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REVIEW ARTICLE

Biodiversity and biotechnological potential of microorganisms from mangrove ecosystems: a review

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Abstract Mangrove forests occurring at the interface of terrestrial and marine ecosystems represent a rich biological diversity of plants, animals and microorganisms. Microbes, being an important component of the mangrove environment, not only play a very critical role in creating and maintaining this biosphere but also serve as a source of biotechnologically valuable and important products. By participating in various steps of decomposition and mineralization of leaf litter, microbes make an essential contribution to the productivity of the mangrove ecosystem. They able to recycle nutrients, produce and consume gases that affect global climate, destroy pollutants, treat anthropogenic wastes and can also be used for biological control of plant and animal pests. Microorganisms from mangrove environments are a major source of antimicrobial agents and also produce a wide range of important medicinal compounds, including enzymes, antitumor agents, insecticides, vitamins, immunosuppressants, and immune modulators. However, the phylogenetic and functional description of microbial diversity in mangrove ecosystems has not been addressed to the same extent as for other environments. Even though the mangrove ecosystem is very rich in microbial diversity, less than 5% of species have been described; in many cases neither their ecological role nor their application potential is known. Recently developed technologies in molecular biology and genetics offer great promise to explore the potential of microbial diversity. Hence, the present paper makes an attempt to review the microbial diversity in mangrove ecosystems and explore their potential applications in various fields such as agriculture, pharmaceutical, industrial, environmental and medical sciences.

Keywords Microbial diversity · Mangrove · Ecological role · Biotechnological potential

Introduction

Mangroves are unique inter-tidal ecosystems of the tropical and sub-tropical regions of the world that support genetically diverse groups of aquatic and terrestrial organisms. Nearly 60–70% of the world's tropical and subtropical coastlines are covered with mangroves, which are known to be highly productive ecosystems of immense ecological value. Despite being fragile and sparsely distributed, these ecosystems are highly productive all over the world (Thatoi and Biswal 2008). They protect and stabilize coastal zones, nourish and nurture the coastal water with nutrients. These ecosystems are characterized by periodic tidal flooding, which makes environmental factors such as salinity and nutrient availability highly variable resulting in unique and

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specific characteristics. Apart from flora and fauna, microbial diversity characterizes one of the important communities of these ecosystems. Because of the abundance of carbon and other nutrient contents, the mangrove ecosystem harbors a large number of microbial communities, which can adapt to the moderate saline and fluctuating environmental conditions. These microbial communities play an important role in cycling of nutrients such as carbon, nitrogen, sulfur and phosphorous, and thus control the chemical environment of the mangrove ecosystem (Alongi et al. 1993). Microbial activity is also responsible for major nutrient transformations within mangrove ecosystems (Alongi et al. 1993; Holguin et al. 1999). In tropical mangroves, bacteria and fungi constitute 91% of the total microbial biomass, whereas algae and protozoa represent only 7% and 2%, respectively (Alongi 1988). Complex interactions of these microbes maintain the harmony of different biogeochemical processes and sustain the nutritional status and ecological balance. Free living bacteria, fungi and yeasts have been reported to play a significant role in the formation of detritus in mangrove ecosystems (Maria and Sridhar 2002). Various groups of bacteria are usually present in the ecosystem (Holguin et al. 2001), performing various activities like photosynthesis, nitrogen fixation, methanogenesis (Das et al. 2006). Several studies have shown the uniqueness of mangrove sediments with respect to their microbial composition (Gray and Herwig 1996; Urakawa et al. 1999). Studies on microbial diversity in the mangrove sediments are important in understanding the process of biogeochemical cycling and pollutant removal (Roy et al. 2002). The microbial diversity of mangrove ecosystems can also provide information on their ecological role and unique biotechnological potential in the field of agriculture, industry, medicine and pharmaceuticals (Lageiro et al. 2007). During the past decade, the development of molecular techniques using nucleic acids has led to many new findings in studies of microbial ecology (Amann et al. 1995). This approach avoids the limitations of traditional culturing techniques for assessing microbial diversity in natural environments. Notwithstanding the existing knowledge of microbes and microbial processes, we are still only scratching the surface of microbial diversity, which needs to be explored for the judicious and gainful utilization of this nature's treasure. The particular conditions of a mangrove, and adaptation of bacterial species to such conditions, represents an important source of biotechnological potential resources to be exploited (Sivaramakrishean et al. 2006). Microorganisms from mangrove ecosystems contain useful enzymes, proteins, antibiotics and salt tolerant genes of much biotechnological significance. This review is an attempt to consolidate the latest studies on mangrove microbial biodiversity and to explore the immense biotechnological potential of mangrove microbial flora in various fields.

Microbial diversity of mangrove ecosystems

Biodiversity can be defined as the variability of life at the genetic, species and ecosystem levels of organization. The mangrove ecosystem provides a unique environment harboring diverse groups of microorganisms. All microbial forms, such as bacteria, fungi, cyanobacteria, microalgae, macroalgae and fungus-like protists, have been reported in this ecosystem. The common bacterial groups of the mangroves are sulfate-reducing (*Desulfovibrio*, *Desulfotomaculum*, *Desulfosarcina*, *Desulfococcus* sp., etc.), N_2-fixing (*Azospirillum*, *Azotobacter*, *Rhizobium*, *Clostridium*, *Klebsiella* sp., etc.), phosphate-solubilizing (*Bacillus*, *Paenibacillus*, *Xanthobacter*, *Vibrio proteolyticus*, *Enterobacter*, *Kluyvera*, *Chryseomonas* and *Pseudomonas* sp., etc.), photosynthetic anoxygenic (*Chloronema*, *Chromatium*, *Beggiatoa*, *Thiopedia*, *Leucothiobacteria* sp., etc.) and methanogenic (*Methanoccoides methylutens* sp., etc.) bacteria. In addition, various groups of fungi, such as ligninolytic, cellulolytic, pectinolytic, amylolytic and proteolytic fungi as well as actinomycetes are present in mangrove ecosystems (Kathiresan and Bingham 2001). Among the algae, groups like *Chlorophyta*, *Chrysophyta*, *Phaeophyta*, *Rhodophyta* and *Cyanophyta* dominate the mangrove ecosystem (Sen and Naskar 2003).

Algae

In mangroves, algal species occur abundantly in planktonic, benthic and periphytic forms. The roots (pneumatophores) of mangrove trees provide a favorable habitat for 50% of the total algal species, the hard substrates for 30% and the soft mud for 20% of the species (Kathiresan and Qasim 2005). Certain algae are associated frequently with mangroves and are considered as characteristic of the ecology. Algal species belonging to the genera *Bostrychia*, *Cologlossa* and *Catenella* are commonly present on the roots and trunks of the mangroves. Species of the genera *Rhizoclonium*, *Enteromorpha* and *Cladophora* normally exist in the sediment along with the cyanobacteria (*Lyngbya* and *Anacystis*), benthic diatoms and the sulfate-reducing bacteria (Kathiresan and Qasim 2005). This microbial community forms a ‘biofilim” that activates the attachment of algae to the mangrove trees. The factors governing the occurrence of these algae are mainly those of a microclimate prevailing in the swamps. Most of these algae are small filament forms that are fairly resistant to desiccation as well as to high salinity.

Algae are widespread in mangrove habitats all over the world. Cordeiro-Marino et al. (1992), recorded 150 algal taxa from New World mangroves, with highest diversity in the red algal groups with 78 species, and lowest in the brown algae with less than 15 species. Maximum algal diversity with 109 species and a high degree of endemism (about 70%) of red algae was reported along the Caribbean coast (Kathiresan and Qasim 2005). In the Indian context, about 558 species of algae from seven families are known to occur (Kathiresan and Qasim 2005). The east coast is represented by 264 species, whereas the west coast has 326 species (Kathiresan and Qasim 2005). Only 71 species have been recorded so far from the Andaman and Nicobar Islands (Kathiresan and Qasim 2005). From the Sundarbans mangroves of West Bengal, 150 different species of algal flora were identified, belonging to different groups viz., *Chlorophyta* (39 species), *Chrysophyta* (44 species), *Phaeophyta* (2 species), *Rhodophyta* (15 species) and *Cyanophyta* (50 species) (Sen and Naskar 2003). Algal species such as *Gloeocapsa* sp., *Chlorella* sp., *Ulva* sp*.*, *Anabaena* sp., *Spirogyra* sp., *Oscillatoria* sp., *Phormidium* sp. were identified from mangroves of Bhitarakanika, Orissa (Mishra 2010).

