Fungal Endophytes of Mangroves: Diversity, Secondary Metabolites and Enzymes

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Abstract

The culturable fungal endophytes of mangrove plants so far investigated appear to be not distinct from those associated with the terrestrial plants. The pattern of distribution of endophytes in a leaf and its species composition is similar in plants of mangrove and other ecosystems. This reflects the ecological success of a few fungal species to lead an endophytic life in plants of different environment and taxonomic affiliation. Despite this commonality, endophytes of mangroves are distinct in possessing certain traits which enable them to survive in the harsh mangrove environment. Their ability to produce novel bioactive compounds and enzymes make them attractive candidates for bioprospecting. Considering the endophyte-mediated improvement of performance of plants of other ecosystems, more studies are needed on mangrove endophytes addressing their role in abiotic and biotic stress tolerance of mangroves. Their functions in mangrove ecosystem including litter degradation and nutrient recycling, as well as their enzyme arsenal and secondary metabolite spectrum, need to be studied in detail in order to improve our understanding of these unique plant endosymbionts. Information gleaned on these aspects may aid in the protection and restoration of deteriorating mangrove vegetation.

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10.1 Introduction

Mangrove forests or tidal forests are found along tropical and subtropical ocean coastlines. Mangrove ecosystem is unique since the life here is adapted to high salinity, hypoxia, tidal fluctuations, strong ultraviolet light, anaerobic soils and high tidal interference (Rothschild and Mancinelli 2001; Sandilyan and Kathiresan 2012) (Plate 10.1). According to Global Mangrove Watch (GMW), the global cover of mangroves for 2010 was 137,600 km^2 (Bunting et al. 2018) with around 75% of mangroves being located in merely 15 countries (Giri et al. 2011). Mangrove ecosystems are biodiversity rich and highly productive; they provide many valuable ecosystem services including nutrient cycling, carbon sequestration, bioremediation of waste and contribution to food security (Lee et al. 2014; Malik et al. 2015; Richards and Friess 2016). They afford protection against shoreline erosion (Alongi 2014) and natural calamities like floods and tsunamis (Menéndez et al. 2020). As a blue carbon reservoir, the mangroves account for 10–15% of global carbon storage (Alongi 2014).

Plate 10.1 Pichavaram Mangrove Forest, Tamil Nadu

10.2 Mangrove Habitats in India

The coastline of India, which is about 7516.6 km^2 including the Island territories (Anonymous 1984), has a mangrove cover of about 4975 km^2 (FSI 2019) (Plate 10.1). The state of West Bengal has the largest mangrove cover of 2112 km^2. The East Coast or the Deltaic Mangrove habitat has larger and more widespread cover when compared to the West Coast Mangroves (Estuarine and Back Water Mangrove Habitat) and Andaman and Nicobar Islands (Insular Mangroves) because of its distinctive geo-morphological setting (Ragavan et al. 2016). Indian mangrove forests harbour a large number of floral and faunal wealth with over 1600 plant and 3700 animal species (Ghosh 2011). As far as the number of obligate or true mangrove plant species are concerned, the estimate varies from thirty (Mandal and Naskar 2008) to thirty-nine (Kathiresan 2008).

10.3 Mangrove Fungi

A mangrove ecosystem supports a variety of microbes including bacteria, protists, microalgae and fungi. Fungi occur on the prop roots, pneumatophores, decaying leaves, roots, and wood of mangrove plants, as well as on drift wood, intertidal grasses, algae, sediments, soil, crustaceans, corals, and calcareous tubes of mollusc shells of the mangrove forests (Kohlmeyer and Kohlmeyer 1979; Hyde et al. 1998; Jones and Mitchell 1996; Sarma and Hyde 2001). The fungal communities associated with a mangrove species of distantly located individuals are more dissimilar than those of closely occurring individuals; furthermore, the fungal associates of the aerial parts of mangroves, which are never submerged, are less diverse than those occurring in the submerged parts of the plants (Lee et al. 2019). Generally terrestrial fungi are associated with the aerial parts of mangroves, while marine fungi (obligate and facultative) appear to dominate the flooded parts (Lee et al. 2019). Such a preferential distribution of these ecological groups of fungi is a reflection of their adaptations to different environmental niches offered by mangrove ecosystem.

10.4 Mangrove Endophytes

Apart from the fungi mentioned above which are associated with various tissues of mangrove plants, some fungi occur as endophytes in their leaves and roots. Endophytes (Class 3 type—Rodriguez et al. 2009) live inside the living tissues of all plants as mutualists or commensals for short or long periods. Latent pathogens also occur as endophytes until environmental signals induce them to switch over to a pathogenic phase and cause diseases (Wheeler et al. 2019). One of the earliest studies on the fungal endophytes (FE) of mangroves is that of Suryanarayanan et al. (1998) which addresses the endophyte assemblages in the leaves of *Rhizophora apiculata* and *R. mucronata*. This study showed that, like in terrestrial plants, the leaves are densely colonised by many FE species, only one or two of them are dominant (Suryanarayanan et al. 2018). Rajamani et al. (2018), in one of the largest surveys of mangroves for their foliar endophytes, studied twenty mangrove species of the Andaman Islands and found that *Phomopsis/Diaporthe* occurs as endophyte in all the plants and *Xylaria*, *Colletotrichum* and *Phyllosticta* are endophytic in most of the plants. Here we collate the available data for the last 22 years (from the year 1998 to 2020) to identify the dominant endophytes (non-sterile and culturable) of mangrove leaf endophyte communities. A total of thirty-eight mangrove plant species from different parts of the world are included in this analysis (Table 10.1). *Guignardia* spp. were present in 38% of the plant hosts, while species of *Glomerella* (*Colletotrichum*) (Plate 10.2a), *Xylaria* (Plate 10.2b) and *Diaporthe* (*Phomopsis*) infected 21%, 18% and 16% of the mangrove species, respectively (Fig. 10.1).

