



REVIEW ARTICLE

# Abiotic stress tolerance in mangroves with a special reference to salinity

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## Abstract

Since mangroves are found near extremely transitional ecosystems, they face a lot of physico-chemical perturbations. As mangroves possess a unique ecotone, they experience many abiotic stressors viz. salinity, metal, oil, humidity temperature, nutrient and a wide range of biotic interactions. Amongst all, salinity is the most important factor affecting mangrove physiology and biochemistry, and thereby regulating the organic matter contribution to the consumers underneath. Exploitation by human, being a dominant biotic interference, is above the rate at which natural replacement of mangrove vegetation occur. Mal-nutrition is a limiting factor in growth and reproduction of many mangroves whereas nutrient replenishment reduces the phytotoxicity of heavy metals. Different environmental pollutants including heavy metals, recalcitrant, cosmetics, petroleum oil and endocrine disrupters have reported impact on various mangroves and associated biota. Stress tolerance in mangroves involves various mechanism including morphological and anatomical features, osmoregulation, water use efficiency, salt secretion, salt exclusion and salt accumulation and molecular regulations. Various aspects of salt tolerance strategies of mangroves related to their growth, biochemical anatomy and physiology were reported by many researchers.

## Keywords

Abiotic stress, Environmental pollutants, Mangroves, Salinity tolerance

## Introduction

Forests are regarded as greatest sink for carbon in the form of stored organic matter and also adding carbon dioxide (CO<sub>2</sub>) to the atmosphere by biodegradation and wildfires (1). Coastal ecosystems are driving force in maintaining environmental balance with unique biogeographic features, ecosystem services and anthropogenic activities (2). Numerous human pathogens, including *Candida albicans*, *Mycobacterium vaccae*, *M. aurum*, *M. smegmatis*, *M. fortuitum* and *Staphylococcus aureus*, were susceptible to various mangrove extracts, including those from *Avicennia* sp., *Bruguiera gymnorhiza*, *Excoecaria agallocha*, and *Acanthus ilicifolius*. These extracts also exhibited antimicrobial, anti-inflammatory (3-5). These ecosystems also provide food and shelter to a number of organisms maintaining the biodiversity (6). To

reiterate, these ecosystems are ultimate sink of several man-made pollutants from industrialization, modern life styles, agricultural run-offs and municipal sewage systems (7, 8). The coastal vegetation is composed of mangroves and associates, which are unique halophytes of tropical and subtropical intertidal forests across the globe (9). Storm and cyclone control mechanisms of mangrove saves lives and property with onset of any geo-hydrological disasters (10). Mangroves are most dominant ecosystems in coastal and estuary bio-geographical zones across the globe (11). Mangroves are worse affected by synergistic effect of climate changes and human activities. The alarming rate of interference by human beings in intertidal zones has caused a variety of environmental problems and worsened the conditions of ecosystem processes (12).

The intertidal regions of tropical and subtropical coastlines are home to a unique type of vegetation known as mangroves. They are mostly facultative halophytes and are thought to be more tolerant to salt than any other species since they can withstand high and changing salinities (13). A sophisticated antioxidant system made up of both enzymatic and non-enzymatic antioxidants effectively defends their cells from the damaging effects of ROS. Reactive oxygen species (ROS) which include the superoxide radical ( $O_2^-$ ), hydrogen peroxide ( $H_2O_2$ ), hydroxyl radical ( $OH\cdot$ ) and singlet oxygen ( $^1O_2$ ) are produced at a higher rate in plants as a result of several environmental stressors, including salt (14). When ROS are not under control, these can significantly impair the normal metabolism of plant cells by oxidatively damaging lipids, proteins and nucleic acids (15, 16). Mangroves degradation has been noticed more frequently since a few decades by human encroachment, cutting off trees, land use policy and freshwater management. The mangrove dwelling animals include a wide range of taxa of vulnerable or threatened categories due to unsustainable human activities. Calculating the economic value of mangroves and other estuarine habitats for these animals depends on their life history strategies, physiology and ecology throughout the dynamic habitats (17). These findings of many researchers show the presence of mangroves influences their life cycle, but paucity of convenient scientific evidence is a key problem to prove it (18). Due to blockage in tidal flows and exchanges by anthropogenic hydrological planning, mangroves has been residing under high risk of habitat loss and fragmentation. The present study reviews the various aspects of abiotic and biotic stress tolerance in mangroves.

International policies have started emphasizing mangrove conservation and rehabilitation as part of a comprehensive protection strategy for vulnerable coastal communities as the importance of mangrove forests in shoreline protection and climate change mitigation has grown (14, 17-19). Mangrove forest restoration projects frequently fall short of expectations or fail entirely, despite the fact that some design criteria have been devised for them (20). These failures are frequently associated with habitat parameters and the limiting factors include both biogeochemical such as light, nutrients, salinity and pre-

dition) and hydrodynamic issues such as wave, current and tidal inundation (21). The three main abiotic factors that affect mangrove growth and spread are inundation, elevation gradient and salinity changes (22). To adapt to the frequently changing intertidal ecology they inhabit, mangroves have special adaptations include vivipary, salt secretion, aerating roots, ultrafiltration, ion sequestration, osmolyte build up and thick waxy leaves (19, 23). Intertidal zones in river deltas, estuaries, coastal lagoons and open coastlines are blessed with dynamic characteristics including variable tidal flow, anoxic habitats and high salinity that make them distinctive niches for mangroves where other types of vegetation struggle to flourish (19).

Mangroves are currently endangered by various anthropogenic activities such as irrigation projects, aquaculture, global warming, sea level rise and climate change. However, irrigation projects bypass freshwater from sea resulting in enhanced salinity whereas aquaculture systems without proper land use plan degrade mangroves primarily through exogenous material inputs and habitat fragmentation. The tidal flux and intensity indicating elevated sea level significantly affect geomorphology of mangroves which has been predicted as climate change indicator (24). Firewood, timber, apiculture, aquaculture and fisheries are some important livelihoods of the mangrove forest tribes, who are affected by loss of the mangrove resource. The productivity, species diversity and socio-economic values of mangroves attract many biologists to explore their significance.

As mangroves are unique ecotone areas, they experience many abiotic stressors viz. salinity, metal, oil, humidity, temperature, nutrient and a range of biotic interactions (25). Alterations in plant-community structure and salt marsh-to-woody shrub ecotone, impacted many mangroves and their associates in chilling seasons as experienced by *A. germinans* in its early life-history stages whereas this canopy provides a fundamental niche overcoming cold stress in Mexican coast (26). Mangroves survive in adverse environmental perturbations maintaining a fair amount of net production. Even during seasons with non-availability of photosynthetic light induction, they overcome this photoinhibition by active leaves resulting sustainable productivity. Previously reported a significant decline in photosynthetic yield when *Rhizophora stylosa*, were directly illuminated (27) whereas other workers observed no photoinhibition in *Bruguiera parviflora* under normal light conditions or in *R. Mangle* under control and water-logging situation (28). It was reported that the salinity, inundation and elevation significantly induced oxidative stress in the leaves of *R. stylosa*, resulting in triggering of the antioxidant defense system (29). The hypocotyls of Rhizophoraceae mangroves especially *B. gymnorhiza*, *B. parviflora*, *Kandelia candel* and *Rhizophora apiculata* had profound multiple shoots inducing ability under ex vitro condition. The hypocotyls of Rhizophoraceae are helpful to maximize the potentiality of shoot regeneration and conservation of the mangrove forest (30).

