

## Review

## Genetic and molecular mechanisms underlying mangrove adaptations to intertidal environments

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**Mangroves are halophytic plants belonging to diverse angiosperm families that are adapted to highly stressful intertidal zones between land and sea. They are special, unique, and one of the most productive ecosystems that play enormous ecological roles and provide a large number of benefits to the coastal communities. To thrive under highly stressful conditions, mangroves have innovated several key morphological, anatomical, and physio-biochemical adaptations. The evolution of the unique adaptive modifications might have resulted from a host of genetic and molecular changes and to date we know little about the nature of these genetic and molecular changes. Although slow, new information has accumulated over the last few decades on the genetic and molecular regulation of the mangrove adaptations, a comprehensive review on it is not yet available. This review provides up-to-date consolidated information on the genetic, epigenetic, and molecular regulation of mangrove adaptive traits.**

## INTRODUCTION

Mangroves are dominant vegetation in saline wetlands which serve as an ideal system to unveil the genetic background of stress tolerance (Duke et al., 1998; Duke, 1992). The mangroves have evolved as a convergent group of plants comprising around 73 species and hybrids derived from 18 plant families (Spalding et al., 2010). During the course of evolution from land plants, mangroves acquired unique adaptive features such as vivipary, salt secretion, aerating roots, ultrafiltration, ion sequestration, osmolyte accumulation, and thick waxy leaves to cope up with rapidly changing intertidal ecosystem they harbor (Duke, 2017; Friess et al., 2019). Intertidal zones found in river deltas, estuaries, coastal lagoons, and open coastlines are endowed with dynamic conditions such as fluctuating tidal flow, anoxic environments, and high salinity which make them unique niches for mangroves where other kind of vegetation fails to flourish (Friess et al., 2019; Spalding et al., 2010). Even though mangroves naturally propagate in hypersaline conditions, they are facultative in nature and can grow equally well in fresh and saline waters which emphasize the tightly regulated gene expression patterns literally drive adaptive characteristics by sensing the surrounding salinity (Krauss and Ball, 2013; Parida and Jha, 2010). There is a growing debate on the halophytic categorization of mangroves and are sometimes considered as obligate halophytes (Clough, 1984; Downton, 1982; Wang et al., 2011b). Nevertheless, even among mangroves, the tolerance level for salinity and adaptive characteristics vary from species to species (Krauss and Ball, 2013). Being the prominent flora of intertidal regions, mangroves offer enormous ecological and economic services such as carbon sequestration, aquaculture, shrimp cultivation, fisheries, timber production, and coastal protection (Maharana, 2021; Numbere, 2018). High carbon storage due to the carbon sequestration mostly in organic rich sediments has placed mangroves among the most important blue carbon ecosystems of the tropics (Donato et al., 2011; Macreadie et al., 2019). The exhaustive root system of mangroves which anchor deep into the sediments not only brings stability during high tides and storms but also reduces coastal erosion and increases coastal resilience during the times of natural disasters. Mangroves are biodiversity-rich ecosystems as they provide home to a variety of flora and fauna including threatened species (Parida and Jha, 2010).

Notwithstanding the extensive roles mangroves play as an ecologically relevant ecosystem, they have been subjected to substantial pollution as well as exploitation of reserves for aquaculture, agriculture, and urban development (Friess et al., 2019; Ouyang and Guo, 2016). Pollutants especially plastics and their more toxic microplastic counterparts suffocate mangrove vegetation by enhancing anoxia beyond limits (Deng et al., 2021; Li et al., 2020b; Meera et al., 2021; van Bijsterveldt et al., 2021). Exploiting mangrove habitats by

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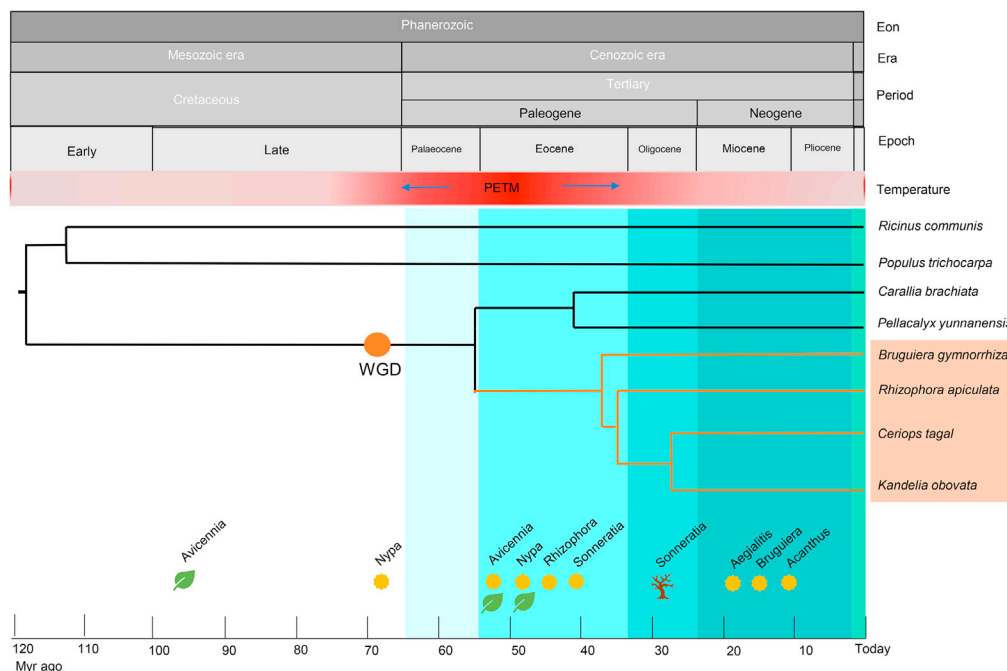
largely converting them into aquaculture ponds for fish, shellfish, and shrimp farming could reduce mangrove areas, alter the hydrology, and eventually cause eutrophication (Friess et al., 2019; Hong et al., 2018). The other deteriorative effects of human activities such as logging and developments near mangrove habitats impart long-term consequences by acting as a barrier of gene flow resulting in low genetic diversity (Azman et al., 2020; Meng et al., 2016). Microsatellite studies on *Rhizophora apiculata* serve as a typical example of a similar situation which revealed low genetic diversity among the populations and reduction in population size due to habitat fragmentation (Azman et al., 2020). Moreover, climate change, rising sea level, and fluctuating tidal cycles have influenced the distribution and growth of mangroves (Friess et al., 2019; Parida et al., 2014; Rippel et al., 2021; Servino et al., 2018). Global warming has also led to an unexpected distribution pattern which drives mangroves to expand far off the habitat territories. They tend to progress inland due to rise in sea level with the gradually increasing global temperature (Donato et al., 2011). The deleterious anthropogenic activities ultimately result in the loss of mangroves. In total, 50% of mangrove flourishing zones have already been lost with clear-cut evidence of species extinction (Feller et al., 2010). Out of 73 true mangrove species and hybrids reported so far, nearly 3% of each are endangered and critically endangered whereas 6% and 7% of them are in vulnerable and near-threatened categories, respectively (IUCN, 2021; Kumar et al., 2021; Spalding et al., 2010). The scenario highlights the necessity of global initiatives for the proper conservation of the mangrove ecosystem which may otherwise disappear within the next 100 years (Duke et al., 2007). To devise better strategies for conservation, understanding various aspects of mangrove adaptations should not be overlooked. The salt tolerance mechanisms of mangroves are reviewed to a great extent by Parida and Jha (2010) stating the lack of sufficient molecular information to unravel the genetic basis of adaptations. The current review provides a comprehensive overview of the genes that regulate mangrove adaptations to intertidal environments. For an easy absorbance of the review content, the whole text is broadly sectioned as (i) the adaptive evolution of mangroves, (ii) the genetic basis of mangrove adaptations, (iii) the epigenetic mechanisms complementing the genomic regulation of mangrove adaptations, (iv) non-nuclear (chloroplast and mitochondrial) genes involved in mangrove adaptations, and (v) the ways to ensure species diversity and conservation using the genomic information of mangrove adaptations.

## EVOLUTION OF MANGROVES AND THEIR ADAPTATIONS TO INTERTIDAL ENVIRONMENTS

### Adaptive evolution

Mangroves are well distinguished as intertidal ecosystems harboring marine habitats but originated from terrestrial flora. Mangroves are supposed to exhibit multiple origins and the adaptive traits of mangrove lineages are inherited from the ancestral characteristics. For example, some of the structural peculiarities of mangroves such as vivipary and pneumatophores have co-adapted from the already evolved ancestral features such as terrestrial vivipary and aerial roots. The co-adaptation (exaptation) modified the ancestral structures for a different purpose and to suit mangrove environments (Sahu et al., 2016). The terrestrial ancestry is unique for diverse mangrove genera, but the evolutionary timescale significantly varies (Ricklefs et al., 2006; Shi et al., 2005; Srivastava and Binda, 1991). Uncertainties still exist regarding the precise period of origin, phylogenetic locale, and species distribution within mangrove families. The evolutionary time point where mangroves denoted the first appearance dates back to the late Cretaceous period of the Mesozoic era that is about 100–60 million years (Myrs) ago (Srivastava and Prasad, 2019). The recovery of leaf and pollen fossils of *Avicennia* (97 Myrs ago) and *Nypa* (69 Myrs ago), respectively, from the late Cretaceous period are the oldest fossil records of modern mangrove genera (Friess et al., 2019; Srivastava and Prasad, 2019). But diversification among terrestrial plants widely occurred during the succeeding Paleocene–Eocene Thermal Maximum (PETM), a period of global rise in temperature that lasted several thousand years from the late Paleocene to early Eocene epochs of the Paleogene period in the modern Cenozoic era. At PETM, polyploidy or the event of whole genome duplication (WGD) complemented speciation in mangroves and the formation of adaptive features to withstand intertidal environments (Guo et al., 2017; Kyriakidou et al., 2018). The major evolutionary events in the emergence of mangroves are depicted in Figure 1.

The Rhizophoraceae is the major mangrove family that emerged during PETM around 50 Myrs ago. The sequence homology (collinear blocks) identified by phylogenetic analysis of Rhizophoraceae genomes suggest two WGD events in the past (Guo et al., 2017; Xu et al., 2017). The second and more recent WGD that occurred ~70 Myrs ago might have led to adaptive evolution of Rhizophoraceae mangroves to the intertidal environments. This event is known to have led to the divergence of mangroves from its



**Figure 1. Major evolutionary events in the evolution of mangroves from terrestrial plants based on genomic studies and fossil records**

Whole genome duplication (~70 Myrs ago) and the subsequent PETM conditions (temperature decreases from dark to light) aided in the emergence of mangroves from the terrestrial flora. PETM is also responsible for the first occurrence of most of the mangrove clades during the Paleocene-Eocene epoch. Diversification of Rhizophoraceae into the mangrove and non-mangrove species represented by black and yellow lines, respectively, is depicted in the phylogenetic tree (Xu et al., 2017). Different mangrove genera are positioned within the geological timescale based on the relative dating of respective leaf (represented with green leaf), wood (represented with tree), and pollen (represented with stars) fossil records (Srivastava and Prasad, 2019).

terrestrial Rhizophoraceae ancestor family (Guo et al., 2017). Similarly, phylogenetic analysis on *Aegiceras corniculatum* and *Kandelia obovata* genome indicated the WGD event as a turning point in adaptive evolution and mangrove emergence from Myrsinaceae and Rhizophoraceae, respectively (Feng et al., 2021; Hu et al., 2020). WGD is often followed by fractionation by which most of the gene duplicates created are lost. Interestingly, duplicated genes retained after fractionation may acquire novel functions or contribute to stress tolerance mechanisms, thereby giving a survival advantage to the plants (Panchy et al., 2016). The genes coding for H<sup>+</sup>ATPase and 14-3-3 regulatory proteins are the gene duplicates in *A. corniculatum* that are responsible for development of adaptation to intertidal zones (Feng et al., 2021). The retained genes are mostly involved in protein phosphorylation, ion transport, transcriptional regulation, energy metabolism, and signal transduction pathways (Feng et al., 2020, 2021).

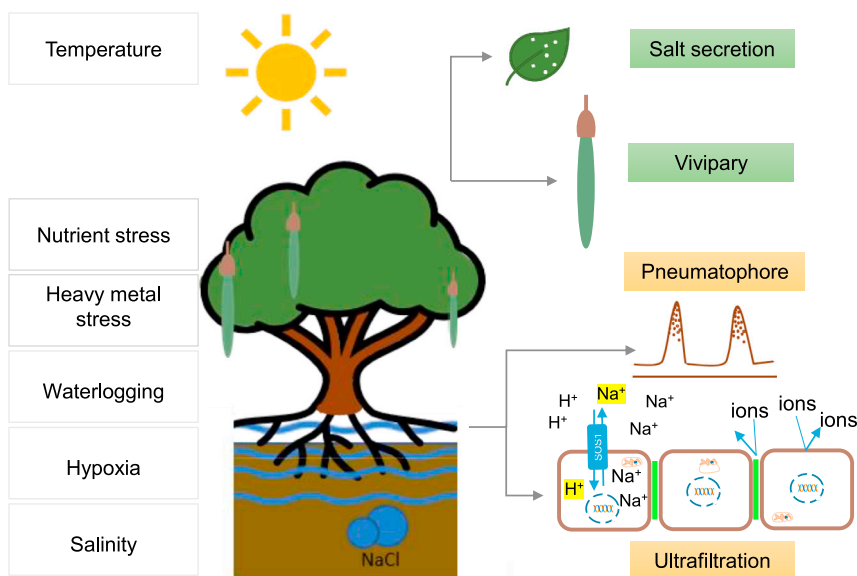
Another perspective of mangrove adaptations to environmental constraints is driven by convergent evolution (Ellison et al., 1999; Tomlinson, 2016). A worth reading review exclusively on genomic convergence of extreme adaptations was published recently by Xu et al. (2020). A brief overview of convergence is given below with latest updates after Xu et al. (2020). The convergent evolution reduces genome size by optimizing the number of genes specific for adaptive pathways as exemplified by pathogen resistant gene families (He et al., 2020; Losos, 2011). Genetic similarity between different mangrove species such as *Avicennia marina* and *A. corniculatum* also shows convergent evolution of mangroves (Feng et al., 2021; Xu et al., 2020). Whole genome sequencing of mangroves revealed two noteworthy genomic convergences viz. unusual substitution in amino acid composition and changes in amino acid usage that may be either over usage (glycine, proline, arginine, and alanine) or under usage (asparagine, lysine, tyrosine, isoleucine, and phenylalanine) (Xu et al., 2020). In mangroves, the amino acid usage preferences are determined based on its hydrophobic nature. Under high saline conditions, amino acids containing larger hydrophobic residues may disrupt protein folding and hence their usage is limited (Paul et al., 2008). Amino acid

substitutions also aid mangrove survival in nutrient-deficient environments by reducing energy cost (He et al., 2020). Adding to this, a comparative analysis between the Rhizophoraceae mangroves (*R. apiculata*, *K. obovata*, *Ceriops tagal*, *Bruguiera gymnorrhiza*, *Rhizophora stylosa*, *Rhizophora mangle*, and *Rhizophora mucronata*) and some non-mangrove plants (*Carallia brachiata* and *Pellacalyx yunnanensis*) showed a pattern of amino acid substitution in mangrove SUMO-activating enzyme-2 (SAE-2) (Xu et al., 2017). SAE-2 uses ATP to activate SUMO (Small Ubiquitin-like Modifier) protein which regulates a specific post translational modification termed as SUMOylation. SAE-2 has multiple roles in cell cycle, protein stability, apoptosis, transcriptional control, cellular transport, and stress response (Hay, 2005). The link between the evolutionary convergence and mangrove adaptation is proven by analyzing convergence at conservative sites (CCS) which suggested 73 convergent genes with amino acid substitutions from *Avicennia*, Rhizophoraceae, and *Sonneratia* mangrove clades (He et al., 2020). The more prominent genes among them which have more than 3 convergent sites and proven roles in salinity tolerance are *BEACH-domain homolog A1 (BCHA1)*, *protein phosphatase 2C (PP2C)*, and peroxidase genes (He et al., 2020). Along with this, gene expression alterations, changes in gene copy number, and GC content can also be associated with mangrove adaptation to extreme environments (Xu et al., 2020). Gene duplication enhances gene expression and improves overall stress tolerance (Van de Peer et al., 2021). On the other hand, GC-rich DNA is often found to be advantageous to cells undergoing severe desiccation and freezing (Šmarda et al., 2014). The evolutionary analysis of mangrove adaptations conclude that most of the mangrove species have evolved during PETM and the evolutionary events such as WGD and genome convergence drove parallel in allocating the individual adaptive features. PETM might have helped in providing favorable ecological conditions whereas WGD and genome convergence might have contributed to the desirable genetic constitution for mangrove speciation and formation of adaptive structures. The evolution of the unique adaptive characters in mangroves has helped them thrive in the highly stressful intertidal zones of the world.