Since specific adaptations are required to survive, only some plant species grow in a mangrove environment; thus, the species diversity of plants in mangrove forests is low, and consequently the density of individual species is high (Gilbert et al. 2002). Considering this low host plant diversity and the fact that the environment would act as a filter in selecting fungi tolerant to the harsh conditions prevailing there, it is conceivable that the diversity of foliar endophytes of mangroves would not be high. Rajamani et al. (2018) concluded that endophytes of 'mangroves are not unique with reference to their species diversity and frequency of occurrence when compared to those of terrestrial plants'. This conclusion is confirmed by the work of Suryanarayanan et al. (2018) in which 224 angiosperm plants of 60 families (including mangroves) were screened for their foliar endophyte assemblages. They showed that species of *Colletotrichum*, *Phyllosticta*, *Phomopsis* and *Xylaria* occurred as endophytes in the leaves of many plant hosts including those that were taxonomically not closely related. A few other studies also endorse the wide host range of these fungi as foliar endophytes (Pandey et al. 2003; Jeewon et al. 2004; Murali et al. 2006; Wei et al. 2007; Tejesvi et al. 2009; Govindarajulu et al. 2013). Such a host generalism is also observed among other guilds of tropical fungi such as wood rotting fungi (Parfitt et al. 2010), mycorrhizal fungi (Zhao et al. 2003; Tedersoo et al. 2010) and epifoliar fungi (Gilbert and Webb 2007). One explanation for such a lack of host specificity among tropical plant-associated organisms is the existence of high plant species diversity in the tropics that results in a non-continuous distribution of hosts (May 1991; Novotny et al. 2002). However, it is not known how such broad host range endophytes are adapted to encounter the different secondary metabolites and co-occurring microbes of different plant species (Suryanarayanan 2013, 2020; Schulz et al. 2015).

Generally, FE of plants of terrestrial habitats exhibit some degree of tissue specificity (Su et al. 2010; Wearn et al. 2012). A similar tissue specificity is also present among mangrove FE. The endophyte assemblages of the bark, petiole and the propagule in *Rhizophora apiculata* differ significantly indicating tissue preference among mangrove FE (Kumaresan et al. 2002).

Table 10.1 Dominant foliar fungal endophytes of mangrove plants

Host	Location	Dominant foliar endophyte(s)	References
Acanthus ebracteatus	Andaman Island, India Luzon Island, Philippines	*Colletotrichum gloeosporioides* *Aspergillus niger*	Rajamani et al. (2018) Ramirez et al. (2020)
Acanthus ilicifolius	Nethravathi Mangrove, Karnataka, India	*Cladosporium* sp.	Maria and Sridhar (2003)
	Ranong Province, Thailand	*Phyllosticta* sp. 1	Chaeprasert et al. (2010)
	Andaman Island, India	*Colletotrichum* sp.	Rajamani et al. (2018)
A. ilicifolius var. *xiamenensis*	Lieyu Township, Kinmen County, Taiwan	*Drechslera dematioidea* and *Fusarium oxysporum*	Chi et al. (2019)
Acrostichum aureum	Nethravathi Mangrove, Karnataka, India	*Acremonium* sp. and *Paecilomyces* sp.	Maria and Sridhar (2003)
Aegiceras corniculatum	Beilun Estuary National Reserve, South China	*Leptosphaerulina chartarum*	Li et al. (2016)
	Andaman Island, India	*Diaporthe pseudomangiferae*	Rajamani et al. (2018)
	Zhanjiang Mangrove National Nature Reserve, South China	Dothideomycetes and Tremellomycetes	Yao et al. (2019)
	Luzon Island, Philippines	*Nigrospora* sp. 2	Ramirez et al. (2020)
Aegiceras floridum	Luzon Island, Philippines	*Cladosporium* sp.	Ramirez et al. (2020)
Avicennia alba	Chanthaburi Province, Thailand	*Phyllosticta* sp.1	Chaeprasert et al. (2010)
Avicennia marina	Pichavaram Mangrove, Tamil Nadu, India	*Phoma* sp. 2	Kumaresan and Suryanarayanan (2001)
	Beilun Estuary National Reserve, South China	*Phyllosticta capitalensis*	Li et al. (2016)
	Andaman Island, India	*Diaporthe pseudomangiferae*	Rajamani et al. (2018)
	Zhanjiang Mangrove National Nature Reserve, South China	Tremellomycetes	Yao et al. (2019)
	Luzon Island, Philippines	*Phialophora* sp.	Ramirez et al. (2020)

(continued)

Table 10.1 (continued)

Host	Location	Dominant foliar endophyte(s)	References
Avicennia officinalis	Pichavaram mangrove, Tamil Nadu, India	*Paecilomyces* sp.	Kumaresan and Suryanarayanan (2001)
	Andaman Island, India;	*Diaporthe pseudomangiferae*	Rajamani et al. (2018)
Avicennia schaueriana	Itamaracá Island, Brazil	*Colletotrichum gloeosporioides*	Costa et al. (2012)
Bruguiera cylindrica	Pichavaram Mangrove, Tamil Nadu, India	*Colletotrichum gloeosporioides*	Kumaresan and Suryanarayanan (2001)
	Andaman Island, India	*Xylaria* sp. 1	Rajamani et al. (2018)
Bruguiera gymnorrhiza	Beilun Estuary National Reserve, South China	*Neofusicoccum australe*	Li et al. (2016)
	Andaman Island, India	*Phyllosticta capitalensis*	Rajamani et al. (2018)
	Zhanjiang Mangrove National Nature Reserve, South China	Dothideomycetes and Tremellomycetes	Yao et al. (2019)
Bruguiera parviflora	Andaman Island, India	*Xylaria* sp. 1	Rajamani et al. (2018)
Ceriops decandra	Prachuap Khiri Khan Province, Thailand	*Phyllosticta* sp. 1	Chaeprasert et al. (2010)
	Luzon Island, Philippines	*Penicillium* sp. 3	Ramirez et al. (2020)
Ceriops tagal	Andaman Island, India	*Xylaria* sp. 1	Rajamani et al. (2018)
	Luzon Island, Philippines	*Penicillium* sp. 3	Ramirez et al. (2020)
Excoecaria agallocha	Pichavaram Mangrove, Tamil Nadu, India	*Glomerella* sp.	Kumaresan and Suryanarayanan (2001)
	Andaman Island, India	*Phyllosticta capitalensis*	Rajamani et al. (2018)
	Zhanjiang Mangrove National Nature Reserve, South China	Dothideomycetes	Yao et al. (2019)
	Luzon Island, Philippines	*Phialophora* sp.	Ramirez et al. (2020)
Kandelia candel	Mai Po Nature Reserve, Hong Kong	*Phomopsis* sp., *Pestalotiopsis* sp., *Guignardia* sp. and *Xylaria* sp.	Pang et al. (2008)
	Beilun Estuary National Reserve, South China	*Phyllosticta capitalensis*	Li et al. (2016)

(continued)

Table 10.1 (continued)

