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Review

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Unique adaptations and bioresources of mangrove ecosystems

Anjana Ramesh[1], Athira Sajan[1], Mina Mobram[1], L.H. Namitha[2], N.D. Brijithlal[2], G. Prakash Williams[2]*

[1]CEPCI Laboratory and Research Institute, Kollam, Kerala, India
[2]P.G. Department of Botany and Biotechnology, Bishop Moore College, Mavelikara, Alappuzha, Kerala, India

*Corresponding author, E-mail: prakash.gw@gmail.com

Abstract

Mangroves are unique ecosystems. As they are present in a transition zone, they harbour a variety of organisms, which include microorganisms, aquatic as well as terrestrial organisms. Being present in an ever-changing and adverse environment, mangroves have developed several adaptations that make them unique. These unique features have been exploited for the isolation of various useful compounds from mangroves. The organisms associated with the mangrove ecosystem will also be well equipped to survive such extreme conditions. Microorganisms such as bacteria, fungi, actinomycetes, algae etc, survive in this changing environment, and they might be producing certain metabolites as a part of their survival mechanism, which can be exploited for the production of various compounds that are useful to mankind. Mangrove microorganisms can be used as an important source of food, medicines, enzymes, antimicrobials etc.

Key words: *Avicennia marina, Bruguiera gymnorrhiza*, mangroves, pneumatophores, *Rhizophora apiculata*, rhizosphere, vivipary.

Introduction

Mangrove ecosystems are located along the intertidal zones and estuaries of tropical and subtropical coastlines (Alongi 2018) and consist of dicotyledonous woody shrubs or trees (Hogarth 2015). Though highly dynamic and fragile, mangroves are considered among the most productive ecosystems on earth (Thatoi, Biswal 2008). They represent a transition zone between land and aquatic biomes (Patra et al. 2020) and have ecological, economic and social significance (Gopal, Chauhan 2006). Mangroves are considered as hotspots of biodiversity (https://www.nature.org/en-us/what-we-do/our-insights/perspectives/state-of-world-mangroves/). Mangroves actually represent a unique ecosystem that has a positive impact on human society, as they help in stabilizing shorelines thereby reducing the damage caused by natural disasters, and provides food, medicine, fuel and various other necessities (Giri et al. 2011; Srikanth et al. 2016).

Environmental conditions in mangrove ecosystems are rather specific (Hogarth 2015). As mangrove plants are mostly flooded with sea water, they have to cope with changing levels of salinity in addition to high temperature, relatively low air humidity and hypoxia. However, mangroves have evolved with various adaptations to exist in such harsh conditions. These include various morphological adaptations as well as production of various compounds that help them to survive. Mangroves possess unique biochemical properties that can be used as a source of novel natural products (Sachithanandam et al. 2019). Various studies have shown that compounds produced by the mangrove ecosystem have great pharmacological importance (Sadeer et al. 2022). Various bioactive compounds obtained from mangroves can be used for synthesizing biomaterials useful for environmental and biomedical applications (Vaish, Pathak 2023).

The aim of the present review was to compile information on unique biological properties of mangrove plants and mangrove-associated microorganisms in order to better understand the ecological and practical importance of mangrove ecosystems.

Distribution of mangroves

According to the satellite mapping images by the National Aeronautics and Space Administration, about 42 % of the worlds mangroves are in Asia, 21% in Africa, 15% in North and Central America, 12% in Australia and the islands of Oceania, and 11% in South America (Giri et al. 2011; Mint et al. 2019). The global land covered by mangrove forests as of 2020 is 145 068 km^2 (Jia et al. 2023). The largest area of mangroves is in Asia – in Southeast Asian countries such as Indonesia, Malaysia, Myanmar, Papua New Guinea and Thailand (Mint et al., 2019). India comes under the category of a mangrove rich country with 2.7% of the global total area of mangroves. The largest tidal mangrove forest in the world, Sundarbans, is situated in Bangladesh and India (Pramanik, Bhattacharyya 2024). Australia, along with Indonesia, Brazil and Nigeria also have a large area of mangroves, especially around residential areas (Bindiya et al. 2023).

