Chapter 5
The Mangrove Ecosystem

> *If there are no mangroves, then the sea will have no meaning.*
> *It is like having a tree without roots, for the mangroves are*
> *the roots of the sea...*
> *Words of a Thai fisher from the Andaman Coast*

The hundreds of islands with mangrove vegetation that constitute Sunderbans in the Gangetic delta region of India, the home of the Bengal tiger, traversed by innumerable creeks and which sustain a million lives is a natural wonder. Equally important and wonderful are the numerous coastal mangrove vegetations and forests in other tropical and subtropical coasts.

Mangroves are autochthonous marine vegetations. They are found along marshy tidal areas of estuaries and coastal shorelines of the tropics and subtropics, between latitudes of 25°N and 25°S. Mangrove vegetations are also called mangal. Mangrove trees are adapted to extreme, fluctuating conditions of salinity and temperature and to the swampy sediments with low oxygen conditions. The total global coverage of mangroves is approximately 24 million hectares of area.

There are around 30 "typical mangrove plants" and more or less equal number of "mangrove associated plants" that occur in mangroves forests around the world (Hutchinson et al. 2014). Mangrove trees have several interesting ecological adaptations. Species of *Rhizophora* support themselves in the marshy soil by producing prop roots. This genus also produces viviparous seedlings in which germination takes place while the seeds are still attached to the trees. Species of *Avicennia* have characteristic "breathing roots" called pneumatophores.

Mangroves are a treasure house for marine mycologists. The enormous amount of decomposing litter generated by the dense vegetation of a variety of mangrove trees, the marshy sediments, and the winding creeks of a mangrove forest are all excellent habitats for fungi (Fig. 5.1)

Net primary production (NPP) of mangrove trees results in the woody trunk, the dense foliage of leaves, underground roots, prop roots of many species that help in supporting the tree in marshy conditions, the aerial roots or pneumatophores of several species, and the viviparous seedlings of species such as *Rhizophora*. The global net primary production (NPP) of mangrove trees

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Fig. 5.1 A mangrove forest with *Rhizophora* trees supported by prop roots, the creek, and marshy sediments (Courtesy: Pieter van Eijk, Wetlands International)

through wood, leaves, and roots is 218 × 10^6 metric tons of C (Fig. 5.2; Bouillon et al. 2008).

The enormous quantity of detritus generated by mangroves serves as a major food source to many estuarine and coastal animals, such as prawns and fish. One of the important aspects of mangroves, therefore, lies in their export of organic matter in the form of detritus to adjacent coastal waters.

- **Fungi play an important role in decomposition of dead lignocellulosic material.** A number of mycetaen and straminipilan fungi carry out this task in the mangrove ecosystem. Most of our knowledge on mangrove fungi comes from those that inhabit dead mangrove wood, prop roots, leaves, and viviparous seedlings. Fungal dynamics of these depends on the physical and chemical nature of the substrates**. Mangrove wood is more recalcitrant to degradation compared to leaves and viviparous seedlings because of several significant differences in their structural and chemical composition** (Marchand et al. 2005). Fungi which grow on wood have a “k” strategy for growth and survival in that they grow slowly, face little competition from other microbes, and break down recalcitrant compounds.

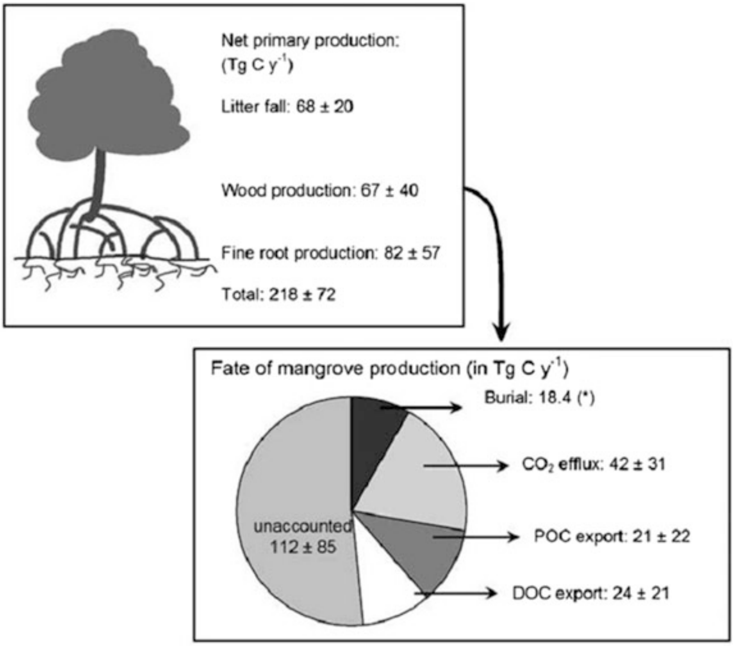


Fig. 5.2 The fate of mangrove primary production (Copyright (2008) Wiley. Used with permission from Bouillon, S., et al. (2008) Mangrove production and carbon sinks: A revision of global budget estimates, Global Biogeochem. Cycles, 22, GB2013. doi: 10.1029/2007GB003052. John Wiley and Sons.)

These features lead to differences in fungal dynamics in leaves and wood.

1. The three distinct phases of decomposition (Chap. 2), namely, leaching, decomposition, and fragmentation phases, are more clearly seen in the case of mangrove leaves than in case of wood.
2. The zoosporic, straminipilan fungi follow the substrate capture or r-strategy in the case of decaying mangrove leaves (Newell 1996a). On the other hand, obligate, marine, lignicolous mycetaen fungi adopt a k-strategy to colonize and exploit the highly recalcitrant nature of decomposing woody and lignocellulosic materials.
3. Leaves are converted to fine POM in a matter of a few weeks, while wood takes several months to totally degrade.

5.1 Fungi in Woody Detritus of Mangroves

The estimated global production of mangrove wood is 67×10^6 metric tons per year (Bouillon et al. 2008). Lignocellulose-degrading, lignicolous fungi are extremely common on decomposing mangrove wood. A.B. Cribb and J.W. Cribb described the first lignicolous mangrove fungi from Queensland, Australia. Subsequently, the research of Jan Kohlmeyer in the 1960s led to the recognition that many obligately marine lignicolous fungi were found exclusively on decomposing mangrove wood, prop roots, or viviparous seedlings. **Lignicolous mangrove fungi include "manglicolous fungi" which are found exclusively in mangroves, as well as other marine, lignicolous fungi.** E.B. Gareth Jones, Kevin Hyde, and others have contributed enormously to our knowledge of the diversity and taxonomy of fungi in woody mangrove substrates.

5.1.1 Diversity of Fungi in Decomposing Mangrove Wood

Most of the lignicolous mangrove fungi belong to the division Pezizomycotina of the Phylum Ascomycota, particularly to the Classes Dothideomycetes and Sordariomycetes, as is the case also with marine lignicolous fungi in general (Sect. 1.2.1).