Host	Location	Dominant foliar endophyte(s)	References
	Zhanjiang Mangrove National Nature Reserve, South China	Dothideomycetes and Tremellomycetes	Yao et al. (2019)
Laguncularia racemosa	Itamaracá Island, Brazil	*Guignardia* sp.	Costa et al. (2012)
Lumnitzera littorea	Chanthaburi Province, Thailand	*Phyllosticta* sp. 1	Chaeprasert et al. (2010)
	Andaman Island, India	*Phyllosticta capitalensis*	Rajamani et al. (2018)
Lumnitzera racemosa	Pichavaram mangrove, Tamil Nadu, India	*Phyllosticta* sp. 4	Kumaresan and Suryanarayanan (2001)
	Andaman Island, India	*Phyllosticta capitalensis*	Rajamani et al. (2018)
Nypa fruticans	Andaman Island, India	*Xylaria* sp. 1	Rajamani et al. (2018)
	Luzon Island, Philippines	*Phialophora* sp.	Ramirez et al. (2020)
Osbornia octodonta	Luzon Island, Philippines	*Phialophora* sp.	Ramirez et al. (2020)
Phoenix paludosa	Andaman Island, India	*Nodulisporium* sp. 1	Rajamani et al. (2018)
Rhizophora apiculata	Pichavaram Mangrove, Tamil Nadu, India	*Phyllosticta* sp. MG 90 and *Sporormiella minima*	Suryanarayanan et al. (1998); Kumaresan and Suryanarayanan (2002)
	Chanthaburi, Prachuap Khiri and Ranong Province, Thailand	*Phyllosticta* sp. 2 and *Cladosporium* sp. 1	Chaeprasert et al. (2010)
	Andaman Island, India	*Aspergillus fumigatus*	Rajamani et al. (2018)
Rhizophora mangle	Itamaracá Island, Brazil	*Phyllosticta* sp.	Costa et al. (2012)
Rhizophora mucronata	Pichavaram Mangrove, Tamil Nadu, India	*Sporormiella minima*	Suryanarayanan et al. (1998)
	Chanthaburi and Ranong Province, Thailand	*Phyllosticta* sp.2 and *Pestalotiopsis* sp.1	Chaeprasert et al. (2010)
	Matang Mangrove Forest Reserve, Malaysia	*Pestalotiopsis* sp.	Hamzah et al. (2018)
	Andaman Island, India	*Diaporthe discoidispora*	Rajamani et al. (2018)
	Hainan Island, China	*Neofusicoccum*	Zhou et al. (2018)
	Luzon Island, Philippines	*Penicillium* sp. 4	Ramirez et al. (2020)

(continued)

Table 10.1 (continued)

Host	Location	Dominant foliar endophyte(s)	References
Rhizophora stylosa	Andaman Island, India Hainan Island, China Zhanjiang Mangrove National Nature Reserve, South China	*Xylaria* sp. 1 *Pestalotiopsis* sp. and *Seiridium* sp. Dothideomycetes	Rajamani et al. (2018) Zhou et al. (2018) Yao et al. (2019)
Scyphiphora hydrophyllacea	Andaman Island, India	*Phyllosticta capitalensis*	Rajamani et al. (2018)
Sesbania bispinosa	Nethravathi Mangrove, Karnataka	*Aspergillus niger*	Anita et al. (2009)
Sonneratia alba	Chanthaburi Province, Thailand Andaman Island, India Luzon Island, Philippines	*Phyllosticta* sp. 1 *Pestalotiopsis* sp. *Phialophora* sp.	Chaeprasert et al. (2010) Rajamani et al. (2018) Ramirez et al. (2020)
Sonneratia apetala	Hainan Province, China	*Phomopsis* sp. 3	Xing et al. (2011)
Sonneratia caseolaris	Hainan Province, China	*Stemphylium solani*	Xing et al. (2011)
Sonneratia ovata	Hainan Province, China	*Glomerella* sp.	Xing et al. (2011)
Sonneratia paracaseolaris	Hainan Province, China	*Phoma* sp.	Xing et al. (2011)
Suaeda microphylla	Songyuan Guaibodian, Jilin, China	*Alternaria alternata*	Sun et al. (2011)
Suaeda corniculata	Songyuan Guaibodian, Jilin, China	*Alternaria alternata*	Sun et al. (2011)
Xylocarpus granatum	Ranong Province, Thailand Andaman Island, India	*Colletotrichum* sp. 3 *Colletotrichum gloeosporioides*	Chaeprasert et al. (2010) Rajamani et al. (2018)
Xylocarpus moluccensis	Ranong Province, Thailand	*Phyllosticta* sp.2	Chaeprasert et al. (2010)

10.5 Adaptations of Mangrove Foliar Endophytes

The core endophyte species of the leaves of mangrove plants are not unique as those of terrestrial plants. Considering the distinctiveness of mangrove environments, they should exhibit at least some trait difference to survive in this ecosystem. Mangroves have evolved mechanisms to tolerate a wide range soil salinities (Reef and Lovelock 2015). The leaves of *Aegiceras* and *Avicennia* have salt glands on their epidermis

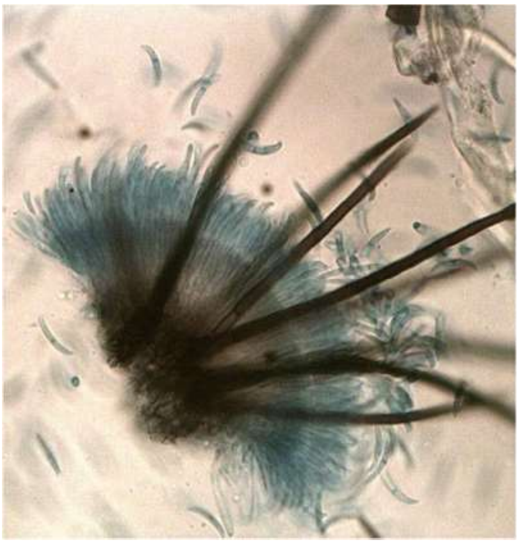

Plate 10.2a *Glomerella* sp. (*Colletotrichum*) endophytic in leaves of many mangrove species

Plate 10.2b *Xylaria* sp.

through which the excess salt absorbed by the plant is secreted. Leaves of *Bruguiera* and *Kandelia* do not possess salt glands on their leaves and sequester the salt in their vacuoles. Endophytes thus need to be salt tolerant to survive in mangrove leaves. Kumaresan et al. (2002) showed that several mangrove endophytes tolerate 7% NaCl in the growth medium which is equal to twice the concentration of salt present in seawater. It is known that in *Cirrenalia pygmea*, a fungus associated with mangrove roots, polyols regulate turgor and the activities of its polyol metabolism enzymes increase with salinity (Ravishankar and Suryanarayanan 1998). Additionally, this fungus also uses amino acids as compatible solutes for turgor regulation (Ravishankar et al. 1996). Exposure to salinity decreases the unsaturation index of