There are about 20 families and roughly 70 species of mangroves across the world (Alongi 2009). There are mainly two categories of mangrove species: true mangroves that occur exclusively in the typical mangrove habitat and nowhere else, and mangrove associates that occur on the landward margin of mangrove forests and can also be found in non-mangrove habitats (Hogarth 2015).

Unique adaptations of mangroves

Root modifications

As mangroves are always present in a highly heterogeneous environment, where their morphological and physiological features exhibit certain unique properties that helps the plants survive. One of the most peculiar features is the branching and root system. Various root adaptations help mangrove plants to increase their physical stability to hold on to the soft sediments and also to withstand currents and storms. In order to survive under anoxic conditions, mangrove roots have developed numerous lenticels and extensive aerenchyma that help them facilitate oxygen availability (Yabuki et al. 1990). Some of the structural adaptations include pneumatophores, knee roots, stilt roots etc which aid in the ventilation of roots, and also above ground roots that have the ability to photosynthesize (Srikanth et al. 2016).

Root adaptations of various mangroves include prop roots that are seen in *Rhizophora mangle* and *Rhizophora apiculate*, which helps to anchor the plant in the substrate. Buttress roots in *Heritiera littoralis, Xylocarpus granatum, Pelliciera rhizophora* and *Ceriops* sp. provide physical support and prevent tree fall (Clair et al. 2003). Surface roots occur in *Excoecaria agallocha*, stilt roots seen in *Rhizophora stylosa*, cable roots with pneumatophores and knee roots in *Bruguiera gymnorrhiza* and *Bruguiera cylindrica*, cone roots in *Avicennia* species and pencil roots in *Sonneratia caseolaris* (Clair et al. 2003).

In some mangroves, their root to shoot ratio is relatively high with increasing salinity and the relative ratio of salt content and fresh water prevents ice formation (Ball 1988; Zhou et al. 2024). As the plants are always located in a semifluid substratum, the roots are extremely strong that aids attachment. Another peculiarity of their root system is that they can selectively permit or reject various salts and other compounds, thereby acting as a filter system. The salt exclusion mechanism of some mangrove species is possible because of an ultrafiltration mechanism occurring at the root cell membranes of cortical cells (Scholander 1968; Wang et al. 2002; Zheng et al. 1999).

Another peculiarity associated with the roots of mangroves is the presence of specialized structures called pneumatophores. These aerial roots help mangroves breathe in waterlogged soil habitats (Chen 2016). Pneumatophores emerge from the soil and grow upward, i.e. they are negatively geotropic (Sahoo 2018). They provide the respiratory needs of underground roots in anoxic soil (Hogarth 2015).

Reproductive strategy

Mangroves have a unique reproductive strategy called vivipary (precocious germination). The seeds germinate while they are still attached to the parent plant, and the seedlings are buoyant, photosynthetically competent and are transported across long distances along with the tidal waves (Nettel, Dodd 2007). Vivipary is seen in most of the mangrove families and it occurs due to low levels of abscisic acid within the embryonic tissues (Farnsworth, Farrant 1998).

In respect to reproduction, mangrove species are classified into three groups: viviparous, crypto-viviparous and non-viviparous. Crypto-vivipary is a situation when the growing embryo breaks through the seed coat but not the fruit wall. The viviparous group includes *Bruguiera, Ceriops, Kandelia,* and *Rhizophora*, crypto-viviparous group includes *Avicennia, Aegiceras*, and *Aegilitis*, and the non-viviparous group includes *Lumnitzera, Excoecaria, Barringtonia, Xylocarpus, Scyphiphora*, and *Sonneratia*. There are mainly two pollen discharge mechanisms: explosive and non-explosive. Explosive pollen discharge mechanism occurs in *Bruguiera* spp. and *Ceriops tagal*, while non-explosive pollen discharge occurs in the other mangrove species (Aluri 2022).