Fungi

Mangrove forests are biodiversity 'hotspots' for marine fungi (Shearer et al. 2007). Although the mangrove trunks and aerating roots are submerged, permanently or intermittently, the upper parts of the roots and trunks are rarely or never wetted by the salt water. Thus, terrestrial fungi and lichens occupy the upper part of the trees and marine species occupy the lower part; at the interface there is an overlap between marine and terrestrial fungi (Sarma and Hyde 2001). Since they were first reported from mangrove roots in Australia by Cribb and Cribb (1995), there has been considerable increase in information on mangrove-associated fungi. The latest estimate of marine fungal species in the world is 1,500, which excludes lichens and many fungi that are newly isolated or inadequately described (Hyde et al. 1998). Out of large number of estimated fungal species, Hyde listed only 120 species of fungi from 29 mangrove forests around the world (Hyde 1990). These included 87 *Ascomycetes*, 31 *Deuteromycetes* and 2 *Basidiomycetes*. There are some 169 fungal species from Malaysia (Alias et al. 1995), 44 fungi associated with standing senescent *Acanthus ilicifolius* from Mai Po mangrove, Hong Kong (Sadaba et al. 1995), 76 species from Pearl River Estuary, China (Vrijmoed et al. 1991), 91 fungi from Egyptian Red Sea (Abdel-Wahab 2005) and 112 species reported from the Bahamas islands (Jones and Abdel-Wahab 2005). In the Indian context, about 48 fungal species were reported to occur in decomposing *Rhizophora* debris in Pichavaram, South India (Ravikumar and Vittal 1996). Seven species of fungi that exist on mangrove leaf surfaces in the Sundarbans of West Bengal have been reported by Pal and Purkayastha (1992). From a Mangalvan mangrove ecosystem, 31 fungal isolates were recorded from soil, and 27 species from decaying mangroves; 7 species from floating plants were reported, with dominance of *Aspergillus* followed by *Penicillium*, *Fusarium* and *Trichoderma*. Sarma and Hyde (2001) reported 73 species of fungi from the Krishna estuaries of India. Similarly, 31 fungal species have been studied from sediment and 27 species from decaying leaves, stems, roots and pneumatophores of an estuarine mangrove ecosystem in Cochin (Prabhakaran et al. 1990). Raghukumar et al. (1995) studied the colonization of thraustochytrids on leaf litter of *Rhizophora apicula* at Caorao mangrove, Goa. Higher groups of fungi have been reported from the mangrove woods on the Maharashtra coast, with 41 species of *Ascomycetes*, 2 *Basidiomycetes*, and 12 *Deuteromycetes* with predominance of *Massarina velatospora* (Borse 1988). In Bhitarkanika, Orissa (India), Gupta et al. (2009a, b) reported the population status of fungi associated with the phyllopsphere of different mangrove plants viz., *Avicennia*, *Aegiceras*, *Bruguiera*, *Ceriops*, *Excoecaria*, *Heritiera*, *Kandelia*, *Rhizophora* and *Sonneratia*. A total of 33 fungi from Godavari and 67 fungi from the Krishna estuary, India, was reported by Venkateswara Sarma et al. (2001). Relatively few fungi have been reported as pathogens of mangrove plants compared to the number of saprophytic fungi identified on decaying mangrove wood and leaves (Hyde et al. 1998). The intertidal fungus *Cytospora rhizophorae* is thought to be parasitic on *Rhizophora* spp. prop root (Kohlmeyer and Kohlmeyer 1979). *Phomopsis mangrovei*, which is probably pathogenic, was described from dying prop roots of *Rhizophora apiculata* in Thailand (Hyde 1996). An intertidal *Phytophthora* species was described to cause terminal dieback of *Avicennia marina* (Pegg et al. 1980; Gadek 1998) and a *Phytophthora* species was also found to be pathogenic on *Avicennia marina* var. *resinifera* in New Zealand (Maxwell 1968). *Halophytophthora* species were also thought to be responsible for diseased mangrove forests over vast areas in Sydney (Garrettson-Cornell and Simpson 1984).

Endophytic fungi were found in large numbers in mangrove environments. More than 200 species of endophytic fungi—mainly *Alternaria*, *Aspergillus*, *Cladosporium*, *Colletotrichum*, *Fusarium*, *Paecilamyces*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Phyllosticta* and *Trichodema*—were isolated and identified from mangroves (Liu et al. 2007). Chinese researchers surveyed and reported the occurrence of several arbuscular mycorrhizal fungi (AMF) on root system mangroves plants in QinZhou Bay, Guangxi, China (Wang et al. 2003). In India, 25 endophytic fungi comprised of 3 ascomycetes, 20 mitosporic fungi and 2 sterile fungi were recovered from 2 halophytes (*Acanthus ilicifolius* and *Acrostichum aureum*) of a west coast mangrove habitat. Endophytic fungi were also isolated from leaves of *Rhizophora apiculata* and *Rhizophora mucronata*, two typical mangrove plants grown in the Pichavaram mangrove of Tamil Nadu, Southern India (Suryanarayanan et al. 1998). Vazquez et al. (2000) first isolated a marine phosphate-solubilizing fungus, *Aspergillus niger*, together with several phosphate-solubilizing bacterial strains, from the rhizosphere of black mangrove *Avicennia germinans*, and proposed the production of organic acids by these mangrove rhizosphere microorganisms as a possible mechanisms involved in the solubilization of insoluble calcium phosphate. Arbuscular mycorrhizal (AM) colonizing mangrove and mangrove associates from river estuary of Ganges have been reported by Sengupta and Chaudhuri (2002).

Actinomycetes

Actinomycetes have been looked upon as potential sources of bioactive compounds and are the richest sources of secondary metabolites. The mangrove ecosystem is a largely unexplored source of actinomycetes with the potential to produce biologically active secondary metabolites (Hong et al. 2009). Several reports from different geographical locations around the world have described the occurrences of actinomycetes in different mangrove habitats. Eccleston et al. (2008) reported the occurrence of actinomycetes belongs to genus *Micromonospora* from the Sunshine Coast in Australia. A rifamycin-producing *Micromonospora* from mangroves of the South China Sea was reported by Huang et al. (2008) and Xie et al. (2006). Several genera of actinomycetes, such as *Actinomadura*, *Microbispora*, *Nonomuraea*, *Actinoplanes*, *Micromonospora*, *Verrucosispora*, *Arthrobacter*, *Isoptericola*, *Micrococcus, Microbacterium, Nocardia*, *Rhodococcus* and *Streptomyces* were reported from mangrove soils and plants in China (Hong et al. 2009). Similarly, genera like *Brevibacterium*, *Dermabacter*, *Kocuria*, *Kytococcus*, *Microbacterium*, *Nesterenkonia* and *Rothia* were reported from a mangrove sediment in Brazil (Dias et al. 2009). Ara et al. (2007) reported novel actinomycetes (*Nonomuraea maheshkhaliensis*) from a mangrove rhizosphere mud in the southern area of Bangladesh.

In the Indian context, Sivakumar (2001) reported 23 actinomycete species from Pichavaram mangrove, with most species identified belonging to the genus *Streptomyces*. Laksmanaperumalsamy et al. (1978) isolated 518 *Streptomyces* strains from mangrove environments of Porto Novo. As many as 107 different actinomycetes were isolated from marine sediments off the Konkan coast of Maharashtra by Gulve and Deshmukh (2011), and 17 actinomycetes isolates were identified from the Karangkadu mangrove forest of Tamil Nadu, India by Ravikumar et al. (2011b). Sahu et al. (2005) reported several Streptomycetes, viz., *Streptomyces alboniger*, *S. violaceus*, *S. moderatus* and *S. aureofasciculus* from the Vellar estuary on the south east coast of India. Similarly, Ravikumar et al. (2011a, 2011b) reported the biodiversity of actinomycetes from sediments of the Manakkudi mangrove ecosystem of the southwest coast of India. Sivakumar et al. (2005) reported the occurrence of *Streptomyces albidoflavus*, which has antitumor properties, from the Pichavaram mangrove. A number of *Streptomyces*, such as *S. albidoflavus*, *S. atroolivaceous*, *S. auranticus*, *S. canus*, *S. chromofuscus*, *S. exfoliates*, *S. griseoluteus*, *S. helstedii*, *S. lavenduale*, *S. longisporoflavus*, *S. luridus*, *S. lydicus*, *S. nogalator*, *S. pactum*, *S. prasinosporus*, *S. purpureus*, *S. tubercidus*, *S. versoviensis*, *S. viridochromogenes* and *S. xanthochromogenes* have been reported by Gupta et al. (2009a, b) from different plant species of the Bhitarkanika mangrove forest of Orissa, India. Phosphate-solubilizing actinomycetes such as *Streptomyces galbus* in the Vellar Estuary of the Parangipettai estuarine environment on the south east coast of India have been reported by Sahu et al. (2007), and five phosphate-solubilizing *Streptomyces* spp. from the mangrove ecosystem of Bhitarkanika, Orissa, India were reported by Gupta et al. (2010). Distribution of actinomycetes in the Sundarbans mangrove of West Bengal, India has been reported by Mitra et al. (2008). This relatively large distribution of actinomycetes species throughout the world's mangrove ecosystems appears to reason that mangrove forests represent a treasure trove of actinomycetes.