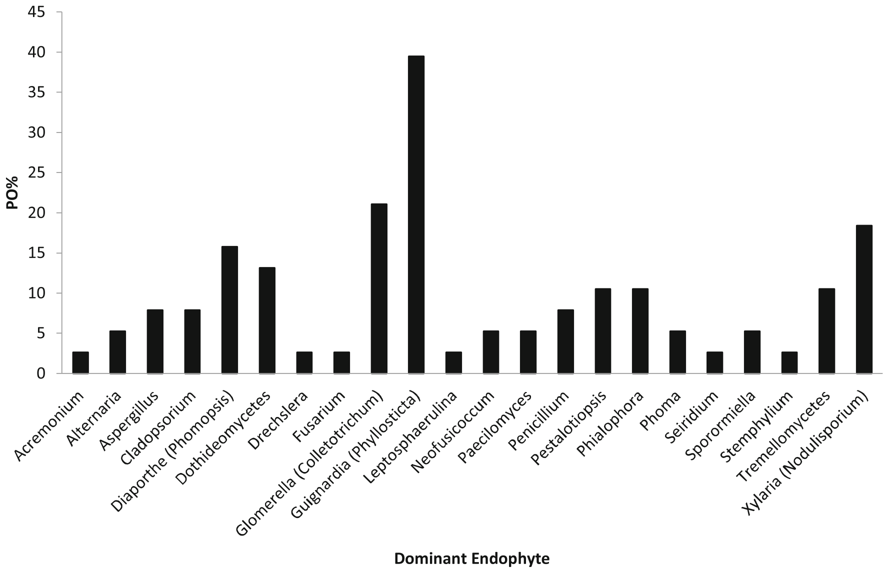

Fig. 10.1 Percentage Occurrence (PO%) of dominant endophytic genera in 38 mangrove hosts

fatty acids in this fungus suggesting a reduction of membrane fluidity for turgor regulation (Ravishankar et al. 1994). It is likely that such alterations at the metabolic level work in the mangrove endophytes also for survival in a saline milieu. Leaves of many mangrove plants contain tannins (Lin et al. 2007) which are antifungal in nature (Anttila et al. 2013). Mangrove leaf endophytes tolerate and even degrade tannins indicating that they are adapted to survive in mangrove leaves (Kumaresan et al. 2002). Dominant mangrove endophytes such as *Phyllosticta* have melanised hyphal walls and melanin protects fungi from sudden osmotic shocks (Ravishankar et al. 1995).

10.6 Bioactive Compounds of Mangrove Endophytes

FE produce an array of secondary metabolites with several exploitable bioactivities (Suryanarayanan et al. 2009; Prado et al. 2013). In a few cases, the endophytes produce their host plant's secondary metabolites in culture (Mohana Kumara et al. 2012; Gandhi et al. 2015). Reciprocal influence of the plant host and its endophyte could result in the production of novel metabolites (Ludwig-Müller 2015). Mangrove fungal endophytes too are a promising source of novel chemical scaffolds which could lead to the synthesis of many useful drugs. The environmental conditions of the mangrove ecosystem determine the composition of its microbes; thus, some of these microbes, even though are not taxonomically different from other ecosystems, exhibit trait difference. This raises the hope of identifying novel bioactive compounds from mangrove endophyte assemblages. A majority of the

850 new bioactive compounds characterised from mangrove-associated fungi in the last decade are produced by FE (Ancheeva et al. 2018). Many mangrove endophytes produce novel metabolites exhibiting a variety of activities including antibacterial, anti-inflammatory, antiviral, α-glucosidase inhibitory, acetylcholinesterase inhibitory, anticancer, antiproliferative, cytotoxic, COX-2 and Protein kinase G (PknG) inhibitory activities (Table 10.2).

10.7 Enzymes of Mangrove Endophytes

It is well known that fungal enzymes find use in various industrial processes. As the demand for such enzymes increases, enzymes vested with higher activity and stability are being sought. Although directed evolution along with site-directed mutagenesis (Piscitelli et al. 2011) and protein engineering are being used for obtaining better enzymes (Böttcher and Bornscheuer 2010); the search for novel biocatalysts from hitherto unexplored microbes would be profitable. FE qualify for being such a novel source, since they have hardly been explored for enzymes (Suryanarayanan et al. 2012). FE of plants of extreme environments such as the mangroves may produce enzymes adapted to such harsh conditions which may find use in industrial applications. A few studies endorse this because endophytes produce novel pharmaceutically important enzymes (Govinda Rajulu et al. 2011; Thirunavukkarasu et al. 2011; Nagarajan et al. 2014) and enzymes for food and biofuel production (Suryanarayanan et al. 2012). Marine-derived endophytes produce ionic liquid-tolerant xylosidases which could find use in conversion of lignocellulosic biomass to biofuel (Sengupta et al. 2017). Some FE utilise toxic furaldehydes, the most abundant volatiles produced during biomass conversion to biofuel (Govinda Rajulu et al. 2014). Since furaldehydes inhibit the downstream process in biomass to biofuel conversion, these FE could find use in improving the efficiency of the process. Mangrove endophytes produce amylase, cellulase, laccase, lipase, pectate transeliminase, protease and tyrosinase (Kumaresan et al. 2002; Kumaresan and Suryanarayanan 2002; Maria et al. 2005) (Table 10.3). Paranetharan et al. (2018) reported that *Talaromyces stipitatus,* an endophyte of the root of the mangrove tree *Avicennia marina*, elaborates salt-tolerant chitinase and chitosanases. This endophyte is halotolerant and produces such chitin-modifying enzymes even in the presence of a high concentration of NaCl in the growth medium, and NaCl induced the production of isoforms of chitinase and chitosanase by this fungus. Mangrove fungal endophtes have hardly been explored for their enzyme arsenal to be used in various industries. Modern methodologies such as genome mining and metagenomics should be employed for identifying enzymes of non-culturable endophytes as has been done for bacteria (Kennedy et al. 2008).