Salinity tolerance

Many species of mangrove possess salt glands on their leaves (Parida, Jha 2010). Salt excretion is another mechanism performed by mangroves, which includes the deposition of salt crystals on the leaf surface (Cheng et al. 2020). Depending on their salt excretion mechanism, mangroves can be classified into three groups: salt excluders, salt secretors and salt accumulators (Parida, Jha 2010). Salt excluders eliminate excess salt by ultrafiltration performed by their roots. Salt accumulation occurs by the sequestration of sodium and chloride ions into the vacuoles of storage tissue in leaves (Mimura et al. 2003). Root suberization also helps in tolerating salt stress (Cheng et al. 2020). In some species, salt is deposited also on the bark of stem and roots (Scholander 1968). It has also been found that decreased leaf size, increased thickness and increased water content in leaves are also responses to salinity (Ball 1988; Sobrado 2005). Studies have found that the viviparous propagules during their development have relatively lower salt concentration, compared to other plant parts, which could be a protection mechanism for the embryo from extreme salt concentration until its maturity (Hogarth 1999; Wang et al. 2002).

Biological properties associated with mangroves

Leaves, bark and roots of mangroves contain various valuable compounds that could be significant commercial use in pharmaceutical industries (Rajendra et al. 2016). Important biochemical properties associated with mangroves are summarized in Table 1.

Antimicrobial activity

Antimicrobial properties have been extensively studied in several mangrove species around the world. Methanol extract of *Sonneratia alba* was found to have activity against bacteria such as *Staphylococcus aureus, Bacillus cereus, Escherichia coli* and the yeast *Cryptococcus neoformans* (Saad et al. 2012; Dela Cruz Carnaje et al. 2023). *Rhizophora apiculata* and *Bruguiera gymnorrhiza* exhibit antimicrobial activity (Rajendra et al. 2016). All parts of the plant *Rhizophora apiculate*, especially their leaf and stem show bactericidal activity (Jhurani, Jadhav 2010). The mangroves A*vicennia marina, Avicennia officinalis, Bruguiera sexangula, Exoecaria agallocha, Lumnitzera racemosa*, and *Rhizophora apiculata* showed promising antibacterial activity against the pathogens *Staphylococcus aureus* and *Proteus* sp. (Abeysinghe 2010).

Antiviral and anticancer activity

Bark of *Rhizophora mucronata* and leaves of *Rhizophora apiculata* were found to exhibit antiviral activity by acid polysaccharides that inhibited the cellular binding mechanism of HIV (Premanathan et al. 1999). *Avicennia officinalis* also has shown antiviral, antidiabetic and anticancer activity among other ethnomedicinal uses (Thatoi et al. 2016; Kavunkal, Vasu 2023).

Ethyl acetate extract of the whole plant of *Acanthus ilicifolius* showed significant anticancer activity (Khajure Rathod 2011). It has also been observed that alkylated benzoquinones isolated from the stem and twigs of *Aegiceras corniculatum* had varying degrees of selective cytotoxicity against cell lines HL-60, HepG2, BGC-823, and A2780 (Li et al. 2020). Two flavonoids obtained from methanol extracts of aerial parts of *Avicennia marina* proved to be cytotoxic against the cell line BT 20 (Cerri et al. 2022).

Antidiabetic activity

A study revealed that the extract of the mangrove species *Ceriops decandra* had promising anti diabetic activity (Nabeel et al. 2010). The presence of alkaloids such as xylogranatinin, granatoin, acanthicifoline and trigonellin that can have anti-hyperglycaemic effect has been reported in the mangrove *Xylocarpus granatum* and *Acanthus* species (Li et al. 2009; Das et al. 2016). A complex polysaccharide molecule present in *Sonneratia alba* was reported to have hypoglycaemic properties (Morada et al. 2011). The anti-diabetic potential of *Avicennia marina* was found to be due to a particular saponin α-amyrin (Mahera et al. 2011; Abu Zeid 2017). Mangrove plants can be used to treat diabetes mellitus through their unique chemical properties