Bacteria

Next to trees, bacterial flora dominates the biomass and productivity of mangrove forests (Kathiresan and Qasim 2005). Among microbes, bacterial populations in mangroves are many fold greater than those of fungi (Kathiresan and Qasim 2005). Microbially generated detritus in mangrove ecosystems acts as the major substrate for bacterial growth in mangroves (Bano et al. 1997). The bacteria may act as primary decomposers that utilize dissolved organic substances at low concentration and assimilate dissolved inorganic substances like nitrate and phosphate. Bacteria with different ecological roles have been reported from mangrove ecosystems.

N_2 fixing bacteria

Nitrogen fixation is a process of conversion of gaseous forms of nitrogen (N_2) into combined forms, i.e., ammonia or organic nitrogen by some bacteria and cyanobacteria. Free-living as well as symbiotic microbes known as diazotrophs fix N_2 into proteins. Nitrogen-fixing (diazotrophic) microorganisms can colonize both terrestrial and marine environments. In mangrove ecosystems, high rates of nitrogen fixation have been associated with dead and decomposing leaves (Mann and Steinke 1992), pneumatophores (Hicks and Silvester 1985; Toledo et al. 1995) and the rhizosphere soil (Holguin et al. 1992). N_2 fixation in mangrove sediments is likely to be limited by insufficient energy sources. The low rates of N_2 fixation by heterotrophic bacteria detected in marine water are probably due to lack of energy sources. Nitrogen fixation by heterotrophic bacteria can be regulated by specific environmental factors such as oxygen, combined nitrogen and the availability of carbon source to support energy requirements. Energy for N_2 fixation can also be derived from leaves and roots decomposed by non-diazotrophic microflora that colonize dead mangrove leaves (Zuberr and Silver 1978). Nitrogen-fixing bacteria such as members of the genera *Azospirillum*, *Azotobacter*, *Rhizobium*, *Clostridium* and *Klebsiella* were isolated from the sediments, rhizosphere and root surfaces of various mangrove species. Nitrogen-fixing bacteria, *Azotobacter* species are repeatedly isolated from sediments of Pichavaram mangroves, and they were more in the mangrove habitats than in the backwaters and estuarine systems (Lakshmanaperumalsamy 1987). Several strains of diazotrophic bacteria such as *Vibrio campbellii*, *Listonella anguillarum*, *Vibrio aestuarianus* and *Phyllobacterium* sp. were isolated from the rhizosphere of mangroves in Mexico (Holguin et al. 1992). N_2-fixing bacteria such as *Azotobacter* sp. which can be used as biofertilizers, are abundant in mangrove habitats of Pichavaram (Ravikumar 1995). Two halotolerant N_2-fixing *Rhizobium* strains were isolated from root nodules of *Derris scandens* and *Sesbania* species growing in the mangrove swamps of Sundarbans (Sengupta and Choudhury 1990). Nitrogen-fixing cyanobacteria such as *Aphanocapsa* sp., *Nodularia* sp., and *Trichodesmium* sp., were isolated from Pichavaram mangroves (Ramachandran and Venugopalan 1987). N_2-fixing bacteria are efficient at using a variety of mangrove substrates despite differences in carbon content and phenol concentrations (Pelegri and Twilley 1998). However, their abundance may be dependent on physical conditions and mangrove community composition. Both symbiotic and asymbiotic N_2-fixing bacteria play a vital role in the nitrogen enrichment of mangrove ecosystems (Holguin et al. 2001). One may conclude from the available information that N_2 fixation is a major bacterial activity in mangrove ecosystems, second only to carbon decomposition of detritus by sulfate-reducing bacteria.

Phosphate-solubilizing bacteria

Muddy mangrove soils have a strong capacity to absorb nitrates and phosphates carried by the tides (Hesse 1962). Most of the inorganic phosphate present in the sediment is bound to calcium, iron and aluminium ions as insoluble phosphates (Alongi et al. 1992). Fungi and inorganic phosphate-solubilizing bacteria present in the mangrove rhizosphere participate in releasing soluble phosphate into pore water (Vazquez et al. 2000). Certain bacteria exhibit high phosphatase activity, capable of solubilizing phosphate (Sundararaj et al. 1974). Phosphorous is one of the major plant nutrients, second only to nitrogen (Vassileva et al. 1998), so phosphate-solubilizing microorganisms (PSMs) play an important role in supplementing phosphorus to plants and allowing the sustainable use of phosphate fertilizers (Gyaneshwar et al. 1998). In an arid mangrove ecosystem in Mexico, nine strains of phosphate-solubilizing bacteria, such as *Bacillus amyloliquefaciens*, *B. atrophaeus*, *Paenibacillus macerans*, *Xanthobacter agilis*, *Vibrio proteolyticus*, *Enterobacter aerogenes*, *E. taylorae*, *E. asburiae* and *Kluyvera cryocrescens* were isolated from black mangrove (*Avicennia germinans*) roots. A further three strains, viz. *B. licheniformis*, *Chryseomonas luteola* and *Pseudomonas stutzeri* were isolated from white mangrove (*Laguncularia racemosa*) roots (Vazquez et al. 2000). Very little information is available about phosphate-solubilizing bacterial diversity and their activity in Indian mangroves. However, some studies related to phosphate-solubilizing bacterial activity have been done in the Vellar estuary at Parangipettai on the south eastern coast of India (Kathiresan and Selvam 2006), the Bhitarkanika mangrove environment of Orissa (Gupta et al. 2007; Mishra 2010), the Sundarban mangroves of West Bengal (Ramanathan et al. 2008) and the Great Nicobar mangroves of India (Kothamasi et al. 2006). A preliminary isolation and screening of phosphate-solubilizing bacteria from mangrove soil from Bhitarkanika, on the Orissa coast, by Gupta et al. (2007) revealed the presence of 33 soil bacteria showing phosphate-solubilizing capacity. Ramanathan et al. (2008) quantified phosphorus-solubilizing bacteria along with cellulose-degrading and N_2-fixing bacteria from Sundarban mangroves of India. Kothamasi et al. (2006) reported two strains of phosphate-solubilizing *Pseudomonas aeruginosa* (designated GM01 and GM02) in mangrove soils of Great Nicobar. Nine phosphate-solubilizing bacteria have been isolated and characterized phenotypically from mangrove soil of Bhitarkanika (Mishra 2010). Genera of phosphate-solubilizing bacteria, like *Pseudomonas*, *Bacillus*, *Corynebacterium*, *Vibrio*, *Micrococcus* and *Alcaligenes*, were studied by Venkateswaran and Natarajan (1983) in mangrove biotopes in Porto Novo, Chennai water and sediment. Endophytic phosphate-solubilizing bacteria were isolated from leaf samples of mangrove plants of Pichavaram, Tamil Nadu by Gayathri et al. (2010).

Sulfur-oxidizing bacteria

Bacteria also play a major role in the chemical and biological redox reactions that create the sulfur cycle. Sulfur and sulfide-oxidizing bacteria generate sulfate, which is used by sulfate-reducing bacteria (SRB) as an alternative electron acceptor in anaerobic respiration to create hydrogen sulfide. SRB cycle hydrogen sulfide through the atmosphere for use by anaerobic photosynthetic bacteria and sulfur-oxidizing bacteria, while returning carbon dioxide to the atmosphere (Holmer and Storkholm 2001). Mangrove sediments are mainly anaerobic with an overlying thin aerobic sediment layer. Degradation of organic matter in the aerobic zone occurs principally through aerobic respiration, whereas in the anaerobic layer decomposition occurs mainly through sulfate-reduction (Sherman et al. 1998). Sulfur-oxidizing bacteria play an important role in the detoxification of sulfide in sediments. Symbiotic sulfur-oxidizers, e.g., those within members of the bivalve family Lucinacea, are commonly found in muddy mangrove areas (Liang et al. 2006). Sulfate reduction accounts for almost 100% of the total emission of CO_2 from the sediment (Kristensen et al. 1991). Some sulfur-oxidizing bacteria like Gammaproteobacteria, e.g., *Chromatiales*, and Deltaproteobacteria, e.g., *Desulfobacterales*, were reported from oil-contaminated soil of Brazilian pristine mangrove sediment (Santos et al. 2011; Holguin et al. 2001). The bacterial diversity present in sediments of a well-preserved mangrove in Ilha do Cardoso, located in the extreme south of the São Paulo State coastline, Brazil, was assessed using culture independent molecular approaches [denaturing gradient gel electrophoresis (DGGE)]. The data revealed a bacterial community dominated by Alphaproteobacteria (40.36% of clones), Gammaproteobacteria (19.28% of clones) and Acidobacteria (27.71% of clones) besides minor components of Firmicutes, Actinobacteria and Bacteroidetes (Dias et al. 2010). Some free-living and symbiotic sulfur oxidizing bacteria were reported from the Futian mangrove swamp of China (Liang et al. 2006). In Florida, SRB were the most numerous bacterial group in the rhizosphere of *Rhizophora mangle* and *A. germinans* mangroves, reaching a population density of 10^6 cfu g^{-1} fresh weight (Zuberr and Silver 1978). In Goa's mangrove (India), 10^3 cfu g^{-1} dry sediment of SRB, mostly spore-forming species, were associated with mangroves (Saxena et al. 1988). Further, In Goa's mangroves, eight species of SRB such as *Desulfovibrio desulfuricans*, *Desulfovibrio desulfuricans aestuarii*, *Desulfovibrio salexigens*, *Desulfovibrio sapovorans*, *Desulfotomaculum orientis*, *Desulfotomaculum acetoxidans*. *Desulfosarcina variabilis* and *Desulfococcus multivorans* were isolated and tentatively classified within four different genera (Loka Bharathi et al. 1991). In mangrove sediments, availability of iron and phosphorus may also depend on the activity of SRB (Holguin et al. 2001). It appears that, as the main decomposers of organic matter in anaerobic sediments, SRB play a major role in the mineralization of organic sulfur and production of the soluble iron and phosphorus used by organisms in mangrove ecosystems.

