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An Overview of the Adaptive Variations in Mangroves

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ABSTRACT

Mangrove species grow on saline soils of the tropical and subtropical coasts, which are permanently or periodically flooded. The mangroves are halophytes having certain traits which help them to survive in differing levels of salinity, drought, inundation and extreme temperatures. They can remarkably normalize ion homeostasis in brackish conditions by salt secretion, ultra filtration and ion appropriation. These plants have different developmental, physiological and anatomical adaptations as compared to a normal tree, which allow their survival in high stress habitat. This review is focused on those features of the mangroves that help them to adjust and grow extensively in the saline rich coastal regions, which make mangrove species physiologically different from other trees.

HIGHLIGHTS

⦿ Mangroves possess various unique physiological features that allow them to withstand harsh environmental conditions.

Keywords: Mangroves, salt stress, physiological adaptations, harsh environment

The word 'mangrove' refers to woody plants of intertidal forest communities. Mangroves are known to grow in over 123 countries and occur in geo-morphologically similar location with highly varying floristic compositions depending on the salinity attributes of the region (Tomlinson 1986; Hamilton and Casey, 2016). The estimated global cover of mangroves is about 1, 50,000 km². Regionally, over 40% of the global mangroves are in the south and south-east Asian region. India is bestowed with 45.8% of the mangrove cover within this south-east Asian territory (Spalding *et al.* 2010). Indian mangrove habitats are classified into three major groups *viz.*, Deltaic (east coast), Non-Deltaic (west coast) and Island (Andaman Nicobar and Lakshadweep). In India, the mangrove cover is 57% in the east coast, 30% in west coast, and 13% is within the Andaman Nicobar and Lakshadweep islands. Sundarbans, West Bengal in the east coast and Gujarat in the west coast are the major regions in India, comprising 43% and 23% of the total mangrove cover, respectively. 'Mangrove

community' is the general term for differentiating the plant assemblage from the individual mangrove species. The mangrove trees have enthralled physiologists for many decades (Saenger 2002; ICFRE, 2020).

All mangrove plants have special adaptations that allow them to survive in their harsh environment, though there are contradictory views regarding whether the mangroves are obligate or facultative halophytes. Morphological and physiological characteristics for adaptation include aerial roots, viviparous embryos, tidal dispersal of propagules, rapid rates of canopy production, absence of growth rings, wood with narrow densely distributed vessels, highly efficient nutrient retention mechanism, the ability to cope with salt, and to maintain water and carbon balance (Naskar and Palit 2014; Nizam *et al.*

2022). Other vegetation fails to flourish in the unique niches of mangroves. Adaptations in mangrove tree species which make them different from normal trees, are in physical stability, salt tolerance, anaerobic segments, reproduction, and at biochemical and molecular level, and these are reviewed herein. The adaptive mechanisms are followed by these salt tolerant plants particularly grown on the reverie shore in inter-tidal environment, where salinity plays a significant role in regulating the distribution of mangroves. This review offers an insight into all the mechanisms governing the unique traits, though there are prior reports on the underlying mechanisms of these adaptive features.

Adaptations in Mangrove Trees

The various physical, anatomical, biochemical and molecular adaptations of different mangroves are discussed hence forth. The leaves of mangroves are evergreen owing to the precipitation, tropical atmosphere and consistent temperatures throughout the year. The leaf surfaces are thick and stringy to avoid the water loss due to transpiration. They also have different orientations in the direction of leaves to circumvent the harsh noon time sun and thereby reduce loss from the leaves (Vinoth *et al*. 2019). Mangrove seeds are light and appropriate for water dispersal. The fruits of *Avicennia* spp. can be diverted by the water to another area where they will flourish, due to its buoyancy. The sprouted seedlings of *Rhizophora* spp. develop either inside or out through the fruit to form propagules which can produce its own nourishment through photosynthesis; once seedling is developed, it will drop into the water. These propagules survive drought and remain inactive for a long duration prior to development in an appropriate environment. Mangrove species extend their roots shape as vertically rather than parallel, whereby it is more possible to lodge in the mud. The most important of adaptations in mangroves are the various kinds of specialised roots (Srikanth *et al*. 2015). Natural root graft formation in *A. marina* has benefitted in resource sharing through these root networks providing advantage for better growth under stressful conditions (Vovides *et al*. 2021). The roots of mangrove species contain salt rejection mechanism, with a higher extent of gaseous exchange in waterlogged and high salinity condition. The most remarkable effects of salinity are on the mineral nutrition of the plants, and regulation of ion homeostasis. Salinity affects the nutritional status of plants by osmotic effects of salts, competitive interactions among ions in the substrate, and effects on membrane selectivity. As root elongation slows, the amount of ions reaching the roots by diffusion decreases. Different modifications also include the capability to expel abundant salt from leaves, vivipary or the development of seeds before they are scattered, and having distinctive seeds and propagules (Vinoth *et al*. 2019).