About 300 species of lignicolous fungi are known from decomposing mangrove wood (Kohlmeyer and Kohlmeyer 1979; Jones et al. 2009; Sridhar et al. 2012a). While members of Halosphaeriaceae with unitunicate asci are dominant in allochthonous wood, members of both Halosphaeriaceae and also those of the Class Dothideomycetes with bitunicate asci are common on mangrove wood, prop roots, and seedlings (Sarma 2012).

- **Nearly 80 species form the core group of lignicolous mangrove fungi that are frequent on mangrove wood.** Some of these are shown in Fig. 5.3.
- **Fungi belonging to the Dothideomycetes, which are characterized by bitunicate asci, are important inhabitants of mangrove wood in the intertidal region.** Nearly 110 species of marine Dothideomycetes, belonging to 64 genera, are known. Nearly all of these are intertidal species (Suetrong et al. 2009). Bitunicate asci of Dothideomycetes have a "jack-in-the-box" mechanism, wherein the inner wall of the two-walled asci is capable of expanding under moist conditions when mature. It expands beyond the outer wall and discharges the ascospores forcibly. This mechanism is well adapted for intertidal conditions. These fungi do not have the elaborate appendages found in marine lignicolous fungi belonging to the Halosphaeriaceae (Chapt. 4). However, ascospores of many of their species have a mucilaginous sheath, often in the form of polar appendages (Jones 2006).
- Some of the common manglicolous ascomycete fungi are:
  - *Aigialus mangrovei* Borse.
  - *A. grandis* Kohlm. & S. Schatz.
  - *Dactylospora haliotrepha* Kohlm. & E. Kohlm.) Hafellner.
  - *Halorosellinia oceanica* (S. Schatz) Whalley, E.B.G. Jones, K.D. Hyde & Lassøe)
  - *Halosarpheia marina* (Cribb & J.W. Cribb) Kohlm.

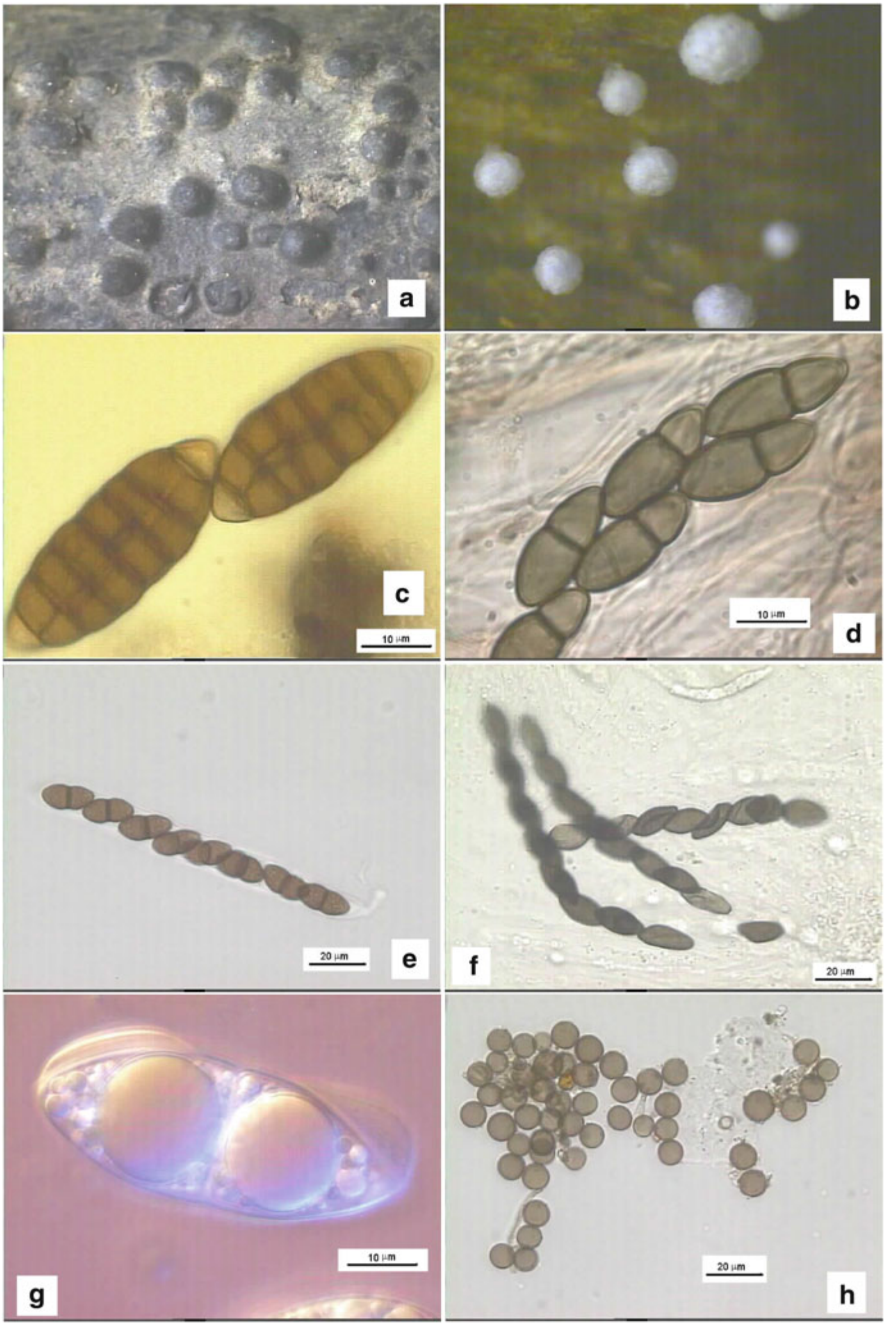


Fig. 5.3 Some common lignicolous marine fungi of decomposing mangrove wood. (**a**) Ascocarps of *Halorosellinia oceanica*. (**b**) Basidiocarps of *Halocyphina villosa*. (**c**) Ascospores of *Aigialus mangrovei*. (**d**) Ascosores of *Dactylospora haliotrepha*. (**e**) Ascospores of *Verruculina enalia*. (**f**) Ascospores of *Halorosellinia oceanica*. (**g**) Ascospores of *Saagaromyces ratnagiriensis*.

  - *Natantispora retorquens* (Shearer & J.L. Crane) J. Campb., J.L. Anderson & Shearer.
  - *Quintaria lignatilis* (Kohlm.) Kohlm. & Volkm.- Kohlm.
  - *Saagaromyces abonnis* (Kohlm.) K.L. Pang & E.B.G. Jones.
  - *S. ratnagiriensis (*S.D. Patil & Borse) K.L. Pang & E.B.G. Jones.
  - *Verruculina enalia* (Kohlm.) Kohlm. & Volkm.- Kohlm.