Table 10.2 Various secondary metabolites of mangrove endophytes and their bioactivities

Endophytes	Host and Location	Compounds	Activity tested	References
Alternaria longipes	*Avicennia officinalis*, India	2,4,6–triphenylaniline	Antidiabetic activity	Ranganathan and Mahalingam (2019)
Annulohypoxylon sp.	*Rhizophora racemosa*, Cameroon	Daldinone H, Daldinone I, Daldinone J, Daldinone C, Hypoxylonol C, Daldinone B, 3,4-dihydro-3,4,6,8-trihydroxy-l(2*H*)-naphthalenone, (*R*)-scytalone, 1-hydroxy-8-methoxynaphthalene	Cytotoxic activity	Liu et al. (2017)
Aspergillus flavus	*Kandelia obovata,* Guangdong Province, China	Diphenyl ethers and Phenolic bisabolane sesquiterpenoids	α- glucosidase inhibitory activity	Wu et al. (2018a)
Aspergillus flavus	*Sonneratia alba*, Kupang, East Nusa Tenggara Province, Indonesia	Kojic acid	Antibacterial activity	Ola et al. (2020)
Aspergillus sp.	*Acanthus ilicifolius,* Hainan Island, China	Aspergisocoumrin A–B, 8-dihydroxyisocoumarin-3-carboxylic acid and Dichlorodiaportin	Anticancer activity	Wu et al. (2018b)
Aspergillus sp.	*Avicennia marina,* Red Sea coast close to Hurgada, Egypt	1-(2′,6′-dimethylphenyl)-2-*n*-propyl-1,2-dihydropyridazine-3,6-dione and Dioxoauroglaucin	Antiploriferative activity	Elissawy et al. (2019)
Basidiomycetous fungus XG8D	*Xylocarpus granatum,* Samutsakorn province, Thailand	Chamigrane sesquiterpenes: Merulinol A–F	Cytotoxic activity	Choodej et al. (2016)

Botryosphaeria sp.	*Kandelia candel,* Guangdong Province, China	Botryosphaerin A, Orthosporin, 1*RS* 2*SR*,4*SR*-1,2,3,4-tetrahydronaphthalene-1,2,4,5-tetrol, 1*RS*,2*RS*,4*RS*1,2,3,4-tetrahydronaphthalene-1,2,4,5-tetrol, 11-epiterpestacin and Fusaproliferin	Antimicrobial activity, COX-2 inhibitory and Cytotoxic activity	Ju et al. (2016)
Campylocarpon sp.	*Sonneratia caseolaris*, China	Campyridone A–D and Ilicicolin H	Anticancer activity	Zhu et al. (2016)
Cladosporium sp.	*Ceriops tagal*, South China Sea	4-*O*-α-D-ribofuranose-3-hydroxymethyl-2-pentyl- phenol, (-)-trans-(3*R*,4*R*)-3,4,8-trihydroxy-6,7-dimethyl-3,4-dihydronaphthalen-1(2*H*)-one, (3S)-3,8-dihydroxy-6,7-dimethyl-α-tetralone, (-)-trans-(3*R*,4*R*)-3,4-dihydro-3,4,8-trihydroxy-1(2*H*)-napthalenone, (-)-(4*R*)-regiolone, 1,8-dimethoxy naphthalene, (2*S*)-5-hydroxy-2-methyl-chroman-4- one and (2*R**,4*R**)3,4-dihydro-5- methoxy-2-methyl-1(2*H*)-benzo pyran-4-ol	Cytotoxic activity and Antibacterial activity	Wu et al. (2019)
Cladosporium sp.	*Ceriops tagal,* South China	1,1′-dioxine-2,2′-dipropionic acid and 2-methylacetate-3,5,6-trimethylpyrazine	Antibacterial activity	Bai et al. (2019)

(continued)

Table 10.2 (continued)

Endophytes	Host and Location	Compounds	Activity tested	References
Clonostachys rosea	*Bruguiera gymnorrhiza, Santolo Garut Beach, West-Java, Indonesia*	(-)-dihydrovertinolide, Clonostach acids A–C And (-)-Vertinolide	Antimicrobial activity	Supratman et al. (2019)
Cytospora sp.	*Ceriops tagal*, China	Seiricardine D, Xylariterpenoid A, Xylariterpenoid B, Regiolone, 4-hydroxyphenethyl alcohol, (22*E*, 24*R*)5, 8-epidioxy-5a, 8a-ergosta-6,22*E*-dien-3ß-ol, (22*E*, 24*R*)5, 8-epidioxy-5a, 8a-ergosta-6,9(11), 22-trien-3 ß-ol, ß-sitosterol and Stigmast-4-en-3-one	Antimicrobial activity	Deng et al. (2020)
Daldinia eschscholtzii	*Bruguiera sexangula* var. *rhynchopetala*, South China Sea	Cytochalasin: [11]-cytochalasa-5(6),13-diene-1,21-dione-7,18-dihydroxy-16,18-dimethyl-10-phenyl-(7*S**,13*E*,16*S**,18*R**), [11]-cytochalasa-*n*(12),13-diene-1,21-dione-7,18-dihydroxy16,18-dimethyl-10-phenyl-(7*S**,13*E*,16*S**,18*R**), 1-(2,6-dihydroxyphenyl)butan-1-one and 1,8-dimethoxynaphthalene	Antibacterial activity	Yang et al. (2018)
Diaporthe phaseolorum	*Acanthus ilicifolius*, China	Alkaloids: Diaporphasine A–D Meyeroguilline A, Meyeroguilline C, Meyeroguilline D, 5-deoxybostrycoidin and Fusaristatin A	Cytotoxic and Growth inhibitory activity	Cui et al. (2017)

Diaporthe sp.	*Rhizophora stylosa*, Sanya City, Hainan Province, China	Octaketides (Dothiorelone O, (15*R*)-acetoxydothiorelone A) Chromone (Pestalotiopsone H), Phthalides ((±)-microsphaerophthalide H, microsphaerophthalide I) and α-pyrone (methyl convolvulopyrone)	Anti-influenza A virus (H1N1)	Luo et al. (2018a)
Diaporthe sp.	*Rhizophora stylosa*, Sanya city, Hainan Province, China	Isochromophilones A−F, Azaphilone derivatives	Cytotoxic activity	Luo et al. (2018b)
Diaporthe sp.	*Bruguiera sexangula,* South China	Sesquiterpenoids, 1-methoxypestabacillin B, 11-nor-8,9*R*-drimanediol, chrodrimanin type meroterpenoids	Antiviral activity	Luo et al. (2019)
Eupenicillium sp.	*Xylocarpus granatum,* South China Sea	Penicilindole A–C	Cytotoxic activity and Antibacterial activity	Zheng et al. (2018)
Eupenicillium sp.	*Xylocarpus granatum*, South China Sea	Phenol derivative, 3-chloro-5-hydroxy-4-methoxyphenylacetic acid methyl ester, Methyl 4-hydroxyphenylacetate, Cytosporone B, (*R*)-striatisporolide A, (*R*)-butanedioic acid and Ergosterol	Insecticidal activity	Mei et al. (2020)
Eurotium rubrum	*Suaeda salsa,* BoHai, China	Rubrumol	Anticancer activity	Zhang et al. (2017a)
Fusarium solani	*Avicennia officinalis*, Dive agar and Shrivardhan, Maharashtra, India	3-Pyridylacetic acid, Aloe-emodin, Antipyrine, Mitoxantrone and Sulfabenzamide. 2, 4, 6-Trimethylacetophenone	Anticancerous compounds, Antioxidant activity, Anti-inflammatory activity and Antimicrobial activity	Sonawane et al. (2020)