### Adaptive traits

Apart from the nature of evolutionary events, the adaptations to saline and anaerobic conditions in the habitats led to convergent evolution of mangrove species from different plant families (Duke, 2017). This in turn enriched mangrove flora with diverse members from 18 different families of angiosperms spanning 28 genera namely *Acanthus*, *Acrostichum*, *Aegialitis*, *Aegiceras*, *Aglaia*, *Avicennia*, *Bruguiera*, *Camptostemon*, *Ceriops*, *Conocarpus*, *Cynometra*, *Dolichandrone*, *Diospyros*, *Excoecaria*, *Heritiera*, *Kandelia*, *Laguncularia*, *Lumnitzera*, *Mora*, *Nypa*, *Osbornia*, *Pelliciera*, *Pemphis*, *Rhizophora*, *Scyphiphora*, *Sonneratia*, *Tabebuia*, and *Xylocarpus* (Duke, 2017; Spalding et al., 2010). Within these genera, species diversity comprising a total of 73 true mangrove species and hybrids has been identified as mentioned in the introductory part. The distinctive adaptive features of individual mangrove species add to the ecological success in addition to the species diversity they own. Regardless of the molecular basis, most of the adaptive features are more or less comprehended earlier (Parida and Jha, 2010). Here, we discuss some of the exceptional features mangroves possess.

Among the various adaptive features evolved in mangroves, salt glands, thickening of leaves, viviparous seeds, and waxy epidermis are the important morphological and anatomical adaptations (Liang et al., 2008). Anatomical structures mostly resist salt uptake whereas salt glands secrete excess salt (Parida and Jha, 2010). Salt glands in leaves are characteristic to many mangrove genera including *Aegiceras*, *Avicennia*, *Acanthus*, and *Aegialitis*. Salt secretion via salt glands and the underlying molecular mechanism has been well described in *A. marina* (Natarajan et al., 2021). Analogous structures of salt glands resembling tiny bumps are present in *Laguncularia* and *Conocarpus* (Tomlinson, 2016). Water imbibition and subsequent thickening of leaves to induce leaf succulence during salinity stress is an adaptive feature in *Laguncularia racemosa* (Sobrado, 2005; Suárez and Sobrado, 2000). Thick leaves are also seen in *R. mucronata* and *B. gymnorrhiza* (Lechthaler et al., 2016). The epidermal coating with wax maintains water loss by lowered transpiration rates and thus dilutes absorbed salt (Werner and Stelzer, 1990). The other adaptive features include deposition of salt via senescent leaves, vacuoles for trapping excess sodium and chloride ions, root elongation, and cell wall suberization (Peterson, 1988; Stelzer et al., 1988; Taura et al., 1988; Werner and Stelzer, 1990; Zheng et al., 1999). Morphological adaptations of mangroves to survive in saline conditions mainly include viviparous propagules. Vivipary permits mangrove to exclude salinity at germination phase and is a key morphological peculiarity in *Bruguiera*, *Kandelia*, and *Rhizophora* (Tomlinson, 2016). Some of the notable physio-biochemical and anatomical adaptations that some mangrove species share include osmolyte accumulation, antioxidative response, salt exclusion by roots, salt sequestration,



**Figure 2. Environmental stresses dominating intertidal zones and unique mangrove adaptive traits to these conditions**

The exposure of mangroves to harsh environmental stresses such as temperature shifts (heat stress and cold stress), heavy metal toxicity, difficulty in uptaking nutrients, waterlogging, hypoxia, and salinity (shown on left side) share and overlap various signaling pathways ultimately leading to the emergence of adaptive features in mangroves (shown on right side). Salt glands in leaves excrete excess salt whereas root ultrafiltration resists its intake. Vivipary helps propagules to escape salinity during germination while attached to the parent plant. Aerenchyma of pneumatophores ensures oxygen supply under hypoxia and water logging.

pneumatophores, and specialized root structures (Liang et al., 2008; Takemura et al., 2000). Knee roots, buttress roots, prop roots, stilt roots, and cable roots provide support, transport of water and nutrients in addition to supplying oxygen to survive anoxic environment (Kitaya et al., 2002; Srikanth et al., 2016). A recent study on natural root graft formation in the *A. marina* population discusses benefits of resource sharing through these root networks which gives advantage to grow better under stressful conditions (Vovides et al., 2021). Studies on genes governing the aforementioned adaptive responses are of great importance and are discussed below in separate sections for individual adaptive features. An overview of prominent mangrove adaptive features and environmental stress factors characteristic of intertidal zones are graphically represented in Figure 2.

## GENETIC AND MOLECULAR BASIS OF MANGROVE ADAPTATIONS TO INTERTIDAL ENVIRONMENTS

Over the past decade, the advances in sequencing technologies have provided genomic information regarding the mangrove stress tolerance mechanisms. To characterize genes, including stress responsive ones of non-model organisms like mangroves, DNA or RNA sequence analysis is performed followed by *de novo* assembly (Margulies et al., 2005). If the genome or transcriptome of an organism is already available, read alignment to the reference sequence pool can be done. Individual gene characterization is also possible rather than going for whole genome sequencing. All the subsequent biological characteristics are retrieved from this sequence information. For example, the abundance of a particular transcript read count directly represents the gene expression level. In addition, the functional elements, which are the protein-coding regions of a genome, are identified from the sequence information. Variations of gene expression patterns between populations can also be analyzed (Wolf, 2013). After a thorough evaluation of the reference papers, *de novo*/reference grade and comparative genome/transcriptome/proteome analyses, differential/relative gene expression studies, analyses of expressed sequence tags, suppression subtractive hybridization, molecular cloning/overexpression/transgenic approaches, agrobacterium functional screening, genomic/multi-gene phylogenetic analyses, genome evolutionary convergence/divergence analyses, and quantitative phosphoproteomics are summarized as different practical approaches followed for

the identification and characterization of mangrove stress-responsive genes. Although most of the genes involved in a particular adaptive response are similar, the tissue/species-specific gene expression levels significantly vary. But the differences in mode of analysis make it difficult to compare and analyze these variations in stress-responsive gene expression levels. Therefore, irrespective of the mode of analysis, we attempt to connect a sufficient number of well characterized genes involved in various adaptive responses such as cellular homeostasis, ultrafiltration mechanisms of root, survival in anoxic environment, specialized leaf patterns, vivipary, and the hormonal regulations. Studies show that stressful intertidal environments due to stress factors such as temperature shift, heavy metal stress, nutrient stress, fluctuating water level, hypoxia, and salinity preferentially retained specific stress-responsive genes which span over the aforesaid adaptive features and might have aided in the exceptional adaptations in mangrove taxa (Feng et al., 2020; He et al., 2020; Lyu et al., 2018; Xu et al., 2020). Even though intertidal zones where mangroves flourish are exposed to a range of fluctuating conditions, the primary stress among them is salinity (Ball, 1988). Moreover some of the unique adaptive features such as ultrafiltration, vivipary, salt glands, and thick waxy leaves have specifically evolved to fight off salinity stress. Adding to this, the salt tolerance mechanisms of mangroves have been the focus of several studies compared to other abiotic stresses (Barnuevo and Asaeda, 2018). In the following sections, we have comprehensively discussed the genetic background of prominent adaptive features in response to various abiotic stresses with an emphasis on salinity.

### Cellular homeostasis for optimal functioning of mangrove plant cell

Abiotic stresses trigger mangrove-specific pathways involved in redox and ionic homeostasis as well as osmotic balance to attain overall cellular homeostasis. Although these networks possess shared features and the pathway elements cross talk, the three aspects are discussed under separate sections to highlight the unique adaptive characteristics.

#### Redox homeostasis

The physiological steadiness is equally maintained by redox homeostasis indistinguishable from the well-accepted concept of ion homeostasis (Ursini et al., 2016). Salt stress primarily accumulates ions and inflicts osmotic and ionic stress which induces genes associated with reactive oxygen scavenging, osmolyte biosynthesis, molecular chaperones, transporters, and signaling components (Parida and Jha, 2010). One of the first cellular changes under any kind of stress is toxic accumulation of reactive oxygen species (ROS) such as peroxides, superoxide, hydroxyl radical, singlet oxygen, and alpha-oxygen (Hayyan et al., 2016; Sharma et al., 2012). Superoxide dismutases (SOD) are enzymes which convert superoxide radicals ( $O_2^-$ ) to  $H_2O_2$ , minimizing cellular damage.  $H_2O_2$  thus produced is often utilized for secondary cell wall thickening in plants (Gómez Ros et al., 2006; Sharma et al., 2012). The cellular concentration of cytosolic Cu/Zn SOD (CSD) is reported to increase under salinity stress in *A. marina* (Prashanth et al., 2008). Root epidermis of *K. obovata* accumulated FeSOD and CSD under cadmium stress with a hindered metal ion transfer. On the other hand, *SaFeSOD* and *SaCSD1* of *Sonneratia alba* are highly expressed in leaf and fruit tissues against accumulating ROS (Wang et al., 2013a; Yang et al., 2016). The tissue-specific changes in expression patterns of SOD show that the gene is more expressed where the oxidative stress and ROS count are the highest. The buildup of SODs has a proven role in the induction of root exodermis lignification (Pan et al., 2020, 2021). From the literature, it is apparent that both SOD and its end product  $H_2O_2$  improve anatomical resistance for the external stress by secondary cell wall thickening in addition to preventing plant cell components from oxidative damage. But the said role of SOD and  $H_2O_2$  in anatomical adaptation of mangroves is not yet clearly studied. As mangroves primarily rely on expelling external stress, investigation of the probable connections of antioxidative pathway genes in inducing the anatomical barriers against stresses is required to better understand the anatomical/structural defense mechanisms.

Besides the role of genes encoding CSD in oxidative stress relief, the catalase and ferritin genes of *A. marina* are found to be induced by external stimuli such as light, mannitol,  $H_2O_2$ , iron, and salt (Jithesh et al., 2006). SOD and catalase maintain ROS balance via enzymatic mechanism whereas ferritin contributes to the same by metal ion sequestration (Lobréaux et al., 1995). The genes encoding another ROS scavenging protein, glutathione S transferase (GST), responsible for GSH-dependent peroxidase activity is observed to be upregulated in *B. gymnorrhiza* and *R. mucronata* under stressed conditions (Kumar and Trivedi, 2018; Meera and Augustine, 2020; Wong et al., 2007). While SODs, GSTs, and catalases maintain cytosolic redox levels, stress-induced DNA damage is reversed by repair mechanisms in which genes such as *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 *Kandelia*

*candel* (Wang et al., 2016). The balancing of oxidative pressure and the repairing of oxidative damage work together until a stable cellular state is attained.

While discussing redox homeostasis, it is not possible to ignore redox signaling, a prime feature of ROS. Although ROS are produced as a consequence of environmental stresses, they can act as secondary messengers in subsequent tolerance mechanisms at lower concentrations. Among the well-studied ROS, H<sub>2</sub>O<sub>2</sub> can easily diffuse through plasma membranes via aquaporins (AQP), thereby establishing its role as prominent ROS signaling molecule in abscisic acid (ABA)-induced stomatal closure (Bienert et al., 2007; Sharma et al., 2012). In plants, redox signaling is already recognized as a major part of redox homeostasis (Foyer and Noctor, 2013). But the redox signaling in mangroves is not properly addressed till date. Again, the stressful environment of mangroves sufficiently supplies ROS to the cell interior of mangroves, where they undergo redox homeostasis and the remnants may take part in stress survival signaling pathways. This major gap invites future research on genomic regulation of signaling networks and the redox signaling molecules of mangroves so that the process of inland to intertidal adaptation could be better understood.

### Ion homeostasis

Maintenance of intracellular ion concentration with respect to the varying ionic strength of surrounding estuarine water is essential for mangrove survival. The constant absorbance of Na<sup>+</sup> and Cl<sup>-</sup> ions enhances osmotic pressure of the cell interior. The ions in excess are either compartmentalized through vacuoles or excreted to cell exterior (Golldeck and Dietz, 2001; Shabala, 2013). Transporter proteins regulate the movement of molecules into the cell and vice versa. Na<sup>+</sup>/H<sup>+</sup> antiporters transport excess sodium ions and rely on the electrochemical gradient created by the energy utilizing action of H<sup>+</sup>ATPases (Janicka-Russak and Kabala, 2015). Increased copy number of genes for H<sup>+</sup> ATPase and its regulatory protein "14-3-3" together with photosynthesis and oxidative phosphorylation pathway proteins suggest their role in cellular homeostasis (Feng et al., 2021). 14-3-3 proteins bind to phosphorylated form of H<sup>+</sup> ATPase and modify functional characteristics (Camoni et al., 2018). The energy production for the transport of ions by H<sup>+</sup> ATPase is facilitated by dihydrolipoamide dehydrogenase (DLDH) and lipoic acid synthase (LAS) which catalyze the synthesis of cofactors dihydrolipoic acid and lipoic acid, respectively. Genes for DLDH and LAS are upregulated in *B. gymnorrhiza* with respect to the external stress (Banzai et al., 2002). In the case of ion sequestration by vacuoles in maintaining cytosolic ion concentration, tonoplast H<sup>+</sup> ATPase comes first into action. Tonoplast H<sup>+</sup> ATPase and vacuolar acid phosphatase production increased along with vacuolar volume in *Bruguiera sexangula* under salt stress which indicates their importance in vacuolar transport of ions (Mimura et al., 2003). *A. marina* is also known for its peculiarity to adjust salinity by storing inorganic ions in vacuoles and organic solutes in non-vacuolar spaces, but the genes involved are not studied yet (Aspinwall et al., 2021). Similar to these findings, genes involved in Ca<sup>2+</sup> signaling and thus regulating both cell membrane and vacuolar ion transport are upregulated specifically in *B. gymnorrhiza* leaf tissues (Miyama and Tada, 2008). This leaves the possibility that membrane transporters in the leaf may be connected to adaptations like shedding of ion-filled senescent leaves. Apart from transporters, ferritin encoding genes also contribute to ion homeostasis similar to its role in ROS homeostasis. In *A. marina*, ferritin-encoding genes are found to be stress-dependent and efficiently take part in cellular rescue (Mehta et al., 2005). Generally, ROS concentration and transportation of ions are controlled in accordance with salinity stress in roots, stem, and leaves. Moreover, transporter proteins facilitate filtration mechanisms in roots of mangrove plants that we will be discussing later.

### Osmotic homeostasis

Environmental stresses especially drought and salinity affect water balance which increases intracellular salt concentration and osmolarity. Ion homeostasis alone cannot maintain a balanced osmotic and water potential across the plasma membrane. Compared to other land plants, mangroves experience a very high cellular osmolarity with respect to the surrounding salinity. Osmoregulation by means of synthesis and buildup of osmolytes or compatible solutes within the cytoplasm or vacuoles aid mangroves to combat increased osmotic pressure they encounter (Takemura et al., 2000). Pinitol, mannitol, betaine, proline, starch, polysaccharides, aspartic acid, and sterols are the major types of osmolytes produced in mangroves (Liang et al., 2008). In *A. marina*, *BADH* gene codes for glycine betaine, an osmolyte belonging to the group of betaines under high salt conditions (Hibino et al., 2001). Correlating with this, *AmT1*, *AmT2*, and *AmT3* betaine/proline transporter genes are also up-regulated in leaves of the given species (Hibino et al., 2001; Waditee et al., 2002). The co-expression of *BADH* and transporter genes emphasises the active involvement of osmolytes in the osmoregulation of various cellular compartments. Similarly, genes encoding

raffinose synthase and mannitol dehydrogenase are expressed in leaves of *Acanthus ebracteatus* which catalyze synthesis or modification of osmolytes (Nguyen et al., 2006). Biochemical characterization of proline, one of the efficient osmoprotectants, has been done long ago in *Xylocarpus*, *Avicennia*, and *Heritiera* (Popp et al., 1985). But now it is evident that the genes that take part in proline-mediated osmoprotection mainly include those from the proline biosynthetic pathway which have been reported to be positively regulated in *Acanthus ilicifolius* (Yang et al., 2015b). An important gene participant of the proline synthetic pathway encoding delta-1-pyrroline-5-carboxylate synthase (AcP5CS) enzyme is upregulated in leaf tissues of *A. corniculatum* indicating its prime role in osmoprotection (Fu et al., 2005). The transcriptome analysis of *C. tagal* root also revealed differential expression of proline biosynthetic genes where the active gene expression lasted from 3h to 12h of salt treatment (Xiao et al., 2016). The discussion highlights the fact that most of the genetic studies are related to proline whereas the genes encoding other osmolytes are least studied.