### Salinity stress in mangroves

All mangrove species have the mechanism to reject excess amount of salt but the mechanism varies from one species to another. *Avicennia* sp. and *Sonneratia* sp. have salt excretion glands whereas some accumulate salt in their stems by increasing succulence. Above or below certain salinity levels their growth is inhibited and even death occurs (31). Though many mangroves develop well at salt 5-20‰ levels they are able to tolerate more than these reported ranges, which, however, appreciably vary with the species (32). According to the data revealed with the distribution of mangroves with respect to soil salinities, one who grows in salinities as high as threefold of sea water and another hardly up to 40‰ salt (33). Salinity can affect stomatal conductance and transpiration thereby causing wilting due to water accumulation on excessive dehydration in mangroves (34). Stomatal and non-stomatal gas exchange were severely affected by higher salt concentrations (35) which may lead to photorespiratory carbon loss and photosystem-II damage (36). Salinity put a considerable adverse effect on propagule establishment of *A. germinans* and seedling development whereas 10% propagules could be able to root at 75 ppt (13). Elevated levels of salt reduced nitrogen accumulation in *K. candel* and *E. agallocha* (37) and hindered the transport of  $K^+$  by *A. marina*, thereby disintegrating photosynthetic apparatus (38). By measuring the intensity and nature of fluorescence of photosynthetic pigments, plant ecophysiology can be investigated under salt stress.

Salt tolerance in terms of photosynthesis, transpiration and stomatal conductance has been studied in skimpily as far as physiological response is concerned. The correlation between photosynthesis and transpiration rates had been tested in many mangroves indicating their differential salt tolerances (39). Salinity stress induces low stomatal conductance which ranges between -2.5 and -6.0 MPa resulting in declining rate of transpiration and  $CO_2$  availability to inter-mesophyll milieu (36). There is hardly any evidence of increased respiration and reduced photosynthesis due to high salt levels in Rhizophoraceae mangroves. Stomatal closure led to reduced transpiration and also reduced carbon gain in elevated levels of salinities in certain mangroves (32).

Varied mangrove species exhibit different salinity preferences and grow best at different salinity levels. For example, *Sonneratia caseolaris* grows best at low salinity (<5 ‰), but *Ceriops tagal* grows best at 50‰ seawater (40). Seedlings thrive when exposed to 25‰ seawater, but growth is negatively impacted by high salinity or a complete lack of salt. True mangroves can be found on the beaches of south and southeast Asia, from western India to Borneo, with *K. candel* and *R. stylosa* being the dominant species and considered to be a representative of all mangrove species (23). The increased levels of enzyme activity and lower levels of lipid peroxidation may help to partially explain how mangrove plants have adapted to their salty environment, while there are many other mechanisms involved in reducing oxidative stress (16). The unique genes in *A. ilicifolius* are mostly connected to rhythmic

processes, reproductive processes and reaction to stimuli, according to Gene Ontology (GO) enrichment. *Acanthus* travelled from terrestrial to intertidal settings, where 311 pairs may be subject to positive selection, according to the fast evolution and positive selection studies. Functional enrichment analysis showed that the adaptation of *A. ilicifolius* to intertidal habitats, which are characterised by high salinity and hypoxia, is related to these genes associated with essential metabolism and biosynthetic pathways, such as oxidative phosphorylation, plant hormone signal transduction, photosynthetic carbon fixation and arginine and proline metabolism (41).

Mangroves are facultative in nature, which means they can grow equally well in freshwater and saltwater. This highlights how tightly controlled gene expression patterns literally drive adaptive features by sensing the surrounding salinity (13, 15). Mangroves, the dominant plant species in intertidal areas, provide vast ecological and economic functions, including the storage of carbon, aquaculture, shrimp farming, fisheries, lumber production and coastal protection. By raising anoxia levels over safe levels, pollutants, particularly plastics and their more hazardous microplastic cousins, choke mangrove plants (42).

### Effect of nutrient in mangroves subject to salt stress

Nutrient deficiency is another problem limiting mangrove development (43). Water-logging reduces nitrification, which leads to minimal nitrogen availability in mangrove habitats (44). Exogenous supply of nutrients significantly enhances shoot elongation in *Rhizophora mangle*, improves leaf and branch growths of *A. germinans*, increases LAI of *C. tagal*, induces higher rates of stomatal conductance and photosynthetic rate in *K. obovata* (45, 46). It was also reported that addition of nutrient reduces phytotoxicity of heavy metals (44), contribute to osmoregulation (46) and stimulate antioxidant systems (47), resulting in higher tolerance capacity of mangroves to varying salinity regimes. Nutrient supplements also enhanced  $P_N$ ,  $E$ ,  $g_s$  and water use efficiency of *E. agallocha* (48), *K. candel* (46) and dwarfed *R. mangle* trees (49). Conversely, nutrient deficiency significantly hampered biomass accumulation and root growth rate in *E. agallocha* (48), *A. marina* and *B. parviflora* (38) and *K. candel* (46). Global studies on distribution of *R. mangle* in mangrove habitats suggested that these are P limited (49).

Both an increase in water availability, which would assist plant development, and a decrease in oxygen supply, which will hinder it, are potential impacts of persistent waterlogging on plants. Less root biomass will be required to absorb water from the root environment in a species that is more resilient to waterlogging because the increase in accessible water will out-compete the suppression of oxygen deficiency after being waterlogged for some time. For *K. candel*, a biomass shifts from root to shoot (an increase in S/R) during protracted waterlogging may help it maintain its RGR by increasing nutrient intake per unit of root biomass (50). The viviparous mangroves showed varying levels of resistance to waterlogging, and one defense involved morphological and structural changes that

allowed roots to maintain aerobic metabolism for prolonged durations of submersion (51). It was reported that chlorophyll contents and photosynthesis decreased in many species with waterlogging whereas *K. candel* enhanced the synthesis of chlorophyll and showed better photosynthetic response under prolonged waterlogging (50, 52, 53). Shorter vessel components were seen to emerge in *B. gymnorrhiza* in the mangrove *Laguncularia racemosa* under higher and longer flooding levels. In several mangroves, including *S. alba*, *B. gymnorrhiza* and *L. racemosa*, gelatinous fibres appear to have a functional role in sustaining stems and the normal ontogeny or architectural development of woody axes, as well as in leaves under low waterlogging situations (54). The capacity of *A. marina* seedlings to oxidise the rhizosphere and save oxygen allows them to maintain aerobic metabolism for extended periods of time while submerged in glasshouse water (51). *A. marina* seedlings' anatomical variances would respond favourably to modest flooding, but would be adversely affected by extreme flooding (55).

#### Effect of metals, oil and other toxicants in salinity tolerance of mangroves

Wetlands are well-known sink for metals because of different physico-chemical and biological phenomena involving mass wasting and sediment development (56). Coastal zones receive enormous amounts of industrial effluents and become rich in heavy metals (57). Antioxidative enzymes induce defence against oxidative damage by Cd and Pb in *B. gymnorrhiza* and *K. candel* (44). An impermeable barrier formation in rhizospheric region to radial oxygen loss (ROL) under Cu stress in *B. gymnorrhiza* and *R. stylosa* is has been noted as a unique stress tolerance mechanism by immobilising the metals (44). The common ion effect of Cd was observed in both *R. apiculata* and *A. alba* against salt, which established an antagonistic relationship of Cd over elevated salinity (58). This result was in agreement with other heavy metals such as Pb, Ni, Cr etc. in three mangroves in their order of tolerance under increasing salinities are *S. caseolaris* followed by *S. apetala* and *K. candel* (59). High rhizospheric accumulation of Cu, Cd, Pb, Zn and Cr in roots with low translocation index was found in the order as *C. tagal* followed by *B. sexangula* and *K. candel* (60). The metals like Cu, Zn, Co exhibited higher rates of accumulation whereas Pb and Cr showed a strong coupling with each other (61). But these metals demonstrated a reverse trend i.e., accumulation is maximum in stems and leaves than in roots of *A. alba*, *C. decandra*, *X. granatum* and *R. mucronata* species (62).

