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REVIEW

Mangrove root: adaptations and ecological importance

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Abstract

Key message **This review gives a comprehensive overview of adaptations of mangrove root system to the adverse environmental conditions and summarizes the ecological importance of mangrove root to the ecosystem.**

Abstract In plants, the first line of defense against abiotic stress is in their roots. If the soil surrounding the plant root is healthy and biologically diverse, the plant will have a higher chance to survive in stressful conditions. Different plant species have unique adaptations when exposed to a variety of abiotic stress conditions. None of the responses are identical, even though plants have become adapted to the exact same environment. Mangrove plants have developed complex morphological, anatomical, physiological, and molecular adaptations allowing survival and success in their high-stress habitat. This review briefly depicts adaptive strategies of mangrove roots with respect to anatomy, physiology, biochemistry and also the major advances recently made at the genetic and genomic levels. Results drawn from the different studies on mangrove roots have further indicated that specific patterns of gene expression might contribute to adaptive evolution of mangroves under high salinity. We also review crucial ecological contributions provided by mangrove root communities to the ecosystem including marine fauna.

Keywords Mangrove root · Abiotic stress · Salinity balance · Tidal inundation · Lenticels · Pneumatophore

Introduction

Mangrove ecosystems are one of the major types of natural wetlands along tropical and subtropical shores, and play a vital role in estuarine ecosystems (Peters et al. 1997). Mangrove forests are among the most productive and biologically important ecosystems of the world, because they provide an important and unique ecosystem that impacts positively human society by stabilizing shorelines and reducing the devastating impact of natural disasters, as well as providing food, medicines, fuels and building materials (Tomlinson 1986; Giri et al. 2011). There are 9 orders, 20 families, 27 genera, and roughly 70 species of trees found in mangroves across the world (Alongi 2009). The principal genera are *Avicennia* (Avicenniaceae), *Laguncularia* and *Lumnitzera* (Combretaceae), *Nypa* (Palmae), *Bruguiera, Ceriops, Kandelia* and *Rhizophora* (Rhizophoraceae), and *Sonneratia* (Sonneratiaceae) (Tomlinson 1986). Indonesia, Australia, Brazil, and Nigeria accommodate roughly 43 % of the world's mangrove forests, which represent a total area of approximately 160,000 km^2 (FAO 2003). Mangrove forests are a characteristic feature of the intertidal zone of tropical and subtropical coasts. Since these forests are regularly flooded with seawater, mangrove trees not only have to cope with high temperatures and low relative air humidity, but also with high and changing salt concentrations, and hypoxia due to regular inundation (MacFarlane et al. 2007; Agoramoorthy et al. 2008; Robert et al. 2012). However, these plants have adapted in various ways, with features such as aerial roots, vivipary, salt exclusion and salt secretion to

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overcome these threats and thus are able to survive in intertidal zones (Scholander 1968; Tomlinson 1994; Shi et al. 2005).

The success of mangrove plants growing in intertidal zones is generally ascribed to anatomical adaptations (Youssef and Saenger 1996; Liu et al. 2009; Pi et al. 2009) that facilitate O_2 supply to submerged roots (Thomson et al. 1990; Colmer 2003; Evans 2003). Mangrove roots must cope with short periods of anoxia, as survival and sustained growth of the plants depend on maintaining oxygen levels in the roots (Alongi 2009). Their shallow nature and the presence of numerous lenticels and extensive aerenchyma facilitate oxygen availability. Most species have structural features (pneumatophores, knee roots, stilt roots or plank roots) to provide root ventilation via atmospheric exposure, at least during low tides (McKee 1993). Some species have above-ground roots with the ability to photosynthesize and thus provide oxygen directly to underground roots (Yabuki et al. 1985; Dromgoole 1988).

This review article gives a comprehensive overview of studies on different morphological, anatomical and physiological adaptations of mangrove root system to the adverse environment. This article also summarizes the positive impact of mangrove roots to costal ecosystems such as protection against floods and hurricanes, reduction of shoreline and riverbank erosion, controlling water pollution, and maintenance of marine fauna.

Mangrove root adaptations to adverse environmental conditions

The most typical adaptations of mangrove species resulted in many types of specialized roots: buttress roots (*Xylocarpus granatum*), flying buttresses (*Rhizophora* sp.), surface roots (*Excoecaria agallocha*), prop roots (*Rhizophora apiculata*), stilt roots (*R. stylosa*), spreading roots (*Rhizophora* sp.), cable roots with pneumatophores, knee roots (*Bruguiera gymnorrhiza and B. cylindrica*), pencil roots (*Sonneratia caseolaris*) and cone roots (*Avicennia* sp.) (Fig. 1a–k). Mangrove species have roots with a higher proportion of gas space when waterlogged and are capable of salt exclusion, or are tolerant to high tissue salt concentrations. Other adaptations include the ability to excrete excess salt from leaves, vivipary or the development of the embryo in seeds before they are dispersed, and seeds and propagules having different morphological adaptations that facilitate flotation (Baskin and Baskin 2001; Hogarth 1999; Tomlinson 1986).