Balanced with compatible solutes, some secondary metabolites of biochemical pathways and free amino acids can also exhibit osmotic regulatory function. Phenylpropanoid biosynthetic pathway is one of the major metabolic routes producing secondary metabolites such as lignin, flavonoids, anthocyanins, and phenols under salinity stress to keep osmotic balance and ROS scavenging inside plant cells (Wang et al., 2016; Wen et al., 2020). It should also be noted that not all metabolic intermediates are connected to stress responses. Among the secondary metabolites such as dolichols and polyprenols, concentration of the latter is found to change in response to abiotic stress. Moreover, only dolichols (formed by the action of polyprenol reductase on polyprenols) are detected in mangrove roots while leaves contain both of the secondary metabolites. A genetic study predicted 3 mangrove-specific gene sequences of polyprenol reductase from the *K. obovata* genome (Basyuni et al., 2018a). Transcriptome analysis of *R. apiculata* under different salt treatments revealed that the gene *dihydroflavonol reductase B* (encoding bifunctional enzyme essential for the metabolism of flavonoid) is expressed at a high level and can be correlated with tannin content, a polyphenolic secondary metabolite (Xu et al., 2017). The increase in transcription of glyoxalase genes such as *lactoylglutathione lyase (GLYI)*, *hydroxyacylglutathione hydrolase (GLYII)*, and *D-lactate dehydratase (GLYIII)* in *R. mucronata* indicates their role in detoxification of methylglyoxal, a toxic metabolite formed in presence of salinity stress. In this, not the metabolite but the enzymes perform osmoregulatory function by removing excess methylglyoxal (Meera and Augustine, 2020). Similarly, metal ion detoxifying protein chitinase gene expression in *A. corniculatum* (*AcCHI I*) and *A. marina* (*AmCHI III*) is particularly upregulated in root tissues under cadmium stress (Wang et al., 2015a, 2015b). A metallothionein gene product from *K. candel* also has a high affinity toward metal ions and detoxifies excess ion (Zhang et al., 2012). Expression of osmotin, a member of the pathogenesis-related-5 protein family, is highly induced in leaves and slightly in the stem and roots of *K. obovata*. As a mechanism of osmoregulation, *KoOsmotin* gene product accumulates within the plant cell under cold stress (Fei et al., 2021). Free amino acids in mangrove osmoregulation are equally relevant to secondary metabolites. Genes related to biosynthetic as well as signaling pathways of amino acids and secondary metabolites (flavonoids and anthocyanins) upregulated during high salinity in *K. candel* include *Phenylalanine ammonia-lyase (PAL)*, *Trans-cinnamate 4-monooxygenase (C4H)*, *4-coumarate-CoA ligase 2 (4CL)*, *anthocyanidin reductase (ANR)*, *leucoanthocyanidin reductase (LAR)*, *glutamic acid decarboxylase (GAD)*, and *phosphatidylinositol 4-phosphate kinase (PIP4K)* (Wang et al., 2016). Transcriptome analysis of a semi-mangrove species *Millettia pinnata* also revealed differential expression of genes involved in synthesis of metabolites and proteins where most of the genes are upregulated in leaves than in roots. The genes commonly expressed in root and leaf tissues are more related to oxidation and amino acid metabolism. The differentially expressed genes (DEGs) specific for roots are involved in sulfur metabolism whereas those specific for leaves are connected to oxidative phosphorylation, and photosynthesis (Huang et al., 2012).

Finally, the maintenance of membrane potential is exceptionally important to achieve cellular osmotic homeostasis. The membrane permeability fundamentally decides the ionic flow across the cell membrane and the resultant membrane potential. Hence, the genes responsible for membrane structure formation are differentially expressed as part of osmotic regulation. At higher saline conditions, the genes for membrane lipids and triterpenoids are upregulated in mangroves such as *K. candel* and *B. gymnorrhiza* (Basyuni et al., 2012). When it is necessary to block material flow to and fro, sterol content of the membrane is enhanced, presence of which reduces membrane permeability (Guo et al., 2019). The stress-responsive *cytochrome P-450* genes, *KcCAS* (root) and *RaCAS* (leaf) from *K. candel* and *R. apiculata*, respectively, are thought to catalyze sterol biosynthesis (Basyuni et al., 2007). Terpenoids and triterpenoids are another

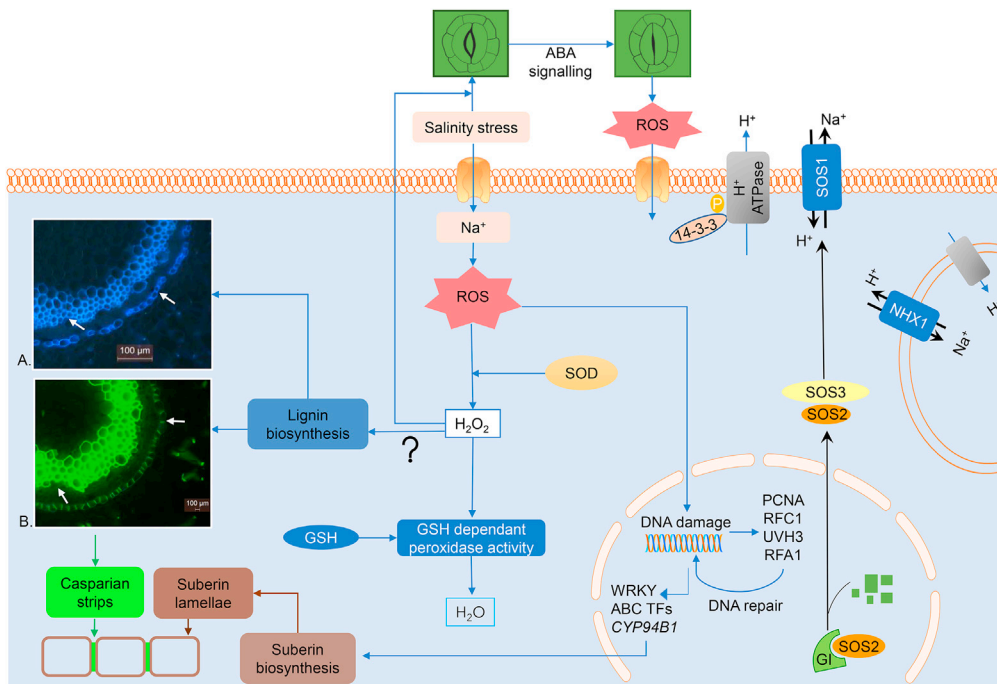


group of membrane lipids which have a role in maintaining membrane permeability (Basyuni et al., 2006; Oku et al., 2003). Terpenoid biosynthesis genes are upregulated on salt stress in *K. candel* and *B. gymnorrhiza*. The expression values show higher terpenoid mRNA levels in roots compared with leaves (Basyuni et al., 2009, 2012). The expression status of  $\beta$ -amyrin synthase (*BgbAS*) and lupeol synthase (*BgLUS*) involved in triterpenoid biosynthesis of *B. gymnorrhiza* is induced in root but decreased in leaves under saline conditions. Contrary to this, enhanced expression level of triterpenoid synthase gene (*KcMS*) is observed in both roots and leaves of *K. candel*. The acclimation of *K. candel* to salinity stress is more visible compared with that of *B. gymnorrhiza*. Despite the tissue-specific differences in gene expression, the triterpenoid contents returned to optimal level upon replanting the experimental plants in freshwater, hinting that they are crucial during the adaptive stage (Basyuni et al., 2012). Briefly, in osmotic homeostasis, compatible solutes, free amino acids, and secondary metabolites balance the osmoticum of cell interior whereas membrane lipids regulate the ionic inflow.

### Ultrafiltration to sieve out surplus salt

Mangroves may be salt excluders, secretors, or accumulators depending upon the mode of salt elimination mechanisms they follow (Parida and Jha, 2010). Salinity primarily affects roots and causes disruption in the effective uptake of water, nutrients, and solutes. Ultrafiltration at the membrane surface of root cells is deployed by salt excluder mangroves such as *Rhizophora*, *Bruguiera*, *Ceriops*, *Excoecaria*, and *Lumnitzera* to eliminate excess salt (Khan and Aziz, 2001; Scholander, 1968; Takemura et al., 2000). It prevents  $\text{Na}^+$  from entering the xylem sap by simply excluding those ions (Krishnamurthy et al., 2014). Non-salt secretor mangrove species exhibit higher salt filtration through roots than their counterparts with salt-secreting organs (Krishnamurthy et al., 2014). *A. corniculatum* is a mangrove species exhibiting salt secretion while *K. candel* lacks salt secretory structures such as salt glands or salt hairs (Reef and Lovelock, 2015). A significant part of the ultrafiltration mechanism is through membrane transporters which selectively permit ions and water molecules to get into and out of the plant cell. Osmotic balance under saline stress in *K. candel* is achieved by suppression of membrane proteins such as tonoplast intrinsic protein (*KcTIP1*), a class of aquaporin to minimize water loss (Huang et al., 2003). In *A. ilicifolius*, TIP seems to be positively selected, probably as a part of adaptive evolution and impart resistance to salt stress (Yang et al., 2015b). Root-specific expression of ABC transporter gene may also be connected to ultrafiltration of ions by mangrove roots (Su et al., 2019). Among the genes differentially expressed in the roots of *B. cylindrica*, *GIGANTEA* (*GI*) establishes its role as a transporter regulator (Wong et al., 2007). It has been reported that *GI* forms a complex with salt overly sensitive protein (*SOS2*) and inhibits its function of activating  $\text{Na}^+/\text{H}^+$  antiporter (*SOS1*). *GI* is degraded under salinity stress thereby releasing *SOS2*, which forms a complex with *SOS3* and activates  $\text{Na}^+/\text{H}^+$  antiporter anchoring the plasma membrane (Kim et al., 2013). The lipid metabolism-related genes such as *UDP-3-O-acyl-N-acetylglucosamine deacetylase* and *acyl-CoA synthetase* impose regulatory functions by changing plasma membrane lipid composition and thus aiding membrane bound ion transporters to efficiently exclude or compartmentalize excess  $\text{Na}^+$  ions in the vacuoles under salt stress (Wong et al., 2007). *Ubiquitin-specific protease 16* (*UBP16*) homologous gene of *A. ilicifolius* is also involved in regulating plasma membrane  $\text{Na}^+/\text{H}^+$  antiporter activity (Yang et al., 2015a).

To infer the wholesome picture of ultrafiltration, the genes involved in anatomical expulsion of salt in addition to the genes related to transporters and their regulators need to be explored. Plant cell wall normally consists of cellulose, hemicellulose, pectin, lignin, and proteins where its composition alters as a method to withstand stress (Liu et al., 2021). Primary cell wall contains cellulose and pectin whereas the thicker secondary cell wall contains cellulose, hemicellulose, and lignin providing extra strength (Somssich et al., 2016; Tenhaken, 2015). Secondary cell wall modifications such as casparian bands are present in the intercellular space of endodermis, while suberin lamellae cover the primary cell wall in epidermis and endodermis of plant root (Graça, 2015; Krishnamurthy et al., 2009). Apoplastic barriers such as the casparian bands and suberin lamellae confer the ability to block bypass flow of ions to xylem, thereby maintaining osmotic equilibrium (Cheng et al., 2020; Krishnamurthy et al., 2014). In mangroves, an extensive study on genes related to apoplastic barrier formation is done in *Avicennia officinalis*. *Cytochrome P450* (*CYP94B1*), a peroxidase gene of *A. officinalis*, is involved in the apoplastic cell barrier that aids in suberin biosynthesis. Expression of *AoCYP94B1*, homologue of *CYP94B1*, in *A. officinalis* is also induced on salt stress treatments (Krishnamurthy et al., 2020). Similarly, *AoCYP86B1* gene upregulated in root tissues of the given mangrove species in response to salt stress is also correlated to suberin synthesis (Krishnamurthy et al., 2014). Although characterization of *WRKY33*, an upstream regulator of *CYP94B1*, is identified in the model plant *Arabidopsis thaliana*, regulation of suberin synthesis in mangrove ultrafiltration mechanisms is yet to be characterized (Krishnamurthy et al., 2021). Not much information is available on the genetic basis of secondary wall formation



**Figure 3. Cellular homeostasis pathways in connection to ROS induced anatomical variations**

The process of accumulating apoplastic barriers (lignification, suberin lamellae formation, and casparian thickening) within the root structures give anatomical resistance to salt invasion which may complement ultrafiltration by mangrove root cell transporters. The activation of SOS1 ( $\text{Na}^+/\text{H}^+$  antiporter of plasma membrane) is facilitated by the SOS2-SOS3 complex whereas GI inhibits SOS1 by holding back SOS2. The mechanism of SOS1 ion transport relies on  $\text{H}^+$  ATPases for the generation of electrochemical gradients which in turn are regulated by "14-3-3" protein. On the other hand, vacuolar  $\text{Na}^+/\text{H}^+$  antiporters (NHX1) are responsible for compartmentalization of excess ions. ROS, the primary accumulators within the stressed mangrove cell directly damage nuclear DNA which is reversed by repair mechanisms involving replication factor C 1 (RFC1), proliferating cell nuclear antigen (PCNA), UV hypersensitive protein 3 (UVH3), and replication factor A1 (RFA1). The intact DNA encodes proteins involved in suberin synthesis like ABC TFs, CYP94B1, and WRKY33. The enzymatic activity of superoxide dismutase (SOD) detoxifies ROS into  $\text{H}_2\text{O}_2$  which may have different fates within the cell.  $\text{H}_2\text{O}_2$  easily diffuses through plasma membranes via aquaporins and acts as ROS signaling molecule in abscisic acid (ABA)-induced stomatal closure.  $\text{H}_2\text{O}_2$  is also supposed to be mediating lignin biosynthesis. Excess  $\text{H}_2\text{O}_2$  is finally converted to  $\text{H}_2\text{O}$  by peroxidases. Within the figure, A and B represent lignin (Blue) deposition in the stellar region and casparian strips (Green) in the endodermis of mangrove root.

and the way it helps in ultrafiltration by mangrove roots. Future studies need to be concentrated on dissecting the genes involved in biosynthesis of casparian bands and their potential to regulate ultrafiltration. A particular focus should be given to the probable interconnection of redox pathways (section [redox homeostasis](#)) to the anatomical resistance that has been depicted in [Figure 3](#).

Some other root-specific findings which may be related to ultrafiltration include preferential expression of specific genes encoding Zinc finger transcription factor, ankyrin repeat protein, lipid transfer protein, ACC oxidase, DnaJ-like protein, and BURP domain-containing protein in lateral and main roots of *B. gymnorhiza* (Yamanaka et al., 2009). Among these, ankyrin repeat protein takes part in protein-protein interactions whereas lipid transfer proteins en route lipid molecules for the synthesis of cutin and waxy layers of plant cell wall (Kader, 1997; Mosavi et al., 2004). DnaJ-like protein, ACC oxidase, and BURP domain-containing proteins have diverse functions such as senescence, fruit ripening, and protein folding (Cyr et al., 1994; Hattori et al., 1998; Zhang et al., 1995). However, further investigation is required to infer whether these stress-responsive genes and their proteins are tightly linked to ultrafiltration in mangrove roots or not.

### Skillful breathing under hypoxic and anaerobic conditions

Intertidal zones are flooded during tidal peaks and mangrove roots remain periodically submerged in water (Jia et al., 2019). Recent global warming events have also contributed to root submergence due to rising

sea levels which causes mangroves to remain in anoxic environments for a longer time (Lovelock et al., 2017). Besides climatic factors, anthropogenic pollutants especially plastic debris brings about irreversible anoxia and suffocation to the mangrove vegetation (van Bijsterveldt et al., 2021). Specialized root systems such as prop roots, buttress roots, cable roots, feeding roots, anchor roots, and stilt roots succor mangrove adaptations by a number of ways (Srikanth et al., 2016). Among them, cable roots, feeding roots, and anchor roots facilitate proper gaseous exchange during anoxic conditions such as high tides and increased sedimentation. Cable roots possess erected aerial structures called pneumatophores with higher percentages of lenticels (porous tissues) and aerenchyma cells to ensure oxygen availability to the mangrove root cells (Okello et al., 2020). Although aerenchymae and pneumatophores are normally present in mangroves, the respective percentage of occurrence varies with respect to the degree of root submergence. The genes involved in the formation/distribution of aerenchymae and pneumatophores are discussed separately in the following subsections to get an overview of the genomic basis of mangrove adaptation to cope with hypoxic/anoxic conditions.