Mangrove plants can't alleviate salt stress under oil contamination as the salt resistance process competes over oil induced degradation (63). It is anticipated that oil-induced damage to mangrove plants would be more serious under salt stress with marked synergism (64). Numerous laboratory and field studies have shown that oil biodegradation could be enhanced by nutrient addition (65). Different degrees of sublethal damages on the growth of four mangrove species seedlings: *B. gymnorrhiza*, *K. obovata*, *A. corniculatum* and *A. ilicifolius* were observed in response to lubricating oil-contaminated sediments (66). It

was reported that some mangrove plants are resistant to an optimal concentration of Persistent Organic Pollutants (POPs) by their unique adaptive mechanisms (66). Extensive fishing by boats, prosperous shipping, vehicular exhausts and sewage discharges etc. may also add PAH (Poly-Aromatic Hydrocarbons) into the mangrove sediments (67).

#### Mechanisms of salt tolerance in mangroves

##### Morphological and anatomical features

Mangroves possess many mechanisms associated with morphological features against salt stress (68). It was observed that the root to shoot ratio was linearly related to salt-injury in *Avicennia* and *Aegiceras* (69). Furthermore, viviparous mode of germination is one of the salt tolerance strategies in many mangroves (70). Salt secreting glands in the leaves of *L. racemosa* (71) and salt excretory system "extra floral nectarines" (EFN) in *conocarpus* (72) were typically observed as salt reduction strategies in mangroves. Leaf succulence with thick leaves of mangroves facilitates increased leaf water content, photosynthesis and CO<sub>2</sub> uptake (28). The waxed leaf epidermis is a salt tolerance mechanism in mangroves by resisting transpiration and maintaining the tissue water balance (21). Development of Kranz anatomy, reduction in stomatal density and wider stomata are typical features of succulence (21), while expanded hyalinous hypodermal cells in *R. mangle* is a salt-induced increase in succulence (28).

##### Physiological mechanism

Halophytes possess an optimal growth or physiological response under salinity conditions (Fig. 1). Alterations in morphological to physiological characteristics in mangroves were reported under salt stress (22). Mangroves grown in green-house conditions without salt exhibited nutrient limitation (73). Certain iso-enzymes of antioxidant enzymes were salt-induced and removable in fresh water conditions in *B. gymnorrhiza* leaves. Similarly, in many mangroves under salt-induced oxidative stress, the stress was alleviated through expression or overexpression of antioxidative enzymes (74). Distribution of salts in rhizospheric-zone led to decrease in stomatal conductance disproportionately, which was influenced by phytohormone signalling from roots (75). ABA plays an important role in

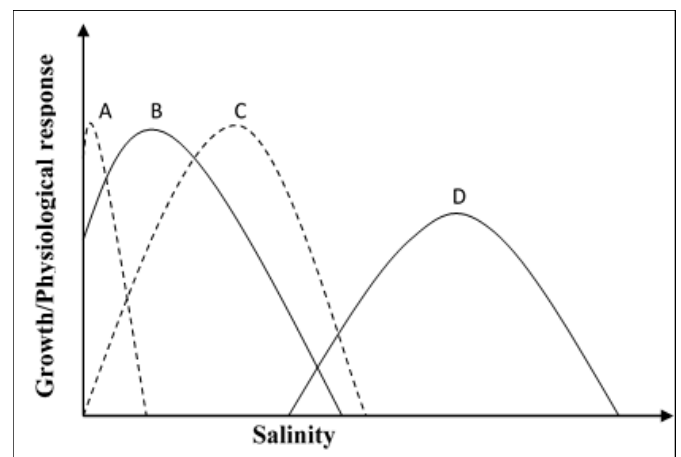


Fig. 1. Hypothetical growth/physiological response curves in relation to salinity in mangroves. (A) non-halophytes, (B) facultative halophytes (C) obligate halophytes and (D) extreme halophyte (*Halobacterium* sp.).

shoot signalling by root in salt stressed as well as water-scarce plants (76). It was also reported that enhanced ABA concentrations in xylem and leaves of salt-treated plants and low transpiration rate (77). However, in *A. officinalis* ABA-independent pathways triggered by 1404 and 5213 genes were significantly up- and down-regulated respectively in reducing salinity stress (78). Transcriptome analysis of *K. obovata* resulted in 26 genes out of which six were involved in chilling stress, seed germination and oxidation-reduction processes, revealing their adaptive role to these stressors (79).

### Salt secretion, rejection and accumulation strategy

Mangroves are divided into 3 types based on their salt adaptation strategies viz. (1) salt excluders (e.g. *Rhizophora* sp. and *Exocaria* sp.), (2) salt secretors (e.g. *R. mangle* and *B. gymnorrhiza*) and (3) salt accumulators (e.g. *B. cylindrica*, *Avicennia rumphiana* and *A. marina*) (Table 1). Transpiration-induced negative hydrostatic pressure can overcome negative osmotic pressure in roots of salt-excluding mangrove (80). The ultra-filtration and  $K^+/Na^+$  exchange helps to maintain the salt level in shoots of mangroves (33). Another strategy to protect against salt injury is expropriating of ions to the vacuoles and translocation and cuticular water loss in leaves of some mangrove species such as *Lumnitzera* and *Excoecaria* (40). There are many competing processes being executed in mangroves against salt stress (Table 1). Hyper-accumulation of  $Na^+$  fused with decline in  $Ca^{2+}$  and  $Mg^{2+}$  uptake or carbon sequestration in the leaves of *B. cylindrica*, *A. rumphiana* and *A. marina* have emerged as a novel strategy (81).

### Osmotic adjustment

Osmo-regulation in certain mangroves such as *B. gymnorrhiza*, *K. candel* and *R. stylosa* is maintained by many compatible solutes e.g. pinitol and mannitol (82) (Table 2). Glycinebetaine and O-methylmucoinositol also act as osmoprotectant by catabolising chlorophyll and reducing  $Na^+$ -toxicity in *A. marina* and *B. gymnorrhiza*, respectively (50). Under salt stress, Chl a, b and carotenoid degradation have been observed in mangroves (83). Allometric responses of the mangrove *A. germinans* to increasing salinity indicated

morphological plasticity that was an adaptive mechanism to adverse situations (84).

Proteins that accumulate in plants under saline conditions may be stored as N-source and help in osmoprotection. The concentration of different molecular weight proteins especially 23 kDa in *B. parviflora* decreased and 33 kDa over-expressed in *B. gymnorrhiza* (85) under salt stress whereas a particularly 23 kDa protein band reappeared when the plant was desalinized indicating its possible involvement in osmotic adjustment (84). Previous workers observed that a unique protein (mangrin) induced salt tolerance in *B. sexangula* (86). There was a decrease in amino acid concentration with increasing salinity in *A. corniculatum* (87).

Proline is a compatible osmolyte to function as an osmoregulator of the cytoplasmic compartment of cells and an osmoprotectant for cellular component (88). The increasing NaCl salinity has increased the proline content in *A. ilicifolius* (89). Soluble sugar level was found to be high in monsoon and low in summer in many mangroves (90). It was also reported that low salt level enhanced sugar content in *Salicornia brachiata* resulting in improved metabolic and photosynthetic performance. It was a reported fact that ascorbic acid level increased in the leaves of *R. stylosa* and *B. parviflora* against oxidative stress due to salt stress. The decrease in ascorbic acid and glutathione level in *B. parviflora* due to consumption of antioxidants via ascorbate-glutathione oxidative pathway (87).

### Molecular mechanism of salinity tolerance in mangroves

Stress-induced genes that cover the adaptive features in mangroves were preferentially retained in stressful intertidal environments due to stress factors like temperature shift, heavy metal stress, nutrient stress, fluctuating water level, hypoxia and (91-94). Ionic and osmotic stress caused by salt stress, which predominantly results in ion accumulation, activates genes involved in reactive oxygen scavenging, osmolyte production, molecular chaperones, transporters and transduction components (15). Toxic accumulation of reactive oxygen species (ROS) such perox-

**Table 1.** Reported mechanisms of salt adaptation and their known distribution in some mangrove species. Exclude, Secrete and Accumulate are the terms for salt management by plant tissues.