Specialized root for physical stability

In some mangrove species relative root depths differ by both species and growth conditions such as soil compaction, competition for assimilates, water logging, wind force, direction of wave or storm surges, which in turn affects the tree stability (Mickovski and Ennos 2003; Ong et al. 2004). To overcome these adverse circumstances, some mangrove species develops above-ground, functional, modified, spreading root systems such as stilt roots/prop roots and buttress roots instead of consistent below-ground tap root system (Ong et al. 2004). 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. Also, thigmomorphogenetic responses of some mangrove roots might aid in resisting the tension and compression forces created as the crown moves with surging storms by resisting tree toppling.

R. mangle and *R. apiculata* (Fig. 1d) have prop roots descending from both trunk and branches, providing a stable support system. Submerged prop roots or stilt roots (Fig. 1d, e) help to anchor the plant in place and collect water-borne silt and debris to build soil beneath it. Furthermore, based on the biomechanical adaptations of the rhizophore system (prop roots/flying buttresses from trunk) in *R. mangle*, it is proven that they can act as a defensive hindrance against storm surges and is higher than that of other mangrove species (Bayas et al. 2011; Ohira et al. 2013; Mendez-Alonzo et al. 2015).

Buttress root development is stimulated in trees parallel to the predominant wind heading, especially on the leeward side. Furthermore, the shape of the roots becomes more oval in weaker soils looking like the “I” shafts regular in engineering (Nicoll and Ray 1996; Clair et al. 2003; Dupuy et al. 2005; Mendez-Alonzo et al. 2015). These roots develop from stress-induced cambial activity found in some species such as *Heritiera littoralis, X. granatum* (Fig. 1a), *Pelliciera rhizophora* and *Ceriops* sp. and provide physical support to prevent tree fall (Clair et al. 2003; Duke 2011). 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 serve as conduits for long distance transport of water, nutrients, and metabolites (Tomlinson 1986; Day et al. 2010). When these roots spread horizontally, they are able to cover a wider area for collecting nutrients from the soil surface. They spread near the upper soil layer where the main nutrients are available (Crook et al. 1997; Mickovski and Ennos 2003; Mendez-Alonzo et al. 2015). Buttresses are tension elements, being larger on the side away from the stress of asymmetrical canopies (Young and Perkocha 1994). Other species of mangrove trees, which grow at higher elevations in drier soils, do not require specialized root structures for physical balance.

Fig. 1 Morphology of different kinds of mangrove root adaptations. **a** Buttress roots of a *Xylocarpus granatum*. **b** Flying buttress roots of *Rhizophora* sp. **c** Surface roots of *E. agallocha*. **d** Prop roots hanging from branches in *R. apiculata*. **e** Stilt roots of *R. stylosa*. **f** Spreading roots of *Rhizophora* sp. **g** Cable roots. **h** Knee roots of *B. cylindrica*. **i** Knee roots of *B. gymnorrhiza*. **j** Pencil roots (*S. caseolaris*). **k** Cone roots of *Avicennia* sp. **l** Leaf bases of mangrove palm *Nypa fruticans*

Tidal inundation

In mature mangrove trees, different root systems such as cable roots, pneumatophores, feeding roots and anchor roots facilitate gas exchange when they are subjected to tidal inundation. Pneumatophores (Fig. 2a) arise vertically from cable roots and have evolved independently in at least five mangrove families and genera: *Laguncularia* (Combretaceae), *Avicennia* (Acanthaceae), *Bruguiera* (Rhizophoraceae), *Xylocarpus* (Meliaceae), and *Sonneratia* (Sonneratiaceae) (Tomlinson 1986). They have abundant lenticels (Fig. 2b), and aerenchyma may account for up to 70 % of root volume (Hogarth 1999). The pneumatophores of *Sonneratia* and *Avicennia* are slender and cone shaped (Fig. 2), standing erect and aligned on the cable root of 1–20 m or more in length, which spread horizontally in the soil (Yanez-Espinosa and Flores 2011). Curran et al. (1986) demonstrated that the conductance of pneumatophores in *A. marina* was sufficient to resupply the root internal gas space during a normal low tide when they exposed to the atmosphere. Curran et al. (1996) measured that the gas space in the roots of the same species was 40–50 % by volume. Upon exposure to low tide, pressure recovers immediately to atmospheric level, but oxygen slowly rises to a plateau below the concentration in the atmosphere. These changes in oxygen concentration are consistent with continuous oxygen diffusion through the pneumatophores (Allaway et al. 2001).

The anatomy of mangrove roots has been extensively studied in relation to development and function (Tomlinson 1986). Prolonged flooding alters physical and chemical properties of soil, as well as bacterial composition, directly affecting the adapted mangrove roots (Rajaniemia and Allison 2009). The affected root vascular system in turn affects the stem vascular system and leaf structure of mangrove species (Visser and Pierik 2007).