Cellulose-degrading bacteria

Cellulose is the primary product of photosynthesis in terrestrial environments and the most abundant renewable bioresource product in the biosphere (Zhang and Lynd 2004). Cellulose biodegradation by cellulases and cellulosomes, produced by numerous microorganisms, represents the major carbon flow from fixed carbon sinks to atmospheric CO_2, and is very important in several agricultural and waste treatment processes (Haight 2005). In anaerobic environments, which are rich in decaying plant material, decomposition of cellulose is brought about by complex communities of interacting microorganisms (Odum and Heald 1972). As the substrate, i.e., cellulose, is insoluble, bacterial and fungal degradation occurs exocellularly to degrade cellulose into carbon and energy sources that are required by other microorganisms present in the mangrove environment. Several marine bacterial species such as *Rhodospirillum rubrum*, *Cellulomonas fimi*, *Clostridium stercorarium*, *Bacillus polymyxa*, *Pyrococcus furiosus*, *Acidothermus cellulolyticus*, *Saccharophagus degradans* have been reported as degrading cellulose (Taylor et al. 2006). Five promising cellulose-producing bacteria such as *Bacillus cereus*, *Bacillus licheniformis*, and *Bacillus pumilus* and *Bacillus* sp., have been reported from mangroves in the Philippines (Tabao and Moasalud 2010). Sediment associated with dense Sunderban mangroves showed highest counts of cellulose-degrading bacteria in comparison to other bacterial diversity (Ramanathan et al. 2008). Compared to other bacterial groups, much less information is available on the diversity of cellulose-degrading bacteria from mangrove ecosystems, which may be due to the lack of suitable technologies for their isolation and identification. A detailed study is required to assess the diversity of cellulose-degrading bacteria from various mangrove ecosystems.

Photosynthetic anoxygenic bacteria

Two main types of photosynthetic bacteria are seen in mangrove ecosystems, viz., purple sulfur bacteria (PSB; family Chromatiaceae), and purple non-sulfur bacteria (PNB; family Rhodospirillaceae, strains belonging to *Rhodopseudomonas* spp.,). These bacteria are capable of using light to grow, fix nitrogen and release hydrogen gas in this environment. PSB range in color from pink to purple and contain bacteriochlorophyll *a* as their major pigment. These phototrophic anaerobes require sulphide, which they oxidise to sulphate for growth. Carbon dioxide is the usual source of cell carbon, but they also utilise various organic acids as carbon sources and are usually distributed widely in sulfide-rich reducing environments such as mangroves (Vethanayagam 1991). PNB range in color from brown to red and also contain bacteriochlorophyll *a* as their major pigment. They have the ability to utilize a remarkably wide spectrum of reducing carbon compounds, like malate or succinate, as electron donors as well as carbon sources for growth. Sulfur-rich mangrove ecosystems, with their mainly anaerobic soil environment, provide favorable conditions for the proliferation of these bacteria. The predominant bacteria belonging to this group in the mangrove ecosystem of Cochin (India) were identified as members of the genera *Chloronema*, *Chromatium*, *Beggiatoa*, *Thiopedia* and *Leucothiobacteria* (Vethanayagam and Krishnamurthy 1995). In mangrove on the coast of Red Sea in Egypt, 225 isolates of PNB, belonging to 10 species of 4 different genera, were identified. Nine of the ten species inhabited the rhizosphere and root surface of the trees. The most common bacteria (*Rhodobacter* and *Rhodopseudomonas*) were detected in 73% and 80% of the sample, respectively (Shoreit et al. 1994). Some of the anoxygenic photosynthetic bacteria were also diazotrophic. Although there is as yet no published evidence, one can hypothesise that photosynthetic anoxygenic bacteria—the predominant photosynthetic organisms in anaerobic environments—contribute substantially to ecosystem productivity (Saho and Dhal 2009).

Methanogenic bacteria

An important characteristic of mangrove sediments is the absence of oxygen at a few millimeters below the surface (Lyimo et al. 2002). This lack of oxygen, coupled with the abundance of organic matter, creates an optimal environment for several groups of anaerobic organisms, such as SRB and methanogens (Dar et al. 2008). Since the presence of these groups in most coastal sediments is selected by the redox potential (Dar et al. 2008), these groups are expected to be found in discrete niches. However, these organisms are known to share similar niches in organic matter (OM)-rich environments like mangroves (Oremland et al. 1982). Niche superimposition between SRBs and methanogens is restricted to certain substrates, such as hydrogen and acetate (Oremland et al. 1982). Simple substrates (e.g., methanol, mono-di-trimethylamine) are important for methanogens (Lyimo et al. 2002), but not for SRB, which are capable of degrading more complex substrates, such as long-chain and aromatic hydrocarbons (Muyzer and Stams 2008). The presence of SRB limits the proliferation of these bacteria (Ramamurthy et al. 1990). There are several reports of methanogenic bacteria occurring in mangrove ecosystems, such as a strain of methanogenic bacterium, *Methanococcoides methylutens* (Mobanraju et al. 1997) and four strains of unidentified thermotolerent methanogenic bacteria isolated from the sediment of a mangrove forest (Marty 1985). A methanogenic bacterium, *Methanococcoides methylutens*, was isolated and characterized from the sediment of the mangrove environment of Pichavaram, southeast India (Mobanraju et al. 1997). Lyimo et al. (2008) also reported the methanogenic bacteria *Methanococcoides methylutens* and *Methanosarcina semesiae* from sediment samples of Tanzanian mangrove, and Taketani et al. (2010) reported the occurrence of methanogenic bacteria such as *Methanopyrus kandleri* and *Methanothermococcus thermolithotrophicus* from a pristine tropical mangrove soil of Brazil.

Ecological role of microorganisms in mangrove environment

Mangrove ecosystems provide large quantities of organic matter to adjacent coastal waters in the form of detritus, which serves as a nutrient source and is the base of an extensive food web. The diverse microbial communities living in mangrove ecosystems continuously transform nutrients from dead mangrove vegetation into sources of nitrogen, phosphorus and other nutrients that can be used by mangrove plants (Fig. 1). In turn, plant root exudates serve as a food source for the microorganisms living in the ecosystem. The degradation of mangrove vegetative material that produces detritus can be defined as organic matter in the active process of decomposition. It is rich in energy and contains a large active microbial population—both attached and free living (Odum and Heald 1975a). In addition to bacteria and fungi, other organisms may also colonize the vegetative material and contribute to detritus formation (D'Croz et al. 1989). Microscopic examination of decomposing mangrove leaves reveals a complex community composed of bacteria, fungi, protozoa and microalgae (Odum and Heald 1975b).