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

ides, superoxide, hydroxyl radical, singlet oxygen and alpha-oxygen is one of the first cellular alterations that occurs under any form of stress (95). Superoxide dismutases (SOD) are enzymes that reduce cellular damage by converting superoxide radicals ( $O_2^{\cdot-}$ ) to  $H_2O_2$ . When *A. marina* is exposed to saline stress, it has been shown that the cellular concentration of cytosolic Cu/Zn SOD (CSD) increases (96). Under cadmium stress, *K. obovata*'s root epidermis accumulated FeSOD and CSD with a hampered metal ion transport. In contrast, *Sonneratia alba* SaFeSOD and SaCSD1 are highly expressed in leaf and fruit tissues to combat accumulated ROS (97, 98).

Under stressful conditions, it has been seen that the genes for glutathione S transferase (GST), a different ROS-scavenging protein that is necessary for GSH-dependent peroxidase activity, are elevated in *B. gymnorrhiza* and *R.*

**Table 2.** Compatible solutes synthesized and accumulated as a salinity stress management strategy in mangroves and associates.

Compatible solutes	Mangrove species	References
Pinitol	<i>K. candel</i> , <i>R. stylosa</i> , <i>B. gymnorrhiza</i> , <i>A. marina</i>	Hibino <i>et al.</i> (2001)
	<i>C. tagal</i>	Popp <i>et al.</i> (1985)
	<i>K. candel</i> , <i>R. stylosa</i> , <i>B. gymnorrhiza</i>	Hibino <i>et al.</i> (2001)
Mannitol	<i>S. alba</i>	Yasumoto <i>et al.</i> (1999); Ashihara <i>et al.</i> (2003)
	<i>L. racemosa</i>	Ashihara <i>et al.</i> (2003)
	<i>K. candel</i> , <i>R. stylosa</i> , <i>B. gymnorrhiza</i>	Hibino <i>et al.</i> (2001)
	<i>B. parviflora</i>	Parida <i>et al.</i> (2002)
Proline	<i>A. corniculatum</i>	Fu <i>et al.</i> (2005)
	<i>B. sexangulata</i> , <i>A. alba</i> , <i>X. granatum</i>	Datta and Ghosh (2003)
	<i>A. ilicifolius</i> , <i>H. tiliaceus</i>	Datta and Ghosh (2003)
	<i>A. marina</i>	Datta and Ghosh (2003); Hibino <i>et al.</i> (2001)
	<i>C. roxburghiana</i>	Rajesh <i>et al.</i> (1999)
	<i>C. tagal</i>	Aziz and Khan (2001)
	<i>A. marina</i>	Hibino <i>et al.</i> (2001); Ashihara <i>et al.</i> (2003); Popp <i>et al.</i> (1985)
Glycinebetaine	<i>C. roxburghiana</i>	Rajesh <i>et al.</i> (1999)
	<i>H. tiliaceus</i>	Popp <i>et al.</i> (1985)
O-methyl- muconiositol	<i>R. stylosa</i> , <i>B. gymnorrhiza</i>	Ashihara <i>et al.</i> (2003)
Starch/Polysaccharide	<i>A. corniculatum</i>	Parida <i>et al.</i> (2004d)
Aspartic acid	<i>A. corniculatum</i> , <i>A. ilicifolius</i>	Datta and Ghosh (2003)
Sterol	<i>C. roxburghiana</i>	Suarez and Medina (2006)

*mucronata* (42, 99). Stress-induced DNA damage is reversed by repair mechanisms in which genes like Replication factor C 1 (RFC1), Proliferating cell nuclear antigen (PCNA), UV hypersensitive protein 3 (UVH3) and Replication factor A1 (RFA1) are involved with an enhanced expression status in *K. candel*. SODs, GSTs and catalases keep cytosolic redox levels in check (97). Mangrove survival depends on maintaining intracellular ion concentration in relation to the fluctuating ionic strength of the surrounding estuary water. The energy-using activity of  $H^+$ ATPases creates an electrochemical gradient that is used by  $Na^+/H^+$  antiporters to transport surplus sodium ions (100). Under salt stress, tonoplast  $H^+$ ATPase and vacu-

olar acid phosphatase production in *B. sexangula* increased together with vacuolar volume, indicating their significance in vacuolar ion transport (101). Glycine betaine, an osmolyte from the betaine family under high salt conditions, is encoded by the *A. marina* BADH gene (102).

In the leaf tissues of *A. corniculatum* suggests that the upregulated gene encoding the enzyme delta-1-pyrroline-5-carboxylate synthase (AcP5CS) plays a key role in osmoprotection (103). Additionally, the transcriptome study of the *C. tagal* root indicated differential expression of proline biosynthesis genes, with the active gene expression lasting between 3 and 12 hrs after salt treatment (104). In *K. candel*, genes involved in the biosynthesis and signalling of amino acids and secondary metabolites (flavonoids and anthocyanins) are upregulated when the environment is salty. These genes include phenylalanine

ammonia-lyase (PAL), trans-cinnamate 4-monooxygenase (C4H), 4-coumarate-CoA ligase 2 (4CL), anthocyanidin reductase (97). GIGANTEA (GI) genes expressed in *B. cylindrica* roots, establishes its role as a transporter regulator (105). By altering the composition of plasma membrane lipids, lipid metabolism-related genes such acyl-CoA synthetase and UDP-3-O-acyl-N-acetylglucosamine deacetylase help membrane-bound ion transporters effectively exclude or compartmentalise excess  $Na^+$  ions in the vacuoles during salt stress (105). *A. officinalis* Cytochrome P450 (CYP94B1), a peroxidase gene, functions in the apoplastic cell barrier to support suberin production. The production of suberin is also associated with the expression of

AoCYP94B1, a CYP94B1 homologue that is elevated in root tissues of the particular mangrove species in response to salt stress (106).

Abiotic stress causes aerenchymae, which are larger gas gaps between cells, to grow in the cortical area (107). In order to promote the development of aerenchyma in the mangrove root system, type 2C protein phosphatases (PP2C), which are significantly expressed under hypoxia, downregulate genes involved in the ABA pathway. In order to guarantee that the majority of ABA-related cellular activities are shifted to a lower level, genes encoding SNF1-related protein kinase 2 (SnRK2), an active booster of ABA substrate proteins, are likewise maintained downregulated (108-110). To maintain the integrity of the mangrove root system that is submerged, more pneumatophores must grow in response to challenges like hypoxia. When pneumatophore production occurs, granule-bound starch synthase (WAXY) and glucose 1-phosphate adenylyl transferase (GLGC) act in pathways that convert UDP glucose to starch (108). The gene (AoNHX1) that codes for the vacuolar Na<sup>+</sup>/H<sup>+</sup> exchanger is selectively expressed in the tonoplast of *A. officinalis* leaves (106). With the help of nitric oxide (NO) signalling, the increased expression of the genes for the plasma-membrane-specific H<sup>+</sup>ATPase (HA1) and Na<sup>+</sup>/H<sup>+</sup> antiporter (SOS1) further enhanced the transcription of the genes for the vacuolar H<sup>+</sup>-ATPase (VHA-c1) and the vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter (NHX1), which in turn facilitated the accumulation of Na<sup>+</sup> in vacuoles (111). A greater level of OEE expression suggests that mangroves are better able to tolerate the detrimental effects of salt on photosynthesis by providing PSII with more stability and capacity as well as improved oxygen-evolving activity. *A. ilicifolius* has been shown to possess the positively selected gene BRAP2 RING ZnF UBP domain-containing protein 2 (BRIZ2), which is required for seed germination and growth. In *A. officinalis*, differential gene expression analysis revealed activation of ethylene and auxin signalling genes and downregulation of ABA signalling genes and transcription factors such MYBs, ABA-responsive element binding factors (ABFs) and basic Leucine Zipper genes (bZIPs) (112).