Transverse sections of matured pneumatophores show enlarged polygonal or irregular aerenchymatous cells in the cortical region (Fig. 3a). These cells are described as lacunae, which are distributed between epidermis and endodermis without any cell sap (Purnobasuki and Suzuki 2005). Matured pneumatophores consist of more extensive lacunose cortex and a little focal stele in contrast to the young pneumatophores. Usually the root tissue of halophytes shows differential growth responses to different saline concentrations. Hajibagheri et al. (1985) reported that *Suaeda maritima* grown in the presence of 340 mM NaCl had greater root stele diameter and cortical thickness than those grown in the absence of NaCl. *Kandelia candel* had a larger ratio of stele to root cross section in low and moderate salinities, suggesting the influence of NaCl on the growth (Hwang and Chen 1995a). The trend was reversed when *K. candel* was cultured in high salinities (400 and 550 mM NaCl), which could be the result of salt stress caused by the accumulation of Na^+ and Cl^- in the tissues (Hwang and Chen 1995b). The lower salt concentration or lower rate of exposure to higher salt concentration might be the reason for larger stele regions in young pneumatophores. Early development of the Casparian strips, and their location close to the root apex was observed in salt-grown *Puccinellia intermedia* (Stelzer and Lauchli 1977) and in *S. maritima* (Hajibagheri et al. 1985). Moreover, early lignification of secondary tissues, such as metaxylem, was believed to be a general characteristic of plants growing in habitats with a low water potential (Saadeddin and Doddema 1986). These could be the reasons for smaller stele with reduced pith in matured pneumatophores. The clorenchymatous cortex of pneumatophores might be the reason for green color in aerial surface of pneumatophores (Fig. 2).

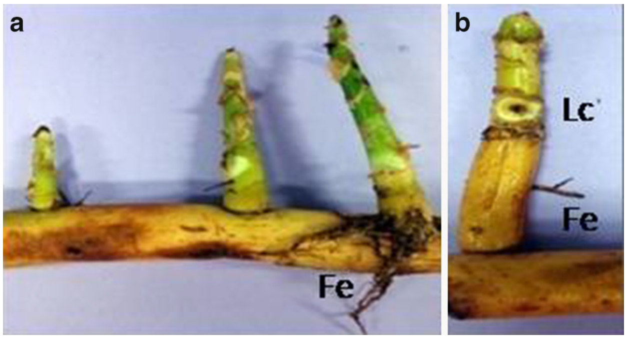

Fig. 2 Morphology of young pneumatophores. **a** Immature cable root with small pneumatophores with green color in superficial area and feeding root (Fe). **b** Pneumatophore with lenticel (Lc) and feeding roots (Fe)

Lenticels can be seen noticeably on aerial parts of pneumatophores and also on young stilt roots or prop roots and helps to supply oxygen for the underground roots. These are varied in size and morphology, and composed of a complementary tissue (Fig. 3c) with thin-walled spheroidal cells (Purnobasuki and Suzuki 2005). Generally, lenticels develop from the parenchymatous cells adjoining the aerenchyma in cortical region. These parenchymatous cells become specialized and increase in size and then divide. The resulting cells are aligned as complementary cells with intercellular spaces (Fig. 3c). In older pneumatophores, which are covered by periderm, the lenticels arise from the phellogen. At certain places, it also produces complementary tissues in an uninterrupted cortical layer and thus acts as lenticellular meristem (Purnobasuki and Suzuki 2005). The pressure of rapidly dividing and expanding complementary tissue causes the epidermis to protrude outward and finally to rupture exposing the complementary tissue to air.

Apart from the morphological adaptations of mangrove root systems, the vital anatomical modification that enables tolerance to inundation and soil anoxia is the development

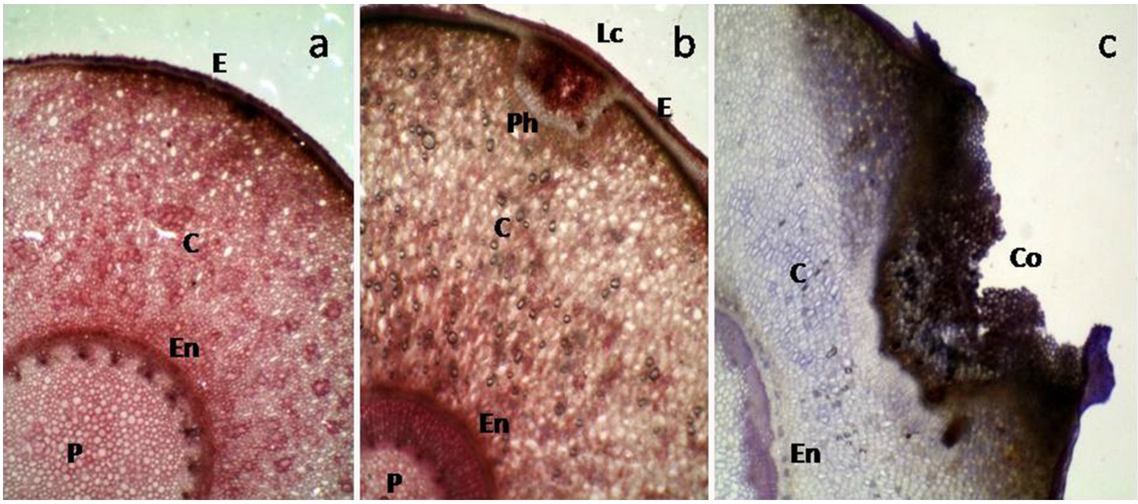

Fig. 3 Free hand transverse sections (T.S) of pneumatophores. **a** T.S of pneumatophore with normal epidermis (*E*), cortex (*C*), endodermis (*En*) and stele with central pith (*P*) region. **b** T.S of pneumatophore through an immature lenticel (*Lc*) with specialized phellogen (*Ph*). **c** TS of pneumatophore through a mature lenticel showing complementary tissue (*Co*) with regular alignment and intercellular spaces

of aerenchyma with interconnected air channel frameworks throughout the plant. *N. fruticans* Wurmb. is the only extant mangrove palm which has no specialized root structures to provide oxygen supply to the submerged roots (Chomicki et al. 2014). Since *Nypa* does not produce any breathing roots, it is believed that the leaves play the role of a 'giant pneumatophore', as they are the only emergent parts of the plant (Tomlinson 1994). As an aftermath of senescence, the leaf rachis abscised from the leaf base (petiole) at the zone of intersection and lenticels develop at the same time on the leaf base (Fig. 11). Soon after, these leaf bases will develop aerenchyma with increasing porosity towards the stem junction. Subsequently, a network of mature lenticels covers the leaf base and connects with aerenchyma network which helps in gases exchange up to 4 years following abscission (Chomicki et al. 2014).