Physical Stability

The physical stability of mangroves is one of the most important adaptation, which also prevents shoreline erosion and shields inland areas from severe damage during hurricanes and tidal waves. The most typical physical adaptations of mangrove species are the many types of specialized roots (Fig. 1): buttress roots (*Xylocarpus granatum*), flying buttresses and spreading roots (*Rhizophora* spp.), surface roots (*Excoecaria agallocha*), prop roots (*R. apiculata*), stilt roots (*R. stylosa*), cable roots with pneumatophores, knee roots (*Bruguiera gymnorrhiza* and *B. cylindrica*), pencil roots (*Sonneratia caseolaris*) and cone-shaped roots (*Avicennia* sp.) (Srikanth *et al*. 2015).

In some mangrove species, relative root depth and tree stability depend on the growth conditions such as soil compaction, competition for assimilates, water logging, wind force, direction of wave or storm (Mickovski and Ennos 2003). To overcome these adverse circumstances, some mangrove species develop functionally modified, spreading root systems above-ground such as stilt roots, prop roots, and buttress roots, instead of consistent below-ground tap root system (Ong *et al*. 2004). Such root adaptations increase physical stability of mangrove trees in the soft sediments along shorelines in unstable mud, and enable them to withstand currents and storms. Some modifications of mangrove roots aid in resisting tree toppling as in *R. mangle* and *R. apiculata*, with prop roots descending from both trunk and branches, providing a stable support system to resist the tension and compression forces created as the crown moves with surging storms. Submerged prop roots or stilt roots help to anchor

(a) Stilt roots of *Rhizophora* sp.

(b) Prop roots hanging from branches

(c) Surface roots of *Excoecaria* sp.

(d) Cone roots and Pneumatophores of *Avicennia* sp.

(e) Prop roots of *A. marina*

Fig. 1: Morphology of mangrove root adaptations

the plant in place and collect water-borne silt and debris to build soil beneath it. Furthermore, based on the biomechanical adaptations of the root system, it is proven that the prop roots or flying buttresses from the trunk of *R. mangle* can act as a defensive hindrance against storm surges (Mendez-Alonzo *et al.* 2015; Srikanth *et al.* 2015).

Buttress roots develop in mangrove trees parallel to the predominant wind direction, especially on the leeward side (Mendez-Alonzo *et al.* 2015). Furthermore, the shape of the roots becomes more oval in weaker soils, and offer physical support to prevent tree fall in *Pelliciera rhizophora* and *Ceriops* species (Nicoll and Ray 1996). A buttress root bears a narrow strip of bark along the base, which covers its underlying cambium and conductive tissue, and connects vertical or inclined root branches with the stem. In addition to anchorage, buttress roots also serve in long distance transport of water and nutrients (Tomlinson 1986). They spread near the upper soil layer where the main nutrients are available. When these roots spread horizontally, they are able to cover a wider area for absorbing nutrients from the soil surface (Mickovski and Ennos 2003; Mendez-Alonzo *et al.* 2015).