Table 1. Mangroves and their biological properties

Mangrove species	Activity exhibited	Active constituents	Reference
Rhizophora mucronata, Rhizophora apiculata	Antiviral	Polysaccharides	Premanathan et al. 1999
Xylocarpus granatum, Acanthus sp.	Antidiabetic	Xylogranatinin, granatoin, acanthicifoline, trigonellin	Li et al. 2009
Avicennia marina, Avicennia officinalis, Bruguiera sexangula, Exoecaria agallocha, Lumnitzera racemosa, Rhizophora apiculata	Antibacterial		Abeysinghe 2010
Rhizophora apiculata	Bactericidal		Jhurani, Jadhav 2010
Ceriops decandra	Antidiabetic		Nabeel et al. 2010
Acanthus ilicifolius	Anticancer		Khajure, Rathod 2011
Avicennia marina	Antidiabetic	α-amyrin	Mahera et al. 2011
Sonneratia alba	Hypoglycaemic property	Polysaccharide	Morada et al. 2011
Sonneratia alba	Antimicrobial		Saad et al. 2012
Rhizophora apiculata	Alpha-glucosidase inhibition		Selvaraj et al. 2015
Rhizophora apiculata, Bruguiera gymnorrhiza	Antimicrobial		Rajendra et al. 2016
Aegiceras corniculatum	Anticancer	Alkylated benzoquinones	Li et al. 2020
Avicennia marina	Anticancer		Cerri et al. 2022

(Sachithanandam et al. 2019). A study revealed that leaf extract of *Rhizophoa apiculata* exhibited significant alpha-glucosidase inhibitory activity (Selvaraj et al. 2015).

In addition, mangrove plant extracts can be considered an excellent source of various bioactive compounds, which can be used as alternatives for existing compounds, as they are safe and environment friendly. Several mangrove extracts can be used as mosquito repellents, especially against *Aedes aegypti* (Sudhir et al. 2022).

Microorganisms associated with mangroves and their benefits

A mangrove ecosystem is a reservoir of diverse microbial communities, which plays significant roles in various processes (Thatoi et al. 2013). They harbour a diverse group of microorganisms such as actinomycetes, bacteria, fungi, cyanobacteria, microalgae, macroalgae etc. (Xu 2014). Bacteria and fungi constitute about 91% of the mangrove microbiome, and the remaining 7% constitutes algae and only 2% are protozoa (Palit et al. 2022). The major reason for such a wide variety of microorganisms is the abundance of organic carbon and other nutrients. The mangrove ecosystem provides huge amounts of organic matter, which when utilized by microorganisms leads to their conversion into sources of nitrogen, phosphorus and other essential nutrients. Thus, they play a major role in the cycling of various nutrients, thereby maintaining the nutrient balance of the mangrove ecosystem (Alongi et al. 1993). The complex interactions occurring between the mangroves and their associated microorganisms play a major role in maintaining the ecological balance of the ecosystem. As the mangroves are present in a fluctuating environment, the microorganisms present there will also have the ability to adapt to such changing environmental conditions (Thatoi et al. 2013). These microorganisms may be used to produce enzymes, proteins, antibiotics, salt tolerant genes etc. that have practical use. Plastic degrading microorganisms have been isolated from mangrove soil (Kathiresan 2003). Mangrove microorganisms are very much beneficial also for agricultural practices (Kathiresan, Selvam 2006). Information on microorganisms associated with mangroves and their properties are summarized in Table 2.

Actinomycetes

Actinomycetes isolated from mangroves have wide application in industries as they can be exploited as producers of antibiotics, enzymes, enzyme inhibitors, antitumour agents etc (Rajivgandhi et al. 2024). Various antibiotic producing actinomycetes have been isolated from mangrove ecosystems. *Streptomyces albidoflavus* isolated from Pichavaram mangrove forest has exhibited antitumour activity (Kumar et al. 2005).