Morphological adjustments such as pneumatophores and lenticels are believed to increase the rate of oxygen diffusion from the aerated parts to the flooding root and eliminate by-products of anaerobic metabolism (ethanol, CO_2 and CH_4), which is required for the mangrove survival and growth. It is reported that lenticel formation is associated with ethylene and auxin accumulation due to stress caused by O_2 deficiency in flooded soil (Bruna et al. 2012; Patel et al. 2014). Flooded roots contain more amount of ethylene and its precursor (acid-1 aminocyclopropane-1-carboxylic acid—ACC), and high activity of ACC synthase and ACC oxidase compared with normal roots (He et al. 1996; Rieu et al. 2005; Vidoz et al. 2010). Even though their presence is often linked to flooding tolerance in plants, the actual physiological responsibility of lenticels is still unclear (Parelle et al. 2006; Liu et al. 2014).

Anaerobic conditions

In submerged mangroves, specialized root structures (Fig. 1) facilitate oxygen supply to live in oxygen-poor or anaerobic sediments. These root adaptations to anaerobic condition help to conserve the atmospheric oxygen by diffusion into the underground root parts. A part of this conserved O_2 inside the roots is used for aerobic respiration, while the excess O_2 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 and Pedersen 2008). To prevent O_2 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 (a barrier to ROL) (Visser et al. 2000; Vasellati et al. 2001; Colmer et al. 2006). Variations in lignin and suberin composition of exodermal cell walls determine the function of this impermeable barrier (Armstrong and Beckett 1987; Soukup et al. 2007). External environmental factors interact perpetually with the root architecture and ROL (Kotula et al. 2009). Some adverse environmental factors, such as continuous flooding (Armstrong et al. 1988), heavy metal attack (Liu et al. 2009; Cheng et al. 2010) and potential phytotoxins (Armstrong and Armstrong 2005) increase the levels of lignification and suberization within cell walls of the exodermis. Lignin deposition within the exodermis could regulate the fluxes of gas, water, and solutes at the interface between root and rhizosphere (Degenhardt and Gimmler 2000; Pollard et al. 2008; Colmer and Greenway 2011).

Halophytic nature

Mangrove communities represent marine halophytes whose different life history stages were framed within the context of salinity tolerance (Tomlinson 1986; Ball 1988; Parida and Jha 2010). No other environmental factors other than salinity admitted more in the mangrove history. Some authors have also categorized mangroves under obligate halophytes (Downton 1982; Clough 1984; Wang et al. 2011). Several mangrove tree species reach an optimum growth at salinities of 5–25 % of standard seawater (Downton 1982; Clough 1984; Ball 1988; Burchett et al. 1989; Ball and Pidsley 1995). However, the range of salinity in which the plant is able to survive varies across the species (Ball 1988); 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). Krauss and Ball (2013) reported mangroves as a group of facultative halophytes since they can survive and tolerate fresh water. But when these mangroves are grown in normal terrestrial land provided with ample amount of oxygen and fertility, they might not develop any specialized roots with lenticels. As an example, a true mangrove species of *S. caseolaris* developed pencil roots when it grew in the fresh water (Fig. 4b) as compared to its relative *S. alba* (Fig. 4a) which produces pencil roots in tidal inundation. In contrast, this species did not produce any specialized roots when it grew under normal terrestrial conditions (Fig. 4c). However, different species exhibit a wide range of tolerance from salt sensitive to those that require higher levels of salt for optimal growth and reproduction (Krauss and Ball 2013).

Salinity balance

It is important for mangroves to control cytosolic salt concentration when living in intertidal zones with high salinity (Tomlinson 1986). Mangrove species develop diverse mechanisms associated with anatomic or physiological characteristics to regulate salt absorption and exclusion, such as ultra-filtration, salt secretion (Tomlinson 1986) and ion sequestration (Mimura et al. 2003; Kura-Hotta et al. 2001). Some species can even accumulate saline ions to balance transmembrane osmotic potentials (Kura-Hotta et al. 2001). Diverse anatomic and physiological strategies of salt management enable mangrove species to adapt to high salinity. Many mangrove species (e.g., *K. obovata*, *Avicennia marina*) are able to accumulate inorganic ions to maintain osmotic and water potential (Kura-Hotta et al. 2001; Suarez and Medina 2006). This characteristic confers a survival advantage to these species in a saline environment (Tomlinson 1986).