Salt Tolerance

Salinity affects almost all aspect of plant development including germination, vegetative growth and reproductive development. Increased salinity often upsets the nutritional balance of plants by one or more mechanisms including osmotic effects of salts, competitive interactions among ions in the substrate, and effects on membrane selectivity. As root elongation slows, the amount of ions reaching the roots by diffusion decreases. High concentration of chloride reduces nitrate uptake by plants, whereas high concentration of nitrate inhibits phosphate uptake. Salinity condition often decreases uptake of K, Ca and Mg ions leading to nutritional imbalance (Dutt *et al.* 1991). High salinity can damage the plants by salt toxicity and dehydration due to low water potential (Naskar and Palit 2014).

Munns (2002) hypothesised the effect of salinity on plant growth by decrease in soil water potential, creating water stress and effects such as salt accumulation in leaves. These leaves die out because of rapid increase of salt in cell wall or cytoplasm, when vacuoles can no longer sequester incoming salts. The loss of leaves decreases the

supply of carbohydrates or growth hormones to meristematic regions, there by inhibiting growth. It is thus important for mangroves to control cytosolic salt concentration when living in intertidal zones with high salinity. Mangroves develop varied mechanisms associated with some physiological and anatomical characteristics to regulate salt absorption and exclusion, such as salt secretion, ultra filtration and ion sequestration (Tomlinson 1986; Mimura *et al.* 2003). Naskar (2014) observed that some species of mangroves can even accumulate saline ions as osmolytes to balance transmembrane osmotic potential.

The main ionic constituents of majority of the saline soil are Na^+ and Cl^-. Excess of these two salts in the soil solution poses a challenge to the plant. Na^+ and other ions taken up by roots and transported to shoot in the transpiration stream accumulate over time (Munns and Tester 2008). Elevated concentration of salts is built up in the apoplast and eventually inside the cell as water evaporates, and this accumulation of ions in plant tissues results in progressive damage. The presence of specific transport systems in mangroves for low affinity Na^+ uptake from soil, and the exact mechanisms for root Na^+ and Cl^- uptake involving transporters from many gene families and transport classes was debated before two decades (Hasegawa *et al.* 2000; Xiong and Zhu 2002). Salt stress regulates the expression and activity of K^+ and Na^+ transporters and H^+ pumps that generate the driving force for the transport (Brini and Masmoudi 2012). Also, Zhu (2003) reported some evidences suggesting that a protein kinase complex consisting of the myristoylated calcium-binding protein -SOS_3 and the serine/threonine protein kinase -SOS_2 is activated by a salt stress elicited calcium signal. This protein kinase complex gets phosphorylated in salinity condition and activates various ion transporters, such as the plasma membrane Na^+/H^+ antiporter SOS_1 to export the salt ions from the cell through plasma membrane.

Mangrove species also have many salt resistance-associated anatomic structures. One typical characteristic is thickening leaves that can reserve abundant water. For example, *Lumnitzera racemosa* have more leaf thickness and stores water during stress with high salinity by which absorbed salt is diluted thereby reducing the damage from salt

stress to some extent. Some mangroves have waxed epidermis in the leaves, which contributes to low transpiration efficiency (Ye *et al.* 2005). Some species like *Rhizophora*, *Bruguiera* and *Ceriops spp.* have ultra filters in their root frameworks. These ultra filters act as channels to prohibit salts while separating water from the dirt. Other species like *Avicennia marina*, *Acanthus illicifolius* and *Aegiceras corniculatum* intake salt and discharge it through specific salt organs in the leaves (Fig. 2). The mangrove species like *L. racemosa* and *Excoecaria agallocha* collect salts in leaf vacuoles and end up becoming succulent, or transfer the salts into senescent leaves, or store them in the bark or the wood (Tomlinson 1986). Many mangrove species like *Kandelia obovata* or *A. marina* can accumulate inorganic ions and use them as osmolytes to maintain osmotic and water potential (Zhao *et al.* 1999). Excessive ions imported into the cells would be harmful to the structure and activity of cytosolic proteins (Zhu 2003). Thus, while sequestering excessive ions into vacuoles, mangroves could also accumulate organic osmolytes like hydroxyl compounds, free amino acids and polysaccharides in cytoplasm to maintain the osmotic equilibrium across the tonoplast (Ru *et al.* 2006; Liang *et al.* 2008). These diverse strategies of salt management indicate that mangroves are adaptive to high salinity at the histological and physiological levels.