- Several marine lignicolous fungi which are not confined to mangroves and which are also found on allochthonous wood grow on dead mangrove wood. Some of these are *Antennospora quadricornuta* (Cribb & J.W. Cribb) T.W. Johnson*, Aniptodera chesapeakensis* Shearer & M.A. Mill.*, Leptosphaeria australiensis* (Cribb & J.W. Cribb) G.C. Hughes*, Lignincola laevis* Höhnk, *and Lulworthia* sp.
- Halocyphina villosa Kohlm. & E. Kohlm. is the most frequent manglicolous basidiomycete.
- The anamorphic fungus *Hydea (Cirrenalia) pygmea* (Kohlm.) K.L. Pang & E.B.G. Jones is common in mangrove substrates.

The fungal assemblage of dead mangrove wood comprises two components.

1. **Endophytic fungi that were already growing in living woody trunks of mangrove trees may continue as decomposers upon the death of the trees**. Twigs of the mangroves *Aegiceras corniculatum, Avicennia marina, Bruguiera gymnorrhiza*, and *Kandelia candel* in Guangxi, China, have been observed to possess high endophytic colonization rates of 30–58%, which were higher than in leaves (6–25%) (Li et al. 2016). Among various fungi, *Phomopsis, Phyllosticta, Xylaria, Leptosphaerulina,* and *Pestalotiopsis* were dominant. Some endophytic fungi showed host and tissue preference. The endophytic fungal community composition was different among four mangrove species and between leaf and twig tissues.
2. **Lignicolous fungi colonize dead mangrove wood.** Wood of living trees is covered by a protective bark that is rich in antimicrobial tannin. Prop roots are also protected likewise. Viviparous seedlings are covered by a protective, waxy cuticle. Only a few bark-inhabiting fungi such as *Etheirophora blepharospora* (Kohlm. & E. Kohlm.) Kohlm. & Volkm.-Kohlm., *Mycosphaerella pneumatophorae* Kohlm., *Lulworthia grandispora* Meyers, *Alisia salsuginosa* Nakagiri & Tad, and *Rhabdospora avicennia* Kohlm. & E. Kohlm. colonize dead wood where a bark is retained (Kohlmeyer and Kohlmeyer 1979; Hyde and Jones 1988; Hyde 1991; Leong et al. 1991).

   Lignicolous mangrove fungi colonize dead wood only following decomposition of the bark by bark-inhabiting fungi or by removal of the bark by abiotic means.

Fig. 5.3 (continued) (**h**) Conidia of *Periconia prolifica* (Photographs: V.V. Sarma and S. Raghukumar. Marine Lignicolous fungi. A Database on taxonomy. With kind permission of CSIR-National Institute of Oceanography, Goa, India. Under Creative Commons 4.0. http://www.niobioinformatics.in/fungi/index.htm)

Ascospores, basidiospores, and conidia become attached to mangrove wood and other lignocellulosic material in a passive manner, through impaction, entrapment, and adhesion owing to their sticky ascospores or appendages. Attachment of ascospores of many mangrove dothideomycete fungi is aided by the mucilaginous sheath present on them. Many fungi with unitunicate asci possess ascospores with various forms of sticky appendages which too are of importance in their adhesion to wood. Further germination and colonization takes place as with other marine lignicolous fungi (Sect. 4.2.1).

Species assemblage and diversity of lignicolous fungi in mangrove wood is determined by various factors.

1. **Many mangrove fungi display specific host preferences or even specificity towards wood from particular mangrove tree species** (Table 5.1). Mangrove trees differ in terms of their wood anatomy. They may also differ with reference to their chemistry such as the presence of tannins and other inhibitory compounds and the composition of lignocelluloses. These factors are probably important determinants of the preference of individual species to wood of different mangrove trees.

   Wood of mangrove species belonging to *Rhizophora* is a highly favorable substrate for mangrove fungi. Along the mangroves of the west coast of India, *Rhizophora apiculata* Blume has the highest diversity, followed by *Avicennia officinalis* L. and *A. marina* (Forssk.) Vierh. Decomposing prop roots of *R. apiculata*, in particular, are excellent substrates for growth of mangrove fungi (Sarma and Vittal 2000). More than 201 lignicolous fungi belonging to 139 genera are known from *Rhizophora* spp. Thus, approximately two-thirds of total number of lignicolous marine fungi are known to occur on this host. Some species prefer substrates belonging to *Rhizophora* sp., while others prefer those of *Avicennia*. Many others are known to prefer the fronds of the mangrove palm *Nypa fruticans*. Several fungi show no host preference and colonize lignocellulosic material from a wide variety of mangrove species.
2. **Several species of mangrove fungi display distinct geographical distributions** (Table 5.2). Lignicolous fungi have been studied from a wide range of tropical and subtropical mangrove ecosystems of the Indian (India, Malaysia, Thailand, Philippines, Hong Kong, Seychelles, New Zealand, and Australia), Atlantic (Sierra Leone in West Africa, Florida in USA, Baja California in Mexico, Bermuda, Brazil, South Africa, and Egypt), and the Pacific Oceans (Peru, Hawaii, Fiji). Diversity of fungi is greater in tropical mangroves, particularly in the Indian Ocean, than in subtropical ones. This might correspond with the greater mangrove tree diversity of tropics. Although similar fungi are found both in tropical and subtropical mangroves, frequency of certain species differs in the two (Abdel-Waheb and El-Sharouny 2002).
3. **Location of the wood in the intertidal zone is an important determinant of the diversity present in it** (Table 5.3). Mangroves are subject to strong tidal variations. Hence, different parts of mangroves occurring at different zones from the highest high tide to the lowest low tide are inundated by seawater or exposed

Table 5.1 Host preference of lignicolous mangrove fungi (Gratefully acknowledge: Md. Farid Hossain, Md. Anwarul Islam. Utilization of Mangrove Forest Plant: Nipa Palm (*Nypa fruticans* Wurmb.) American Journal of Agriculture and Forestry 2015; 3(4): 156–160 for the photograph of *Nypa fruticans*)

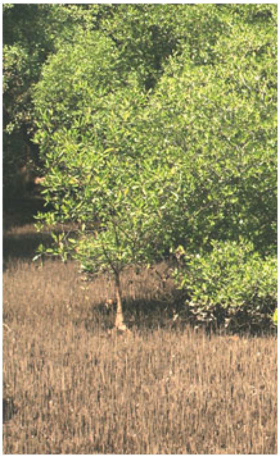
 *Rhizophora apiculata*	*Caryosporella rhizophorae*, *Cryptosporella mangrovei*, *Etheirophora blepharospora*, *Hypophloeda rhizospora*, *Lophiostoma rhizophorae*, *Pedumispora rhizophorae*, *Rhizophila marina*, *Sacardoella rhizophorae*, *Trematosphaeria mangrovei*, *Phomopsis mangrovei*, *Robillarda rhizophorae*, *Xylomyces rhizophorae*	*Leptosphaeria australiensis*, *Savoryella lignicola*, *Verruculina enalia*, *Halorosellinia oceanica*, *Hypoxylon* sp., *Lophiostoma mangrovei*, *Lulworthia* sp., *Lulworthia grandispora*, *Trichocladium achrasporum*
 *Avicennia marina*	*Adomia avicenniae*, *Camarosporium roumeguerii*, *Bathyascus avicenniae*, *Cryptovalsa* sp, *Didymella avicenniae*, *Eutypa bathurstensis*, *Eutypella naqsii*, *Julella avicenniae*, *Leptosphaeria avicenniae*, *Mycosphaerella pneumatophorae*, *Rhabdospora avicenniae*, *Zopfiella latipes*, *Z. marina*	
 *Nypa fruticans*	*Aniptodera nypae*, *A. intermedia*, *Anthostomella nypae*, *Astrosphaeriella striatispora*, *Fasciatispora nypae*, *Helicascus nypae*, *Helicorhoidion nypicola*,, *Lignincola nypae*, *Linocarpon appendiculatum*, *L. bipolaris*, *L. angustatum*, *Oxydothis nypae*, *Tirisporella beccariana*, *Trichocladium nypae*	