### Aerenchymae

Aerenchymae are enlarged gas spaces between cells formed in the cortex region due to abiotic stress, usually hypoxia (Evans, 2004). They provide sufficient oxygen supply to the mangrove root cells (Allaway et al., 2001; Pi et al., 2009). Aerenchymae formed by cell separation and cell death are termed schizogenous and lysigenous respectively (Evans, 2004). Schizogenous aerenchyma formed on the basis of cell separation and expansion, rather than cell lysis, is observed in *A. marina* roots (Purnobasuki and Suzuki, 2005). Accumulation of ethylene has been reported to cause programmed cell death that subsequently results in the formation of lysigenous aerenchyma (Allaway et al., 2001). In mangroves, distribution and emergence of aerenchyma is supposed to be closely regulated by the plant hormones especially ethylene and abscisic acid (ABA) as demonstrated in *A. marina* anchor roots and pneumatophores (Hao et al., 2021; Ma et al., 2009; Wang et al., 2013b). It is known that ethylene-responsive genes positively regulate aerenchyma formation whereas ABA-responsive genes negatively affect it (Shimamura et al., 2014). Ethylene response factor 1 (ERF 1), a downstream component of ethylene pathway in *A. marina* root tissues, is found to be directly involved in increased aerenchyma formation (Hao et al., 2021). Some other root-specific ethylene-related genes such as AP2/EREBP transcription factor, ethylene response factor (ERF) 2, and ACC oxidase that we discussed in ultrafiltration (section [ultrafiltration to sieve out surplus salt](#)) and hormonal regulation (section [plant hormones as stress messengers](#)) may also be connected to aerenchyma formation (Basyuni et al., 2011; Yamanaka et al., 2009). Under hypoxia, ABA pathway genes are downregulated by highly expressed type 2C protein phosphatases (PP2C) to enhance aerenchyma formation in the mangrove root system. At the same time, genes encoding SNF1-related protein kinase 2 (SnRK2), an active booster of ABA substrate proteins, is also kept downregulated to ensure most of the ABA involving cellular actions are switched to a lower level (Hao et al., 2021; Ma et al., 2009; Wang et al., 2013b). It is evident that a balance between ethylene- and ABA-responsive genes is necessary for ample numbers of aerenchyma in the specialized root structures, especially pneumatophores. Now, the genetic mystery of pneumatophores themselves is another area of scientific interest that is detailed below.

### Pneumatophores

Compared to the gravitropic anchor roots, pneumatophores are negatively gravitropic that grow vertically upward against the gravity exposing their tips to the atmosphere (Hao et al., 2021). Gas exchange between lenticels on the pneumatophore root surface and atmosphere delivers sufficient oxygen to the submerged root system (Purnobasuki and Suzuki, 2005). The stresses such as hypoxia demand more pneumatophores to be formed to keep the submerged root system intact. Auxin metabolism is reported to be a vital part of pneumatophore development in *A. marina* (Hao et al., 2021). Auxin-responsive genes encoding indoleacetic acid-induced protein 3 (IAA3), and auxin-responsive factor 3 (ARF3) are upregulated during pneumatophore initiation in *A. marina*, while ARF3 is downregulated in the anchor root initiation. The pneumatophores are capable of negative gravitropism at an early stage of their development. Normally, statocytes, specialized cells of root cap tissues, are filled with starch-enriched statoliths to respond to gravity and thus exhibit gravitropism. For the pneumatophores to acquire negative gravitropism, it should reduce the number of starch granules within the statoliths. So, the genes involved in the starch and sucrose metabolism are suppressed to control the negative gravitropism of pneumatophore structures (Leitz et al., 2009). *Starch synthase* (GLGA) is the key gene involved in starch synthesis from ADP glucose which is downregulated during pneumatophore formation (Hao et al., 2021). On the contrary, *granule-bound starch synthase* (WAXY) and *glucose 1-phosphate adenylyltransferase* (GLGC) functions in pathways converting UDP

glucose to starch is upregulated during pneumatophore formation (Hao et al., 2021). This may be explained by the biochemical role of ADP glucose and UDP glucose. The gene related to ADP glucose, the major glucosyl donor for starch synthesis in seeds, tubers, and fruits may be downregulated in root cap tissues to block the major supply of starch to statoliths and thus facilitate negative gravitropism of pneumatophores. To keep the optimal supply of starch for basic cellular activities of root cap tissues, the genes involved in UDP-glucose mediated sucrose metabolism in the cytosol may be upregulated (Deschamps et al., 2008; Hao et al., 2021). Downregulating *GLGA* directly reduces starch and statolith formation, the root cells escape gravitropisms and pneumatophores grow upward to interact with the gaseous atmosphere. *Trehalose-6-phosphate synthase (TPS)* and *trehalose 6-phosphate phosphatase (TPP)* are among the upregulated genes converting UDP glucose to D-glucose complementing to decreased statolith formation in pneumatophores (Hao et al., 2021). As discussed above, the genetic aspects of pneumatophore formation in *A. marina* is more or less identified by Hao et al. (2021). Still, the genetics of adaptive regulations concerning pneumatophore development in other mangrove species need to be investigated to gain more information about pneumatophore formation in mangroves.

### Leaf modifications: how the lateral appendages fight off salinity?

Mangrove leaves are unique to defend stress with specialized structures and mechanisms such as waxy epidermis, salt glands, salt hairs, senescence of salt embedded leaves, salt compartmentalization, and stringent regulation of stomatal closure. Some of the stress-responsive genes at leaf level adaptations to expel or cope up with extreme salinity overlap with other features such cytosolic ion homeostasis (section ion homeostasis). Briefly, at high saline conditions, the salt secretory glands are in demand for more energy to remove  $\text{Na}^+$  ions from the cell to outward via the combined action of antiporter and  $\text{H}^+$  ATPase regulated by 14-3-3 protein-coding genes (Feng et al., 2020). At the same time, some of the ionic load is compartmentalized to leaf cell vacuoles to attain cellular homeostasis. In *A. officinalis* leaves, vacuolar  $\text{Na}^+/\text{H}^+$  exchanger encoding gene (*AoNHX1*) is preferentially expressed and is localized in tonoplast (Krishnamurthy et al., 2019). The *AoNHX1* gene expression is controlled by ABA-dependent transcription factors such as bHLH and MYC (Krishnamurthy et al., 2019). Comparably, in *A. marina*, the increased expression level of genes encoding plasma-membrane specific  $\text{H}^+$  ATPase (*HA1*) and  $\text{Na}^+/\text{H}^+$  antiporter (*SOS1*) further enhanced the transcription of vacuolar  $\text{H}^+$ -ATPase (*VHA-c1*) and vacuolar  $\text{Na}^+/\text{H}^+$  antiporter (*NHX1*) genes by means of nitric oxide (NO) signaling and facilitated accumulation of  $\text{Na}^+$  in vacuoles (Chen et al., 2010).

Another set of genes with increased expression status in mangrove leaves are those encoding AQP isolated from *A. corniculatum*, *R. mucronata*, and *K. obovata* (Fei et al., 2015b; Hibino et al., 2001; Menon and Soniya, 2014). The membrane transporters such as AQP which carry water and other tiny neutral molecules play an equal role to ion transporters in alleviating overabundance of intracellular salt under stressed conditions. AQPs belong to the major intrinsic protein (MIP) superfamily of proteins and are of five different types such as X intrinsic proteins (XIPs), small basic intrinsic proteins (SIPs), nodulin 26-like intrinsic proteins (NIPs), tonoplast intrinsic proteins (TIPs), and plasma membrane intrinsic proteins (PIPs) (Kapilan et al., 2018). *NHX1* genes along with *TIP* and *PIP* are upregulated in leaf tissues of *S. alba* (Feng et al., 2020). The gene expression regulation of ion transporters and AQPs are essential to keep the cellular osmoticum at an optimal range and thus help mangrove leaf cells to perform under stressful conditions.

Besides affecting osmotic balance, the external stress factors adversely alter other leaf characteristics such as stomatal conductance, chlorophyll content, leaf area, and ultimately photosynthesis (Tester and Davenport, 2003). The phytohormone ABA regulates most of the downstream stress signaling and hence the genes related to ABA are found to be involved in stomatal variations as well (Chen et al., 2020a). In *A. marina*, highly divergent and differentially expressed gene involved in stomatal conductance is *9-cis-epoxycarotenoid dioxygenase (NCED)* encoding the rate-limiting enzyme of ABA biosynthesis (Friis et al., 2021; Huang et al., 2018). Drought stress-induced ABA signaling activates  $\text{K}^+$  efflux in stomatal guard cells of *K. candel* mediated by a chloroplast localized thioredoxin-f protein encoding gene (*KcTrxf*). *KcTrxf* reduces stomatal aperture and promotes stomatal closure to retain water balance in leaves to overcome drought conditions (Jing et al., 2020). Heat shock protein expression induced in response to oxidative stress is also correlated with induction of stomatal closure as acclimatization to heat stress (Bajay et al., 2018). Sooner or later, the stress-driven changes in stomatal opening and closure upset photosynthesis in the leaves. Expression of genes related to photosynthesis and oxidative phosphorylation are highly specific for leaves in *M. pinnata* (Huang et al., 2012). Salinity stress particularly affects reaction centers of

photosystem II (PSII) by reducing electron transfer rates (Salim Akhter et al., 2021). Maintenance of the PSII is thus a crucial factor in coping with salinity stress in mangroves, specifically *B. gymnorrhiza* (Sugihara et al., 2000). Oxygen-evolving enhancer protein 1 (OEE1) is attached to PSII that helps in oxygen-evolving activity. Expression level of the three *B. gymnorrhiza*-specific enhancer proteins (OEE1, OEE2, and OEE3) is increased with NaCl treatment (Sugihara et al., 2000). A higher expression level of OEEs implies that the mangroves withstand negative effects of salinity on photosynthesis by giving extra stability and capacity to PSII with a better oxygen-evolving activity.

In conjunction with stomatal closure, cuticles act as a barrier to water loss and the genes related to cuticle formation are clustered with that of oxidative stress response (Bajay et al., 2018). *3-Ketoacyl-CoA synthase* is the key gene involved in cutin, suberin, and wax formation which is highly expressed in *K. obovata* (Su et al., 2019). Another gene participating in leaf cuticle development, *Glycerol-3-phosphate acyltransferase (GPAT4)*, has been reported in *A. marina* (Friis et al., 2021). Upregulation of ABC transporters in *A. officinalis* leaves can also be related to formation of thick cuticular layers under increased salinity by means of their ability to transport fatty acids. The leaves of *A. officinalis* are evolved with salt glands, the salt secretory structures on the surface. Like leaf surface cuticles, ABC transporters contribute to cuticle deposition around salt glands which is mandatory to maintain structural integrity and resist water loss under saline conditions. An elevated expression level of *dehydrin* gene (*AoDHN1*) coding for a cellular protein protector is also observed in the salt glands of *A. officinalis* (Jyothi-Prakash et al., 2014; Shimony et al., 1973). Other highly expressed genes of *A. officinalis* leaf tissues enriched with salt glands are *Leucine-Rich Repeat Receptor*, *3-Ketoacyl-CoA Synthase*, *1-Amino-Cyclopropane-1-Carboxylate Oxidase (ACC Oxidase)*, *AQP*, *R2R3 transcription factor*, *Thioredoxin H*, and *ATP Citrate Lyase* (Jyothi-Prakash et al., 2014). The genetic information on mangrove leaf adaptations is not yet complete and it needs further studies to get in-depth detailing about the adaptive mechanisms in the leaves. Still, it is evident that a major proportion of mangrove leaf adaptation is contributed by the genes related to ionic/water transporters as well as the photosynthetic machinery.

### Vivipary: Plantlets steer clear of salinity during germination

Vivipary is an adaptation facilitating dispersal and colonization of mangrove plants in hostile intertidal zones (Qiao et al., 2020). In vivipary, the propagules germinate without dormancy period while attached to the parent tree (Hong et al., 2018). Development of propagules on maternal trees gives advantage of avoiding salinity during normal seed dispersal (Elmqvist and Cox, 1996). Vivipary has multiple evolutionary origins (Shi et al., 2005). Members of Rhizophoraceae exhibit true vivipary while members of Avicenniaceae, Myrsinaceae, Palmae, Pellicieraceae, and Plumbaginaceae show cryptovivipary where the developed zygote does not penetrate the pericarp before dispersal (Elmqvist and Cox, 1996; Xu et al., 2017). Table 1 provides an overview of true mangroves and mangrove associates possessing vivipary, cryptovivipary, or nonvivipary. Because vivipary lacks dormancy period, the genes inducing dormancy are either lost or switched off to achieve this peculiar adaptation in mangroves. The *Delay of germination 1 (DOG1)* gene which regulates seed dormancy is found to have lost in mangrove plants expressing true vivipary such as *K. obovata*, *C. tagal*, and *R. apiculata* (Carrillo-Barral et al., 2020; Qiao et al., 2020). In contrast, the loss of heme-binding activity of the *DOG1* gene in *A. corniculatum* might have resulted in the appearance of crypto vivipary (Elmqvist and Cox, 1996; Feng et al., 2021). The loss of heme-binding activity in the *DOG1* gene is attributed to the replacement of histidine residues by glutamate that might have altered its function (Feng et al., 2021). The genes regulating signal transduction and embryo development are equally important to genes involved in dormancy in development of vivipary. Among the convergent genes, those involved in signal transduction (N-glycan biosynthesis) and embryo development (ubiquitin-mediated proteolysis pathways), *DNA damage-binding protein 1 (DDB1)*, *Cullin 3 (CUL3)*, and *SAE-2 genes* are reported to be positively selected in mangroves (Xu et al., 2017). Transcriptome analysis of *B. gymnorrhiza*, *K. obovata*, *R. apiculata*, *C. tagal*, and a closest terrestrial relative (*C. brachiata*) revealed that 10 genes are positively selected during their evolution of which a *eukaryotic translation factor eIF6* plays a vital role in embryogenesis (Guo et al., 2017). Another positively selected gene *BRAP2 RING ZnF UBP domain-containing protein 2 (BRIZ2)* needed for seed germination and growth is reported in *A. ilicifolius*. The study also suggested major genes involved in embryo development (Yang et al., 2015a). Overexpression of *N. fruticans*-specific gene namely *hydroxysteroid dehydrogenase (HSD1)* in *A. thaliana* terminated seed dormancy which catalyzes seed lipid biosynthesis and may be responsible for the unusual viviparous seed germination in mangroves (He et al., 2015). *Ent*

**Table 1. Viviparous and non-viviparous germination among true mangroves and mangrove associates**

Sl. No.	Mangrove species	TM <sup>b</sup> /MA <sup>c</sup> ; family	Reference(s)
Viviparous			
1	<i>Aegiceras corniculatum</i> (L.) Blanco <sup>a</sup>	TM; Myrsinaceae	(Farnsworth and Farrant, 1998; Feng et al., 2021; Quadros and Zimmer, 2017)
2	<i>Aegiceras floridum</i> Roem. & Schult. <sup>a</sup>	TM; Myrsinaceae	(Duke, 2017; Farnsworth, 2000; Kasim et al., 2019; Quadros and Zimmer, 2017)
3	<i>Aegialitis annulata</i> R. Brown <sup>a</sup>	TM; Plumbaginaceae	(Clarke and Kerrigan, 2002; Farnsworth and Farrant, 1998; Feng et al., 2021; Quadros and Zimmer, 2017)
4	<i>Aegialitis rotundifolia</i> Roxb. <sup>a</sup>	TM; Plumbaginaceae	(Aluri and Karyamsetty, 2017; Duke, 2017; Quadros and Zimmer, 2017)
5	<i>Avicennia marina</i> (Forssk.) Vierh. <sup>a</sup>	TM; Avicenniaceae	(Baleta and Casalamitao, 2016; Clarke and Kerrigan, 2002; Duke, 2017; Quadros and Zimmer, 2017)
6	<i>Avicennia officinalis</i> L. <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Feng et al., 2021; Quadros and Zimmer, 2017)
7	<i>Avicennia alba</i> Blume <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017; Raju et al., 2012)
8	<i>Avicennia bicolor</i> Standl. <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
9	<i>Avicennia germinans</i> (L.) L. <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
10	<i>Avicennia integra</i> N.C.Duke <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
11	<i>Avicennia rumphiana</i> Hallier f. <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
12	<i>Avicennia schaueriana</i> Stapf & Leechn. ex Moldenke <sup>a</sup>	TM; Avicenniaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
13	<i>Barringtonia racemosa</i> (L.) Spreng.	MA; Lecythidaceae	(Duke et al., 2007; Farnsworth, 2000)
14	<i>Bruguiera gymnorhiza</i> (L.) Lam.	TM; Rhizophoraceae	(Clarke and Kerrigan, 2002; Duke, 2017; Farnsworth and Farrant, 1998; Quadros and Zimmer, 2017)
15	<i>Bruguiera exaristata</i> Ding Hou	TM; Rhizophoraceae	(Clarke and Kerrigan, 2002; Duke, 2017; Farnsworth and Farrant, 1998; Quadros and Zimmer, 2017)
16	<i>Bruguiera cylindrica</i> (L.) Blume	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)
17	<i>Bruguiera hainesii</i> C.G.Rogers	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)
18	<i>Bruguiera parviflora</i> (Roxb.) Wight & Arn. ex Griff.	TM; Rhizophoraceae	(Clarke and Kerrigan, 2002; Duke, 2017)
19	<i>Bruguiera sexangula</i> (Lour.) Poir	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)
20	<i>Ceriops tagal</i> (Perr.) C.B. Rob.	TM; Rhizophoraceae	(Farnsworth and Farrant, 1998; Quadros and Zimmer, 2017)
21	<i>Ceriops decandra</i> (Griff.) W.Theob	TM; Rhizophoraceae	(Clarke and Kerrigan, 2002; Duke, 2017; Farnsworth and Farrant, 1998; Quadros and Zimmer, 2017)
22	<i>Ceriops australis</i> (C.T.White) Ballment, T.J.Sm. & J.A.Stoddart	TM; Rhizophoraceae	(Clarke and Kerrigan, 2002; Duke, 2017; Quadros and Zimmer, 2017)
23	<i>Ceriops zippeliana</i> Blume	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)
24	<i>Kandelia candel</i> (L.) Druce	TM; Rhizophoraceae	(Duke, 2017; Farnsworth and Farrant, 1998; Quadros and Zimmer, 2017)

