes and 527 of the remaining 547 ESTs represent singletons. Real-time quantitative RT-PCR analysis of four transcripts’ expression pattern showed that all of their transcripts were up-regulated during 24 h after salt shock. Their sequences showed high homology to the delta-1-pyrroline-5-carboxylate synthetase, Na^+/H^+ antiporter and plasma membrane intrinsic proteins, respectively.

Another salt secreting mangrove species *Acanthus ebracteatus* has also been of concern recently. *A. ebracteatus* was chosen as a source for the generation of ESTs to isolate genes involved in salt tolerance of this mangrove plant (Nguyen et al. 2006). In this study, they isolated and sequenced 864 randomly selected cDNA clones from the primary cDNA library of *A. ebracteatus*. Sequence analyses demonstrated that 349 of these ESTs showed significant homology to functional proteins, of which 18% are particularly interesting as they correspond to genes involved in stress response. Some of these clones, including putative mannitol dehydrogenase, plastidic aldolase, secretory peroxidase, ascorbate peroxidase, and vacuolar H^+-ATPase, may be related to osmotic homeostasis, ionic homeostasis, and detoxification (Nguyen et al. 2006). Hundred seven salinity tolerance candidate genes have been identified and isolated from the mangrove plant, *A. ebracteatus* by using bacterial functional assay (Nguyen et al. 2007). Sequence analysis of these putative salinity tolerant cDNA candidates revealed that 65% of them have not been reported to be stress related and may have great potential for the elucidation of unique salinity tolerant mechanisms in mangrove. Among the genes identified were also genes that had previously been linked to stress response including salinity tolerance (Nguyen et al. 2007). Even though many of these mangrove genes or gene products were reported in stress tolerance of higher plants, the mangrove proteins may display unique properties and function. For example, the mangrove allene oxide cyclise (AOC) homolog or “mangrin” (Yamada et al. 2002b), containing an usual sequence of 70 amino acids that is essential to salt tolerant phenotype, is not found in *Lycopersicon* and *Arabidopsis* AOC homologs. The successful identification and isolation of salt-tolerant candidates from

A. ebracteatus provide a basis for further function elucidation, in addition to providing useful information for plant breeding and genetic engineering of crop plants with greater salinity tolerance that allow agriculture on saline soil.

Conclusion and future prospects

Salinity is a major abiotic stress that greatly affects plant growth and crop production globally. Sodium ions in saline soil are toxic to plants because of their adverse effects on potassium nutrition, cytosolic enzyme activities, photosynthesis, and metabolism. Mangroves tolerate high salinity by rejecting potentially harmful salts. Some species of mangroves actively excrete those salts leaking into the plant by means of specialized salt glands in their leaves and some species excrete salt by ultra filtration at the root cell membranes of cortical cells. Salt accumulators avoid the toxic effects of salt by compartmentation of Na^+ and Cl^- ions into the vacuoles by Na^+/H^+ antiporter system. Accumulation of compatible solutes and induction of antioxidative enzymes are other mechanisms of salt tolerance in mangroves. Mangroves also provide a reservoir for some of the best known, and at times, novel genes and proteins, involved in tolerance to salinity stress, that are likely at work in other plants. The salt tolerance genes listed in this review most likely represent only the tip of the iceberg, and continuous efforts to isolate and identify novel useful genes and promoters from mangroves are necessary; DNA microarray technology in particular is likely to become a powerful tool for this purpose. Eventually, the largest challenge will be to combine these genes and promoters in a systematic and logical way in order to maximize plant salinity tolerance. When realized, genetic engineering of crop and industrial plant for salinity tolerance using genes isolated from mangroves will be a vitally important tool in the quest to alleviate the earth's future problems concerning food, energy, and the environment.

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