Among the 2000 actinomycetes isolated from mangrove sites in China, about 20% inhibited the growth of Human Colon Tumuor 116 cells, 10% inhibited the growth of *Staphylococcus aureus*, 5% inhibited *Candida albicans* and 3% inhibited protein tyrosine phosphatase 1B that is associated with diabetes. Some of these are rich sources

Table 2. Mangrove-associated microorganisms and their properties

Group	Activity exhibited	Species	Reference
Actinomycetes	Antitumor activity	*Streptomyces albidoflavus*	Kumar et al. 2005
Actinomycetes	Anti infection, antitumor		Hong et al. 2009
Actinomycetes	Antibacterial	*Micrococcus* H2, *Nocardia* H3, *Corynebacterium* H6, *Streptomyces* H8, Actinomycetes H10	Rozirwan et al. 2020
Actinomycetes	Antibacterial	*Streptomyces* strains	Lu et al. 2019
Bacteria	Nitrogen fixation	*Azospirillum, Azotobacter, Rhizobium, Clostridium, Klebsiella*	Thatoi et al. 2013
	Phosphate solubilization	*Bacillus licheniformis, Chryseomonas luteola, Pseudomonas stutzeri*	Ravikumar et al. 2007
	Sulfur oxidation	*Chromatiales, Desulfobacterales*	
	Cellulose degradation	*Bacillus cereus, Bacillus licheniformis, Bacillus pumilus*	
	Biofertilizer activity	*Azotobacter chroococcum, Azotobacter vinelandii, Azotobacter beijerinckii*	
Fungi (manglicolous fungi)	Production of cellulose, amylase, pectinase, xylanase etc.		Thatoi et al. 2013
Fungi	Aquaculture, medical applications	*Aureobasidium* spp.	Jia et al. 2020
	Polyunsaturated fatty acid production	*Schizochytrium* sp. LU310	Patel et al. 2016
Algae	Biological indicator for metal contamination	*Enteromorpha*	Say et al. 1990
Algae	Atmospheric carbon and nitrogen fixation		Nedumaran et al. 2008

of anti-infectious compounds and can also be used for treating neurodegenerative diseases (Hong et al. 2009).

Five isolates of actinomycetes (*Micrococcus* H2, *Nocardia* H3, *Corynebacterium* H6, *Streptomyces* H8, and *Actinomycetes* H10) obtained from mangrove sediments of South Sumatra, Indonesia showed strong inhibitory activity against *Escherichia coli* (Rozirwan et al. 2020). Four *Streptomyces* strains (B475, B486, B353, and B98) isolated from mangroves of Maowei Sea showed strong inhibition against Gram-positive bacteria (Lu et al., 2019). Also, new antibiotics were discovered from the *Streptomyces* B475 strain. These included quinomycin A, quinomycin monosulfoxide etc., which are included in the group quinoxaline-type antibiotics.

Bacteria

Among the microorganisms of a mangrove ecosystem, the most important contributor of biomass and productivity is bacteria. The population of bacteria is several fold higher than that of fungi (Kathiresan, Qasim 2005). Bacteria performing several ecological functions have been isolated from mangrove ecosystems. These include nitrogen fixing bacteria (*Azospirillum, Azotobacter, Rhizobium, Clostridium*, and *Klebsiella*), phosphate solubilizing bacteria (*Bacillus licheniformis, Chryseomonas luteola* and *Pseudomonas stutzeri*), sulfur oxidizing bacteria (Chromatiales, Desulfobacterales), cellulose degrading bacteria (*Bacillus cereus, Bacillus licheniformis, Bacillus pumilus*), methanogenic bacteria, photosynthetic anoxygenic bacteria etc. (Vazquez et al. 2000; Tabao, Monsalud, 2010; Santos et al. 2011; Thatoi et al. 2013). Bacteria of the rhizospheric region of mangroves are the most beneficial, and they perform various activities like fixing molecular nitrogen, solubilizing phosphates, ammonia production, plant growth regulator production etc. (Patra et al. 2020). Thus, there is a beneficial interaction between plants and microorganisms either directly or indirectly. Furthermore, the quantity of bacteria in the rhizosphere soil is relatively large compared to any other region of the soil (Gislin et al. 2018). Also, the rhizosphere microorganisms exhibit high levels of antagonistic activity (Khandan, Janardhana 2015).

In addition to those mentioned above, some microorganisms associated with mangroves have biofertilizer effects. A study showed that some *Azotobacter* strains (*Azotobacter chroococcum, Azotobacter vinelandii* and *Azotobacter beijerinckii*) isolated from mangrove soils of Pichavaram exhibited biofertilizer effect which resulted in the increased growth of the mangroves *Ceriops decandra* and *Avicennia marina* (Ravikumar et al. 2007).