(Continued on next page)

**Table 1. Continued**

Sl. No.	Mangrove species	TM <sup>b</sup> /MA <sup>c</sup> ; family	Reference(s)
25	<i>Kandelia obovata</i> Sheue, H.Y. Liu & J. Yong	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)
26	<i>Mora oleifera</i> (Hemsl.) Ducke	MA; Fabaceae	(Duke, 2017; Farnsworth, 2000)
27	<i>Pelliciera rhizophorae</i> Planch. & Triana	TM; Pellicieraceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
28	<i>Nypa fruticans</i> Wurmb. <sup>a</sup>	TM; Arecaceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
29	<i>Rhizophora mangle</i> L.	TM; Rhizophoraceae	(Duke, 2017; Farnsworth, 2000; Quadros and Zimmer, 2017)
30	<i>Rhizophora stylosa</i> Griff.	TM; Rhizophoraceae	(Clarke and Kerrigan, 2002; Duke, 2017; Farnsworth and Farrant, 1998; Quadros and Zimmer, 2017)
31	<i>Rhizophora apiculata</i> Blume	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017; Takayama et al., 2013)
32	<i>Rhizophora racemosa</i> G.Mey.	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017; Takayama et al., 2013)
33	<i>Rhizophora mucronata</i> Lam.	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)
34	<i>Rhizophora samoensis</i> (Hochr.) Salvoza	TM; Rhizophoraceae	(Duke, 2017; Quadros and Zimmer, 2017)

**Non-viviparous**

35	<i>Acanthus ebracteatus</i> Vahl	MA; Acanthaceae	(Duke, 2017; Farnsworth, 2000)
36	<i>Acanthus ilicifolius</i> L.	TM; Acanthaceae	(Duke, 2017; Farnsworth, 2000)
37	<i>Acrostichum aureum</i> L.	TM; Pteridaceae	(Duke, 2017; Quadros and Zimmer, 2017)
38	<i>Acrostichum speciosum</i> Willd	TM; Pteridaceae	(Duke, 2017)
39	<i>Acrostichum danaeifolium</i> Langsd. & Fisch.	TM; Pteridaceae	(Duke, 2017)
40	<i>Brownlowia tersa</i> (L.) Kosterm.	MA; Malvaceae	(Duke, 2017)
41	<i>Camptostemon philippinense</i> (S.Vidal) Becc.	TM; Fabaceae	(Duke, 2017)
42	<i>Camptostemon schultzei</i> Mast.	TM; Fabaceae	(Duke, 2017; Quadros and Zimmer, 2017)
43	<i>Conocarpus erectus</i> L.	TM; Combretaceae	(Duke, 2017; Farnsworth, 2000)
44	<i>Crenea patentinervis</i> (Koehe) Standl.	MA; Lythraceae	(Duke, 2017)
45	<i>Cynometra iripa</i> Kostel.	MA; Fabaceae	(Duke, 2017)
46	<i>Diospyros littorea</i> (R.Br.) Kosterm.	MA; Ebenaceae	(Duke, 2017)
47	<i>Dolichandrone spathacea</i> (L.f.) Seem.	MA; Bignoniaceae	(Duke, 2017; Farnsworth, 2000)
48	<i>Excoecaria agallocha</i> L.	MA; Euphorbiaceae	(Duke, 2017)
49	<i>Shirakiopsis indica</i> (Willd.) Esser.	MA; Euphorbiaceae	(Ahmed et al., 2007)
50	<i>Heritiera littoralis</i> Aiton	MA; Malvaceae	(Baleta and Casalamitao, 2016; Duke, 2017)
51	<i>Heritiera fomes</i> Buch.-Ham.	MA; Malvaceae	(Duke, 2017)
52	<i>Hibiscus tiliaceus</i> L.	MA; Malvaceae	(Jiang et al., 2017; Shi et al., 2020)
53	<i>Laguncularia racemosa</i> (L.) C.F.Gaertn.	TM; Combretaceae	(Duke, 2017; Quadros and Zimmer, 2017)
54	<i>Lumnitzera racemosa</i> Willd.	TM; Combretaceae	(Duke, 2017; Quadros and Zimmer, 2017)
55	<i>Lumnitzera littorea</i> (Jack) Voigt	TM; Combretaceae	(Duke, 2017; Quadros and Zimmer, 2017)
56	<i>Muellera moniliformis</i> L.f.	MA; Fabaceae	(Duke, 2017)
57	<i>Osbornia octodonta</i> F.Muell	TM; Myrtaceae	(Duke, 2017; Quadros and Zimmer, 2017)
58	<i>Pavonia paludicola</i> Nicolson ex Fryxell	MA; Malvaceae	(Duke, 2017)
59	<i>Pavonia rhizophorae</i> Killip ex Kearney	MA; Malvaceae	(Duke, 2017)
60	<i>Pemphis acidula</i> J.R. & G. Forst	MA; Lythraceae	(Duke, 2017)
61	<i>Sonneratia caseolaris</i> (L.) Engl.	TM; Lythraceae	(Duke, 2017; Quadros and Zimmer, 2017)
62	<i>Sonneratia alba</i> Sm.	TM; Lythraceae	(Duke, 2017; Quadros and Zimmer, 2017)

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**Table 1. Continued**

Sl. No.	Mangrove species	TM <sup>b</sup> /MA <sup>c</sup> ; family	Reference(s)
63	<i>Sonneratia apetala</i> Buch.-Ham.	TM; Lythraceae	(Duke, 2017; Quadros and Zimmer, 2017)
64	<i>Sonneratia griffithii</i> Kurz.	TM; Lythraceae	(Duke, 2017; Quadros and Zimmer, 2017)
65	<i>Sonneratia lanceolata</i> Blume	TM; Lythraceae	(Duke, 2017; Quadros and Zimmer, 2017)
66	<i>Sonneratia ovata</i> Backer	TM; Lythraceae	(Duke, 2017; Quadros and Zimmer, 2017)
67	<i>Scyphiphora hydrophyllacea</i> C.F.Gaertn	TM; Rubiaceae	(Duke, 2017; Quadros and Zimmer, 2017)
68	<i>Tabebuia palustris</i> Hemsl.	MA; Bignoniaceae	(Duke, 2017; Farnsworth, 2000)
69	<i>Thespesia populnea</i> (L.) Sol. ex Corrêa	MA; Malvaceae	(Leperlier et al., 2020; Shi et al., 2020)
70	<i>Xylocarpus granatum</i> J.Koenig	TM; Meliaceae	(Duke, 2017; Quadros and Zimmer, 2017)
71	<i>Xylocarpus moluccensis</i> (Lam.) M.Roem	TM; Meliaceae	(Duke, 2017; Quadros and Zimmer, 2017; Wang et al., 2011a)

<sup>a</sup>indicates crypto vivipary.

<sup>b</sup>Tm indicates true mangrove.

<sup>c</sup>Ma indicates mangrove associate.

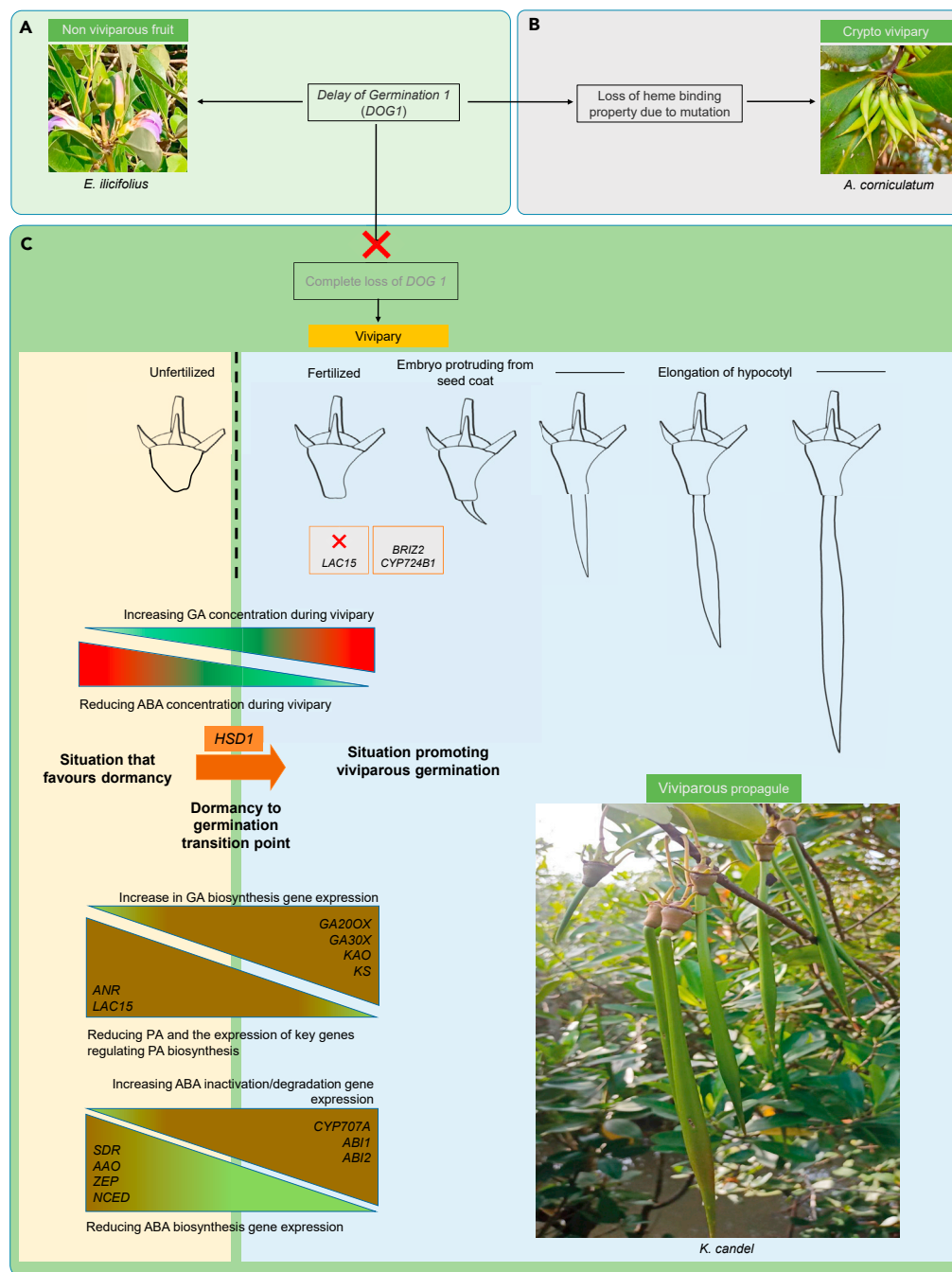
*kaurene synthase* (KS) gene and SAE-2 which underwent duplication and amino acid substitution, respectively, in Rhizophoreae mangroves may also be linked to vivipary (Bajay et al., 2018; Xu et al., 2017).

In non-viviparous mangroves, ABA-mediated signaling results in seed dormancy (Skubacz and Daszkowska-Golec, 2017). The ABA is important for dormancy in flowering plants. In contrast, relatively low levels of ABA and its biosynthetic genes (*NCED*, *SDR*, *AAO1*, and *ZEP*) are maintained to impart vivipary in mangroves. In *K. obovata*, increased expression of ABA-degrading enzymes ABA 8'-hydroxylases (*CYP707A*) and ABA negative regulator *ABI1/2* (group A type 2C protein phosphatases (*PP2Cs*)) are observed during the development of viviparous propagules. Another *K. obovata*-specific transcription factor, *ABI4*, regulates primary seed dormancy by inhibiting the promoter activity of *CYP707A*. This provides a strong evidence for the relationship between repressed ABA signaling and lack of seed dormancy in mangroves (Hong et al., 2018; Qiao et al., 2020). Differential gene expression analysis of *A. officinalis* reported upregulation of genes involved in ethylene and auxin signaling and down regulation of genes and transcription factors involved in ABA signaling such as *MYBs*, *ABA-responsive element binding factors* (*ABFs*), and *basic Leucine Zipper genes* (*bZIPs*) (Hong et al., 2018). Upon analyzing seeds of non-viviparous mangrove *Lumnitzera littorea*, starch biosynthesis genes are found to be downregulated while auxin and gibberellic acid (*GA*) biosynthetic genes which are key factors in fruit initiation are differentially expressed (Zhang et al., 2021). Another seed germination-related gene *CYP724B1* is specifically expressed in fruits of *K. obovata* (Su et al., 2019). *K. obovata* is further mined for genes encoding *GA* biosynthetic enzymes (*KS*, *KAO*, *GA20OX*, and *GA3OX*) and some positive regulators (*GID1* and *PIF4*) which could be promoting hypocotyl elongation. Expression of proanthocyanidin (*PA*) synthetic enzymes, known to prevent seed germination, is also found to be lowered during vivipary in the embryos and seeds of *K. obovata* as well as *C. brachiata*. Among them, *LAC15* and *ANR* genes having key roles in *PA* biosynthesis are more regulated in *C. brachiata* than *K. obovata* (Qiao et al., 2020). The salient gene candidates with potential involvement in mangrove vivipary are summarized in Figure 4.

### Plant hormones as stress messengers

A complex network of plant hormone signaling mediates stress response mechanisms in plants (Verma et al., 2016). Plant hormones such as abscisic acid (*ABA*), gibberellic acid (*GA*), cytokinins, auxins, and ethylene primarily participate in abiotic stress tolerance mechanisms where *ABA* act as a typical abiotic stress messenger (Khan et al., 2017; Shu et al., 2018; Zwack and Rashotte, 2015). Genes encoding some peptide hormones, phytoalexins (*PSK*), are also reported in mangroves like *A. marina* which act as signaling component and are highly expressed in leaves upon cadmium stress (Zhang et al., 2017). Cross talk between *ABA* and other plant hormones such as ethylene is equally responsible for regulation of stomatal activity and specialized reproductive structures like viviparous propagules (Xiong, 2007). We have already discussed the role of *ABA* in various stress regulations under different subsections of mangrove adaptations; all the functions of *ABA* as well as other plant hormones known to activate genes related to salt stress response are detailed below.





**Figure 4. Evolution of mangrove vivipary**

(A–C) *Delay of germination 1 (DOG1)* is the key gene determining type of seed germination in mangroves. Active *DOG1* promotes normal fruit development (A) whereas modified *DOG1* without heme-binding property results in cryptovivipary (B) A complete loss of *DOG1* is responsible for the development of viviparous propagules (C) which in turn is initiated once ABA-mediated signaling is switched off and GA comes into action. The ABA concentration decreases during vivipary and GA increases. Hence, genes related to ABA degradation and GA biosynthesis are upregulated during propagule development. Other genes related to seed germination are *BRIZ2*, *HSD*, *CYP724B1*, and *LAC15*, of which, *LAC15* acts as a negative regulator and hence maintains a lower expression status of the said gene to attain vivipary. *HSD* acts as the terminator of seed dormancy whereas *LAC15* promotes proanthocyanidin (PA) biosynthesis. The expression of *LAC15* is blocked to reduce PA concentration and help loosen seed coat to attain viviparous germination.

First of all, the role of plant hormones in mangrove vivipary is considered. A study conducted on variations in ABA level and the seed dormancy indicates a negative role of ABA in seed germination. Hence, the ABA concentration is maintained at lower levels in mangroves exhibiting vivipary to promote seed germination (Farnsworth and Farrant, 1998). Negative feedback regulation of ABA by suppressing the genes encoding different ABA types (*ABA1* and *ABA2*) while enhancing expression of their respective negative modulators (*ABI1* and *ABI2*) is reported upon external ABA application (Hong et al., 2018). Repressed expression level of ABA biosynthetic genes and induction of ABA signaling genes (*PYL9* and *SnRK2.2*) are observed in *K. obovata* (Hong et al., 2018). The study on *K. obovata* genome also reports changes in ABA/GA dynamics and high expression of PA synthesis genes are thought to facilitate vivipary (Qiao et al., 2020). Furthermore, brassinosteroid genes are upregulated in *K. obovata* fruit tissue which is consistent with its role in signaling pathways along with ABA and GA in seed germination (Su et al., 2019). Apart from inducing vivipary, ABA plays a vital part in stomatal conductance of water by regulating expression of transporter proteins in guard cells during salinity stress (Xiong, 2007). *AmNCED* coding for an enzyme catalyzing the rate-limiting enzyme of ABA biosynthesis comes first in its importance in stomatal conductance followed by *KcTrxf*. *KcTrxf* stimulates stomatal closure by inducing ABA-activated  $K^+$  efflux to retain water balance in leaves to overcome drought conditions (Friis et al., 2021; Huang et al., 2018; Jing et al., 2020).