Nevertheless, intracellular K^+/Na^+ balance is fundamental to the physiology of living cells and is crucial for plant normal growth (Chen et al. 2007; Shabala and Cuin 2008). Hence excessive ions in the cells would be harmful to the structure and activity of cytosolic proteins (Zhu et al. 2012). In order to maintain the optimal cytosolic K^+/Na^+ balance and to avoid the adverse effects of high salinity on plant growth and development, halophytes have developed different strategies to avoid excessive Na^+ accumulation and to maintain osmotic balance in plants. A common strategy involves the transport restriction of excess Na^+ via inhibiting non-selective cation channels (NSCCs) in the root cells (Sun et al. 2010). Moreover, halophytes can elevate the Na^+ extrusion from the cytosol to external medium and/or Na^+ compartmentation into the vacuoles through transmembrane transport proteins like plasma membrane (PM)-located Na^+/H^+ antiporter (SOS1) and tonoplast located Na^+/H^+ antiporter (NHX1) (Wu et al. 2009; Chen et al. 2010). Vacuoles of root cells 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 subsequent cell layers (Werner and Stelzer 1990). Chen et al. (2013) reported that nitric oxide greatly contributes to K^+/Na^+ balance in high salinity-treated *K. obovata* roots, by activating AKT1-type K^+ channel and Na^+/H^+ antiporter, which are the critical components in K^+/Na^+ transport system. AKT1, the most important inward-rectifying shaker K^+ channel, whose gene is mainly expressed in root epidermal cells, is involved in K^+ acquisition by plants (Ardie et al. 2010).

While sequestering excessive ions into vacuoles, mangroves could also accumulate organic osmolytes in cytoplasm to obtain osmotic equilibrium across the tonoplast. Organic osmolytes of mangroves mainly include hydroxyl compounds, free amino acids (especially proline), and polysaccharides (e.g., starch) (Ru et al. 2006). As water salinity increases, some species of mangroves simply become increasingly conservative in their water use, thus achieving greater tolerance (Ball and Passioura 1995). Some species actively excrete excess salt by ultra-filtration at the root cell membrane of cortical cells (Parida and Jha 2010). Since 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 (*R. 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

Fig. 4 Root adaptations of mangrove (*Sonneratia* spp.) in coastal region. **a** The tree (*S. alba*) on left side developed specialized pencil roots for oxygen supply, whereas the same species tree on the right side did not develop any specialized roots as it is acclimatized in aerated soil. **b** *S. caseolaris* growing well in fresh water. **c** *S. caseolaris* growing on fertile land without specialized roots. *Center figure* showing its characteristic mangrove apple

mangrove trees to save water. The viscous, polymeric substances in the xylem sap limit the rate of water flow and decrease transpiration (Zimmermann et al. 1994, 2002). Combined with high water-use efficiency this mechanism 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).

Oxidative stress is a secondary effect of salinity, which causes the formation of reactive oxygen species (ROS), such as the superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), the hydroxyl radical (·OH) and singlet oxygen ($^1O_2$). Wang et al. (2014) reported the effect of salt stress on antioxidant defense system in the root of a mangrove *K. candel*. The results showed that a certain salt concentration (<300 mmol/L) was required for the growth of *K. candel* seedlings. At the early stage of high salt stress, *K. candel* can rapidly activate antioxidant defense system to resist the salt induced oxidative stress, thus reducing the damages of oxidative stress to plasma membrane, which could be an effective means for *K. candel* to resist high salt stress (Wang et al. 2014).

The tolerance of mangroves to a high saline environment is also tightly linked to the regulation of gene expression (Parida and Jha 2010). In *A. marina*, salt stress induces transcription of betaine/proline transporter genes (*AmT1, AmT2 and AmT3*) in roots and leaves (Waditee et al. 2002). Wong et al. (2007) have identified and isolated 126 cDNA sequences that confer tolerance to salinity from the root of a mangrove plant, *B. cylindrica* (L.) Blume by suppression subtractive hybridization (SSH) and bacterial functional screening. Among these 75 cDNA sequences of *B. cylindrica* that conferred salinity tolerance to *Escherichia coli* 29 tentative unique genes (TUGs) have putative functions in transportation, metabolism and other functions. 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*. Miyama et al. (2006) identified 14,842 expressed sequence tags from leaves and roots of *B. gymnorrhiza* under high salinity or hormone treatments. In total, 129 statistically confident genes were grouped into four clusters depending on their expressed sequence tag (EST) frequency and each group has a specific pattern of transcript profiling under high salinity.

Unique gene collections obtained from the assembly of those ESTs were later used in microarray experiments to obtain transcript profiles in leaves and roots of salt-stressed *B. gymonorrhiza* (Miyama and Hanagata 2007). Totally 228 genes displayed transcript levels fivefold higher than controls, while 60 genes were down-regulated to one-fifth of control levels. Among these remarkably differentially expressed genes, only 32.5 % up-regulated and 3.3 % down-regulated genes were co-regulated in upper and lower leaves, as well as in roots (Miyama and Hanagata 2007).