Bacteria are responsible for most of the carbon flux in tropical mangrove sediments. The element carbon, which forms the basis of all organic matter, undergoes a constant cycle in nature by various heterotrophic bacteria. The latter process most of the energy flow and nutrients and act as a carbon sink. Roughly 30–50% of the organic matter in mangrove leaves are leachable, containing water soluble compounds such as tannins and sugars (Cundell et al. 1979). The remaining fraction of organic matter consists of structural polymers such as lignocelluloses, which are used directly by the bacteria present in the soil and sediment of the mangrove. Nitrogen—a constituent of protein—is cycled in aquatic environments by several bacteria. The nitrate present in sediments, and derived from the degradation of nitrogenous organic compounds, is probably converted to ammonium ions by bacteria and is then assimilated by plants and bacteria. This process conserves the nitrogen within the ecosystem (Rivera-Monroy et al. 1995a, b). However, high rates of denitrification have been found in mangrove ecosystems into which wastewater are discharged, suggesting a correlation between denitrification rates and nitrate concentration (Rivera-Monroy et al. 1995b). Fixation of molecular nitrogen is carried out intracellularly by various bacteria, e.g., *Azotobacter*, *Clostridium*, etc. Some mangrove ecosystems are nutrient deficient especially in nitrogen and phosphorus (Sengupta and Choudhury 1991). Usually, phosphates precipitate because of the abundance of cations in the interstitial water of mangrove sediments, making phosphorus largely unavailable to plants. As potential suppliers of soluble forms of phosphorus, phosphate-

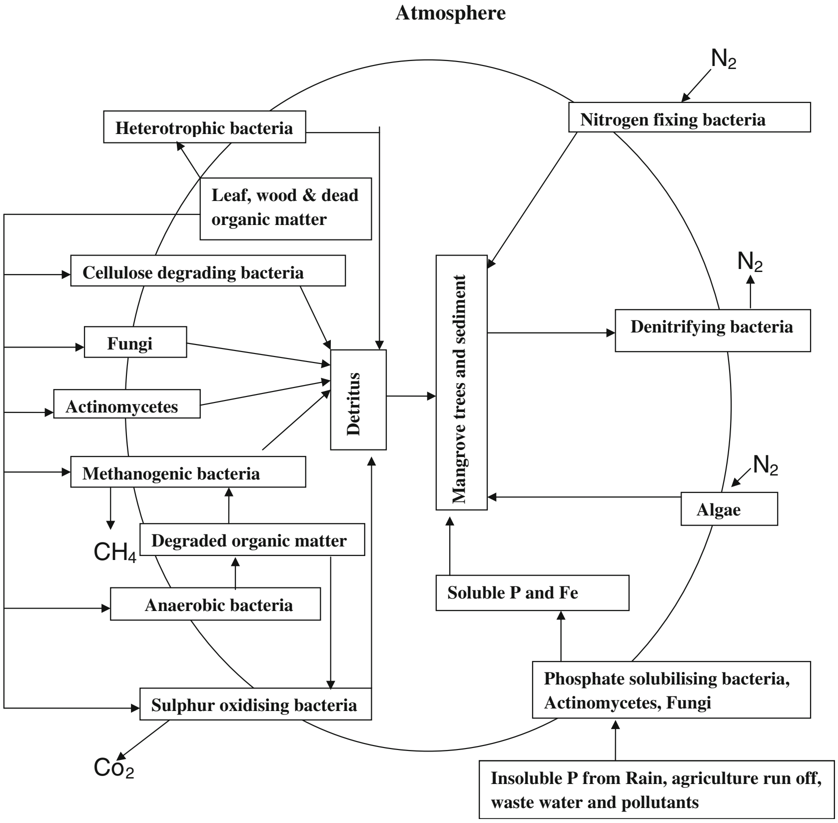

Fig. 1 Conceptual model of ecological role of microbes in a mangrove ecosystem

solubilizing bacteria would have a great advantage for mangrove plants. Microorganisms also play an important part in sulfur transformations in mangrove ecosystems. Mangrove sediments are mainly anaerobic, with a thin overlying aerobic sediment layer. Degradation of organic matter in the aerobic zone occurs principally through aerobic respiration, whereas in the anaerobic layer decomposition occurs mainly through sulfate-reduction (Nedwell et al. 1994; Sherman et al. 1998). Previous investigations also suggest that sulfate-reduction may be an important pathway of organic matter mineralization in the organic-rich deposits typical of mangrove forests (Alongi et al. 1998). When sulfate is reduced by SRB, soluble sulfur compounds such as H_2S and HS are produced. These soluble sulfur compounds react with iron, reducing Fe (III) to Fe (II) and yielding pyrite (FeS_2). Reduction of Fe (III) to Fe (II) releases soluble phosphate. It appears that SRB, as the main decomposers of organic matter in anaerobic sediments, play a major role in the mineralization of organic sulfur and in the production of soluble iron and phosphorus used by organisms in mangrove ecosystems. SRB can also contribute to the well-being of the ecosystem by fixing N_2 (Holguin et al. 2001).

Fungi are decomposers of dead organic substrates associated with the decay of mangrove leaves (Fig. 1) (Nakagiri et al. 1996). Their importance lies in their ability to aggressively degrade lignocelluloses. They may be important in the degradation of dead animals and animal parts. Marine fungi are important pathogens of plants and animals and also form symbiotic relationships with other organisms (Hyde et al. 1998). Mangrove fungi decompose vegetative material and thereby allow secondary colonization by bacteria and yeasts that further decompose the organic matter (Matondkar et al. 1981). In an Indian mangrove, the first colonizers of fallen mangrove leaves were fungi and thraustochytrids (fungi-like unicellular protists). Degradation of fallen mangrove vegetation starts immediately after its colonization by fungi and bacteria residing in the sediment and may last for 2–6 months, or more for degradation of wood (Steinke et al. 1990).

Phytoplankton and benthic micro-algal communities make an important contribution to the functioning of the mangrove environment. Due to the tidal influence and mixing of fresh and marine water in the mangrove ecosystem, several species of green-, and blue-green algae and seaweeds enter mangrove waters. Certain algae, which are colonised frequently and submerged in the surface area of sediments, roots, aerial roots, branches and trunks of mangrove, constitute one of the commercially most important marine resources, having the unique characteristic of fixing atmospheric carbon and nitrogen (Nedumaran et al. 2008). Algae and cyanobacteria also act as primary producers in the food chain of mangrove ecosystems. They harness solar energy and transform inorganic substances into food for other organisms. The consumption of food (phytoplankton) by the benthic organism, with their rapid assimilation of local carbon sources highlights the importance of mangrove algal species in influencing carbon cycling and increasing the productivity in estuaries. Algal flora probably plays an important role in stabilizing and improving the physical properties of the soil by aggregating particles and adding organic matter to the ecosystem.

Besides bacteria, algae and fungi, actinomycetes are also reported to contribute to the breakdown and recycling of organic compounds. The production of several enzymes, such as cellulolytic, proteolytic, amylolytic, lipolytic, chitinolytic, phosphate-solubilizing activities, has been reported from marine actinomycetes (Sivakumar et al. 2007), which play a role in biodegradation of organic matter, thereby enhancing the productivity of the marine environment. Along with the phosphatase enzyme, actinomycetes play a major role in solubilizing phosphate in estuarine ecosystems and increasing the soluble phosphate concentration, thereby enhancing plant growth and increasing productivity (Sahu et al. 2007). Actinobacteria also play an important role by supplying food for other organisms by producing secondary metabolites that enhance the growth of juvenile fish, shrimp and prawn in the ecosystem (Sivakumar et al. 2007).

Biotechnological potential of mangrove microorganisms

Microbial diversity is the key to human survival and economic wellbeing and provides a huge reservoir of resources that we can utilize for our benefit. Mangrove microorganisms have proven to be an important source of food, feed, medicine, enzymes and antimicrobial substances (Lin et al. 2001; Maria et al. 2005). Both halotolerant and halophilic bacteria and other microbes from mangrove ecosystem have large numbers of industrial applications in terms of their unique enzymes (Sabu 2003) that are capable of producing biosurfactants (Yakimov et al. 1999), bioplastics (Steinbüchel and Fuchtenbusch 1998), compatible solutes (Margesin and Schinner 2001), natural bioproducts and other commercially important products. Filamentous fungi—the principal commercial sources of xylanolytic enzymes—have many industrial uses, such as in paper manufacturing, animal feed, bread making, juice preparation, the wine industry and in xylitol production (Polizeli et al. 2005). Marine algae are the only source of industrially important phycocolloids like agar, carrageenan and alginate (Shanmugam and Mody 2000). They are also reported to have blood anticoagulant, anti-tumor, anti-mutagenic, anti-complementary, immunomodulating, hypoglycemic, antiviral, hypolipidemic and anti-inflammatory activities. Actinomycetes isolated from mangrove habitats are a potentially rich source of anti-infection and anti-tumor compounds and of agents for treating neurodegenerative diseases and diabetes (Hong et al. 2009). Besides the above, mangrove microorganisms have wide applications in the agricultural industry as well as in the production of various secondary metabolites (Table 1) for human use , as described below.