## Conclusion

Mangroves face many environmental constraints as well as human interference in their growth and distribution. Apart from many abiotic factors affecting mangrove growth and development, salinity has its own significance. It may be considered that some mangroves are facultative or some are obligate halophytes. In both cases 'salinity' is a known stressor above or below an optimal level. Nutrients, human-mangrove conflict, different environmental pollutants such as heavy metals, recalcitrant, persistent pollutants, cosmetics, petroleum oil and Endocrine Disrupters have reported impact on various mangroves and associated biota. Stress tolerance in mangroves involves various mechanism including morphological and anatomical features, osmo-regulation, water use efficiency, salt secretion, salt exclusion and salt accumulation and molec-

ular regulations. This report reveals various aspects of salt tolerance strategies of mangroves related their growth, biochemical anatomy and physiology.

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## Authors contributions

SA made the conceptualization, data curation, interpretation and design of this work; MP and GM review, formatting manuscript and arrangement of data; RB, SP and PKM editing revised manuscript and data curation. All the authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest:** Authors have no conflicts of interest to declare.

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## References

- Gibbs HK, Brown S, Niles JO, Foley JA. Monitoring and estimating tropical forest carbon stocks, making REDD a reality. *Environ Res Lett.* 2007;2:045023. <https://doi.org/0.1088/1748-9326/2/4/045023>
- Li DL, Li XM, Peng ZY, Wang BG. Flavanol derivatives from *Rhizophora stylosa* and their DPPH radical scavenging activity. *Molecules.* 2007;12:1163-69. <https://doi.org/10.3390/12051163>
- Han L, Huang X, Dahse HM, Moellmann U, Fu H, Grabley S, Sattler I, Lin W. unusual naphthoquinone derivatives from the twigs of *Avicennia marina*. *J Nat Prod.* 2007;70:923-27. <https://doi.org/10.1021/np060587g>
- Patra JK, Panigrahi TK, Rath SK, Dhal NK, Thatoi HN. Phytochemical screening and antimicrobial assessment of leaf extracts of Bhitarkanika, Orissa, Indian Adv Nat Appl Sci. 2009;3:241-46.
- Acharya S, Patra DK, Pradhan C, Mohapatra PK. Anti-bacterial, anti-fungal and anti-oxidative properties of different extracts of *Bruguiera gymnorrhiza* L. (Mangrove). *Eur J Int Med.* 2020;36:101140. <https://doi.org/10.1016/j.eujim.2020.101140>
- Rodrigues CS, Souza SS, Rezende RP, Silva A, Andrioli JL, Costa H *et al.* Application of denaturing gradient gel electrophoresis for detection of bacterial and yeast communities along a salinity gradient in the estuary of the Cachoeira River in Brazil. *Genet Mol Res.* 2013;12:1752-60. <http://dx.doi.org/10.4238/2013.May.21.6>
- Bastami A, Kazemzadeh KJ, Esmailian M. Bioaccumulation of heavy metals in sediment and crab, *Portunus pelagicus* from the Persian Gulf, Iran. *Mid-East J Sci Res.* 2012;12:886-92.
- Gan WQ, McLean K, Brauer M. Modeling population exposure to comm <https://doi.org/10.1016/j.envres.2012.04.001>unity noise and air pollution in a large metropolitan area. *Environ Res.* 2012;116:11-16. <https://doi.org/10.1016/j.envres.2012.04.001>
- Duke NC, Ball MC, Ellison JC. Factors influencing biodiversity and distributional gradients in mangroves. *Globoal Ecol Biogeogr.* 1998;7:27-47. <https://doi.org/10.1111/j.1466-8238.1998.00269.x>

10. Zhang K, Liu H, Li Y, Xu H, Shen J, Rhome J et al. The role of mangroves in attenuating storm surges, Estuar. Coast Shelf S. 2012;102:11-23. <https://doi.org/10.1016/j.ecss.2012.02.021>
11. Acharya S, Patra DK, Mahalik G, Mohapatra PK. Quantitative ecological study of Rhizophoraceae mangroves of Bhitarkanika Wildlife Sanctuary regions of Odisha coast, India. Proc Natl Acad Sci India Sect B Biol Sci. 2021;91(4):897-908. <https://doi.org/10.1007/s40011-021-01295-2>
12. Cui Y, Zhang LJ, Luo XX, Zhang X. Study on the water pollution and eutrophication in the Xiaoqing River Estuary. J Ocean U China. 2013;43:60-66.
13. Krauss KW, Ball MC. On the halophytic nature of mangroves. Tree. 2013;27:7-11. <https://doi.org/10.1007/s00468-012-0767-7>
14. Kathiresan K, Rajendran N. Coastal mangrove forests mitigated tsunami. Estuar Coast Shelf Sci. 2005;65(3):601-06. <https://doi.org/10.1016/j.ecss.2005.06.022>
15. Parida AK, Jha B. Salt tolerance mechanisms in mangroves: a review. Trees. 2010;24:199-217. <https://doi.org/10.1007/s00468-010-0417-x>
16. Hossain MD, Inafuku M, Iwasaki H, Taira N, Mostofa MG, Oku H. Differential enzymatic defense mechanisms in leaves and roots of two true mangrove species under long-term salt stress. Aquatic Botany. 2017;142:32-40. <https://doi.org/10.1016/j.aquabot.2017.06.004>
17. Murdiyarsa D, Purbopuspito J, Kauffman JB, Warren MW, Sasmito SD, Donato DC, Manuri S, Krisnawati H, Taberima S, Kurnianto S. The potential of Indonesian mangrove forests for global climate change mitigation. Nat Clim Chang. 2015;5(12):1089-92. <https://doi.org/10.1038/nclimate2734>
18. Global Mangrove Alliance, 2018. Goals and Objectives. Global Mangrove Alliance, Washington DC. <https://www.mangrovealliance.org/about/>
19. Friess DA, Rogers K, Lovelock CE, Krauss KW, Hamilton SE, Lee SY et al. The State of the World's Mangrove Forests: past, present and Future. Annu Rev Environ Resour. 2019;44(1):89-115. <https://doi.org/10.1146/annurev-environ-101718-033302>
20. Lewis RR. Ecological engineering for successful management and restoration of mangrove forests. Ecol Eng. 2005;24(4):403-18. <https://doi.org/10.1016/j.ecoleng.2004.10.003>
21. Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biol Rev. 2012;87(2):346-66. <https://doi.org/10.1111/j.1469-185X.2011.00198.x>
22. Asaeda T, Barnuevo A. Oxidative stress as an indicator of niche-width preference of mangrove *Rhizophora stylosa*. Forest Ecology and Management. 2019;432:73-82. <https://doi.org/10.1016/j.foreco.2018.09.015>
23. Duke NC, Ying Lo, EY, Sun M. Global distribution and genetic discontinuities of mangroves – emerging patterns in the evolution of *Rhizophora*. Trees. 2002;16:65-79. <https://doi.org/10.1007/s00468-001-0141-7>
24. Sakthivel K. Survey of molluscs in Killai backwaters of South India. Indian J Ecol. 2020;47:190-95.
25. Manson FJ, Loneragan NR, Skilleter GA, Phinn SR. An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. Oceanogr Mar Biol Annu Rev. 2005;43:483-513. <https://doi.org/10.1201/9781420037449>
26. Selvam PP, Geevarghese GA, Ramachandran P, Ramachandran R. Spatial assessment of net canopy photosynthetic rate and species diversity in Pichavaram mangrove forest, Tamil Nadu. Indian J Ecol. 2018;45:717-23.
27. Alimov AF. Theory of ecosystem functioning: application to estuarine ecology. Abstracts of the symposium ECSA42 “Estuarine ecosystem: structure, functional management.” Svetlogorsk, Russia. 2007; p. 8-9.
28. Pickens CN, Sloey TM, Hester MW. Influence of salt marsh canopy on black mangrove (*Avicennia germinans*) survival and establishment at its northern latitudinal limit. Hydrobiologia. 2019;826:195-208. <https://doi.org/10.1007/s10750-018-3730-9>
29. Björkman O, Demmig B, Andrews TJ. Mangrove photosynthesis: response to high-irradiance stress. Aust J Plant Physiol. 1988;15:43-61. <https://doi.org/10.1071/PP9880043>
30. Cheeseman JM, Clough BF, Carter DR, Lovelock CE, Eong OJ, Sim RG. The analysis of photosynthetic performance in leaves under field conditions: a case study using *Bruguiera* mangroves. Photosynthesis Research. 1991;29:11-22. <https://doi.org/10.1007/BF00035202>
31. Asaeda T, Barnuevo A. Oxidative stress as an indicator of niche-width preference of mangrove *Rhizophora stylosa*. Ecol Manag. 2019;432:73-82. <https://doi.org/10.1016/j.foreco.2018.09.015>
32. Rout P, Kumar Mohapatra P, Chand Basak U. *Ex vitro* multiple shoot regeneration potential of hypocotyls of four Rhizophoraceae mangroves. Sci Agr. 2016;14:210-15. <https://doi.org/10.15192/PSCP.SA.2016.14.1.210215>
33. Clarke LD, Hannon NJ. The mangrove swamp and salt marsh communities of the Sydney district III. Plant growth in relation to salinity and water logging. J Ecol. 1970;58:351-69. <https://doi.org/10.2307/2258276>
34. Naidoo G. Effects of nitrate, ammonium and salinity on growth of the mangrove *Bruguiera gymnorhiza* (L.) Lam. Aquat Bot. 1990;38:209-19. [https://doi.org/10.1016/0304-3770\(90\)90006-7](https://doi.org/10.1016/0304-3770(90)90006-7)
35. Werner A, Stelzer R. Physiological responses of the mangrove *Rhizophora mangle* grown in the absence and presence of NaCl. Plant Cell Environ. 1990;13:243-55. <https://doi.org/10.1111/j.1365-3040.1990.tb01309.x>
36. Khan MA, Aziz I. Salinity tolerance in some mangrove species from Pakistan. Wetl Ecol Manag. 2001;9:219-23. <https://doi.org/10.1023/A:1011112908069>
37. Ashraf M, Harris PJC. Photosynthesis under stressful environment. Photosynthetica. 2013;51:163-90. <https://doi.org/10.1007/s11099-013-0021-6>
38. McMillan C. Environmental factors affecting seedling establishment of the black mangrove on the central Texas Coast. Ecology. 1971;52:927-30. <https://doi.org/10.2307/1936046>
39. Chen Y, Ye Y. Effects of salinity and nutrient addition on mangrove *Excoecaria agallocha*. PLoS ONE. 2014;9. <https://doi.org/10.1371/journal.pone.0093337>
40. Aziz I, Khan MA. Physiological adaptations to seawater concentration in *Avicennia marina* from Indus delta, Pakistan. Pak J Bot. 2000;32:171-89.
41. Ma D, Song S, Wei L, Ding Q, Zheng HL. Comparative transcriptome analysis on the mangrove *Acanthus ilicifolius* and its two terrestrial relatives provides insights into adaptation to intertidal habitats. Gene. 2022;839:146730. <https://doi.org/10.1016/j.gene.2022.146730>
42. Meera SP, Augustine A. De novo transcriptome analysis of *Rhizophora mucronata* Lam. furnishes evidence for the existence of glyoxalase system correlated to glutathione metabolic enzymes and glutathione regulated transporter in salt tolerant mangroves. Plant Physiol Biochem. 2020;155:683-96. <https://doi.org/10.1016/j.plaphy.2020.08.008>
43. Patel NT, Gupta A, Pandey AN. Salinity tolerance of *Avicennia marina* (Forssk.) Vierh. from Gujarat coasts of India. Aquat Bot. 2010;93:9-16. <https://doi.org/10.1016/j.aquabot.2010.02.002>