Table 5.2 Preference of lignicolous mangrove fungi to tropical and subtropical regions

Tropical mangroves	Subtropical mangroves
Antennospora quadricornuta	*Cirrenalia macrocephala*
Aigialus grandis	*Dactylospora haliotrepha*
Dactylospora haliotrepha	*Halosarpheia fibrosa*
Caryosphaerella rhizophorae	*Leptosphaeria australiensis*
Aniptodera mangrovei	*Lignincola laevis*
Halocyphina villosa	*Periconia prolifica*
Kallichroma tethys	*Phomopsis* sp.
Lulworthia grandispora	*Zalerion varium*
Massarina velatospora	
Halorosellinia oceanica	
Halosarpheia marina	
Antennospora quadricornuta	

Table 5.3 Vertical distribution of lignicolous mangrove fungi in the littoral zone

Lower littoral or tidal	Mid-littoral or intertidal zone	Upper littoral zone
Ascomycetes: *Antennospora quadricornuta, Thalassogena sphaerica, Acrocordiopsis patilii*	Dothideomycetes (bitunicate ascomycetes): *Aigialus grandis*, *Caryosporella rhizophorae, Pyrenographa xylographoides, Julella avicenniae, Massarina velatospora, M. ramunculicola*	*Cytospora rhizophorae, Halorosellinia oceanic*a, *Savoryella lignicola*
Anamorphic fungi: *Trichocladium achrasporum, Trichocladium alopallonellum*	Unitunicate ascomycetes: *Cucullosporella mangrovei*, *Marinosphaera mangrovei*, *Lulworthia* sp.,	
Basidiomycete: *Nia vibrissa*		
Cryptovalsa sp., *Lulworthia* sp., *Leptosphaeria australiensis* and the anamorphic fungus *Hydea pygmea*		

to air for different periods. Objects in upper littoral or intertidal region are wetted only briefly and remain exposed to air for a large part of the tidal cycle. Those at the lower littoral region are mostly submerged in water and are exposed to air only for a short period. These variations strongly influence the distribution of species in mangrove wood, prop roots, and seedlings. Distinct species assemblages of fungi occur in wood of *Rhizophora apiculata, R. mucronata, Sonneratia griffithii*, *and Xylocarpus granatum* at different zones of the tidal region (Hyde 1988; Hyde et al. 1993; Hyde and Lee 1995; Sridhar et al. 2012a). On the other hand, no evidence of vertical distribution of fungi has been found on the palm *Nypa fruticans* (Besitulo et al. 2010).

   a. **Wood in the lower littoral close to subtidal area is frequently colonized by fungi with unitunicate asci of the family Halosphaeriaceae** and other ascomycete families. Such fungi are also found on allochthonous wood (Chap. 4). Fungi with ascomata having membranous walls and immersed ascomata appear to be common on wood below mean tide level. Ascospores of these fungi have typical appendages for floatation and attachment.
   b. **Wood in the mid-littoral or intertidal zone has the greatest diversity of fungi** (Hyde 1990; Alias and Jones 2000). Wood at this zone is inundated or exposed to air at regular and almost equal intervals within each day. Fungi belonging to Dothideomycetes are common in this zone. Adaptations to this intermittently wet and dry zone appear to be superficial, carbonaceous ascomata, bitunicate asci with an active spore dispersal mechanism and colored or ornamented ascospores, often with a mucilaginous wall. Other ascomycetes characterized by unitunicate asci and passive dispersal of ascospores are also found. *Halocyphina villosa* J. & E. Kohlm. is the most frequent basidiomycete on wood in the intertidal. Several anamorphic fungi are common inhabitants. Most of these fungi are not found on allochthonous driftwood samples. They are adapted to withstand exposure to sunlight, desiccation, and dryness.
   c. **Wood in the upper littoral zone** also has its characteristic fungal diversity.
   d. **Some fungi are versatile and are found on wood throughout the littoral zone.** In general, these versatile fungi possess passive spore dispersal and have immersed ascocarps with membranous walls.
   e. **Several facultative marine fungi**, such as the ascomycetes *Anthostomella* sp., *Hysterium* sp., and *Lecanidion atratum,* as well as anamorphic fungi, such as *Epicoccum purpurascens, Trimmatostroma* sp., *Helicoma hyalonema, Helicosporium pannosum, H. hongkongense*, and *Thozetella nivea,* are also common in intertidal mangrove wood and fronds of the mangrove palm *Nypa* (Sarma and Vittal 2001; Loilong et al. 2012).

4. **Salinity is an important determinant of species diversity in mangrove wood** (Sridhar et al. 2012a). Salinity gradients may exist in mangrove ecosystem depending on proximity to the sea or salinity changes may take place depending on the season. Salinity closer to freshwater is found in the upper reaches of an estuary. Strong monsoonal rains lead to rain and freshwater inflow from land and lower salinities in mangroves along the west and east coast of India. Compared to allochthonous wood immersed in the sea, mangroves are exposed to a wide range of salinities during various seasons.

   a. **Low salinities promote colonization of mangrove wood by facultative marine fungi** belonging to terrestrial as well as freshwater species. Thus, species of *Alternaria, Arthrobotrys, Aspergillus, Penicillium, Phoma*, and

Tetracrium, as well as several freshwater and aero-aquatic fungi, colonize mangrove wood during monsoon periods along the Indian coasts. The mangrove palm *Nypa fruticans* is found along a large salinity gradient ranging from freshwater to seawater conditions. Fronds of this palm along low salinity reaches are colonized by facultative marine fungi such as freshwater species belonging to *Acrogenospora, Helicoma*, and *Helicosporium* spp. and the basidiomycete *Grammothele fuligo.*

b. **Salinities approaching that of seawater promote colonization of mangrove wood by typical manglicolous fungi**. Thus, summer months along Indian coasts accompanied by higher salinities promoted colonization of typical mangrove fungi (Sridhar and Maria 2006). Diversity of fungi as judged by sporulating structures was also higher during summer (Ananda and Sridhar 2004). Dead fronds of *Nypa fruticans* growing at higher salinity reaches of 17–26 ppt are colonized by species belonging to *Halosarpheia, Helicascus, Lulworthia, Saagaromyces*, and *Savoryella.* (Sridhar et al. 2012a).

c. **Many manglicolous fungi show a broad salinity tolerance.** Thus, *Aigialus mangrovei, Halosarpheia cincinnatula, Hydea pygmea, Lignincola laevis, Matsusporium tropicale, Oceanitis cincinnatula, Lulworthia grandispora, Passeriniella mangrovei, Savoryella lignicola, Verruculina enalia, Bactrodesmium linderi*, and *Zalerion maritimum* are found both during monsoon and summer periods in mangroves of Indian coasts.