Fig. 2: Salt excretion through leaves of
Aegiceras corniculatum

Anaerobic Segments

Mangrove trees possess specialized root structures as adaptation for survival in oxygen-deprived

or anaerobic sediments. Plants require oxygen in all living tissues for respiration, including the underground roots. When the soil is not waterlogged, this requirement is supplied by air diffusion between the sediment grains. However, during waterlogged soil conditions, the air spaces are filled with water resulting in lower oxygen levels than air (Srikanth *et al.* 2015).

In contrast to most plants, mangroves have poorly developed, shallow below-ground root systems, but possess well-developed specialized aerial roots. These specialized aerial root structures facilitate atmospheric oxygen to underground water roots. A part of this oxygen supply inside the roots is used for aerobic respiration, while the excess oxygen may be released through aerenchyma into the rhizosphere or soil sediments. This mechanism is defined as radial oxygen loss (ROL) in wetland plants (Armstrong 1978; Colmer 2002). To prevent oxygen loss from aerenchyma of the root while transporting it to aerial parts of plant, mangrove plants have developed an impermeable layer within the exodermis to mitigate ROL (Visser *et al.* 2000). Variations in lignin and suberin composition of exodermal cell walls determine the function of this impermeable barrier (Soukup *et al.* 2007). External environment factors like continuous flooding, heavy metals attack and potential phytotoxins, affect the root architecture and ROL by increasing the levels of lignification and suberization within cell walls of the exodermis (Armstrong and Armstrong 1988; Kotula *et al.* 2009; Liu *et al.* 2009; Cheng *et al.* 2010). Also, the deposition of lignin in the exodermis can regulate the fluxes of gas, water and solutes between the root and rhizosphere (Colmer and Greenway 2011).

The red mangroves have prop roots which extend from the trunk and adventitious roots extending from the branches. Though the black mangroves do not possess prop roots, smaller air roots extend vertically from the soil surrounding the trunk. These air roots are called pneumatophores or breathing roots (Fig. 1), and extend upward from the underground roots above the soil surface as in *Avicennia* and *Sonneratia sp*. During low tides, air is taken up through open passages in the pneumatophores and transported to root tissues (Srikanth *et al*. 2015).

Adaptations to Reproduction

Many mangrove trees also have unique methods of reproductive adaptations *viz*., vivipary and propagule dispersal. Similar to terrestrial plants, mangroves reproduce by flowering with pollination occurring through wind and insects. Once pollination occurs, the seeds remain attached to the parent tree without falling to the soil. They germinate into propagules before dropping into the waters below, and float upright until they reach shallow water suitable for their roots to take hold in the mud. This ability is referred to as "vivipary" (Fig. 3), and is seen in *Avicennia marina* and *Lumnitzera racemosa*. In *Rhizophora stylosa*, aeronautical roots become infant trees which can drift for rather a while before it locates an appropriate place to inhabit (Vinoth *et al*. 2019).

(a) Germinated propagules attached to parent tree

(b) Growth after dropping in mud

Fig. 3: Vivipary in mangroves

Adaptations in Molecular Level

The mangroves are known to have evolved as a convergent plant group comprising about 73 species (Spalding *et al.* 2010). The evolution of their unique adaptive modifications may be a result of a host of genetic and molecular changes. *Avicennia marina* accumulated betaine serving as an osmolyte under salt stress, and the Betaine-2-aldehyde dehydrogenase gene that is involved in betaine synthesis was identified first in this species (Hibino *et al.* 2001). Other salt stress related genes identified in mangrove species are listed in Table 1. Additionally, Nizam *et al.* (2022) have recently summarised the various mechanisms for optimal functioning of mangrove plant cells, and the genes involved in redox, ion and osmotic homeostasis, ultrafiltration to sieve out surplus salt, breathing under hypoxic and anaerobic conditions using aerenchymae and pneumatophores, leaf modifications, vivipary, and plant hormone signalling mediated stress response mechanisms. Specific patterns of gene expression may contribute to adaptive evolution under adverse condition. Gene expression alterations, changes in gene copy number, GC content, and epigenetic regulations like DNA methylation and non-coding RNAs could also have resulted in adaptation of mangroves to harsh environments (Xu *et al.* 2020; Nizam *et al.* 2022).