Agricultural applications

Plant growth promotion

It has been already reported that the mangrove microorganisms are beneficial for agriculture (Kathiresan and Selvam 2006). The rhizosphere soil of mangrove plants harbors a large number of beneficial bacteria with a large number of agricultural applications (Kathiresan and Selvam 2006). These strains have the ability to (1) fix nitrogen, (2) solubilize phosphate, (3) produce ammonia, and (4) produce the plant growth hormone indole acectic acid (IAA). Two strains identified from rhizosphere soil of mangroves viz., *Azotobacter vinelandii* and *Bacillus megaterium* have shown their ability to enhance mangrove seedlings (Kathiresan and Selvam 2006). Soil bacteria present in root regions are known to enhance plant growth. This beneficial effect is mediated through either direct or indirect mechanisms. The direct effects are commonly attributed to the supply of biologically fixed nitrogen and the production of plant hormones such as auxins. The indirect effects are suppression of bacterial, fungal and nematode pathogens, and production of siderophores, ammonia, antibiotics and volatile metabolites (Glick 1995). Further, it has been suggested that halophilic nitrifying bacteria can be used for removal of salinity and nitrate from waste water for recycling (Denariaz et al. 1989). The purified water could be used for irrigation of plants grown in arid soils. One of the problems with saline and hypersaline lands such as salt-affected soils is the relatively low microbial activity in these soils, which affects the vegetal and crop productivity of that soil. Therefore, the isolation of active bacteria from saline soil will allow the use of these bacteria in the reclamation of saline soils. The N_2-fixing bacteria isolated from saline soil could be good candidates for use to improve the fertility of reclaimed arid and saline soils (Zahran et al. 1995). The inoculation of plants with plant-growth-promoting bacteria is a common tool in agriculture to enhance crop yields (Bashan and Holguin 1997).

Biopesticides

Natural marine products have the potential to replace chemical pesticides and other agents used to maximize crop yields and growth (Cardellina 1986). Nowadays, reports about mangrove fungi also reveal that many of them are able to produce insecticidal metabolites. According to Xiao et al. (2005), 188 marine-derived fungi were collected from

Table 1 Natural products from mangrove microorganisms and their biotechnological applications

Natural product	Sources	Application	Reference
Xylanolytic enzyme	*Aspergillus niger, A. aculeatus, A. awamori, A. fumigates, Penicillium brasilianum, Chaetomium thermophile, Humicola insolens, Humicola lanuginosa, Humicola grisea, Melanocarpus albomyces* and *Bacillus* sp.	Paper manufacturing, animal feed, bread making, juice and wine industries and xylitol production	Polizeli et al. 2005
Phyllacoid, agar, carrageenan and alginate	*Codium fragile, C. latum, C. dwarkense, C. tomentosum*	Blood anticoagulant	Shanmugam and Mody 2000; Srivastava and Kulshreshtha 1989
Ethyl acetate extract, broth extract	Fungi	Biopesticide	Xiao et al. 2005; Chen et al. 1893
Polyketide synthases (PKSs)	Halophilic bacteria	Biosynthesis of secondary metabolites such as Erythromycin, Rapamycin, Tetracycline, Lovastatin and Resveratrol	Ventosa and Nieto 1995
Catalase, peroxidase, oxidase, polyphenol oxidase and ascorbic acid oxidase	*Pseudomonas aeruginosa, P. alcaligenes, Methylococcus* sp.	Industrial application	Mishra 2010
Amylase, protease, esterase and lipases	*Vibrionales, Actinomycetales* and *Bacillales*	Industrial application	Armando et al. 2009
Phytase	*Bacillus circulans, B. licheniformis, B. pantothenicus*	Industrial application	Joseph and Paul Raj 2007
Lipopeptides and glycolipids	*Bacillus subtilis* and *Pseudomonas aeruginosa*	Bio-surfactant	Pornsunthorntawee et al. 2008.
Auranticins A and B.	*Preussia aurantiaca*	Antimicrobial	Poch and Gloer 1989
Aigialomycins A-E, hypothemycin	Fungus, *Aigialus parvus* BCC 5311	Antimicrobial	Isaka et al. 2002
Secondary metabolites	Actinomycetes	Anti-tumor, anti-cancer and anti-infection properties	Hong et al. 2009
Xyloketals A (**1**), B (**2**), C (**3**), D (**4**), and E **(5)**	*Xylaria* sp.	Inhibitor of acetylcholine esterase (bioactive compound)	Lin et al. 2001
Isoflavone and prostaglandin analog	*Phomopsis* sp., *Paecilomyces* sp., *Sargassum* sp., *Halorosellinia* sp.	Anti-cancer	Tao et al. 2010
Poly aromatic hydrocarbon and oil degrading enzyme	*Pseudomonas, Shewanella, Sphingomonas, Arthrobacter Pseudomonas, Marinobacter, Alcanivorax, Microbulbifer, Sphingomonas, Micrococcus, Cellulomonas, Dietzia* and *Gordonia*	Bioremediation	Desai et al. 2010; Brito et al. 2006; Ramsay et al. 2000; Yu et al. 2005; Ke et al. 2003; Ventosa et al. 1998; Mishra et al. 2011
Laccase	*Basidiomycetes*	Bioremediation	D'souza et al. 2006; Sabu 2003
Phosphatase	*B. licheniformis, Chryseomonas luteola, Pseudomonas stutzeri, Aspergillus niger* etc.	Agriculture	Vazquez et al. 2000; Gyaneshwar et al. 1998
L-Asparaginase	*Halococcus*	Industrial	Sudha 1981
Xylanase, ligninase	*Aspergillus niger* and *Phlebia* sp.	Industrial	Li et al. 2002
Biosurfactant	*Leucobacter, B. subtillis, P. aeruginosa,*	Industrial	Saimmai et al. 2011
Enniating G	*Fusarium* sp.	Antimicrobial	Lin et al. 2002a
Enalin A & B	*Verruculina enalia*	Antimicrobial	Lin et al. 2002b
2-Pyronone derivative	*Nocardia* sp.	Bioactive compound	Lin et al. 2001
Azapilones, P-terphenyles, shearinines D-K	*Penicillium* sp.	Bioactive compound	Huang et al. 2011; Xu et al 2007
β-Carboline, adenosine, 8-hydroxyl-3, 5-dimethyl-isochroman-1-one	Fungi	Antitumor	Song et al. 2004

the sediment in Zhoushan Sea area, the mangrove at Yunxiao and jiulongjang estuary in Fujian Province, China, of which the ethyl acetate extract of strain 164 exhibited a strong lethal effect on nematode *Rhabditis* sp. Chen et al. (2003, 2006) isolated an endophytic fungus, *Kandelia candel* from an estuarine mangrove on the South China Sea coast, the broth extract of which exhibits cytotoxicity towards NCI4460 and Bel-7402, and high activities against *Heliothis armigera* (Hüehner) and *Sinergasilus* sp. As the potentiality of mangrove-associated fungi in insecticidal activity has been investigated sporadically, continued research and development in this area will result in the discovery of new natural pesticides. The high potential of mangrove fungal metabolites has been anticipated as an alternative source of novel pesticide compounds. Also in Australia, *Bacillus thuringiensis*, which exhibits insecticidal activity against mosquito larvae of *Anopheles maculatus, Aedes aegypti* and *Culex quinquefasciatus*, has been isolated from mangrove sediments (Lee and Seleena 1990).

Industrial applications

Enzymes

Mangrove microorganisms have a diverse range of enzymatic activity and are capable of catalyzing various biochemical reactions with novel enzymes. Especially, halophilic microorganisms possess many hydrolytic enzymes (amylases, nucleases, phosphatases, and proteases) and are capable of functioning under conditions that lead to precipitation or denaturation of most proteins (Ventosa and Nieto 1995). It is believed that sea water, which is saline in nature and chemically closer to human blood plasma, could provide microbial products, in particular enzymes, that could be safer (i.e., having no or less toxicity or side effects) when used for therapeutic applications in humans (Sabu 2003). The hydrolase enzymes produced by halophilic bacteria are currently of commercial interest (Ventosa and Nieto 1995). Polyketide synthases (PKSs) are a class of enzymes involved in the biosynthesis of secondary metabolites such as Erythromycin, Rapamycin, Tetracycline, Lovastatin and Resveratrol, which have all now been isolated and purified from halophilic bacteria. A halophilic bacterium (*Halococcus*) producing L-asparaginase was also reported from a mangrove environment (Sudha 1981). From Brazil mangrove sediment, *Vibrionales* appeared to be the predominant enzyme-producing group within the community when compared with other groups (*Actinomycetales* and *Bacillales*), mainly for the production of amylase and protease (Dias et al. 2009). The order *Vibrionales* has been revealed to be metabolically versatile with a high production of enzymes. An isolate of *Vibrio fluvialis* from mangrove sediments was used to produce an alkaline extracellular protease with high efficiency for use in industrial detergents (Venugopal and Saramma 2006). Mishra et al. (2010) evaluated and reported the activity of some stress enzymes such as catalase, peroxidase, oxidase, polyphenol oxidase and ascorbic acid oxidase from six Gram-negative bacteria isolated from mangroves of Bhitarkanika, Orissa, India. Bacteria isolated from mangrove sediment of Brazil were found to produce diverse extracellular enzymes such as amylase, protease, esterase and lipases (Dias et al. 2009). Joseph and Paul Raj (2007) reported five phytase-producing *Bacillus* strains from mangrove ecosystems of Kochin, Kerala, India. Three bacterial and one fungal strain producing tanase have been isolated from the mangrove forest of North malbar, Kerla, India. Wu (1993) identified 15 genera (42 strains) of fungi from mangroves in the Tansui Estuary near Taipei, Taiwan, and found that most of the *ascomycetes* were able to secrete a wide range of enzymes potentially capable of decomposing mangrove litter. Raghukumar et al. (2004) reported that a mangrove fungus, *Aspergillus niger*, can produce a thermostable, cellulose-free alkaline xylanase that showed activity in biobleaching of paper pulp and its crude enzyme with high xylanase activity could bring about bleaching of sugarcane bagasse pulp by a 60-min treatment at 55°C. A marine hypersaline-tolerant white-rot fungus, *Phlebia* sp. MG-60, screened from mangrove stands (Li et al. 2002), has shown excellent lignin degrading ability. It can degrade more than 50% of lignin incubated with whole sugarcane bagasse and the whole sugarcane bagasse might be used to produce animal feed after fermentation (Li et al. 2003).