Analyzing the genes involved in cell signaling regulated by plant hormones especially ABA is highly significant to understand the various adaptive mechanisms. Important signaling pathways in salt tolerance are SOS,  $Ca^{2+}$ -dependent, and ABA-dependent signaling pathways (Feng et al., 2020; Ji et al., 2013). SOS signaling pathway is triggered by the cytoplasmic  $Ca^{2+}$  abundance caused due to salinity stress. The gene encoding calcium-dependent protein kinase (CDPK) (a subfamily of Serine/Threonine kinases) which act as calcium mediator phosphorylating downstream elements such as ion channels, transcription factors, and metabolic enzymes in the calcium signaling pathways is upregulated in *A. marina* under heat stress (Delormel and Boudsocq, 2019; Liu et al., 2020). Similar to the previously discussed roles in aerenchyma formation and vivipary, SnRK2 phosphorylates and activates proteins in ABA signaling and plays a major role in dehydration response. In order to negatively regulate ABA signaling, *SnRK2* activity is inhibited by PP2AC, a group of protein phosphatases (Shinozawa et al., 2019). In *K. obovata*, the *SnRK2* genes are highly expressed during the freezing events indicating its role in cold tolerance also (Su et al., 2019). Another key element in signaling cascade, cycloartenol promoter, is also studied in *K. candel*. It has ABA, gibberellic acid, salicylic acid, and auxin-responsive elements in common (Basyuni et al., 2018b). *K. obovata* specific-CBF/DREB1 transcription factor gene (*KoCBF3*) is reported to increase its expression under cold, salinity, and heavy metal stresses, thereby offering tolerance through  $Ca^{2+}$  signaling-mediated hormonal stress response (Peng et al., 2020b). Calmodulin-like protein (CML40) identified in a semi-mangrove plant *M. pinnata* maintains cellular homeostasis through  $Ca^{2+}$ -dependent signaling and can be initiated by abiotic stress or ABA induction (Zhang et al., 2021). Late embryogenesis protein and *B. gymnorrhiza*-specific mangrin protein sequences have serine-rich regions which account for its close association with hormone signaling pathways and in maintaining protein and membrane structures under stress conditions (Yamada et al., 2002). These studies suggest that the hormone-induced signaling pathways take part in response to various stressors such as salinity, heat, drought, cold, and heavy metal but the available information is limited.

Plant hormones possess a potent role in redox homeostasis also which in turn is revealed by the investigation of genes encoding SOD isozymes (*KoCSD3* and *KoFSD2*) of *K. obovata* root tissues. *KoCSD3* and *KoFSD2* genes participate in the ABA- and auxin (IAA)-mediated stress responses to cadmium. The exogenous application of ABA alone is sufficient to induce *KoCSD3*, but *KoFSD2* requires a combination of ABA and IAA for the gene induction (Pan et al., 2020). Expression patterns of these two genes differ as *KoCSD3* expression is relatively confined to exodermis and epidermis compared with the widespread presence of *KoFSD2* in root (Pan et al., 2020). The hormonal responses by auxin are initiated by the binding of auxins to receptor molecules and then regulated by induction of *IAA13* and suppression of *IAA19*, *IAA8*, aldehyde dehydrogenase (*ALDH*), and tryptophan aminotransferase of arabidopsis 1 (*TAA1*) (Hao et al., 2021). The auxin-responsive genes are activated by the upregulation of ubiquitin protein ligases (*SIAH1* and *S1AH1-E3*), ubiquitin-conjugating enzymes (*UBE2D* and *UBE2A*), and *RCHY1* genes for the proper development of pneumatophores and aerenchymae (Hao et al., 2021).

Lastly, the genes encoding transcription factors connected with ABA and the other plant hormone signaling are worth discussing when the importance of hormone regulation in adaptive responses is

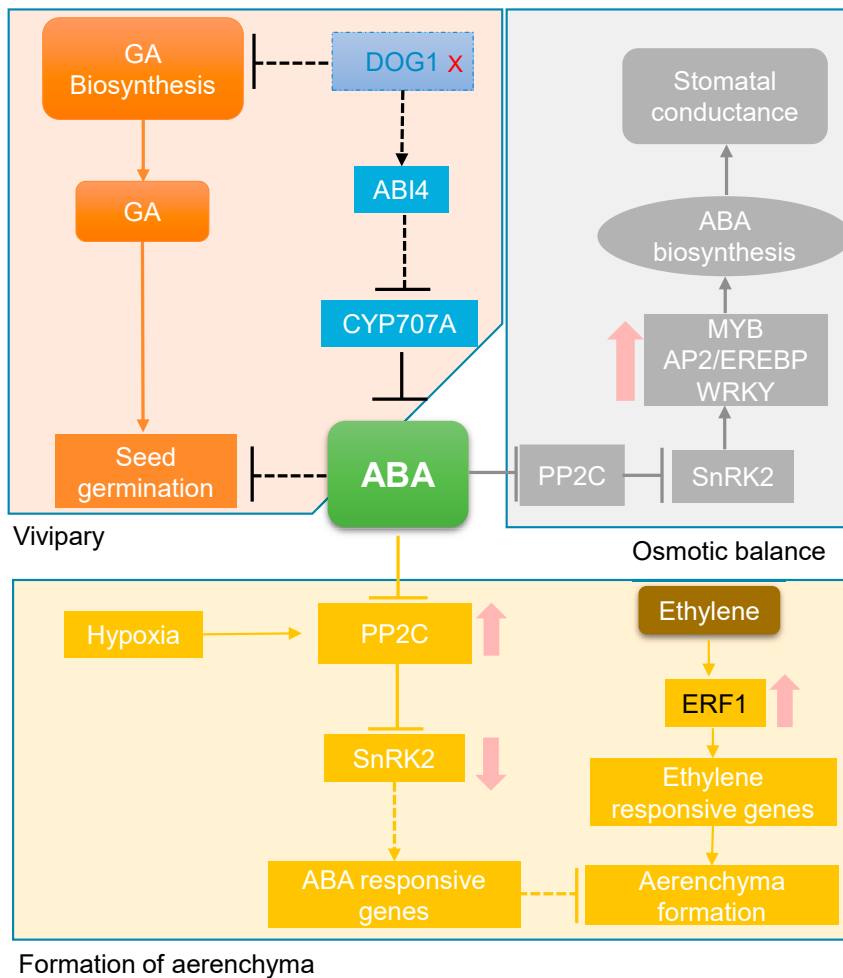
considered. The transcriptome analysis of *A. corniculatum* showed higher expression of the transcription factors such as MYB, AP2/EREBP, and WRKY which promotes gene expression of ABA biosynthesis genes (Fang et al., 2016). Two different transcription factors identified to be involved in ABA-induced hormone signaling of *A. marina* are *AmMYB1* and *AmNAC1* (Ganesan et al., 2008). AP2/EREBP transcription factor, ethylene response factor (ERF)-2, and MADS-domain transcription factor encoding genes are upregulated in *R. stylosa* roots in response to salt stress. Dehydration response element/C-repeat (DRE/CRT) is cis-acting element that bind to the salt stress-responsive genes and mediate their subsequent expression (Basyuni et al., 2011). Genes encoding transcription factor CBF/DREB in mangroves *A. marina* and *B. gymnorrhiza* is upregulated under temperature, salinity, water, heavy metal, and ABA treatments (Peng et al., 2013, 2020b). Regulation of genes at the level of transcription is the most common but essential part of gene control. Therefore, identification of more transcription factors and dissecting their roles during hormonal responses is needed to better understand unique mangrove adaptations. Moreover, the hormonal cross talks in mangrove adaptations (Figure 5) are not completely identified and deserve further scientific studies. The characteristic stress-responsive genes from section [cellular homeostasis for optimal functioning of mangrove plant cell](#) (cellular homeostasis) to section [plant hormones as stress messengers](#) (hormonal regulation) are summarized in Table 2 (See also Table S1). The table provides a list of the genes with their roles in imparting the adaptations to stresses in different mangrove species.

## EPIGENETICS OF MANGROVE ADAPTATIONS TO INTERTIDAL ENVIRONMENTS

Gene expression variations due to DNA methylation, histone modification, and non-coding RNAs (ncRNAs) constitute epigenetic regulations in plants (Ashapkin et al., 2020; Pikaard and Mittelsten Scheid, 2014). The ncRNAs comprise of long non-coding RNAs (lncRNAs) and small RNAs (sRNAs). The ncRNAs might encode small peptides but no proteins for gene regulation (Ben Amor et al., 2009) and also trigger other epigenetic changes such as DNA methylation and chromatin modification (Heo and Sung, 2011; Meyer, 2015). Normally external environmental conditions similar to what mangroves experience may affect gene expression by epigenetic mechanisms (Baulcombe and Dean, 2014). Stress adaptations by gene expression regulations through DNA methylation and sRNA activities have been reported in mangroves although such studies are less. But the salt stress responsive mangrove lncRNAs, and their regulatory role in imparting RNA-directed DNA methylation (RdDM) variations under stress conditions is not yet available. The important mechanisms of epigenetic regulations in mangroves and their impact on adaptations are described in the following paragraphs.

DNA methylation occurs at CHH, CHG, and CG sites (C=Cytosine; G = Guanine; H = any nucleotide except guanine) which may also serve as methylation targets in mangroves (Mounger et al., 2021; Pikaard and Mittelsten Scheid, 2014). The white mangrove *L. racemosa*, an inhabitant of salt marshes, is observed to possess smaller plant and leaf size compared with that of river marsh inhabitants. This can be correlated to hypomethylation due to the action of DNA methylases encoded by the *MET1* gene of *L. racemosa* (Lira-Medeiros et al., 2010). Genetic and epigenetic analyses of *R. mangle* revealed high epigenetic diversity among the populations of maternal plants and garden-grown offsprings. Environmental factors such as fluctuating oceanic currents contributed to epigenetic regulation, which can be observed in populations of *R. mangle* with low genetic but more epigenetic variations. The study also suggests epigenetic variations in mangroves are heritable because some habitat induced epigenetic variations are retained in garden-grown varieties (Mounger et al., 2021).

Small interfering RNAs (siRNA), phased small interfering RNAs (PhasiRNAs), and microRNA (miRNA) are the major types of non-coding sRNAs (Yu et al., 2019). The ncRNA-related epigenetic regulations are primarily mediated by sRNAs which comprise both miRNA and siRNA (Table 3). The sRNAs carry out post-transcriptional gene silencing and also the forementioned DNA methylation (Baulcombe and Dean, 2014; Pikaard and Mittelsten Scheid, 2014). In mangroves, the sRNAs (20–24 nt) which regulate transcriptional or post-transcriptional silencing of gene expression are abundant as exemplified by *A. marina* (Khraiwesh et al., 2013). The tissue-specific or developmental stage-specific expression of miRNAs is responsible for the translational cleavage of target RNAs. *A. marina*-specific miRNAs are reported to target mRNAs of transcription factors such as *SBPs*, *MYBs/TCPs*, *ARFs*, *HD-ZIPs*, *AGO1*, and *CSD1* and are regulated under stress conditions (Khraiwesh et al., 2013). Some families of miRNA such as miR156, miR396, and miR529 are reported in *B. gymnorrhiza* of which miR529 is predicted to target peroxidase and proton-dependent oligopeptide transporter mRNAs (Lee et al., 2011). More mangrove-specific miRNAs are identified later from the transcriptome data of *B. gymnorrhiza* and *K.candel* (Wen et al., 2016). An overview of



**Figure 5. Hormonal crosstalk in mangrove adaptations to intertidal conditions**

The regulatory roles of various plant hormones span over different adaptive responses such as vivipary, osmotic homeostasis, and specialized root structure formation. In the absence of DOG1, ABA pathway is inhibited, while GA biosynthesis is promoted leading to seed germination in vivipary. Dotted lines represent decreased or no action. Binding of ABA to PP2C breaks off its inhibitory action on SnRK2. SnRK2 phosphorylates the transcription factors and promotes gene expression of ABA biosynthesis genes leading to stomatal closure. Stomatal opening and closure is controlled by ABA as a measure to maintain osmotic balance. Under hypoxia, PP2C genes are upregulated which inhibits phosphorylation of TFs by SnRK2, thus lower expression of ABA-responsive genes and increase rate of aerenchyma formation. ERF1 gene is upregulated which promotes gene expression of ethylene-responsive genes and thereby functions in root aerenchyma formation. Upregulated and downregulated genes are represented by upward and downward arrows.

mangrove-specific ncRNAs is given in Table 3. Changes in miRNA expression may be a crucial factor contributing to salt and nutrient stress tolerance because the miRNA profile differed greatly in mangroves compared to non-halophytes. Among them, miR396 and miR394 which recruit target proteins involved in defense and oxidative stress along with unique mangrove-specific changes to tasiRNA (*TAS3*trans-acting siRNAs) might be providing stability in gene expression during stressful conditions (Wen et al., 2016). Further studies revealed that absence of miR827 in both *B. gymnorhiza* and *A. marina* correlates with nitrogen and phosphorus deficiency. The miR827 mediates nitrate-dependent phosphate homeostasis in *A. thaliana* whereas absence of this in mangrove points toward convergent evolution in epigenetic responses (Kant et al., 2011; Khraiweh et al., 2013; Wen et al., 2016). It is hypothesized that in mangroves, miRNAs canalize gene expression buffering as they are constantly exposed to multiple stresses including nutrient stress (Wen et al., 2016).

**Table 2. List of stress-responsive genes with potential roles in the survival of mangroves under extreme conditions in the tropical intertidal environments**

Gene	Mangrove species; part; expression	Functional role(s) in mangroves	Reference(s)
KoHSP70	Ko; Chl; Up	Protein folding and transportation during cold stress	(Fei et al., 2015a)
KoFSD2	Ko; Rt; Up under Cd stress	Stimulate activity of catalase and glutathione reductase enzyme to reduce ROS levels	(Pan et al., 2020)
KoCSD3	Ko; Exodermis and epidermis of Rt; Up under Cd stress	Stimulate ascorbate peroxidase activity to reduce H <sub>2</sub> O <sub>2</sub> levels	(Pan et al., 2020)
AmCBF2	Am; Lv; Up	Involved in the stress-responsive signaling pathway	(Peng et al., 2013)
AcCBF1	Ac; Lv; Up under cold stress	Involved in the stress-responsive signaling pathway	(Peng et al., 2015)
KoCBF1, KoCBF3	Ko; Lv; Rt; Up	Involved in the stress-responsive signaling pathway and crosstalk between hormone signaling pathways	(Peng et al., 2020b)
BgCBF	Bg; Lv; Up	Involved in short-term cold tolerance	(Peng et al., 2020a)
AcCHI I	Ac; Rt; Lv; Up	Heavy metal tolerance and detoxification	(Wang et al., 2015b)
AmCHI III	Am; Lv; Up	Heavy-metal tolerance and detoxification	(Wang et al., 2015a)
KMT	Kc; Sht; Up	Zinc, cadmium, and mercury tolerance	(Zhang et al., 2012)
SaFeSOD	Sa; Lv; Up	Removal of reactive oxygen species	(Wang et al., 2013a)
SaCSD1	Sa; Highly expressed in Fr, moderate in Lv; Up (Lv), Dw (Rt)	Removal of reactive oxygen species	(Yang et al., 2016)
PCNA	Kc; Lv; Up	DNA repair under salinity stress	(Wang et al., 2016)
RFC1	Kc; Lv; Up	DNA repair under salinity stress	(Wang et al., 2016)
RFA1	Kc; Lv; Up	DNA repair under salinity stress	(Wang et al., 2016)
UVH3	Kc; Lv; Up	DNA repair under salinity stress	(Wang et al., 2016)
14-3-3 protein coding gene	Ac; Lv; Gene retained after WGD	Regulates SOS signaling pathway	(Camoni et al., 2018; Feng et al., 2021)
KcTIP	Kc; Rt; Dw	Regulation of water in the cytoplasm during salinity stress	(Huang et al., 2003)
ABCB1	Ko; Rt; Up	Specifically expressed in root tissues	(Su et al., 2019)
OSBP	Ko; Rt; Up	Component of salt tolerance mechanism in root tissues	(Su et al., 2019)
GI	Bc; Rt; Up	Release SOS2 protein involved in SOS-signaling pathway while degrading under salt stress	(Mishra and Panigrahi, 2015; Wong et al., 2007)
UBP16	Ai; Lv; Rt; Positively regulated gene	Increase salt tolerance by positively regulating plasma membrane NA <sup>+</sup> /H <sup>+</sup> antiport activity	(Yang et al., 2015a)
AoCYP94B1 AoCYP86B1	Ao; Rt; Up	Involved in suberin biosynthesis	(Krishnamurthy et al., 2014, 2020, 2021)
ERF 1	Am; Rt; Up	Increases ethylene production and help in the formation of aerenchyma	(Hao et al., 2021)
PP2C	Am; Rt; Up	Negatively regulates ABA signaling	(Hao et al., 2021)
SnRK2	Am; Rt; Dw	Involved in ABA signaling and regulate aerenchyma formation	(Hao et al., 2021)
IAA13	Am; Rt; Up	Initiation of pneumatophore formation	(Hao et al., 2021)
ARF3	Am; Rt; Up	Initiation of pneumatophore formation	(Hao et al., 2021)