Basyuni et al. (2009) studied the molecular mechanisms of salinity tolerance in the halophytic *K. candel* and *B. gymnorrhiza* roots. mRNA level of multifunctional terpenoid synthase *KcMS* was increased with salt concentration in both roots and leaves of *K. candel*. Similarly, salt stress increased the mRNA levels of *BgLUS* lupeol synthase and *BgbAS* β-amyrin synthase in the root of *B. gymnorrhiza*. To isolate anti-salt stress genes from mangrove plants, a cDNA library of *R. stylosa* roots was constructed and screened for stress-related genes by PCR-based suppressive subtractive hybridization (SSH). Basyuni et al. (2011) isolated and sequenced 240 up-regulated ESTs from the SSH library. Significantly increased expression level of 13 genes was found to contribute to the salt tolerance of this plant. Tada and Kashimura (2009) reported that fructose-1,6-bisphosphate (FBP) aldolase and osmotin were related to salt tolerance in *B. gymnorrhiza* roots. Zhu et al. (2012) reported that protein folding and degradation-related proteins and cell organization-related proteins were up-regulated and played important roles in salt tolerance of *B. gymnorrhiza* under severe salt stress. Different concentrations of NaCl treatments revealed differential salt stress mechanisms in this species. Salt-tolerant plants could change their protein expression patterns rapidly to adapt to the saline environment under optimum growth conditions (Pang et al. 2010). Salt stress results in the formation of cytotoxic ROS, which severely disrupt normal metabolism through oxidative damage to lipids, proteins and nucleic acids (Parida and Das 2005). Tolerant plants could overcome oxidative stress, by inducing various defense enzymes and antioxidants (Smirnoff 1995).

Heavy metal exposure

Mangrove roots are also continuously flooded with salty tides of potentially toxic compounds that come from human activities in coastal areas and heavy metal pollutants released into the marine system. Heavy metals in marine water such as copper (Cu), zinc (Zn), lead (Pb), cadmium (Cd), chromium(Cr), iron (Fe), nickel (Ni), manganese (Mn), sulphide (S) and many more trace elements have been reported (Ponnamperuma 1984; Bazzi 2014). Unfortunately, the mechanisms involved in heavy metal tolerance by mangrove plants are poorly understood. Mangrove plants commonly induce changes in the sediment chemistry (e.g., due to O_2 release by roots) that can prevent a potentially deleterious metal uptake and tend to show a low transfer of metals from below-ground to above-ground tissues (Lacerda 1998). Absorption, accumulation and dynamics of seven heavy metal elements were studied in mature *R. stylosa* mangroves (Wen-jiao et al. 1997). In *A. marina,* the root epidermis has been found to form a major barrier to Pb (MacFarlane and Burchett 2000). Machado et al. (2002) identified the trace metals (Zn, Pb, Cu, Ni, and Mn) in *Laguncularia racemosa* (L.) Gaertn with low potential of remobilization and biotic uptake. Heavy metal concentrations in mangrove species tissues are associated with the concentration in sediments (Machado et al. 2002).

Cheng et al. (2010) reported that lignification thickening within the exodermis could directly prevent excessive levels of metals entering the roots. Keshavarz et al. (2012) revealed that the Cd and V were negligible in sediments surrounding roots zones of *A. marina* and *R. mucronata*, whereas Pd concentrations were higher compared to leaves and roots. Cheng et al. (2014) revealed that the three rhizophoraceous species (*B. gymnorrhiza* (L.) Poir, *K. obovata* Sheue, Liu and Yong, and *R. stylosa* (Griff) consistently exhibited higher metal (Pb, Zn and Cu) tolerances than the three pioneer species [*Aegiceras corniculatum* (Linn.) Blanco, *Acanthus ilicifolius* L. and *A. marina* (Forsk)]. Also, metal-tolerant species develop a thick exodermis with high lignification and suberization and this lignified exodermis delays the metal entry into the roots (Cheng et al. 2014). Silica (Si) is another heavy component that present in marine water, which plays a major role in improving plant resistance towards abiotic and biotic stresses. Sahebi et al. (2014) reported that the Si was mainly observed in the epidermal roots' cell walls of mangrove plants compared to other parts. The study showed that the candidate gene of *serine-rich protein* expressed in Si-stressed *R. apiculata*, using the suppression subtractive hybridization technique (Sahebi et al. 2014).

Ecological importance of mangrove roots

The ecological benefits provided by mangroves roots are generally underestimated. Mangroves provide protection against floods and hurricanes, reduction of shoreline and riverbank erosion, and maintenance of biodiversity (Fig. 5). Moreover, a number of food products are harvested directly within the mangrove system through hunting, gathering, and fishing by native populations.

Mitigation of calamities

Mangroves protect coastal communities from cyclones and storms. *Rhizophora* has been documented to act as a protective force against natural calamities (McCoy et al. 1996, Mendez-Alonzo et al. 2015). The ability of mangroves in flood control is due to the root system, which has a large spread and also the ability to promote sedimentation. Mangroves and *Casuarina* plantations reduced tsunami-induced waves and have been shown to protect shorelines against damage (Danielsen et al. 2005). The mitigating effect of mangroves depends on two physical processes of tsunami: (1) wave attack, and (2) towing flow. The protective role of mangroves depends on vegetation characteristics such as, density, height, species composition, density of forest, diameter of mangrove roots and trunks, and elevation of habitats, as well as status of ecological degradation of the forests. Harada et al. (2002) has proved that mangroves form “live seawalls”, and are very cost effective as compared to concrete seawalls and other structures for the protection of coastal erosion. Protection and restoration of mangroves, coastal forests and sand dunes would mitigate the impact of not only tsunamis, but also storms and sea level rise (Kathiresan 2012).