Fungi colonize decomposing wood of any given mangrove tree in a succession of species (Table 5.4).

- Fungal succession is determined by two factors.
  - Fungi that colonize wood may alter the chemistry in such a way that after a while it becomes unsuitable for them. Other fungi which can optimally utilize the wood with altered chemistry then colonize and grow.
  - Fungi may exhibit antagonism against each other. A fungus may not colonize till the presence of an antagonistic fungus declines. The slow growing lignin-degrading fungi colonizing woody substrates in the marine environment are probably k-strategists and may be a good source of antibiotics (Strongman et al. 1987).
- **Fungal succession in wood is deduced by observing the appearance of fruiting bodies of the fungi on the surface of the substrate** (Sect. 2.4.2). We have a fair idea of these processes in mangrove wood through long-term moist chamber incubations and periodic observations (Table 5.4; Alias and Jones 2000; Maria and Sridhar 2003).
  1. (i) **Wood is initially colonized by a few fungi.**
  2. (ii) **Diversity of fungi increases with progressive decomposition of wood.**

Table 5.4 Some examples of successional patterns of lignicolous fungi at different stages of decomposition in mangrove wood

Host	Early colonizer	Intermediate colonizer	Late colonizer	References
Avicennia marina and *Bruguiera parviflora* at Kuala Selangor mangrove stand in Malaysia	*6–18 weeks Halosarpheia marina, Halosarpheia retorquens, Lignincola laevis, Lignincola longirostris*, and *Lulworthia grandispora*	26–54 weeks: *Dictyosporium pelagicum, Halocyphina villosa, Halosarpheia ratnagiriensis, Periconia prolifica, Savoryella lignicola, Trichocladium achrasporum, Trichocladium alopallonellum,* and *Verruculina enalia*	*60–96 weeks: Aigialus parvus, Leptosphaeria australiensis, Nais glitra, Quintaria lignatilis, Saccardoella marinospora,* and *Tirispora unicaudata*	Alias and Jones (2000)
Split wood blocks of *Bruguiera gymnorrhiza* and *Rhizophora muronata* at the intertidal zone at five mangrove sites in Mauritius	*Cumulospora marina, Hydea pygmea*, and *Lulworthia* sp. *Periconia prolifica*	*Lignincola laevis Periconia prolifica* as an early to intermediate colonizer	*Periconia prolifica, Dactylospora haliotrepha*, and a pycnidial fungus as late colonizers	Poonyth et al. (2001)
Avicennia officinalis	*4–12 weeks: Hydea pygmea, Lignincola laevis, Lulworthia sp., Trichocladium achrasporum*	*16–32 weeks: Hydea pygmea, Lignincola laevis, Lulworthia* sp., *Tirispora* sp.	*36–72 weeks: Lulworthia* sp., *Tirispora* sp., *Verruculina enalia, Savoryella lignicola*	Maria and Sridhar (2003)
Avicennia alba	*6–18 weeks: Halosarpheia marina*	22–32 weeks: *Lignincola laevis, Lulworthia* sp., *Verruculina enalia, Payosphaeria minuta*	37–60 weeks: *Halocyphina villosa, Lulworthia* sp., *Verruculina enalia, Payosphaeria minuta*	Leong et al. (1991)

(iii) **Diversity of fungi declines with late stages of decomposition.**
(iv) **Some species colonize wood at late stages of decomposition.**
(v) **A few fungi occur throughout the decomposition, while others are restricted to different stages of decomposition.**

5.1.2 Enzymatic Degradation of Lignocellulosic Material by Mangrove Fungi

Mangrove fungi produce cellulases, hemicellulases, and lignin-degrading enzymes (LDEs) upon colonization of the substrate (Sect. 4.3.2)**. These enzymes break down the substrate and enable them to grow.**

A number of obligate as well as facultative mangrove fungi have been shown to be capable of degrading cellulose and hemicellulose (Raghukumar et al. 1994a; Rohrmann and Molitoris 1992; Pointing et al. 1998; Bucher et al. 2004). Out of 45 marine fungi, 89% showed cellulolytic and 84% showed xylanolytic activities under *in vitro* conditions (Bucher et al. 2004). The lignicolous mangrove fungi *Corollospora maritima*, *Julella avicenniae*, *Lignincola laevis*, *Monodictys pelagica*, *Nia vibrissa*, and *Stagonospora* sp. can utilize cellulose at salinities of 0–34 ppt. Others such as *Aigialus mangrovei, Gongronella* sp., *Lophiostoma mangrovei*, and *Halorosellinia oceanica* produce high levels of xylanase.

Many manglicolous fungi produce various LDEs such as lignin peroxidise, manganese peroxidase, and laccase. *Julella avicenniae, Lignincola laevis, Nia vibrissa*, and *Stagonospora* sp. utilize glucose or cellulose for growth, while simultaneously decolourizing polymeric dyes Poly R-478 and Azure B and oxidation of syringaldazine. This indicates their lignin-degrading capability. *Nia vibrissa* is an excellent lignin degrader. This fungus as well as the anamorphic fungus *Monodictys pelagica* can mineralize lignin to CO_2. *Ascocratera manglicola, Astrosphaeriella striatispora, Cryptovalsa halosarceicola, Linocarpon bipolaris*, and *Rhizophila marina* possess excellent lignin solubilizing abilities and may be comparable to terrestrial white-rot basidiomycetes. An isolate of the facultative marine fungus, *Cerrena unicolor* has been shown to decolorize a number of lignin model compounds and produce extremely high levels of laccase (Raghukumar 2008).

Enzymatic degradation of wood by fungi results in weight loss of mangrove wood. Test wood blocks of *Avicennia* and *Rhizophora* drastically lost weight after 12–18 months in mangroves of Southwest India, coinciding with peak fungal diversity on the wood (Maria et al. 2006). Significant wood borer activity accompanied the weight loss. Mouzouras (1989) using scanning electron microscopy demonstrated differential activity of fungi. The basidiomycetous fungus *Halocyphina villosa* caused significant weight loss of the wood of *Avicennia officinalis* in 24 weeks after inoculation. The anamorphic fungus *Trichocladium achrasporum* caused a rapid weight loss of wood of both *Avicennia officinalis* and *Xylocarpus granatum.* **Decomposition of the recalcitrant lignocellulosic substrate and fungal biomass build up transform mangrove wood into detritus with an enhanced nutritional value** (Sect. 2.4.2).