44. Manikandan T, Neelkandan T, Usha Rani. Effect of salinity on the growth, photosynthesis and mineral constituents of the mangrove *Rhizophora apiculata* L. seedlings, Recent Res Sci Technol. 2009;1:134-41.
45. Reef R, Feller IC, Lovelock CE. Nutrition in mangroves, Tree Physiol. 2010;30:1148-60. <https://doi.org/10.1093/treephys/tpq048>
46. Cheng H, Wang YS, Ye ZH, Chen DT, Wang YT *et al.* Influence of N deficiency and salinity on metal (Pb, Zn and Cu) accumulation and tolerance by *Rhizophora stylosa* in relation to root anatomy and permeability. Environ Pollut. 2012;164:110-17. <https://doi.org/10.1016/j.envpol.2012.01.034>
47. Yates EJ, Ashwath N, Midmore DJ. Responses to nitrogen, phosphorus, potassium and sodium chloride by three mangrove species in pot culture. Trees. 2002;16:120-25. <https://doi.org/10.1007/s00468-001-0145-3>
48. Kao WY, Tsai HC, Tsai TT. Effect of NaCl and nitrogen availability on growth and photosynthesis of seedlings of a mangrove species, *Kandelia candel* (L.) Druce. J Plant Physiol. 2001;158:841-46. <https://doi.org/10.1078/0176-1617-00248>
49. Shi GR, Cai QS, Liu CF, Wu L. Silicon alleviates cadmium toxicity in peanut plants in relation to cadmium distribution and stimulation of antioxidative enzymes. J Plant Growth Regul. 2010;61:45-52. <https://doi.org/10.1007/s10725-010-9447-z>
50. Ye Y, Tam NF, Wong YS, Lu CY. Growth and physiological responses of two mangrove species (*Bruguiera gymnorrhiza* and *Kandelia candel*) to waterlogging. Environ Exp Bot. 2003;49(3):209-21. [https://doi.org/10.1016/S0098-8472\(02\)00071-0](https://doi.org/10.1016/S0098-8472(02)00071-0)
51. Youssef T, Saenger P. Anatomical adaptive strategies and rhizosphere oxidation in mangrove seedlings. Aust J Bot. 1996;44:297-313. <https://doi.org/10.1071/BT9960297>
52. Ashraf M, Yasmin H. Differential waterlogging tolerance in three grasses of contrasting habitats: *Aeluropus lagopoides* (L.) Trin., *Cynodon dactylon* (L.) Pers. and *Leptochloa fusca* (L.) Kunth. Environ Exp Bot. 1991;31:437-46. [https://doi.org/10.1016/0098-8472\(91\)90042-M](https://doi.org/10.1016/0098-8472(91)90042-M)
53. McKevlin MR, Hook DD, McKee JWH. Growth and nutrient use efficiency of water tupelo seedlings in flooded and well-drained soil. Tree Physiol. 1995;15:753-58.
54. Xiao Y, Wang W, Chen L. Stem anatomical variations in seedlings of the mangrove *Bruguiera gymnorrhiza* grown under periodical waterlogging. Flora: Morphol Distrib Funct Ecol Plants. 2010;205(8):499-505. <https://doi.org/10.1016/j.flora.2009.12.004>
55. Xiao Y, Jie Z, Wang M, Lin G, Wang W. Leaf and stem anatomical responses to periodical waterlogging in simulated tidal floods in mangrove *Avicennia marina* seedlings. Aqa Bot. 2009;91(3):231-37. <https://doi.org/10.1016/j.aquabot.2009.07.001>
56. Chen Y, Ye Y. Effects of salinity and nutrient addition on mangrove *Excoecaria agallocha*. PLoS ONE 2014;9. <https://doi.org/10.1371/journal.pone.0093337>
57. Lovelock CE, Ball MC, Choat B, Engelbrecht BMJ, Holbrook NM, Feller IC. Linking physiological processes with mangrove forest structure: phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. Plant Cell Environ. 2006;29:793-802. <https://doi.org/10.1111/j.1365-3040.2005.01446.x>
58. Xin K, Huang X, Hu JL, Li C, Yang XB, Arndt SK. Land use change impacts on heavy metal sedimentation in mangrove wetlands-a case study in Dongzhai Harbor of Hainan, China. Wetlands. 2014;34:1-8. <https://doi.org/10.1007/s13157-013-0472-3>
59. Naser HA. Assessment and management of heavy metal pollution in the marine environment of the Arabian Gulf: a review. Mar Pollut Bull. 2013;72:6-13. <https://doi.org/10.1016/j.marpolbul.2013.04.030>
60. Sari I, Din ZB. Effects of salinity on the uptake of lead and cadmium by two mangrove species *Rhizophora apiculata* Bl. and *Avicennia alba* Bl. Chem Ecol. 2012;28:365-74. <https://doi.org/10.1080/02757540.2012.666526>
61. Zan Q, Wang Y, Wang B. Accumulation and cycle of heavy metals in *Sonneratia apetala* and *S. caseolaris* mangrove community at Futian of Shenzhen, China. Env Sci. 2002;23:81-88.
62. Dai M, Lu H, Liu W, Jia H, Hong H, Liu J, Yan C. Phosphorus mediation of cadmium stress in two mangrove seedlings *Avicennia marina* and *Kandelia obovata* differing in cadmium accumulation, Ecotoxicol Environ Saf. 2017;139:272-79. <https://doi.org/10.1016/j.ecoenv.2017.01.017>
63. Chauhan R, Ramanathan AL. Evaluation of water quality of Bhitarkanika mangrove system, Orissa. Indian J Mar Sci. 2008;37:153-58.
64. Panda SP, Subudhi H, Patra HK. Mangrove forest of river estuaries of Odisha. India Int J Biodivers Conserv. 2013;5:446-54. <https://doi.org/10.5897/IJBC12.004>
65. Page DS, Gilfillan ES, Foster JC, Hotham JR, Gonzalez L. Mangrove leaf tissue sodium and potassium ion concentrations as sublethal indicators of oil stress in mangrove trees. In: Proceedings of the 1985 International Oil Spill Conference. Los Angeles, California, American Petroleum Institute, Washington, DC; 1985. p. 391-93. <https://doi.org/10.7901/2169-3358-1985-1-391>
66. Paliyavuth C, Clough B, Patanaponpaiboon P. Salt uptake and shoot water relations in mangroves. Aquat Bot. 2004;78:349-60. <https://doi.org/10.1016/j.aquabot.2004.01.002>
67. Mills MA, Bonner JS, Page CA, Autenrieth RL. Evaluation of bioremediation strategies of a controlled oil release in a wetland. Mar Pollut Bull. 2004;49:425-35. <https://doi.org/10.1016/j.marpolbul.2004.02.027>
68. Ke L, Zhang C, Wong YS, Tam NFY. Dose and accumulative effects of spent lubricating oil on four common mangrove plants in South China. Eco Toxol Environ Saf. 2011;74:55-66. <https://doi.org/10.1016/j.ecoenv.2010.09.011>
69. Tian Y, Liu HJ, Zheng TL, Kwon KK, Kim SJ, Yan C. PAHs contamination and bacterial communities in mangrove surface sediments of the Jiulong River Estuary, China. Mar Pollut Bull. 2008;57:707-15. <https://doi.org/10.1016/j.ecoenv.2010.09.011>
70. Tomlinson PB. Responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. Plant Physiol. 1986;74:1-6.
71. Saintilan N. Above and below ground biomasses of two patterns of biomass and ANPP in a mangrove ecosystem species of mangrove on the Hawkesbury River estuary, New South Wales. Mar Fresh water Res. 1997;48:147-52. <https://doi.org/10.1071/MF96079>
72. Krauss KW, Lovelock CE, McKee KL, Hoffman LL, Ewe SML, Sousa, W.P., Environmental drivers in mangrove establishment and early development: A review. Aquat Bot. 2008;89:105-27. <https://doi.org/10.1016/j.aquabot.2007.12.014>
73. Biebl R, Kinzel H. Blattbau and Salzhaushalt von *Laguncularia racemosa* (L.) Gaertn. unter Mangroven Blume auf Puerto Rico. Oesterreichische Botanische Zeitschrift. 1965;112:56-93. <https://www.jstor.org/stable/43339272> <https://doi.org/10.1007/BF01372978>
74. Kemis JR. Petiolar glands in Combretaceae: new observations and an anatomical description of the extra-floral nectar of buttonwood (*Conocarpus erectus*). Am J Bot. 1984;71:34.
75. Yan L, Guizhu C. Physiological adaptability of three mangrove species to salt stress. Acta Ecologica Sinica. 2007;27:2208-14. [https://doi.org/10.1016/S1872-2032\(07\)60052-3](https://doi.org/10.1016/S1872-2032(07)60052-3)