(continued)

Table 10.2 (continued)

Endophytes	Host and Location	Compounds	Activity tested	References
		Imine and Daidzein. Anabasamine, Desethylhydroxychloroquine and Mometasone Furoate. Antipyrine, Dihydrodeoxystreptomycin, Phenylacetic acid and Phenylpyruvic acid		
Fusarium sp.	*Kandelia candel*, Dongzhai mangrove, Hainan, China	Cyclic peptide: Beauvericin	Anticancer activity	Tao et al. (2015)
Lasiodiplodia sp.	*Excoecaria agallocha*, Gaoqiao, Zhanjiang city, Guangdong Province, China	Lasidiplodins: 12*E*,15*R*-5-hydroxy-3-methoxy-16-methyl-8,9,10,11,14,15-hexahydro-1*H*-benzo[c][1] oxacyclodocecin-1-one, Ethyl 2,4-dihydroxy-6-(8-oxononyl)benzoate, (*R*)-Zearalane, 2,4-dihydroxy-6-nonylbenzoateand (*R*)-de-*O*-methyllasiodiplodin	Cytotoxic activity	Huang et al. (2017)
Lasiodiplodia theobromae	*Acanthus ilicifolius,* Zhanjiang Mangrove Nature Reserve, Guangdong Province, China	Chloropreussomerin A-B Preussomerin M, Preussomerin K, Preussomerin H, Preussomerin G, Preussomerin F, Preussomerin D, Preussomerin C, Preussomerin A	Cytotoxic and Antibacterial activity	Chen et al. (2016a)

Lasiodiplodia theobromae	*Acanthus ilicifolius*, South China Sea	Lasiodiplactone A	Anti-inflammatory activity and α-glucosidase inhibitory activity	Chen et al. (2017a)
Mucor irregularis	*Rhizophora stylosa,* Hainan Island, China	Rhizovarin A–F Penitrem A, Penitrem C, Penitrem F	Cytotoxic activity	Gao et al. (2016)
Neosartorya udagawae	*Avicennia marina,* Hainan Province, China	Neosartoryadin A–B and Fumiquinazoline	Anti-influenza A virus (H1N1)	Yu et al. (2016)
Penicillium brocae	*Avicennia marina*, China	Penicibrocazine A–F	Antimicrobial activity	Meng et al. (2015)
Penicillium brocae	*Avicennia marina,* Hainan Island, China	Spirobrocazine A–C and Brocazine G	Anticancer activity	Meng et al. (2016)
Penicillium chermesinum	*Heritiera littoralis,* Samut Sakhon province, Thailand	2-chloro-3,4,7-trihydroxy-9-methoxy-1-methyl-6*H*-benzo[c] chromen-6-one	Anticancer activity	Darsih et al. (2017)
Penicillium chrysogenum	*Myoporum bontioides* (Semi-mangrove) Leizhou Peninsula, China	Penochalasin I, Penochalasin J, Chaetoglobosin G, Chaetoglobosin F, Chaetoglobosin C, Chaetoglobosin A, Chaetoglobosin E, Armochaetoglobosin I and Cytoglobosin C	Cytotoxic activity and Antifungal activity	Huang et al. (2016)
Penicillium citrinum	*Bruguiera sexangula* var. *rhynchopetala*, South China Sea	4-chloro-1-hydroxy-3-methoxy-6-methyl-8-methoxycarbonyl-xanthen-9-one and 2'-acetoxy-7-chlorocitreorosein	Antibacterial activity	He et al. (2017)

(continued)

Table 10.2 (continued)

Endophytes	Host and Location	Compounds	Activity tested	References
Penicillium citrinum	*Bruguiera sexangula* var. *rhynchopetala*, South China Sea	Penibenzophenone A–B, (*E*)-*tert*-butyl (3-cinnamamidopropyl)carbamate, Culochrin, Asterric acid and *n*-butyl asterrate	Antibacterial activity and Cytotoxic activity	Zheng et al. (2019)
Penicillium janthinellum	*Sonneratia caseolaris,* Province, China	Penicisulfuranol A–F	Cytotoxic activity	Zhu et al. (2017)
Penicillium sp.	*Ceriops tagal,* Hainan Province, China	Penicieudesmol B	Anticancer activity	Qiu et al. (2018)
Penicillium sp.	*Bruguiera gymnorrhiza*, China	2-deoxy-sohirnone C, 5*S*-hydroxynorvaline-*S*-Ile, 3*S*-hydroxylcyclo(*S*-Pro-*S*-Phe) and Cyclo(*S*-Phe-*S*-Gln)	Antibacterial activity	Jiang et al. (2018)
Penicillium sp.	*Kandelia candel,* Guangxi province, China	3-epiarigsugacin E, Arisugacin D, Arisugacin B, Territrem C, Terreulactone C	Inhibitory activities against acetylcholinesterase	Ding et al. (2016)
Pestalotiopsis clavispora	*Rhizophora harrisonii,* Port Harcourt, Nigeria	Pestalpolyol I, Pestapyrones A, Pestapyrones B, (*R*)-(-)-periplanetin D, Pestaxanthone, Norpestaphthalide A and Pestapyrone C	Anticancer activity	Hemphill et al. (2016)