(Continued on next page)

**Table 2. Continued**

Gene	Mangrove species; part; expression	Functional role(s) in mangroves	Reference(s)
GLGC	Am; Rt; Up	Formation of statoliths and negative gravitropism in pneumatophores	(Hao et al., 2021)
WAXY	Am; Rt; Up	Formation of statoliths and negative gravitropism in pneumatophores	(Hao et al., 2021)
TPS	Am; Rt; Up	Formation of statoliths and negative gravitropism in pneumatophores	(Hao et al., 2021)
TPP	Am; Rt; Up	Formation of statoliths and negative gravitropism in pneumatophores	(Hao et al., 2021)
CDSP32	Ai; Lv; Rt; Positively selected genes	Inhibits oxidative damage caused by ROS in chloroplast	(Yang et al., 2015a)
AcNHA	Ac; Lv; Up	Osmoregulation under salinity stress	(Fu et al., 2005)
AcPIP1,2	Ac; Lv; Up	Regulate water loss under osmotic stress	(Fu et al., 2005)
AoNHX1	Ao; Lv; Up	Regulate osmotic damage by accumulating ions into vacuoles	(Krishnamurthy et al., 2019)
AoNHX6	Ao; Lv; Up	Regulate osmotic damage by accumulating ions into vacuoles	(Krishnamurthy et al., 2019)
HA1	Am; Lv; Up	Salt secretion	(Chen et al., 2010)
VHA-c1	Am; Lv; Up	Provide ATP to vacuolar antiporters	(Chen et al., 2010)
SOS1	Am; Lv; Up	Salt secretion (removes salt from cytoplasm to apoplast)	(Chen et al., 2010)
NHX1	Am; Lv; Up	Ion sequestration in vacuoles	(Chen et al., 2010)
Ko4002	Ko; Lv; Up	Regulate water loss under osmotic stress	(Fei et al., 2015b)
KcTrxf	Ko; Lv; Up	Regulates K <sup>+</sup> efflux and thereby opening and closing of stomatal aperture	(Jing et al., 2020)
OEE1,2,3	Bg; Lv; Up	Maintenance of the PSII system	(Sugihara et al., 2000)
AoDHN1	Ao; Lv; Up	Expressed in salt glands under salinity stress	(Jyothi-Prakash et al., 2014)
BADH	Am; Lv; Up	Role as osmoprotectant under salinity stress	(Hibino et al., 2001)
AmT1,2,3	Am; Lv; Up	Transport of osmoprotectants under salinity stress	(Waditee et al., 2002)
AcP5CS	Ac; Lv; Up	Osmoregulation under salinity and heat stress	(Fu et al., 2005)
KcMS	Kc; Rt; Lv; Up	Synthesis of triterpenoids and osmoregulation	(Basyuni et al., 2012)
KcCAS	Kc; Rt; Up	Regulates plasma membrane fluidity	(Basyuni et al., 2012)
BgbAS	Bg; Rt; Up	Synthesis of triterpenoids and membrane integrity	(Basyuni et al., 2012)
BgLUS	Bg; Rt; Up	Synthesis of triterpenoids and membrane integrity	(Basyuni et al., 2012)
PAL	Kc; Lv; Up	May have role in cell wall formation	(Wang et al., 2016)
C4H	Kc; Lv; Up	May have role in cell wall formation	(Wang et al., 2016)
4CL	Kc; Lv; Up	May have role in cell wall formation	(Wang et al., 2016)
ANS	Kc; Lv; Up	Reactive oxygen species scavenging	(Wang et al., 2016)
ANR	Kc; Lv; Up	Reactive oxygen species scavenging	(Wang et al., 2016)
LAR	Kc; Lv; Up	Reactive oxygen species scavenging	(Wang et al., 2016)
F3H	Kc; Lv; Up	Osmoregulation by accumulating flavonoids in vacuoles and cytoplasm	(Wang et al., 2016)
CHS	Kc; Lv; Up	Osmoregulation by accumulating flavonoids in vacuoles and cytoplasm	(Wang et al., 2016)

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Table 2. Continued

Gene	Mangrove species; part; expression	Functional role(s) in mangroves	Reference(s)
GAD	Kc; Lv; Up	Osmoregulation under salt stress	(Wang et al., 2016)
GDH	Kc; Lv; Up	Production of osmolyte glutamate	(Wang et al., 2016)
GOGAT	Kc; Lv; Up	Production of osmolyte glutamate	(Wang et al., 2016)
PIPK	Kc; Lv; Up	Inositol 1, 4, 5-trisphosphate (IP <sub>3</sub> ) signaling	(Wang et al., 2016)
GLYI	Rm; Lv; Up	Glutathione dependent conversion of cytotoxic methylglyoxal into lactate	(Meera and Augustine, 2020)
GLYII	Rm; Lv; Up	Glutathione dependent conversion of cytotoxic methylglyoxal into lactate	(Meera and Augustine, 2020)
GLY III	Rm; Lv; Up	Glutathione independent conversion of cytotoxic methylglyoxal into lactate	(Meera and Augustine, 2020)
KoOsmotin	Ko; Lv; Up	Osmoregulation under salt stress	(Fei et al., 2021)
MpCML40	Mp; Pm, Nucleus; Up	Help in proline accumulation and salt stress signaling	(Zhang et al., 2021)
GHBHDH	Ai; Lv, Rt; Positively selected gene	Synthesis of glutathione, an antioxidant	(Yang et al., 2015a)
OAT	Ai; Lv, Rt; Positively selected gene	Synthesis of proline, an osmolyte	(Yang et al., 2015a)
Mangrin	Sa; Lv; Up	Participates in the phytohormone-signaling during salt stress	(Feng et al., 2020)
DOG1	Ac, Cb, Ko; Fr, seed, embryo; presence of modified gene product	Loss of heme-binding property could explain emergence of crypto vivipary	(Feng et al., 2021; Qiao et al., 2020)
CYP724B1	Ko; Fr; Dw	Regulation of signaling pathways and seed germination	(Su et al., 2019)
NCED	Ko; Embryo; Dw	Suppression of ABA biosynthesis promotes early germination	(Qiao et al., 2020)
SDR	Ko; Embryo; Dw	Suppression of ABA biosynthesis promotes early germination	(Qiao et al., 2020)
AAO 1	Ko; Embryo; Dw	Suppression of ABA biosynthesis promotes early germination	(Qiao et al., 2020)
ZEP	Ko; Embryo; Dw	Suppression of ABA biosynthesis promotes early germination	(Qiao et al., 2020)
CYP707A	Ko; Embryo; Dw	Control germination and growth of propagules by degradation of ABA	(Qiao et al., 2020)
KAO	Ko; Embryo; Dw	Promotes germination of viviparous propagules	(Qiao et al., 2020)
AB14	Ko; Embryo; Dw	Promotes germination of viviparous propagules	(Qiao et al., 2020)
GA20OX - 1, 2,3	Ko; Embryo; Dw	Promotes germination of viviparous propagules	(Qiao et al., 2020)
GA3OX - 1,2,3	Ko; Embryo; Dw	Promotes germination of viviparous propagules	(Qiao et al., 2020)

Ko, *Kandelia obovata*; Am, *Avicennia marina*; Ac, *Aegiceras corniculatum*; Bg, *Bruguiera gymnorrhiza*; Kc, *Kandelia candel*; Sa, *Sonneratia alba*; Bc, *Bruguiera cylindrica*; Ai, *Acanthus ilicifolius*; Ao, *Avicennia officinalis*; Rm, *Rhizophora mucronata*; Mp, *Milletia pinnata*; Cb, *Carallia brachiata*; Chl, Chloroplast; Rt, Root; Lv, Leaves; Sht, Shoot; Fr, Fruit; Pm, Plasma membrane, Up, Upregulated, Dw, Down regulated.

The table provides species and tissue specific expression status of the genes and their potential functional roles in mangroves. The detailed version of this table is provided as a Table S1 (Table S1).

**Table 3. Non-coding RNAs, their targets, and potential roles in mangroves**

ncRNA; mangrove species	Target; analytical method(s) used	Putative function; tissue specific expression	Reference(s)
siRNA (24 nt); <i>Rhizophora apiculata</i>	Gypsy elements in LTR; computational analysis	Silencing of transposable elements by CHH methylation; Up, Lv	(Wang et al., 2018)
miR156 <sup>a</sup> ; <i>Avicennia marina</i>	Squamosa promoter-binding protein (SBPs); computational analysis and qRT-PCR validation	Transition from vegetative phase to reproductive phase by reducing apical dominance and flowering; Up, Lv, Rt	(Khraiwesh et al., 2013)
miR160; <i>Avicennia marina</i>	Auxin-responsive factor (ARF); computational analysis and qRT-PCR validation	Modulation of hormonal homeostasis to regulate root cap formation and floral organ identity; Up, Lv, Rt	(Khraiwesh et al., 2013)
miR166; <i>Avicennia marina</i>	Homeodomain leucine zipper (HD-ZIPs); computational analysis and qRT-PCR validation	Regulation of plant development including shoot meristem formation, leaf polarity, flower, root, and vascular development. Regulation of stress-responsive pathways; Up, Lv, Rt	(Khraiwesh et al., 2013; Ramachandran et al., 2017)
miR390; <i>Avicennia marina</i>	Trans-acting siRNA 3 (TAS3); computational analysis and qRT-PCR validation	Regulation of plant development including leaf polarity; Up, Lv, Sht	(Khraiwesh et al., 2013)
miR397; <i>Avicennia marina</i>	Beta-6 tubulin and laccase; computational analysis and qRT-PCR validation	Regulation of environmental stress responses. May be involved in cell division and secondary cell wall formation <sup>b</sup> ; Up, Lv	(Huang et al., 2020; Khraiwesh et al., 2013)
miR156/7; <i>Bruguiera gymnorhiza</i>	SPB box gene TFs; computational analysis	Regulation of phase transitions, flowering time, and floral identity. May regulate biosynthesis of anthocyanin <sup>b</sup> ; Up, Lv	(Lee et al., 2011; Zhang et al., 2020d)
miR396; <i>Bruguiera gymnorhiza</i>	Growth Regulating Factor (GRF) TFs; computational analysis	Regulation of plant growth and development, stress, and disease resistance; Up, Lv	(Lee et al., 2011)
miR529; <i>Bruguiera gymnorhiza</i>	Proton-dependent oligopeptide transporter (OPT); computational analysis	Regulation of environmental stress responses, transport of oligopeptides and proteins; Up, Rt	(Lee et al., 2011; Miyama et al., 2006)
TAS3 tasiRNAs; <i>Bruguiera gymnorhiza</i>	TAF5, HRGP; computational analysis and detection of miRNA cleavage site using 5' RACE	Regulation of gene expression and chromatin structure stability to withstand long-term stress exposure; Up, Lv	(Wen et al., 2016)
miR169; <i>Bruguiera gymnorhiza</i>	Nuclear factor Y (NF-Ys); computational analysis and detection of miRNA cleavage site using 5' RACE	Regulation of embryo development, seed germination, hypocotyl elongation, and responses to drought and salt stress; Dw, Lv, Flw bud	(Wen et al., 2016; Zhao et al., 2017)
miR396; <i>Bruguiera gymnorhiza</i>	Rhodanese/cell cycle control phosphatase (RHOD); computational analysis and detection of miRNA cleavage site using 5' RACE	Regulation of leaf senescence and defense responses; Dw, Lv, Flw bud	(Wen et al., 2016)

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Table 3. Continued

ncRNA; mangrove species	Target; analytical method(s) used	Putative function; tissue specific expression	Reference(s)
miR398; <i>Bruguiera gymnorhiza</i>	Cu/Zn superoxide dismutases; computational analysis and detection of miRNA cleavage site using 5' RACE	Regulate gene expression under copper deprivation and oxidative stress <sup>a</sup>	(Wen et al., 2016)
miR395; <i>Bruguiera gymnorhiza</i>	ATP sulfurylase; computational analysis and detection of miRNA cleavage site using 5' RACE	Regulate gene expression under sulfur stress and involved in pathogen defense; Up, Lv	(Anjum et al., 2015; Wen et al., 2016)
bgy_miR1001; <i>Bruguiera gymnorhiza</i>	Casein kinase II; computational analysis and detection of miRNA cleavage site using 5' RACE	Regulation of circadian rhythm <sup>a</sup> Potential role in stress-related hormone signaling and development <sup>b</sup>	(Vilela et al., 2015; Wen et al., 2016)
Bgy-tasiRNA1; <i>Bruguiera gymnorhiza</i>	ARF2; computational analysis and detection of miRNA cleavage site using 5' RACE	Specification of organ polarity and morphogenesis; Up, Lv	(Wen et al., 2016)
Bgy-tasiRNA2; <i>Bruguiera gymnorhiza</i>	ARF4; computational analysis and detection of miRNA cleavage site using 5' RACE	Specification of organ polarity and morphogenesis; Up, Lv	(Wen et al., 2016)
Bgy-tasiRNA3; <i>Bruguiera gymnorhiza</i>	TATA-binding protein-associated factor 5 (TAF5); computational analysis and detection of miRNA cleavage site using 5' RACE	Pol II transcription initiation, histone acetylation, and chromatin modification; Up, Lv	(Wen et al., 2016)
Bgy-tasiRNA4; <i>Bruguiera gymnorhiza</i>	Hydroxyproline-rich glycoprotein (HRGP); computational analysis and detection of miRNA cleavage site using 5' RACE	Regulation of abiotic and biotic stress responses; Up, Lv	(Wen et al., 2016)

Up, Up regulated; Dw, Down regulated; Lv, Leaves; Rt, Root; Sht, Shoot; Flw bud, Flower bud.

<sup>a</sup>Tissue-specific expression is not specified.

<sup>b</sup>Information regarding putative function obtained from non-mangrove study.

One of the notable outputs of epigenetic regulation is the silencing of transposable elements (TEs) which constitute a major proportion of the plant genome. Mangroves have reduced TE load and genome size which is contradictory to the previous findings that TE load increases with stress. The reduced TE loads of mangroves irrespective of the stress combinations they experience highlight their adaptation to intertidal environments. The stress-induced initial rise and subsequent shrinkage of TE load prevent mangroves from its deleterious effects and introduce new genetic components during stress adaptations (Wang et al., 2018). In *A. corniculatum*, TE load is reported to be predominant among the repetitive sequences constituting ~72% of the genome (Feng et al., 2021). RNA-mediated DNA methylation plays a crucial role in silencing highly repetitive TEs which usually involves 24-nt siRNAs (Pikaard and Mittelsten Scheid, 2014). A specific study on the mangrove *R. apiculata* shows preferential silencing of TEs by siRNA-mediated CHH methylation. The 24-nt siRNA specifically targets the Gypsy group of long terminal repeat-retrotransposon (LTR-RT; a type of TE which helped reducing overall TE loads) activation. Prevalence of stresses in the intertidal zones inhabiting mangroves might be responsible for the exposure of LTR-RT to siRNA targeting (Wang et al., 2018). Reduction of TEs in the genome of mangroves can also be correlated with smaller genome sizes as reported in *A. marina*, *R. apiculata*, *S. alba*, and *S. caseolaris*. In addition, the comparative analysis of whole genome sequences of four mangrove (*S. caseolaris*, *S. alba*, *R. apiculata*, and *A. marina*) and 29 non-mangrove plants revealed that mangroves possess less number of LTR-RT clusters. Comparable with these findings, genomes of non-mangrove plants are not subjected to such changes in transposable elements or genome sizes (Lyu et al., 2018). Latest findings on mangrove responses to UV radiation revealed that *A. marina* undergoes stringent silencing of TEs upon UV-B exposure. Contrary to this, a relaxation of TE silencing is observed in *R. apiculata* (Wang et al., 2021). To conclude, mangrove genomes adjust TE load to an optimal range to attain epigenetic control over adaptive responses.

## WHETHER THE GENOMES OF SEMI-AUTONOMOUS CELL ORGANELLES CONTRIBUTE TO MANGROVE ADAPTATIONS?

The organelles like chloroplasts and mitochondria possess their own genetic material and ribosomes to make them semi-autonomous in function. The first one, chloroplasts possess a genome of circular double-stranded DNA with inverted repeats (IR), large single copy region (LSC), and small single copy (SSC) region. Chloroplast genomes normally contain highly conserved genes crucial for plant development and polymorphisms which can be utilized for analyzing genetic diversity. In addition, they carry genes mainly involved in photosynthesis, transcription, and translation. Mangrove chloroplast genomes are also observed to be highly conserved (Han et al., 2020). All of the mangrove chloroplast genomes analyzed contained a typical quadripartite structure with IR, LSC, and SSC regions (Table 4). The other genes excluding the forelisted protein coding genes are specific for transfer RNAs and ribosomal RNAs. The genomic data of mangrove chloroplast are crucial for studying genetic diversity but whether they impart mangrove adaptive characteristics remains to be studied. Further studies must be designed to investigate the roles of chloroplast genes in mangrove adaptations.