Polyploidy, whole genome duplication or convergent evolution is predicted to have set off speciation in mangroves and also the formation of adaptive features to withstand intertidal environments (Nizam *et al.* 2022). For example, the genes coding for H^+ATPase and 14-3-3 regulatory proteins are gene duplicates in *A. corniculatum,* which are responsible for their adjustment to intertidal zones (Feng *et al.* 2021). Convergent evolution of mangroves has resulted in unusual substitution in amino acid composition to aid their survival in nutrient-deficient environments, or in restricting the usage of amino acids containing larger hydrophobic residues that disrupt protein folding under high salinity (Paul *et al.* 2008; He *et al.* 2020; Xu *et al.* 2020). During some circumstances e.g., in reclamation of mangrove areas, the mangrove trees or their parts may be required to be identified by discriminating them from all other tree species. Identifying particular genes or molecular mechanisms involved in the adaptation of mangroves to their harsh environment, may also serve as tools for such

Table 1: Salt stress related genes of mangroves and their function

Species	Gene	Description	Reference
Aegiceras corniculatum P5CS		Delta 1-pyrroline-5-carboxylate synthetase is a key enzyme of Proline synthesis pathway.	Fu *et al.* 2005
Avicennia marina	*AmT1* *AmT2 AmT3*	Betaine/Proline transporter transcription in *Avicennia marina* is salt stress induced in root and leaf.	Waditee *et al.* 2002
	BADH	Betaine-2-aldehyde dehydrogenase transcript level was induced by high salinity, and was accompanied by accumulation of betaine.	Hibino *et al.* 2001
	Cat1 *Fer1*	Catalase and Ferritin 1 were up regulated by saline or oxidative stress.	Jithesh *et al.* 2006
	Sod1	Cu/Zn superoxide dismutase transcript level was decreased by osmotic stress, though high salinity did not lead to transcriptional change.	Jithesh *et al.* 2006
Avicennia, Rhizophoraceae, and *Sonneratia*	*BCHA1* *PP2C*	BEACH-domain homolog A1, protein phosphatase 2C and peroxidase genes were involved in salinity tolerance	He *et al.* 2020
Bruguiera gymnorrhiza	*DLDH* *LAS*	Dihydrolipoamide dehydrogenase and Lipoic acid synthase were up regulated when treated with 500 m mol/L NaCl for 1 d.	Liang *et al.* 2008
	OEE1	Oxygen evolving enhancer 1 is one component of PSĊ and high salinity induced the accumulation of its transcript and protein.	Sugihara *et al.* 2000
Bruguiera sexangula	*Mangrin*	It is partially homologous to gene encoding Allene Oxide Cyclase, and was up regulated by high salinity.	Yamada *et al.* 2002

molecular discrimination. However, it is necessary to first establish that those genes or molecular mechanisms are present only in true mangroves, and not in mangrove associated species or other tree species.

Associate Mangrove Species

Mangrove species are classified as true mangrove and associate mangrove species. True mangrove species differ from mangrove associates physically and ecologically. Generally, true mangroves are grown in a limited environment, restricted to coastal saline and blackish water. They are "exclusive" to particular environment, but associate mangroves are "non exclusive" species that are grown in terrestrial or aquatic habitat, and can also occur in mangrove ecosystem. Associate mangroves are also referred to as semi-mangroves or back mangroves. True mangroves are defined as plant species that, (1) occur only in mangrove forests and are not found in terrestrial communities, (2) play a major role in the structure of the mangrove community, sometimes forming pure stands, (3) have morphological specializations like aerial roots, vivipary etc. according to the mangrove environment, and (4) have some mechanism for salt exclusion / salt excretion (Tomlinson 2016). However, certain mangrove associates also possess these or other adaptations that allow them to endure environmental conditions present in mangrove areas, few of which are listed in Table 2 (Naskar and Mandal 1999).