- Mangroves are tropical and subtropical marine vegetations found along marshy tidal areas of estuaries and coastal shorelines.
- Net primary production (NPP) results in the woody trunk, the dense foliage of leaves, underground roots, prop roots, pneumatophores, and viviparous seedlings of various mangrove tree species.
- Dead mangrove biomass is immediately available as substrates for colonization by bacteria and fungi.
- Fungi play an important role in decomposition of dead lignocellulosic material of mangroves.
- Mangrove wood is more difficult to degrade compared to leaves.
- "Manglicolous fungi" are indigenous, mangrove lignicolous fungi. About 300 species of fungi have been described in dead mangroves, of which nearly 80 species form the core group of manglicolous fungi.
- Fungi which were originally endophytes in living plants, as well as those that colonize from spores occurring in mangrove waters, grow as saprotrophs in dead mangrove wood.
- Diversity of mangrove fungi on wood depends on the host, location in the intertidal region, salinity and geographical location.
- A succession of species colonizes decomposing mangrove wood.
- Wood is initially colonized by a few fungi. Diversity increases with progressive decomposition of wood and declines in later stages. Some species colonize wood late during decomposition, while some are persistent throughout.
- Upon colonization of the substrate, mangrove fungi produce cellulases, hemicellulases, and lignin-modifying enzymes that break down the substrate and enable them to grow. Enzymatic degradation of wood by fungi results in weight loss of mangrove wood.
- Decomposition of the recalcitrant lignocellulosic substrate and fungal biomass build up transform mangrove wood into detritus with an enhanced nutritional value.

Future Directions

1. Fungal diversity of decomposing mangrove wood and woody parts has remained unexplored from many parts of the world. Some examples are Sunderbans in India and Bangladesh, which is the largest mangrove coverage on earth and mangroves along African coasts.
2. Many aspects of fungal degradation of mangrove wood and their contribution to outwelling in coastal waters in the form of fine, particulate organic material have not been quantified.

3. The diversity and role of facultative marine fungi in decomposing marine wood remains to be addressed.
4. The importance of wood-derived detritus in the food web of coastal waters has not been elucidated.

5.2 Fungi in Detritus of Mangrove Leaves and Seedlings

Mangrove leaves contribute approximately 67×10^6 metric tons of NPP per year at a global level. Decomposing mangrove leaves belonging to *Rhizophora mangle*, *R. apiculata*, and *Avicennia marina* and other mangrove trees have been studied intensely for saprotrophic fungi. Many experiments and observations have been carried out by placing the leaves in litter bags in the mangrove environment, recovering them periodically and analyzing for fungi and chemical changes (Fell and Master 1980; Benner and Hodgson 1985; Newell 1996a; Hyde and Jones 1988; Raghukumar et al. 1994b, 1995; Davis et al. 2003; Ananda and Sridhar 2004; Rajendran and Kathiresan 2007; Sridhar et al. 2012a).

Viviparous mangrove seedlings are yet another important nonwoody substrate for marine fungi. Members of the mangrove plant genus *Rhizophora* produce viviparous seedlings that germinate while still on the tree. They fall into the soil when ripe and grow into mature plants. Seedlings that do not establish themselves in the mangrove mud float in the water till they are deposited in a suitable area or decompose and become converted into detritus. Our understanding of fungi inhabiting viviparous mangrove seedlings come mostly from the studies of Steven Y. Newell in mangroves of southern Florida (Newell 1976). Newell studied fungal colonization in detached, uninjured seedlings, as well as those which were artificially injured.

5.2.1 Fungi and Decompositional Phases

Detrital formation from mangrove leaves follows the three typical phases of decomposition of large, particulate, marine detritus (Sect. 2.4.2). Fungi play a key role in detritus formation. Duration and dynamics of the three processes varies according to geographic location and also the nature of the substrates. Thus, decomposition of mangrove leaves leading to fragmentation may take place in a few months, whereas those of the seedlings take over a year. **The important events during detrital formation are (1) mycosere, resulting in changes in species assemblages; (2) microbial biomass buildup; and (3) biochemical changes of detritus.**

(1) The initial phase of leaching and early colonization phase in mangrove leaves lasts about a week.

- Senescent mangrove leaves contain about 50% of lignocellulosic structural polymers and 40 to 60% of soluble, labile organics. Soluble organic compounds comprise sugars, cyclitols, amino acids, and phenolics. **Dead leaves of mangroves undergo a rapid abiotic leaching of soluble organic matter, as well as inorganic minerals such as K, Ca, Mg, and Mn as soon as they fall into the littoral and sublittoral zones of the mangroves.** Decomposition of detached viviparous mangrove seedlings starts if they fail to establish themselves in the soil and drift in the water or when they become senescent or injured and die. In the case of leaves, more than 50% of the phenolics or tannins are lost within 2–3 weeks.
- **Fungal decomposition is initiated during this phase by two different groups of fungi. Fungi from two sources, namely those which are already resident as endophytes and those which colonize from the surrounding waters are responsible for decomposition of mangrove leaves and viviparous seedlings** (Raghukumar et al. 1995).
- Mangrove leaves are inhabited by endophytic fungi even while they are alive and attached to the trees (Kumaresan and Suryanarayanan 2002; Sakayaroj et al. 2012; Li et al. 2016). Species of *Fusarium, Phyllosticta, Phoma, Colletotrichum, Sporormiella minima, Cladosporium, Glomerella cingulata*, and *Mycospharella* sp. are extremely frequent as mangrove endophytes. Some of these species may increase in numbers after the leaves fall and may play an important role in the initial stages of mangrove leaf degradation. Further studies are required to confirm whether these fungi were in an actively growing mycelial state and if they can be truly considered as endophytes. Seedlings too are inhabited by endophytic fungi even while they are alive and attached to the trees. Endophytic fungi persist during the initial stages of decomposition. Species of *Cladosporium, Alternaria alternata, Aureobasidium pullulans, Pestalotia* sp., and *Zygosporium masonii* are some of the fungi that have been found in such seedlings.
- **The initial leaching from leaves encourages colonization by r-strategy bacteria and fungi** (Sect. 2.4.2), **which utilize the soluble organics**. Abiotic removal of phenolics further encourages microbial growth. The straminipilan fungi, *Halophytophthora* spp. (Oomycetes) and the thraustochytrids (Labyrinthulomycetes), are efficient r-strategists in colonization of mangrove leaf detritus (Strongman et al. 1987). Zoospores of *Halophytophthora* and thraustochytrids show a chemotactic attraction to leaf leachates. They swim towards the fallen mangroves leaves which are the source of the leaching and settle on the surface (Leaño et al. 2000).
- **Colonization by the oomycete *Halophytophthora* and members of Labyrinthulomycetes is a significant event during the early decompostional phase.** A total of 13 species and 2 varieties of *Halophytophthora* are known (Fig. 5.4; Nakagiri 2000).