Fungi

A large number of fungal communities inhabit the mangrove ecosystem – they are commonly called manglicolous fungi. They include both marine and terrestrial fungi (Thatoi et al. 2013), which are classified on the basis of their relation to the position of the plant (Kohlmeyer 1969). Mangrove ecosystems can be considered as biodiversity hotspots for marine fungi (Shearer et al. 2007). In order to decompose organic matter, mangrove fungi produce a large number of extracellular degradative enzymes such as cellulose, amylase, pectinase, xylanase etc., which have wide applications in the industry (Behera et al. 2017). Among the different types of mangrove fungi, endophytes were found to be potential candidates that produce novel bioactive metabolites useful in pharmaceutical and nutraceutical industries (Thatoi et al. 2013). Several studies have reported the presence of antimicrobial metabolites in mangrove saprophytic fungi (Deshmukh et al. 2018).

An exopolysaccharide pullulan produced by different species of *Aureobasidium* spp. is found to exhibit physical, chemical and rheological properties and has potential application in the industry (Van Bogaert et al. 2009). Liamosins produced by *Aureobasidium* spp. have applications in aquaculture and medical industries. *Schizochytrium* sp. LU310 isolated from mangroves can be used as a source of polyunsaturated fatty acids such as docosahexaenoic acid. Another mangrove associated fungus, *Pestalotiopsis* sp. NCi6, has been found to secrete two salt-responsive lytic polysaccharide monooxygenases. (Patel et al. 2016; Jia et al. 2020).

Algae

Algae are also associated with mangroves all over the world and they also contribute significantly to mangrove ecology (Yokoya et al. 2023). The roots, hard substrates and soft mud are substrates for algal growth. The marine algae associated with mangroves can be used as food for both humans and livestock (Bandaranayake 1998). Enteromorpha, a benthic algae found in salt marshes, is used as a biological indicator for metal contamination (Say et al. 1990). Certain algae associated with mangroves have the ability of fixing atmospheric carbon and nitrogen and thereby constitute one of the most important marine resources (Nedumaran et al. 2008).

Mangroves: current scenario

Despite being one among the most productive ecosystems, mangroves all around the world are under great threat. Mangrove ecosystems have been declining at a faster rate than any other ecosystems. Mangroves are being destroyed due to several reasons. Anthropogenic activities are the most predominant reasons for their destruction. Mangroves are being destroyed for timber production and their wetlands are used for aquaculture, thereby converting large areas to shrimp and rice aquaculture ponds. Over the past 50 years, about 20 to 35% of the global mangroves have disappeared and it has been warned that if no measures are taken for their conservation, mangroves could disappear from the planet, thereby putting an end to all the benefits they provide (Richards, Friess, 2016; Friess et al. 2020; Goldberg et al. 2020).

However, between the late 20th and early 21st century, the mangrove loss rate has reduced globally by 2 to 4% per year (Friess et al. 2019). Several factors have contributed to this reduction, including changing industrial practices, increased focus on rehabilitation, improved monitoring and data access, increased recognition of the ecological services mangroves provide and others (Friess et al. 2016). This is actually a positive sign and if we are maintaining this pace for mangrove conservation and management, then we can continue to reduce the rate of mangrove loss and with effective rehabilitation techniques, even new areas of mangroves can be gained.

Mangroves are nowadays considered as very valuable ecosystems by scientists as well as by coastal dwellers because of the immense properties associated with them. Several researchers are working on mangroves to discover biologically active compounds with various properties. Studies have already proved that mangroves and their associated microbes possess various properties like antibacterial, anticancer, antiviral, antidiabetic and so on. These ecosystems were neglected before, without knowing their potential, and huge areas associated with mangroves have been destroyed for various purposes. Coastal development, aquaculture, agriculture and climate change are some of the threatening factors that paved the way to their deterioration. But nowadays, the scientific community has understood the value of mangroves and the benefits they are contributing to the environment and as a result various campaigns have been launched with the aim of conservation of mangroves.

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