True mangroves are halophytes, whereas associate mangroves are glycophytes with certain level of salt tolerance. According to Tomlinson (1986), true mangroves or strict mangroves develop morphological adaptations to their tidal environment like aerial roots, salt excretion glands and vivipary

Table 2: Adaptations of mangrove associated species

Family	Species	Adaptive Character
Acanthaceae	*Acanthus ilicifolius*	Shrub with stilt roots; parenchymatous tissue having numerous large schizogenous leaf covered with cuticle
	Acanthus volubilis	Twining shrub with slit; stomata are diacytic, not sunken
Tiliaceae	*Brownlowia tersa*	Tree with aerial roots; dorsiventral leaf with stellate hair
Arecaceae	*Phoenix paludosa*	Palm with trunk and pneumatophores
Malvaceae	*Hibiscus tiliaceus*	Stellate hairs on lower surface of leaf
	Hibiscus tortuosus	Small tree; cuticle on upper surface, and stellate on lower surface of leaf
Rutaceae	*Atalantia correa*	Shrub with conical trunk; oil glands and stomata confined to the lower surface of leaf
Caesalpiniaceae	*Caesalpinia bonduc*	Shrub; leaves covered with thick layered cuticle
	Caesalpinia crista	Shrub; leaves covered with thick layered cuticle
Fabaceae	*Cynometra ramiflora*	Lower epidermal cell has sub-papillose structure
	Dalbergia spinosa	Small tree; lower epidermis has sub-papillose and upper epidermis has papillose structure
Amaryllidaceae	*Crinum defixum*	Herbaceous; stomata - paracytic and confined to both the surfaces, mesophyll-palisade as water storage tissue, leaves are isobilateral
Apocynaceae	*Sarcolobus globosus*	Twining shrub with aerial roots; Laticiferous tuber occurs in both leaf and stem, and trichomes are present
	Sarcolobus carinatus	Twining shrub or herb without aerial roots; stomata confined to ventral side of leaf
	Pentatropis capensis	Twining shrub; stomata present on both sides of leaf
Araceae	*Cryptocorne ciliata*	Herbaceous in the inner estuary
Chenopodiaceae	*Suaeda nudiflora*	Herbaceous; epidermis having thick walled, stomata confined to both surfaces, mesophyll-palisade tissue consisting of water storage tissue
Rubiaceae	*Hydrophylax maritima*	Succulent herb with creeping stem; leaves are fleshy
Lamiaceae	*Clerodendrum inerme*	Leaf hairs of various types; extra-floral nectaries occur on the lower surface of leaf
Poaceae	*Porteresia coarctata*	Hairs - unicellular with blunt tip; Stomata confined to both surfaces of the leaf

of seeds. While associated mangrove species develop these only in very few species (e.g., *Oncosperma*, *Phoenix* and *Raphia*). Some mangrove associated species also have very long stem and root system (*Ipomoea pes-caprae*) that act as sediment binders and stabilize the sand dunes on the coastal zone (Sufia Zaman *et al.* 2014).

CONCLUSION

Physiological behaviour of living plants is mainly dependant on tolerating the ecological conditions under which they grow and develop. The flexibility of mangroves to unfavourable environment makes them perfect natural models to contemplate their adjustment to various abiotic stresses. Mangroves are a repository of the best recognized descriptive qualities and proteins associated with resistance to saltiness, stress and water logging conditions, which can also probably be relevant in other yield plants. Morphological and physiological attributes for adjustment include adventitious roots, viviparous developing nature, tidal dispersal of propagules, fast rates of generation, absence of development rings, wood with thickly disseminated vessels, profoundly effective metabolite maintenance system and the capacity to adapt to saltiness, and to maintain water and carbon regulation. Such differing interrelated qualities constituting the physiological adaption of mangroves species, make them contrasted with other tropical biological systems. Detailed studies on the genes and their sequences related to these mechanisms can also be useful for genetically discriminating mangroves from other plant species. Though some normal tree species also develop physiological adaptations like salt excretion, osmolyte production and ultra filtration in roots under stress condition, mangroves require harsh environment for survival. As a result, mangroves cannot endure in the usual environmental conditions where normal trees exist, making them extraordinary.

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