76. Lv X, Li D, Yang X, Zhang M, Deng Q. Leaf enzyme and plant productivity responses to environmental stress associated with sea level rise in two Asian mangrove species. *Forests*. 2019;10:250. <https://doi.org/10.3390/f10030250>
77. Munns R, Tester M. Mechanisms of salinity tolerance. *Annu Rev Plant Physiol*. 2008;59:651-81. <https://doi.org/10.1146/annurev.arplant.59.032607.092911>
78. Munns R. Plant adaptations to salt and water stress: differences and commonalities. In: Turkan, I. (ed) *Plant Responses to Drought and Salinity Stress: Developments in a Post-Genomic Era*. *Advances in Botanical Research*; 2011;57; Academic, London; p. 1-32. <https://doi.org/10.1016/B978-0-12-387692-8.00001-1>
79. Kefu Z, Munns R, King RW. Abscisic acid levels in NaCl-treated barley, cotton and salt bush. *Aust J Plant Physiol*. 1991;18:17-24. <https://doi.org/10.1071/PP9910017>
80. Krishnamurthy P, Mohanty B, Wijaya E, Lee DY, Lim TM *et al*. Transcriptomics analysis of salt stress tolerance in the roots of the mangrove *Avicennia officinalis*. *Sci Rep*. 2017;7:10031. <https://doi.org/10.1038/s41598-017-10730-2>
81. Su W, Ye C, Zhang Y, Hao S, Li QQ. Identification of putative key genes for coastal environments and cold adaptation in mangrove *Kandelia obovata* through transcriptome analysis. *Sci Total Environ*. 2019;681:191-201. <https://doi.org/10.1016/j.scitotenv.2019.05.127>
82. Wang WQ, Ke L, Tam NFY, Wong YS. Changes in the main osmotic during the development of *Kandelia candel* hypocotyls and after mature hypocotyls were transplanted in solutions with different salinities. *Mar Biol*. 2002;141:1029-34. <https://doi.org/10.1007/s00227-002-0951-1>
83. Li LQ, Ding ZH, Liu JL, Lin HN, Wu H. Distribution of heavy metals in surficial sediments from main mangrove wetlands of China and their influence factors. *Acta Oceanologica Sinica*. 2008;30:159-64.
84. Parida AK, Mitra B, Das AB, Das TK, Mohanty P. High salinity reduces the content of a highly abundant 23-kDa protein of the mangrove *Bruguiera parviflora*. *Planta*. 2005;221:135-40. <https://doi.org/10.1007/s00425-004-1415-2>
85. Akram NA, Ashraf M. Improvement in growth, chlorophyll pigments and photosynthetic performance in salt-stressed plants of sunflower (*Helianthus annuus* L.) by foliar application of 5-aminolevulinic acid. *Agrochimica*. 2011;55:94-104.
86. Vovides AG, Juliane V, Armin K, Uta B, Uwe G, Peters R *et al*. Morphological plasticity in mangrove trees: salinity-related changes in the allometry of *Avicennia germinans*. *Trees*. 2014;28:1413-25. <https://doi.org/10.1007/s00468-014-1044-8>
87. Sugihar K, Hanagata N, Dubinsky Z, Baba S, Karube I. Molecular characterization of cDNA encoding oxygen evolving enhancer protein 1 increased by salt treatment in the mangrove *Bruguiera gymnorhiza*. *Plant Cell Physiol*. 2000;41:1279-85. <https://doi.org/10.1093/pcp/pcd061>
88. Yamada A, Saitoh T, Mimura T, Ozeki Y. Expression of mangrove allene oxide cyclase enhances salt tolerance in *Escherichia coli*, yeast and tobacco cells. *Plant Cell Physiol*. 2002;43:903-10. <https://doi.org/10.1093/pcp/pcf108>
89. Parida AK, Das AB, Mitra B. Effects of salt on growth, ion accumulation, photosynthesis and leaf anatomy of the mangrove *Bruguiera parviflora*. *Trees-Struct Funct*. 2004;18:167-74. <https://doi.org/10.1007/s00468-003-0293-8>
90. Patra DK, Pradhan C, Patra HK. Chromium bioaccumulation, oxidative stress metabolism and oil content in lemon grass *Cymbopogon flexuosus* (Nees ex Steud.) W. Watson grown in chromium rich over burden soil of Sukinda chromite mine, India. *Chemosphere*. 2019;218:1082-88. <https://doi.org/10.1016/j.chemosphere.2018.11.211>
91. Feng X, Xu S, Li J, Yang Y, Chen Q, Lyu H, Zhong C, He Z, Shi S. Molecular adaptation to salinity fluctuation in tropical intertidal environments of a mangrove tree *Sonneratia alba*. *BMC Plant Biol*. 2020;20:178. <https://doi.org/10.1186/s12870-020-02395-3>
92. He Z, Xu S, Zhang Z, Guo W, Lyu H, Zhong C *et al*. The International Mangrove Consortium and Shi, S. Convergent adaptation of the genomes of woody plants at the land-sea interface. *Natl Sci Rev*. 2020;7:978-93. <https://doi.org/10.1093/nsr/nwaa027>
93. Lyu H, He Z, Wu CI, Shi S. Convergent adaptive evolution in marginal environments: unloading transposable elements as a common strategy among mangrove genomes. *New Phytol*. 2018;217:428-38. <https://doi.org/10.1111/nph.14784>
94. Xu S, Wang J, Guo Z, He Z, Shi S. Genomic convergence in the adaptation to extreme environments. *Plant Comm*. 2020;1:100117. <https://doi.org/10.1016/j.xplc.2020.100117>
95. Hayyan M, Hashim MA, AlNashef IM. Superoxide ion: generation and chemical implications. *Chem Rev*. 2016;116:3029-85. <https://doi.org/10.1021/acs.chemrev.5b00407>
96. Prashanth SR, Sadhasivam V, Parida A. Overexpression of cytosolic copper/zinc superoxide dismutase from a mangrove plant *Avicennia marina* in indica rice var Pusa Basmati-1 confers abiotic stress tolerance. *Transgenic Res*. 2008;17:281-91. <https://doi.org/10.1007/s11248-007-9099-6>
97. Wang L, Pan D, Lv X, Cheng C-L, Li J, Liang W *et al*. A multilevel investigation to discover why *Kandelia candel* thrives in high salinity. *Plant Cell Environ*. 2016;39:2486-97. <https://doi.org/10.1111/pce.12804>
98. Yang Y, Li J, Yang S, Li X, Fang L, Zhong C *et al*. Effects of Pleistocene sea-level fluctuations on mangrove population dynamics: a lesson from *Sonneratia alba*. *BMC Evol Biol*. 2017;17:22. <https://doi.org/10.1186/s12862-016-0849-z>
99. Kumar S, Trivedi PK. Glutathione S Transferases: role in combating abiotic stresses including arsenic detoxification in plants. *Front Plant Sci*. 2018;9:751. <https://doi.org/10.3389/fpls.2018.00751>
100. Janicka-Russak M, Kabała K. The role of plasma membrane H<sup>+</sup>-ATPase in salinity stress of plants. In: *Progress in Botany*. U. Lutge and W. Beyschlag, (eds.) (Springer International Publishing); p. 2015. 77-92. [https://doi.org/10.1007/978-3-319-08807-5\\_3](https://doi.org/10.1007/978-3-319-08807-5_3)
101. Mimura T, Kura-Hotta M, Tsujimura T, Ohnishi M, *et al*. Rapid increase of vacuolar volume in response to salt stress. *Planta*. 2003;216:397-402. <https://doi.org/10.1007/s00425-002-0878-2>
102. Hibino T, Meng YL, Kawamitsu Y, Uehara N, *et al*. Molecular cloning and functional characterization of two kinds of betaine-aldehyde dehydrogenase in betaine-accumulating mangrove *Avicennia marina* (Forsk.) Vierh. *Plant Mol Biol*. 2001;45:353-63. <https://doi.org/10.1023/A:1006497113323>
103. Fu X, Huang Y, Deng S, Zhou R, Yang G, Ni X *et al*. Construction of a SSH library of *Aegiceras corniculatum* under salt stress and expression analysis of four transcripts. *Plant Sci*. 2005;169:147-54. <https://doi.org/10.1016/j.plantsci.2005.03.009>
104. Xiao X, Hong Y, Xia W, Feng S *et al*. Transcriptome analysis of *Ceriops tagal* in saline environments using RNA-sequencing. *PLoS One*. 2016;11:e0167551. <https://doi.org/10.1371/journal.pone.0167551>
105. Wong YY, Ho CL, Nguyen PD, Teo SS *et al*. Isolation of salinity tolerant genes from the mangrove plant, *Bruguiera cylindrica* by using suppression subtractive hybridization (SSH) and bacterial functional screening. *Aquat Bot*. 2007;86:117-22. <https://doi.org/10.1016/j.aquabot.2006.09.009>
106. Krishnamurthy P, Jyothi-Prakash PA, Qin L, He J *et al*. Role of root hydrophobic barriers in salt exclusion of a mangrove plant *Avicennia officinalis*. *Plant Cell Environ*. 2014;37:1656-71. <https://doi.org/10.1111/pce.12484>