Maintain biodiversity

Mangrove roots serve as a nursery habitat for juvenile fish and protect them from large fish and birds in shallow water environments (Fig. 5). Furthermore, the survival of juvenile fish is promoted by the long residence time of water amongst the mangroves, which is facilitated by the mangrove roots (Gilber and Janssen 1998). Fish species richness has been reported to be as high as almost 200 species in mangrove-dominated estuaries in Australia and India (Robertson and Blaber 1992). Highly valued food and game fish that have a close association with mangroves in the Indo-West Pacific include mullets (*Liza*, *Mugil*), groupers (*Epinephelus*), snappers (*Lutjanus*), tarpons (*Megalops*), sea-perch (*Lates*, *Centropomus*) and catfish (e.g., *Arius*, *Tachysurus*) (Macintosh 1982). In addition to teleosts, a great number of shark and ray species can also be found in mangrove environments (Matthes and Kapetsky 1988). Fisheries production is believed to constitute the major value of marketed products from an unexploited mangrove forest (Hamilton and Snedaker 1984). Mangrove areas are also used as nurseries or breeding grounds for several commercially important species of marine fauna (Saenger 2002). The limited availability of food and the

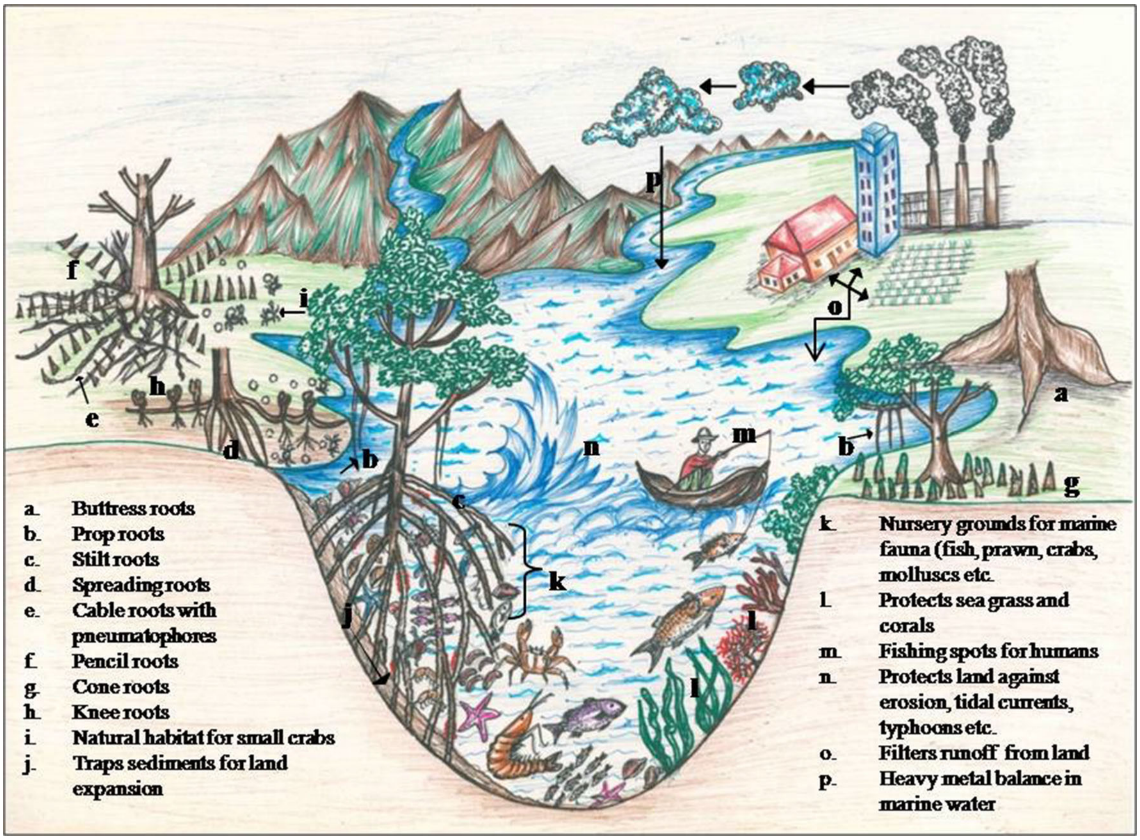

Fig. 5 Schematic representation of root adaptations in mangroves and their ecological importance

smaller habitat size associated with mangrove removal will result in weaker and more exposed fish populations vulnerable to increased rates of predation (Gilber and Janssen 1998). Many species of palaemonid shrimps are also associated with mangroves, including the commercially important giant freshwater shrimp, *Macrobrachium rosenbergii* (Macnae 1974; Matthes and Kapetsky 1988; Singh et al. 1994). The mangrove crab fauna is of major ecological and economic importance (Macnae 1974; Macintosh 1982; Matthes and Kapetsky 1988), including the high-priced mangrove mud crab, *Scylla serrata*. Mangrove-associated fauna are not restricted to the waters and substrate surrounding mangrove roots, as the roots themselves support a thriving and diverse community of molluscs, arthropods and other animals (Ng and Sivasothi 1999). Mangrove roots regulate water quality and this service prevents the deterioration of sea grass or coral reef habitats. Moreover, mangrove-associated mudflats provide feeding grounds not only for resident species, but also for migratory birds that rely on coastal mudflats during their annual migrations to warmer climates.