Biosurfactants

Biosurfactants are getting much more attention compared to chemical surfactants owing to mild production conditions, lower toxicity, higher biodegradability and environmental compatibility (Mulligan 2009). All these qualities of biosurfactants have prompted their numerous applications in environmental protection as well as in the food, cosmetic, biopesticide and pharmaceutical industries (Singh and Cameotra 2004). Based on the types of biosurfactant-producing microbial species and the nature of their chemical structures, biosurfactants can be categorized into four main groups: lipopeptides or lipoproteins, glycolipids, phospholipids, and polymeric surfactants (Fathabad 2011). Among these four groups, the most common biosurfactants that have been isolated and studied are the lipopeptides produced by *Bacillus subtilis* strains, and the glycolipids produced by *Pseudomonas aeruginosa* strains (Pornsunthorntawee et al. 2008). Biosurfactants have advantages over their chemical counterparts because they are bio-degradable, have low toxicity, are effective at extreme temperatures or pH values and show better environmental compatibility (Mulligan 2009). Recently the *Leucobacter komagatae* 183 strain, isolated from mangrove sediment in Trang, southern Thailand, was evaluated as a potential biosurfactant producer (Saimmai et al. 2011).

Pharmaceutical applications

Antimicrobial compounds

The need for diversity and the development of new classes of antimicrobial compounds is increasing, due to trends in antibiotic resistance among different strains of bacteria, fungi and other microorganism, which are causing serious problems in the containment of infectious diseases. A significant number of reports have focused on antimicrobial metabolites isolated from mangrove saprophytic fungi. A fungal strain *Preussia aurantiaca* isolated from mangrove forest was found to synthesize two new despidones (Auranticins A and B) that display antimicrobial activity (Poch and Gloer 1991). Aigialomycins A–E, new 14-membered resorcylic macrolides, were isolated together with a known hypothemycin from the mangrove fungus, *Aigialus parvus* BCC 5311 (Isaka et al. 2002). Enniating G—a novel compound with a structure of cyclohexapeptide was also isolated from the culture broth of the mangrove fungus *Fusarium* sp., (Lin et al. 2002a; Lin and Zhou 2003; You et al. 2006), and displays antitumor, antibiotic, insecticidal and phytotoxic activity. An ascomycete, *Verruculina enalia*, is a common tropical species found on mangrove wood worldwide, reported to produce two new phenolic compounds, enalin A and B, with hydroxylmethyl furfural and three cycloidpeptides from its fermentation broth. Enalin A is a coumaranone—a type of compound distributed widely from microorganisms to higher plants and having antimicrobial, antifungal, phytotoxic and antidiabetic activities (Lin et al. 2002b) Among the mangrove fungi, more and more mangrove endophytes now have been researched, and more and more antimicrobial metabolites have been isolated. One of them is Cytosporone B, which shows broad activities against fungi. In addition to fungi, Wiwin Retnowati (2010) reported an actinomycete *Streptomyces* sp., from mangrove soil in the eastern coast of Surabaya, Indonesia, capable of producing a series of antibiotics that strongly inhibit the growth of Gram-positive and Gram-negative bacteria. Santhi and Jebakumar (2011) reported some *Streptomyces* sp., from mangrove sediment of Manakudi estuary, India, exhibits potent antimicrobial effects against methicillin-resistant *Staphylococcus aureus* (clinical isolate) and methicillin-susceptible *S. aureus* and *Salmonella typhi*.

Bioactive compounds

It is encouraging that bioactive compounds have been obtained from Mangrove plants, fungi, bacteria including actinomycetes (Cheng et al. 2009). Actinomycetes isolated from mangrove habitats are a potentially rich source for the discovery of anti-infection and anti-tumor compounds, and of agents for treating neurodegenerative diseases and diabetes (Hong et al. 2009). Mangrove ecosystems have been considered a "hot-spot" for newer and better drugs naturally produced by the microorganisms living in this environment. In the mangroves situated around the coast of China and surrounding islands, Hong et al. (2009) compiled more than 2,000 fungi-like bacteria or actinomycetes with the potential to synthesize biologically active secondary metabolites that conferred anti-tumor, anti-cancer and anti-infection properties. Using morphological, biochemical and molecular identification techniques and screening tests, approximately 20% showed activity against the growth of human colon tumor 116 cells, whereas only 3% inhibited the protein PTP1B associated with diabetes. Interestingly, it was discovered that, in general, most of the bioactive strains were found in plant tissues although more isolates were identified in rhizophere soils. Lin et al. (2001) also reported three new 2-pyranon derivatives from the mangrove actinomycetes *Nocardiopsis* sp., A00203. Sivakumar et al. (2005) reported a *Streptomyces albidoflavus* from the pichavaram mangrove that showed antitumor properties. Five unique metabolites,

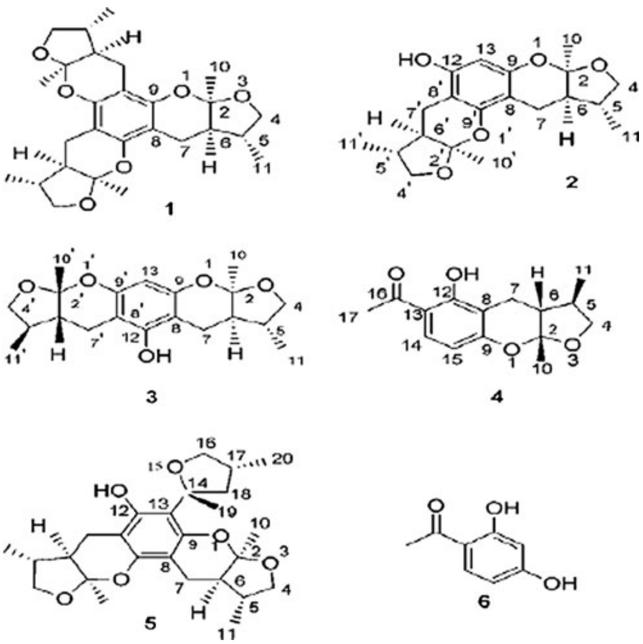

Fig. 2 Five unique metabolites, xyloketals A (**1**), B (**2**), C (**3**), D (**4**), and E **(5),** and the unknown **6** were isolated from mangrove fungus *Xylaria* sp. (no. 2508), obtained from the South China Sea by Lin et al. (2001)

xyloketals A (**1**), B (**2**), C (**3**), D (**4**), and E **(5)** (Fig. 2) were isolated from mangrove fungus *Xylaria* sp. (no. 2508), obtained from the South China Sea. The structures of these compounds were elucidated by spectroscopic and X-ray diffraction experiments. Xyloketal A is a ketal compound with C3 symmetry and xyloketals B–E are its analogues. It was found that xytoketal C slowly rearranged to xytoketal B in DMSO-d_6 solution at room temperature. Xyloketal A exhibited the activity of inhibiting acetylcholine esterase (Lin et al. 2001). Similarly, Tao et al. (2010) reported Isoflavone and Prostaglandin analog compounds (Fig. 3) from mangrove fungi isolated from the South China Sea that appeared to be promising for treating cancer patients with multidrug resistance, which should encourage more efforts to isolate promising candidates for further development as clinically useful chemotherapeutic drugs from mangrove microorganisms. Huang et al. (2011) reported eight secondary metabolites (Fig. 4), including three new azaphilones (chermesinones A–C, **1**–**3**), three new *p*-terphenyls (6′-*O*-desmethylterphenyllin, **4**; 3-hydroxy-6′-*O*-desmethylterphenyllin, **5**; 3″-deoxy-6′-*O*-desmethylcandidusin B, **7**), and two known *p*-terphenyls (**6**, **8**), were isolated from the culture of the mangrove endophytic fungus *Penicillium chermesinum* (ZH4-E2). Terphenyls **4**, **5**, and **6** exhibited strong inhibitory effects against α-glucosidase and Terphenyls **7** and **8** showed inhibitory activity towards acetylcholinesterase.