- [doi.org/10.1111/pce.12272](https://doi.org/10.1111/pce.12272)
107. Evans DE. Aerenchyma formation. *New Phytol.* 2004;161:35-49. <https://doi.org/10.1046/j.1469-8137.2003.00907.x>
108. Hao S, Su W, Li QQ. Adaptive roots of mangrove *Avicennia marina*: structure and gene expressions analyses of pneumatophores. *Sci Total Environ.* 2021;757:143994. <https://doi.org/10.1016/j.scitotenv.2020.143994>
109. Ma Y, Szostkiewicz I, Korte A, Moes D, Yang Y, Christmann A, Grill E. Regulator of PP2C phosphatase activity function as abscisic acid sensors. *Science.* 2009;324:1064-68. <https://doi.org/10.1126/science.1172408>
110. Wang F, Wu Q, Zhang Z, Chen S, Zhou R. Cloning, expression and characterization of iron superoxide dismutase in *Sonneratia alba*, a highly salt tolerant mangrove tree. *Protein J.* 2013;32:259-65. <https://doi.org/10.1007/s10930-013-9482-5>
111. Chen J, Xiao Q, Wu F, Dong X *et al.* Nitric oxide enhances salt secretion and Na<sup>+</sup> sequestration in a mangrove plant, *Avicennia marina*, through increasing the expression of H<sup>+</sup>-ATPase and Na<sup>+</sup>/H<sup>+</sup> antiporter under high salinity. *Tree Physiol.* 2010;30:1570-85. <https://doi.org/10.1093/treephys/tpq086>
112. Hong L, Su W, Zhang Y, Ye C, Shen Y, Li QQ. Transcriptome profiling during mangrove viviparity in response to abscisic acid. *Sci Rep.* 2018;8:770. <https://doi.org/10.1038/s41598-018-19236-x>

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