Pestalotiopsis coffeae	Fishtail palm, Xinglong Hainan Province, China	Isocoumarin derivatives: 6,8-dihydroxy-7-methyl-1-oxo-1*H*-isochromene-3-carboxylic acid, 6,8-dihydroxy-3-methoxy-3,7-dimethylisochroman-1-one (*R*)-periplanetin D, (*R*)-5,7-dihydroxy3-((*S*)-1-hydroxyethyl)- isobenzofuran-1(3*H*)-one, (*S*)-5,7dihydroxy-3-((*S*)-1-hydroxyethyl)-isobenzofuran-1(3*H*)-one, (*R*)-5,7-dihydroxy-3-((*S*)-1-hydroxyethyl)-6-methylisobenzofuran1(3*H*)-one and (*S*)-5,7-dihydroxy-3-((*S*)-1-hydroxyethyl)-6 methylisobenzofuran-1(3*H*)-one	Not mentioned	Wang et al. (2018)
Pestalotiopsis sp.	*Rhizophora mucronata*	Dimethylincisterol, Flufuran, Ergosta-5,7,22-trien-3-ol, Stigmast-4-en-3-one, Demethylincisterol A3, Ergosta-5,7,22-trien-3-ol, Stigmastan-3-one, Stigmast-4-en-3-one, Stigmast4-en-6-ol-3-one, Similanpyrone B, (2-cis, 4-trans)-abscisic acid and 5, 8-epidioxy-5, 8-ergosta-6, 22*E*-dien-3-ol	Anticancer activity	Zhou et al. (2017)

(continued)

Table 10.2 (continued)

Endophytes	Host and Location	Compounds	Activity tested	References
Pestalotiopsis sp.	*Rhizophora stylosa,* Dong Zhai Gang-Mangrove, China	Pestalotiopisorin B, (*R*)-(-)- mellein methyl ether, Pestalotiopyrone G, (*R*)-mevalonolactone, Pestalotiollides A, Pestalotiollides B	Antibacterial activity	Xu et al. (2020)
Phomopsis longicolla	*Bruguiera sexangula var. rhynchopetala,* South China Sea	Biphenyl derivative 5,5′-dimethoxybiphenyl-2,2′-diol	Antibacterial activity	Li et al. (2017)
Phomopsis sp.	*Acanthus ilicifolius*, South China Sea, Hainan Province, China	Phomopyrone A, Acropyrone and Ampelanol	Antibacterial activity	Cai et al. (2017a)
Phomopsis sp.	*Kandelia candel*, Mangrove Nature Conservation Area, Fugong, Fujian Province, China	Polyketides: *Mycoepoxydiene* Deacetylmycoepoxydiene, Phomoxydiene A, 2,3-dihydromycoepoxydiene, Phomoxydiene B and Phomoxydiene C	Cytotoxic activity and Activity against of AMPK	Zhang et al. (2017b)
Phomopsis spp.	*Xylocarpus granatum,* Trang Province, Thailand	Phomopsichalasin D–G	Anticancer activity	Luo et al. (2016)
Phyllosticta capitalensis	*Bruguiera sexangula,* China	Meroterpenes guignardone A, 12-hydroxylated guignardone A, Guignardone J, Guignardone M, and four Polyketides: Xenofuranone B, 6,8-dihydroxy-5-methoxy-3-methyl-1*H*-isochromen-1-one, Regiolone and 3,4-dihydroxybenzoic acid	Antimicrobial activity	Xu et al. (2019)

Pleosporales sp. SK7	*Kandelia candel*, Shankou Mangrove Nature Reserve, Guangxi Province, China	Sesquiterpene: (10*S*,2*Z*)-3-methyl-5-(2,6,6-trimethyl-4-oxocyclohex-2-enyl) pent-2-enoic acid, Methyl 2-(2-carboxy-4hydroxy-6-methoxylphenoxy)-6-hydroxy-4-methylbenzoate, Asterric acid, Methyl asterrate and Methyl 3-chloroasterric acid	Cytotoxic activity	Wen et al. (2019)
Pseudopestalotiopsis theae	*Rhizophora racemosa,* Lagos	Polyketide derivatives: Pestalotheols I–Q and Cytosporins O–W	Cytotoxic activity and Antibacterial activity	Yu et al. (2020)
Rhytidhysteron rufulum	*Bruguiera gymnorrhiza,* Prachuab Kiri Khan Province, Thailand	Rhytidchromones A–E	Anticancer activity	Chokpaiboon et al. (2016)
Talaromyces amestolkiae	*Kandelia obovata*, Zhanjiang Mangrove Nature Reserve, Guangdong Province, China	Isocoumarins and Benzofurans: {6-hydroxy-8-methoxy-3,4-Dimethylisocoumarin, *S*-(_)-5-hydroxy-8-methoxy-4-(10-hydroxyethyl)-isocoumarin, 5,6-dihydroxy-3-(4-hydroxypentyl)-isochroman-1-one. 5-hydroxy-7-methoxy-2-methylbenzofuran-3-carboxylic acid and 1-(5-hydroxy-7-methoxybenzofuran-3-yl) ethan-1-one	α-glucosidase inhibitory and antibacterial activities	Chen et al. (2016b)
Talaromyces sp.	*Kandelia obovata,* Guangdong Province, China	Talaramide A	Protein kinase G (PknG) inhibitor activity	Chen et al. (2017b)

(continued)

Table 10.2 (continued)

Endophytes	Host and Location	Compounds	Activity tested	References
Talaromyces stipitatus	*Acanthus ilicifolius,* Shankou Mangrove, China	Talaromyone A–B	Antibacterial activity and α-glucosidase inhibitory	Cai et al. (2017b)
Trichoderma sp.	*Xylocarpus granatum,* Hainan Island, China	(9*R*,10*R*)-dihydro-harzianone	Anticancer activity	Zhang et al. (2016)
Zasmidium sp.	*Laguncularia racemosa,* Juan Diaz, Panama	Triglyceride and Dehydrocurvularin	α- glucosidase inhibitory activity	Lopéz et al. (2019)