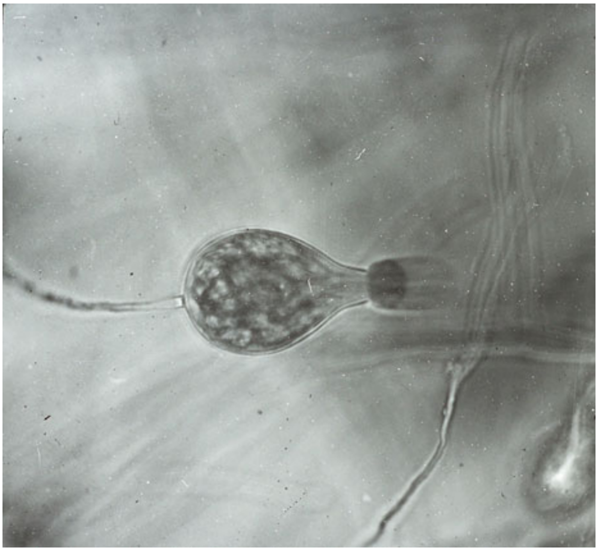


Fig. 5.4 A zoosporangium of *Halophytophthora vesicula* containing zoospores (S. Raghukumar)

Species of *Halophytophthora* show a number of adaptive features that have made them highly successful in colonizing mangrove leaves (Fig. 5.5; Leaño et al. 2000).

Their zoospores can swim for 10 h or more at a rate of at least 100 microns per second. The process by which the zoospores locate mangrove leaves and attach to them takes place in less than 2 h of leaf fall. *Halophytophthora* can be isolated at a frequency of 100% from fallen mangrove leaves within 30 h (Newell et al. 1987). Culturing following surface sterilization has shown that the fungus penetrates the leaf surface and rapidly pervades the decaying leaf. The fungus is not only capable of tolerating the high levels of phenolics that are leached out, but is also capable of degrading them (Raghukumar et al. 1994b). *Halophytophthora* may rapidly utilize the labile organic matter that is leached out. It is further capable of utilizing the cellulose of the leaf cell walls. Different species of *Halophytophthora* show seasonal and salinity preferences. Many such as *H. avicenniae, H. masteri, H. operculata*, and *H. spinosa* var. *lobata* prefer leaves of particular species of mangroves (Nakagiri 2000). Of all the species, *Halophytophthora vesicula* (Anastasiou & Churchl.) Ho & Jong is the most cosmopolitan and versatile.

Although *Halophytophthora* is a very early colonizer in the case of mangrove leaves, it has not been observed to colonize freshly fallen mangrove seedlings. *Halophytophthora vesicula* colonized this substrate only after several months of decomposition.

- **Members of labyrinthulids and thraustochytrids, which are members of Labyrinthulomycetes, are common in mangrove habitats.** Zoospores of *Aurantiochytrium mangrovei* and *Ulkenia* sp. are chemotactically attracted to leaf extracts of many mangrove plants. Glutamic acid and pectin appear to be

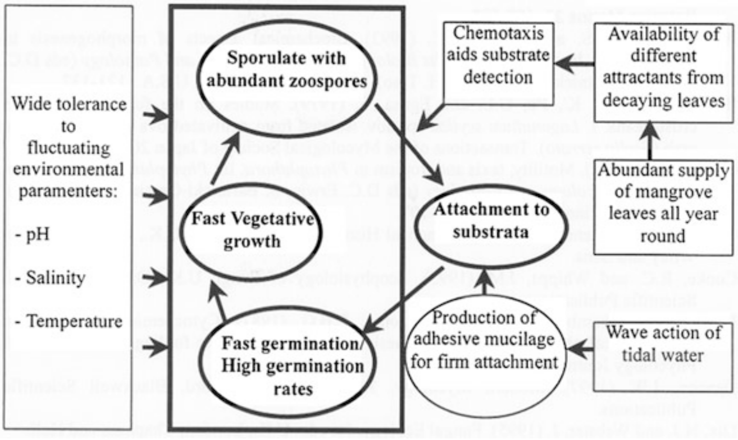


Fig. 5.5 Biological features of the oomycete *Halophytophthora* species that aid them in successfully colonizing decomposing mangrove leaves (Source: Leaño, M. et al. 2000. Fungal Diversity 5: 131–151. With permission from Dr Kevin Hyde.)

some of the specific attractants (Fan et al. 2002). Thraustochytrids colonize mangrove leaves within 24 h of submergence (Bremer and Talbot 1995). Based on analyses of the signature polyunsaturated fatty acids of thraustochytrids, the omega-3 DHA or docosahexaenoic acid (22:6ω3) and the omega-6 docosapentaenoic acid (22:5ω6), Findlay et al. (1986) found that thraustochytrids colonized mangrove leaves immediately upon their fall. They are one of the initial and major colonizers of both mangrove leaf and seedling detritus and play an important role in their degradation. Thraustochytrids have been isolated both from the surface, as well as the interior of decaying leaves, suggesting their pervasion into the leaf. Species of *Thraustochytrium* and *Schizochytrium* have also been isolated from *Sonneratia* and *Rhizophora* leaf disks submerged in mangroves (Bremer and Talbot 1995). Culturable numbers of thraustochytids in leaf detritus of *Kandelia candel* reached values of 4.8×10^3 to 5.6×10^5 CFU g^{-1}(Wong et al. 2005). These species were isolated just after 24 h after immersion of leaf in mangrove waters. *Aurantiochytrium (Schiochytrium) mangrovei* (Raghuk.) R. Yokoy. & D. Honda as well as *A. limacinum* (D. Honda & Yokochi) R. Yokoyama & D. Honda are two of the commonest thraustochytrids in most mangroves. This species has been reported from many mangroves such as the west coast of India (Raghukumar et al. 1995), Panay island, Philippines (Leaño 2001), Hong Kong (Fan et al. 2002), and Viet Nam (Hong et al. 2011).

- **Rapid microbial colonization of dead mangrove leaves takes place following the initial leaching and colonization by *Halophytophthora* species and thraustochytrids.** The rapid leaching out of antimicrobial phenolics from leaves encourages colonization by bacteria and fungi. Following a substantial loss of phenolics, many facultative marine fungi such as species of *Acremonium*, *Aspergillus, Cladosporium,* and *Phoma* colonize fallen mangrove leaves. Endophytic fungi that persist in early stages of mangrove leaf degradation, as well as other early colonizing facultative marine fungi, produce high amounts of various degradative enzymes, such as cellulases, lipases, pectinases, amylases, and proteases (Sakayaroj et al. 2012; Raghukumar et al. 1994b). Few obligate lignicolous mycetaen fungi seem to colonize leaf detritus at this stage. Fatty acid fungal markers increase rapidly from 0 to 2 weeks, indicating their colonization (Mfilinge et al. 2003).