Comparative analysis of chloroplast genomes of *Nypa fruticans*, *B. sexangula*, *Acrostichum aureus*, *A. ilicifolius*, *Acrostichum speciosum*, *R. mangle*, *Sonneratia hainanensis*, *Hernandez sonora*, *Avicennia germinans*, and *L. littorea*, suggests that convergent evolution of mangroves have no effect on chloroplast genomes (Han et al., 2020). Moreover, correlation of chloroplast genome and adaptations could not be established between mangroves and non-mangrove species (Yang et al., 2019), even though the individual gene products of the chloroplast genome may have been complemented in known adaptive responses. Hence, the so far reported protein coding genes of mangrove species need more attention to be characterized to designate the respective proteins and thus to unravel their role in stress responses. Here, we enlist the well-characterized protein encoding genes of mangrove chloroplast genomes which may have direct or indirect role in mangrove adaptations. Whole genome sequencing and comparison of chloroplast genome from 14 mangroves species reported that *A. marina* and *Heritiera littoralis* are the mangroves in which the presence of *translation initiation factor (infA)* is detected. The numbers of mononucleotide, dinucleotide, trinucleotide, tetranucleotide, pentanucleotide, and hexanucleotide simple sequence repeats vary in each of the 14 plant species and can be used as markers for genomic analyses (Shi et al., 2020). The phylogenetic analysis of three mangrove species (*L. littorea*, *Lumnitzera racemosa*, and *L. racemosa*) revealed similarity of their chloroplast genome, while only the gene number in IR regions differed. *Translation initiation factor* gene (*infA*) is completely absent in all the three chloroplast genomes and some genes under relaxed selection are *ycf2*, *ycf2*, and *maturase K (matK)* (Zhang et al., 2020c). The functional role of lost *infA* may be carried out by a copy of the nuclear initiation factor which has been replaced during the loss event (Millen et al., 2001). The evolutionary significance of the loss of *infA* is yet to be determined. Photosynthesis I and II, cytochrome *b6/f* complex, ATP synthase, and Rubisco along with small and large subunit proteins such as ribosomal protein S (*rps*) and ribosomal protein L (*rpl*) are annotated from *A. marina* chloroplast genome (Asaf et al., 2021). Another ribosomal protein gene, *rpl17* from the members of Rhizophoraceae (*R. mangle*, *B. sexangula*, *R. stylosa*, and *K. obovata*) is reported to show signs of positive selection (Han et al., 2020). The basic role of plant ribosomal proteins is in translation but they are also known for their involvement in hormone signaling and developmental processes. An *A. thaliana*-specific *rpl10A* gene is proved to be involved in ABA-induced responses (Ramos et al., 2020). Similarly, the role of *RPL23A* against drought and salt stresses has also been demonstrated (Moin et al., 2017). The *RPL* genes might be involved in similar roles in mangroves. However, further studies are required to unravel the roles of *RPL* and other chloroplastic genes in imparting stress tolerance to mangroves. *KcCSD* gene encoding Cu/Zn SOD is found in the chloroplast genome of *K. candel* which complement its cytosolic counterpart in oxidative homeostasis. When the sodium ion influx increases under prolonged salt stress, *KcCSD* genes are upregulated in order to scavenge ROS. The gene is cloned in tobacco to study its role in salinity tolerance where the transgenic tobacco plant showed increased growth rate than non-transgenic plants under salt stress (Jing et al., 2015). Cu/Zn SOD expression is increased after NaCl treatment as a response to osmotic stress (Takemura et al., 2002). Genes encoding ribosomal subunits, rRNA, DNA-dependent RNA polymerase, ATP synthase subunits, NADH dehydrogenase, cytochrome *b/f* complex, photosystem, rubisco, acetyl CoA carboxylase, envelope membrane protein, c-type cytochrome synthesis protein, protease, translation initiation factor, maturase, and elongation factors are found in the chloroplast genome of *S. hydrophyllacea* (Zhang et al., 2019). The stress-responsive functions related to most of the identified chloroplastic gene candidates are not clearly understood with an exception to *KcCSD*.

**Table 4. Comparison of mangrove chloroplast genomes**

Mangrove species	Total sequence length (bp)	Large single copy (LSC) region (bp)	Small single copy (SSC) region (bp)	Inverted repeat (IR) regions (bp)	No of genes	Protein coding genes	No of genes coding tRNA	No of genes coding rRNA	GC content (%)	Reference(s)
<i>Avicennia marina</i> (forssk.) Vierh.	147,909	88,331	17,772	20,903	112	78	30	4	38.15	(Li et al., 2020a)
	150,279	82,552	17,523	25,117	132	87	37	8	38.6	(Asaf et al., 2021)
	152,288	83,088	17,924	25,638	133	88	37	8	39	(Shi et al., 2020)
<i>Lumnitzera littorea</i> (Jack) Voigt.	159,687	88,323	18,558	26,403	130	85	37	8	37.01	(Zhang et al., 2020c)
<i>Lumnitzera racemosa</i> Willd.	159,473	88,056	18,613	26,402	130	85	37	8	36.97	(Zhang et al., 2020c)
<i>Laguncularia racemosa</i> C. F. Gaertn.	158,311	87,113	18,886	25,156	130	85	37	8	36.97	(Zhang et al., 2020c)
	160,672	89,071	18,886	26,353	130	85	37	8	37	(Shi et al., 2020)
<i>Kandelia obovata</i> Sheue, H.Y. Liu & J. Yong	168,244	94,869	20,088	26,618	129	84	37	8	34.6	(Du et al., 2019)
	160,325	91,156	15,829	26,670	128	80	38	8	35.22	(Yang et al., 2019)
	168,008	95,413	19,955	26,320	129	84	37	8	35	(Shi et al., 2020)
<i>Sonneratia apetala</i> Buch.-Ham.	153,052	87,210	18,026	23,908	131	86	37	8	37.3	(Li et al., 2019)
<i>Ceriops tagal</i> (Perr.) C.B. Robinson	164,439	92,489	20,172	26,390	134	84	42	8	35.32	(Chen et al., 2019)
	164,476	92,697	19,153	26,313	130	85	37	8	35	(Shi et al., 2020)
<i>Rhizophora stylosa</i> Griff.	164,475	92,582	19,243	26,325	131	85	38	8	34.9	(Li et al., 2019)
	163,101	91,208	19,243	26,325	129	84	37	8	35	(Shi et al., 2020)
<i>Acanthus ilicifolius</i> Lour.	150,758	82,963	17,191	25,302	128	84	36	8	38	(Xu et al., 2021)
<i>Pongamia pinnata</i> (L.) Pierre	149,635	83,795	18,534	23,653	127	84	35	8	35	(Shi et al., 2020)
<i>Excoecaria agallocha</i> L.	161,667	89,282	19,336	26,525	132	87	37	8	36	(Shi et al., 2020)
<i>Bruguiera sexangula</i> (Lour.) Poir	162,282	91,332	18,144	26,403	128	83	37	8	35	(Shi et al., 2020)
<i>Hibiscus tiliaceus</i> L.	161,318	89,283	19,717	26,159	130	85	37	8	37	(Shi et al., 2020)
<i>Heritiera littoralis</i> Aiton.	159,401	87,877	19,002	26,261	129	85	36	8	37	(Shi et al., 2020)
<i>Thespesia populnea</i> (L.) Sol. ex Corrêa	160,451	88,981	20,306	25,582	129	84	37	8	37	(Shi et al., 2020)
<i>Pemphis acidula</i> J.R. & G. Forst	160,051	89,775	18,886	25,695	131	86	37	8	37	(Shi et al., 2020)
	160,054	89,785	18,883	25,693	132	87	37	8	36.46	(Jian and Ren, 2019)
<i>Sonneratia ovata</i> Backer	153,057	87,238	18,007	23,906	130	85	37	8	37	(Shi et al., 2020)
<i>Xylocarpus moluccensis</i> (Lam.) M.Roem	159,317	87,319	17,998	27,000	131	86	37	8	38	(Shi et al., 2020)
<i>Scyphiphora hydrophyllacea</i> Gaertn. f.	155,132	85,239	18,165	25,864	132	80	36	8	37.6	(Zhang et al., 2019)
<i>Sonneratia alba</i> Sm.	153,061	87,226	18,033	23,901	106	79	24	4	37.3	(Yu et al., 2018)
<i>Hemandia nymphifolia</i> (C. Presl) Kubitzki	157,762	86,641	18,603	26,260	133	83	42	8	39.3	(Zhang et al., 2018)

Modified after Shi et al., 2020.

The second organellar genome of relevance is mitochondrial genome. The plant mitochondrial genome is comparatively larger and more complex than the animal counterparts. It has a size ranging from 200 to 2,000 kbp consisting of non-coding regions, repeats, and large introns. Contrary to the shape of the

chloroplast genome, the mitochondrial genome is not of large circular shape but mostly linear together with branched and small circular DNAs (Morley and Nielsen, 2017). In plants, some definite functions like cross-compatibility, maintenance of plant vigor, keeping up fertility, and regulating the chloroplast function are carried out by the mitochondrial genes (Chevigny et al., 2020). Mangrove mitochondrial genomes are not explored in detail till date. The mitochondrial genome size of *A. corniculatum* and *B. gymnorrhiza* is reported to be 425,282 bp and 286,503 bp, respectively. *A. corniculatum* seems to contain 39 protein-coding sequences but *B. gymnorrhiza* carries 37 instead (Zhang et al., 2020a, 2020b). Similarly, the mitogenome analysis of *S. hydrophyllacea* and *A. marina* showed 37 and 62 protein-coding genes within the total size of 354,155 bp and 579,000 bp, respectively (Chen et al., 2020b; Natarajan et al., 2021). Monodehydroascorbate reductase (MDAR), encoding an antioxidative pathway enzyme, is distinguished as a salt-tolerant gene from both *A. marina* mitogenome and chloroplast genome (Natarajan et al., 2021). The comparative analysis of chloroplastic genome and mitogenome helps to sort out the evolutionary roots of mangroves but the extent to which these non-nuclear genes take part in adaptive characteristics needs to be examined (Yang et al., 2019). Taken together, the semi-autonomous organellar gene candidates expected to involve in adaptive responses of mangrove primarily take part in antioxidative defense to achieve overall cellular homeostasis with respect to the external stress. However, further studies are required to pinpoint the exact roles of organellar genes in the unique adaptive traits that enable mangrove survival in the intertidal regions.

## MANGROVE CONSERVATION FOR THE PREVENTION OF GENETIC EROSION

Genetic diversity and population structure analysis disclose the variations in genetic structure of mangrove populations which becomes a vital part in devising conservation strategies. It is also inevitable to identify the actual cause of population decline even though the anthropogenic and climatic threats are considered as the prime forces behind population loss (Romañach et al., 2018). The threats to mangroves can also affect the closely related flora and fauna (Sandilyan and Kathiresan, 2012). Decrease in genetic diversity is higher where the mangroves are subjected to more environmental and anthropogenic threats (Sandoval-Castro et al., 2012). Investigation on such an area within a mangrove population may help identify unnoticed anthropogenic stresses (Sandilyan and Kathiresan, 2012). Analysis of DNA methylation patterns in *R. mangle* could reveal that epigenetics also play role in acquiring adaptations if the genetic diversity is low (Mounger et al., 2021). Finding the type of stress factor causing genetic/epigenetic variations makes the initial step of mangrove conservation irrespective of the nature of the adaptive feature it acquired.

Genetic diversity among the mangrove population along the north western coast of Mexico seems to be decreasing due to inbreeding and environmental pressure in the marginal population (Sandoval-Castro et al., 2012). Low genetic diversity among *S. alba* populations may have formed due to the constant shift in climatic conditions during PETM although at species level they show genetic variation (Yang et al., 2017). A study of population decline of mangrove species revealed low genetic diversity among the population of *R. apiculata* also. The change in genetic diversity diagnosed by the excess of homozygotes can be related to habitat destruction due to anthropogenic means and the subsequent inbreeding. Human activities such as logging and developments near mangrove habitats can disrupt the gene flow leading to population size reduction (Azman et al., 2020). Spatial genetic structure analysis among populations of *A. germinans* and *R. mangle* of Pacific and Caribbean coastal lines revealed significant differences in genetic structure of estuaries from the same coastline, while *A. germinans* showed higher levels of genetic diversity as compared to *R. mangle*. It is interesting that both species showed patterns of non-random distribution of genetic variance. *A. germinans* had high genetic diversity in the chloroplast genome with around 22 haplotypes observed, whereas only three are observed in the *R. mangle* population (Cerón-Souza et al., 2012). Genetic diversity of mangrove *A. officinalis* isolated from three different salinity zones namely low salinity, medium salinity, and high salinity zones varied with the level of salt stress. The medium and high salinity zones had greater genetic diversity than that of low salinity zones which indicates genetic diversity is needed for adapting to changing environmental conditions. Adaptive measures developed by the plant in high and medium salinity zones include better resorption efficiency and higher leaf vein density for nutrient retranslocation in these low nutrient availability zones (Alam et al., 2020). Restricted gene flow within the same population and high genetic divergence at species level and between populations of *A. ilicifolius* in the Indo-West Pacific zones resulted from the land barrier between the regions (Guo et al., 2020). Pollen and seed migration rates also affect gene flow and gene diversity. Pollen to seed gene flow ratio indicated that hydrochorious seed dispersal in *A. germinans* and ambophilous seed dispersal in *R. mangle*, respectively, are responsible for lower and higher genetic diversities (Cerón-Souza et al., 2012).

Together with the cause of genetic diversity, species identification serves as the second but important step of mangrove conservation. In mangroves, DNA barcoding with *rbcL* and *matK* gene sequence can help in proper identification and conservation of endangered species (Harisam et al., 2018). The mangrove restoration pivots conservation of endangered mangrove species rather than the mangrove-associated species (Sandilyan and Kathiresan, 2012). The genetic information on differences between species and their hybrids together with species diversity can be used to identify conservational units. On the other hand, information on the physical characteristics of adaptive features gives more insight into the effects of external stress (Sandilyan and Kathiresan, 2012). The review will be an important resource/information for future studies aimed at understanding the molecular biology of adaptive evolution in mangroves. Information on each and every gene candidate taking part in unique mangrove adaptive characteristics is valuable in this context. Hence, documenting the genetic constitution of all mangrove species at the earliest is a matter of concern as mangroves are disappearing at a rate faster than imaginable. Preventing the mangrove genetic erosion itself can serve as the third and final step of mangrove conservation.

## CONCLUSIONS

Mangroves are plants with specialized modifications which are a vital part of the coastal ecosystem as they provide a barrier from ocean currents, a hub of biodiversity, and goods and services for humans. The mangroves have been characterized by the emergence of highly specialized structural, morphological, and physiological modifications such as the development of pneumatophores, aerenchymae, vivipary, ultrafiltration, and salt glands and these unique features are observed only among mangroves. Although there have been many studies on underlying mechanisms of these adaptive features, this review article provides an in-depth insight into the molecular and genetic mechanisms that govern the unique adaptive traits. The evolutionary genetic architecture of mangroves gives rise to highly specialized adaptations through a series of gene/protein interactions and plant hormone-mediated signaling pathways. Epigenetic mechanisms also play an important role in regulation of adaptive characteristics whereas the chloroplastic and mitochondrial genomes are more related to phylogenetic and conservative aspects. Since each mangrove species responds differently to the climate and habitat changes, genetic and molecular studies are crucial for devising conservation strategies as they lay information on molecular level changes pointing toward adaptation and species diversity. Some of the conclusions having broad outlook for the future research are as follows

1. The crosstalk between redox homeostasis and stress-responsive anatomical changes in mangroves must be explored to open up more insight into gene networks behind mangrove stress adaptations.
2. Mangrove cells being constantly exposed to ROS, the possibility of redox signaling cannot be underestimated but need a thorough scientific investigation to portray the entire signaling root map.
3. This review highlights that many gaps still exist at almost all the molecular pathways. Instead of single-gene analysis studies, an entire pathway-specific approach would be crucial in the future to bridge the gaps that exist in the multiple pathways regulating mangrove adaptations and survival in the harsh environmental conditions.
4. The exact role of chloroplastic and mitochondrial genomes in mangrove adaptations deserves more attention to attain a clear understanding of their roles in imparting evolutionary advantages to the mangroves.
5. A comparative evaluation of different species suggest that among the various families of mangroves, those belonging to Rhizophoraceae have been studied to a great extent, still a lot more studies are needed at individual species level.
6. Development of the genetic and genomic resources and framing apt measures for mangrove conservation would be paramount to future projects aimed at mangrove research.

## ETHICAL APPROVAL

Not required.

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2021.103547>.

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## AUTHOR CONTRIBUTIONS

Ashifa Nizam: Writing - Original Draft, Visualization. Suraj Prasannakumari Meera: Writing - Review & Editing. Ajay Kumar: Conceptualization, Supervision, Writing - Review & Editing.

## DECLARATION OF INTERESTS

The authors declare that they have no known competing interests.

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