Furthermore, mangrove rhizosphere is also an excellent habitat for bacteria from estuarine sediments. Alongi (2005) identified sulfate-reducing genera (*Desulfovibrio*, *Desulfotomaculu, Desulfosarcina and Desulfococcu*), and other bacterial types such as methanogens, iron- and manganese-reducers, denitrifiers, nitrogen fixers (e.g., *Azotobacter*, *Rhizobium*) as the major decomposers in the mangrove soils. Gomes et al. (2010) reported that the *R. mangle* rhizosphere samples contained the most distinct composition of the major taxonomic groups included, significantly higher amount of *Acidobacteria*, *Actinobacteria*, *Verrucromicrobia*, *Burkholderiales*, *Caulobacterales* and *Rhizobiales* and significantly lower amount of *Chloroflexi*, *Firmicutes* and *Desulfobacterales*. The microbes in the mangrove habitats are known to decompose mangrove litter (Kathiresan 2012). Nitrogen-fixing bacteria play a major role in re-mineralization processes in mangrove ecosystems which interact with mangrove roots making nitrogen available for plants. Nypa palm roots possessed active nitrogen-fixing endophytic bacteria called *Burkholderia vietnamiensis* (Tang et al. 2010). Understanding the nitrogen-fixing bacteria–mangrove model system is essential to study the interaction of molecular mechanisms involved. Soares Junior et al. (2013) isolated different taxonomical groups of cellulolytic bacteria from mangrove sediments (*Alphaproteobacteria*, *Gammaproteobacteria*, *Actinobacteria*, *Firmicutes* and *Bacteroidetes*) and reported that mangrove soils harbor cellulolytic organisms with distinctive characteristics that can be further explored for cellulose degradation for distinct purposes.

Carbon accumulation

Mangrove root biomass is another important factor in forest ecosystems, which is studied in the yield of wood as a function of age, stand density, and as an indicator of atmospheric, soil pollution input and forest health (Komiyama et al. 2002). Mangrove forests develop massive root biomass to stand upright in the muddy and unstable substrates (Komiyama 2014). The root production may contribute towards half or total standing biomass in mangroves (Briggs 1977). Since they grow in saturated, muddy, low oxygen soils, more amount of carbon is stored in roots, resists decay and can become long-term sinks as mangrove peat (Middleton and McKee 2001). Hence, mangrove roots provide other significant ecological services such as carbon storage. Extensive studies have been conducted on the considerable biomass stored in mangroves, which interestingly have a disproportionately high level of biomass stored in roots compared to other forest systems (Komiyama et al. 2008). The large allocation of biomass to the roots can be understood given the muddy and unstable substrate to which mangroves have to be anchored. Sizeable investments must be made to the roots to ensure that mangroves can stand upright in soft mud (Komiyama 2014). This alone, however, cannot explain the surprising root to shoot biomass allocation, which may be better understood through the nature of decomposition in mangrove roots. Though root decomposition is dependent on a variety of factors (Poungparn et al. 2009), fine root decomposition in mangroves appears to be a slow process; a study of fine root necro-mass in eastern Thailand found an astonishingly high dead to total fine root mass, as much as 98.5 % (Chalermchatwilai et al. 2011). Mangrove peat may be predominantly made up of fine roots (Ono et al. 2015), suggesting that mangroves may play an unappreciated role in carbon sequestration. Ecosystem features of mangroves are not independent. For example, animal richness and density is positively correlated with root biomass (Wada et al. 1987). Most of the substrata in the tropics except under deltaic environments consist of mangrove peat, which mainly derives from mangrove roots. They accumulate sediments via their complex aerial and submerged root systems and play a major role in land expansion (Fig. 5).

Conclusion

The anatomical and morphological characteristics of living plants are commonly correlated with the particular combination of environmental conditions under which individual plants are established and grown (Arens 1997). Mangroves tolerate high salinity by rejecting potentially harmful salts. Some species of mangroves actively excrete those salts 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. Adaptability of mangroves to adverse conditions makes them ideal ecological models to study adaptation of mangroves to different abiotic stresses. Mangroves also provide a reservoir for some of the best known novel genes and proteins, involved in tolerance to salinity stress and water logging conditions that are likely to be applicable in other crop plants.

The rhizosphere of mangrove trees extend into the intertidal and subtidal zones where they turn into a rare feature: hard substrata in a soft sediment environment. As such, mangrove roots have become a good source for terrestrial as well as marine plants, algae, invertebrates and vertebrates. Also, their prolific habitats support coastal fisheries for prawns and fishes (Manson et al. 2005). Apart from the above uses, they are also essential to humans for a variety of reasons, including aquaculture, agriculture, forestry, protection against shoreline erosion, as a source of fire-wood and building materials, and other local subsistence uses (Walters et al. 2008). Mangrove sediments also have a high capacity for absorbing and holding heavy metals thereby preventing the spread of metal pollution in coastal areas. Globally, mangrove forests are being reduced at an alarming rate. They get affected either by direct impacts such as cutting and pollution, or by indirect impacts such as changes in local freshwater management (Dahdouh-Guebas et al. 2005), and are often regarded as unpleasant environments with little intrinsic value. In 26 developing countries, about 90 % of mangroves are critically endangered and in extant condition (Zhila et al. 2014). Therefore, understanding and appreciating the importance of mangrove to the coastal ecosystem is crucial to the wise use and stewardship of this unique plant community.

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