Table 10.3 Extracellular enzymes from fungal endophytes of mangrove plants

Host	Endophytes	Extracellular enzymes	References
Rhizophora apiculata	*Chaetomium globosum, Glomerella* sp. MG 108 *Pestalotiopsis* sp. MG 98, *Sporormiella minima* and Sterile form MG 168	Amylase, Cellulase, Laccase, Lipase, Pectate transeliminase, Pectinase, Protease, Tyrosinase	Kumaresan et al. (2002); Kumaresan and Suryanarayanan (2002)
Avicennia marina, A. officinalis, Bruguiera cylindrica, Ceriops decandra, Lumnitzera racemosa	*Colletotrichum* sp. MG 295, *Paecilomyces* sp. MG 208, *Phoma* sp. MG 190, *Phomopsis* sp. MG 186, *Phyllosticta* sp. MG 123 and Sterile form MG 302.	Amylase, Cellulase, Laccase, Lipase, Pectate transeliminase, Pectinase, Protease, Tyrosinase	Kumaresan et al. (2002)
Acanthus ilicifolius and *Acrostichum aureum*	*Acremonium* sp. *Alternaria chlamydospora, Alternaria* sp., *Aspergillus* sp. 2, *Aspergillus* sp. 3, *Fusarium* sp. and *Pestalotiopsis* sp.	Amylase, Cellulase, Lipase, Protease	Maria et al. (2005)
Avicennia marina	*Talaromyces stipitatus*	Chitinase/ chitosanase	Paranetharan et al. (2018)
Mangroves form Cananeia mangrove forest, Brazil	*Diaporthe* sp., *Fusarium sambucinum Fusarium* sp., *Hypocrea lixii* and *Trichoderma camerunense*	Endo-cellulase, Endo-xylanase, Lignin peroxidase, Manganese peroxidase and Laccase	Martinho et al. (2019)

10.8 Mangrove Endophytes: Not an Insignificant Biotic Component

FE have evolved with the plants and are a constant entity of a plant microbiome. They are an inevitable constituent of a plant and their role in the growth, performance and reproduction of their host plants are being unravelled. Endophytes increase the abiotic tolerance of the plants they colonise. The abiotic stresses include salinity, nitrogen limitation and drought (Rho et al. 2018; Sampangi-Ramaiah et al.

2020). These abilities of endophytes are being viewed as a new avenue for improving crop performance especially under the predicted climate change scenario (Suryanarayananan and Uma Shaanker 2020). Endophytes of plants from extreme habitats which are adapted to the harsh conditions could be inoculated into crops to enhance their stress tolerance. For example, FE of plants of the Antarctic increased salt stress tolerance of lettuce and tomato plants (Molina-Montenegro et al. 2020). Similarly, an endophyte from a salt-tolerant plant confers salt tolerance to salt-sensitive rice (Sampangi-Ramaiah et al. 2020). Mangrove roots have salt-tolerant genes (Basyuni et al. 2011; Krishnamurthy et al. 2017), and leaves have salt glands with such genes to exude salt (Jyothi-Prakash et al. 2014). Endophytes associated with these tissues could be screened for their salt tolerance and selected for their performance in crop plants.

Litter degradation is critical to the nutrient budget of any forest ecosystem. Fungi among the litter degrading organisms play a fundamental role here as deconstructors of recalcitrant biopolymers such as cellulose and lignin in the biomass. It is now established that some FE continue to survive in fallen leaves and contribute to litter degradation by swapping to saprotrophic mode of existence (Unterseher et al. 2013; Yuan and Chen 2014; Prakash et al. 2015). There is a major lacuna with reference to the contribution of FE of mangroves in litter degradation. In mangroves, leaf endophytes of *Rhizophora apiculata* including species of *Glomerella*, *Pestalotiopsis* and *Phialophora* continue to grow as saprotrophs after the leaf fall (Kumaresan and Suryanarayanan 2002). They also elaborate biomass degrading enzymes such as cellulases, xylanases, laccases and pectinases suggesting that they could contribute to mangrove litter degradation (Kumaresan and Suryanarayanan 2002). The persistence of FE in fallen leaves and their ability to elaborate biopolymer degrading enzymes would render the biomass fit for the subsequent saprotrophic players to complete the process of degradation (Voříšková and Baldrian 2013; Prakash et al. 2015) (Fig. 10.2). However, their performance under salinity, a major stress in mangrove ecosystem (Virgulino-Júnior et al. 2020), is not known. Information on the role of FE in litter decomposition may be useful for estimating nutrient recycling and predicting carbon sequestration in mangrove ecosystems.

10.9 Conclusions

The culturable foliar FE of mangrove so far studied are not taxonomically unique when compared to those of plants of other ecosystems. However, they possess unique traits which aid in their survival in the extreme environment of the mangrove ecosystem. It can be expected that the sustained interactions of endophytes with mangrove plants, co-occurring microbes supported by these plants and the unique environment would set these fungi apart from their conspecific endophytes of other ecosystems. Mangrove cover is being lost or fragmented to a great extent mainly due to aquaculture and rice cultivation (Bryan-Brown et al. 2020). Additionally, climate change is predicted to have negative influence on mangrove vegetation due to increased temperature, storminess and salinity (Ward et al. 2016). Restoration of

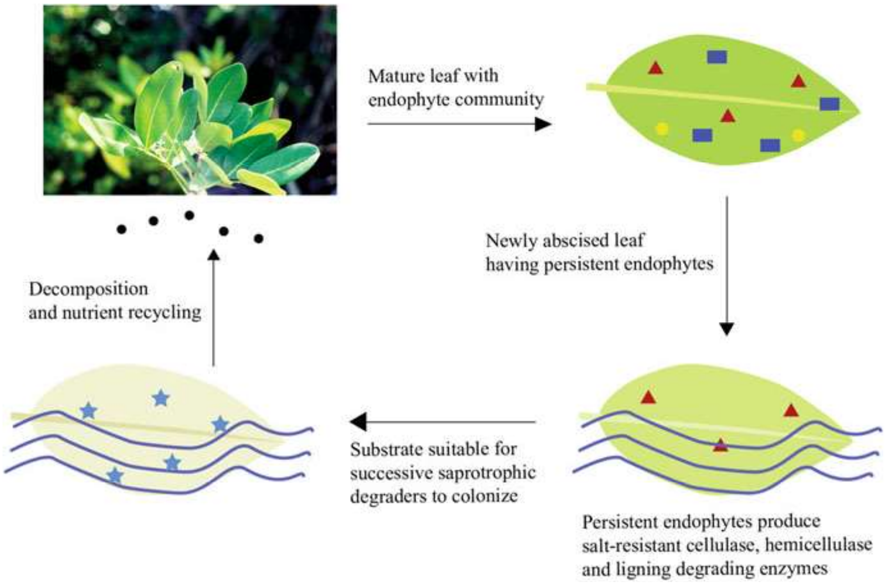

Fig. 10.2 Possible role of leaf endophytes in litter degradation in a mangrove ecosystem

mangrove cover is usually done by propagules planting and/or transplantation of nursery-raised plants (Thivakaran 2017). Although the functional roles played by fungal associates in the maintenance of mangrove ecosystem are hardly understood, the general appreciation that the microbiome (including the endophytes) associated with a plant contribute to its survival and performance (Suryanarayanan 2020) that should motivate studies on endophytes in maintaining mangrove health.

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