Eight new indole triterpenes named shearinines D–K, along with shearinine A, paspalitrem A, and paspaline, have been isolated from the mangrove endophytic fungus *Penicillium* sp., Shearinines D, E, and (with reduced potency) G exhibit significant in vitro biocking activity on large-conductance calcium-activated potassium channels (Xu et al. 2007). β-Carboline, adenosine and 8-hydroxyl-3,5-dimethyl-isochroman-1-one, were isolated from mangrove fungus K32. The interaction of β-carboline with calf thymus DNA was investigated by UV-vis and fluorescence spectra, resulting in the occurrence of a binding reaction, which was proposed to be one possible mechanism of the antitumor activity of β-carboline (Song et al. 2004).

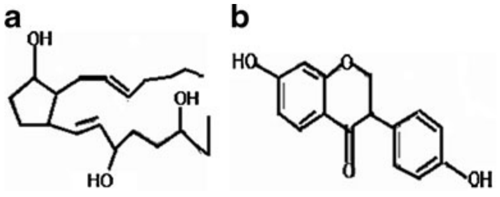

Fig. 3 **a** Prostaglandin- and **b** isoflavone analogs isolated from mangrove fungi of South China Sea by Tao et al. (2010)

Environmental applications

Bioremediation

Bioremediation strategies can be improved by a greater knowledge of microbiology, diversity and function, and new molecular technologies can support this development. Genomics, for instance, provided complete genome sequence data for several microorganisms that are significant for bioremediation, such as *Pseudomonas*, *Shewanella*, *Sphingomonas*, *Arthrobacter* etc. (Desai et al. 2010). In addition to processing nutrients, mangrove bacteria may also help in processing industrial wastes. Iron-reducing bacteria are common in mangrove habitats in some mining areas (Panchnadikar 1993). Eighteen bacterial isolates that metabolize waste drilling fluid were collected from a mangrove swamp in Nigeria (Benka-coker and Olumagin 1995). The presence and activity of the oil-degrading microorganisms in mangrove sediments not only plays a key role in the bioremediation of oil in mangroves but is also considered to represent new prospects for the use of molecular tools to monitor bioremediation processes. The majority of oil from oceanic oil spills (e.g., the recent accident in the Gulf of Mexico) converges on coastal ecosystems such as mangroves. Microorganisms are directly involved in biogeochemical cycles as key drivers of the degradation of many carbon sources, including petroleum hydrocarbons. Various

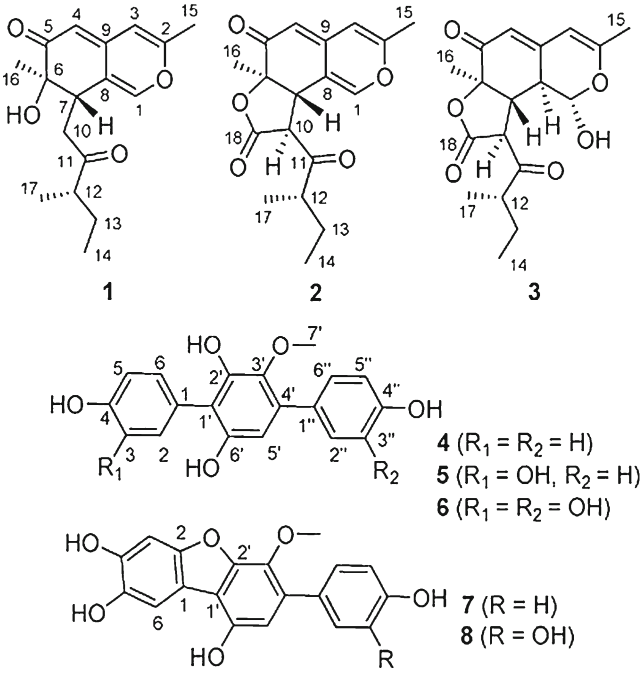

Fig.4 Eight secondary metabolites, (1–3) azaphilones, (4–8) *p*-terphenyls [(4) 6′-*O*-desmethylterphenyllin, (5) 3-hydroxy-6′-*O*-desmethylterphenyllin, (7) 3″-deoxy-6′-*O*-desmethylcandidusin B] from the culture of the mangrove endophytic fungus *Penicillium chermesinum*, isolated from the South China Sea (Huang et al. 2011)

bacterial groups present in mangrove sediment, such as *Pseudomonas*, *Marinobacter*, *Alcanivorax*, *Microbulbifer*, *Sphingomonas*, *Micrococcus*, *Cellulomonas*, *Dietzia* and *Gordonia*, are already known for their capacity to degrade hydrocarbons (Brito et al. 2006). Bacteria were isolated in the sediment of a mangrove located in Hong Kong, China, which demonstrated a great capacity for polyaromatic hydrocarbon (PAH) degradation in vitro and could be used to degrade PAH in contaminated sediment (Ramsay et al. 2000). Similarly, Yu et al. (2005) investigated the biodegradability of PAHs, fluorine (Fl), phenanthrene (Phe) and pyrene by a bacterial consortium enriched with mangrove sediment. The consortium was formed by three bacterial strains: *Rhodococcus* sp., *Acinetobacter* sp., and *Pseudomonas* sp. Ramsay et al. (2000) reported a large number, and wide diversity, of PAH-degrading microorganisms in Australian mangrove sediments. In a study of contaminated mangrove microcosms, Ke et al. (2003) demonstrated the removal of 90 % of pyrane in 6 months. Some bacterial species, such as *Streptococcus*, *Staphylococcus*, *Micrococcus*, *Moraxella* and *Pseudomonas* and fungal species such as *Aspergillus glaucus* and *A. niger* were also reported that degrade polythene and plastic bags from the mangrove environment (Kathiresan 2003). D'Souza et al. (2006) reported a mangrove white-rot basidiomycetous fungus able to produce laccase to decolorize colored effluents and synthetic dyes. The efficiency of this fungus in decolorization of various effluents with laccase that is active at pH 3.0–6.0 and 60 °C in the presence of seawater has great potential in bioremediation of industrial effluent. Enhanced laccase production in the presence of industrial effluents in this fungus is an added advantage during bioremediation of effluents. Recently, two moderately halotolerant *Bacillus megaterium* species isolated from mangroves of Bhitarkanika, Orissa showed potential for reduction of toxic selenite to non-toxic elemental selenium (Mishra et al. 2011).

Molecular methods for microbial taxonomy

Traditionally microbial taxonomy has been studied using a variety of morphological physiological and biochemical tests. However, the phenotypic characterization of bacteria is not sufficient to identify isolates beyond species level (Bakonyi et al. 2003). There also are problems associated with the study of bacterial and fungal diversity in soil due to methodological limitations and lack of taxonomic knowledge. Furthermore, the immense phenotypic and genetic diversity of soil bacteria and fungi make such studies very difficult. Less than 1 % of the bacterial populations found in nature are culturable, while 99 % are unculturable (Stanley 2002). Thus, many fungal populations are non-culturable. Because of this limitation, bacterial biodiversity can be accurately determined only using molecular taxonomic tools that obviate the need for laboratory cultivation of isolates. The cultivation-independent method is called metagenomics or environmental genomics (also called ecogenomics), which is defined as the genomic analysis of microorganisms by direct extraction of nucleic acids from environmental samples (soil, water, sediment, etc.). It involves the amplification by PCR of DNA and cDNA from RNA extracted from environmental samples, and subsequent analysis of the diversity of the amplified molecules. Alternatively, the amplified products may be cloned and sequenced to identify and enumerate bacterial species present in the sample (Tasi and Olson 1991). A number of approaches have been developed to study molecular microbial diversity. These include DNA reassociation, DNA–DNA and mRNA: DNA hybridization, DNA cloning and sequencing, and other PCR-based methods, such as denaturing gradient gel electrophorosis (DGGE), temperature gradient gel electrophoresis (TGGE), ribosomal intergenic spacer analysis (RISA) and automated ribosomal intergenic spacer analysis (ARISA) (Muyzer 1999). FAME (fatty acid methyl ester) analysis, a biochemical method that does not rely on culturing of microorganisms, is also one of the methods to study microbial diversity.

Future perspectives and concluding remarks

Microbial diversity in mangrove ecosystems is very rich and diverse, and has tremendous biotechnological potential. The study of the microbial diversity in mangrove is of vital importance to the understanding of the different processes of the mangrove, which may uncover potent novel microorganisms for screening of bioactive compounds. As evidenced from past and ongoing research, the microbial consortium has a plethora of bioactivity. A number of past reviews have focused the attention of researchers on this tremendous treasure of mangrove microbial diversity but there is still a long way to go. Interdisciplinary research and collaborative endeavors are required amongst scientists, microbiologists and biotechnologists to provide innovative approaches to study the microbial diversity and explore the biotechnological potential of this unique ecosystem. Using culture-dependent technologies reveals only a small percentage (<1 %) of the microbial community, leaving 99 % of microorganisms still undiscovered. Recent developments in molecular techniques will help to explore a good percentage of the microbial community that can be exploited for the welfare of the mankind.

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