Mangrove seedlings are also colonized by facultative marine fungi from the mangrove waters. *Septonema* sp., *Penicillium steckii,* and *Aspergillus repens* have been observed to colonize the seedlings in Newell's study in Florida mangroves.

(2) The intermediate phase of biomass buildup and decomposition of leaves starts after the first week and lasts for several weeks after that. In the case of the seedlings, this phase starts after about 2 months and subsequently lasts for several months. This stage is characterized by a low level of soluble organics, higher concentration of recalcitrant lignocelluloses, and mass loss of detritus. Little is known of such dynamics in mangrove seedlings.

- **Many fungi colonize mangrove leaf detritus in the intermediate phase than during the initial period of rapid leaching and microbial colonization. This includes terrestrial species, the stramenipilan fungus *Labyrinthula*, and a few obligately marine lignicolous fungi.** The latter belong to species of *Lulworthia*, such as *L. grandispora, Lanceispora amphibia, and Corollospora maritima*, and species of *Cirrenalia,* such as *C. basiminuta* and *Zalerion varium*. In a southwest Indian mangrove, the occurrence of marine lignicolous fungi increased after 2 weeks of submersion of fresh and dry leaf litter of *Rhizophora mucronata*. Several other anamorphic marine lignicolous fungi such as *Hydea pygmea, Periconia prolifica,* and *Trichocladium alopallonellum* have also been observed to colonize such leaves (Ananda et al. 2008; Sridhar 2009). The basidiomycete *Clathrus crispus* was reported to occur on the upper mangrove soil and decomposing leaves of *Rhizophora mangle* in Puerto Rico (Maldonado-Ramírez and Torres-Pratts 2005). *Halophytophthora vesicula* continues to inhabit leaf detritus of *Rhizophora apiculata* at this stage (Raghukumar et al. 1995).
- **Decomposing seedlings are also colonized during the intermediate phase by many obligate marine, lignicolous fungi.** These include *Lulworthia grandispora, Zalerion varium*, and *Keissleriella blepharospor*a. The oomycetan stramenipile, *Halophytophthora vesicula*, colonized the seedlings only at this intermediate stage and not during the initial stages. *Thraustochytrium* sp. continued to occur in high numbers even during this phase.
- **Fungal abundance and biomass peak during the intermediate phase of decomposition of mangrove leaves.**
  - Peak densities of *Halophytophthora vesicula* in mangrove leaves occur by about 14 days of submergence (Newell et al. 1987).

- Fatty acid markers showed that thraustochytrid biomass peaked by 14 days in decaying leaves of *Kandelia candel* (Mfilinge et al. 2003).
- Fungi grow better in detritus of intermediate decomposition phase. In vitro studies have shown that their growth on early stages of detritus is poor because of the high amounts of tannins. On the other hand, they grow well on 21–28 days old, intermediate phase detritus (Raghukumar et al. 1994b).
- Peak culturable densities of mycetaen fungi in decomposing leaves of *Rhizophora apiculata* and *Avicennia marina* in Indian mangroves have been recorded by 20 and 30 days of decomposition, respectively (Rajendran and Kathiresan 2007).
- **Biomass of mycetaen fungi in leaf detritus varies from 0.05 up to 1.7% of detrital dry weight depending on different methods of estimation** (Table 5.5). Total microbial biomass in *Rhizophora mangle* leaves from Florida Bay, comprising both bacteria and fungi, was reported to be approximately 0.7% of detritus. An accurate estimate of fungal biomass in mangrove leaf detritus is still lacking. Maximum biomass of mycetaen fungi is generally achieved by 14- to 30-day-old detritus.
- Fungal biomass estimations would be more accurate if the biomass of straminipilan fungi, such as *Halophytophthora vesicula* and thraustochytrids are taken into account. For example, estimations based on fatty acid markers have shown that thraustochytrids can attain a biomass equivalent to 0.043% detrital dry weight (Findlay et al. 1986).

(3) The late, fragmentation phase of mangrove leaf decomposition is characterized by continuing mass loss of detritus, a decrease in C/N ratio, a decline in recalcitrant lignocelluloses and a persistent microbial biomass. Biotic and abiotic processes result in shredding and fragmentation of the detritus into

Table 5.5 Fungal and bacterial biomass in decomposing mangrove leaves

Host	Method	Maximum % biomass in dry wt detritus		Reference
		Fungi	Bacteria	
Rhizophora mangle leaves from Florida Bay	Direct detection	0.08 (30 days)	0.62 (30 days)	Blum et al. (1988)
Rhizophora apiculata, West coast of India	Direct detection	0.05 (21 days)	0.06 (35 days)	Raghukumar et al. (1995)
Rhizophora mangle leaves from Florida Bay	Ergosterol marker	0.17	–	Newell and Fell (1992)
Rhizophora mangle leaves from Florida Bay	Fatty acid marker	0.05	0.005	Findlay et al. (1986)
Kandelia candel	Fatty acid marker	0–14 days	84 days	Mflilinge et al. (2003)
Bruguiera gymnorrhiza	Fatty acid marker	14–28 days	28 and 84 days	
Avicennia marina	Extrapolated from numbers	–	0.17 (40 days)	Robertson (1988)

finer particles (Blum et al. 1988; Raghukumar et al. 1994b, 1995; Mfilinge et al. 2003).

- **Abundance and biomass of mycetaen fungi declines during the final phase**.
- **Field as well as experimental studies have shown that a few fungi, such as *Cirrenalia basiminuta*, appear to prefer detritus during the late decompositional phase**. Fungi grown on aged detritus have been shown to produce high levels of xylanase, in addition to pectinases, proteases, and amylases.
- **Thraustochytrid populations increase in the late stage detritus.** Although mycetaen fungi declined in diversity, abundance, and biomass in late stages of detritus of *Rhizophora apiculata* in mangroves of the west coast of India, thraustochytrids reached a peak by 60 days of decomposition, together with bacteria. High numbers of thraustochytrids have also been isolated in 40-day leaf detritus of *Avicennia marina* from Indian mangroves (Kathiresan et al. 2011). Fatty acid markers have indicated that thraustochytrid and bacterial biomass increase with age of detritus (Findlay et al. 1986). Thraustochytrid numbers were reported to decline only by 80 days in decomposing *Rhizophora mangle* leaves in Florida mangroves. Many thraustochytrids degrade cellulose, and this might help them to multiply during the late phase of detrital decomposition. *Halophytophthora vesicula* also may continue to inhabit leaf detritus at this stage.
- **Bacterial biomass may increase in late stages of decomposition**. Bacterial numbers may be high throughout decay. However, they are known to peak by 35 days on decomposing *R. apiculata* leaves and by 84 days on *Kandelia candel* and *Bruguiera gymnorrhiza*.

Decompositional activities by fungi and bacteria cause significant biochemical changes in mangrove leaf detritus. Initial abiotic leaching of soluble organics results in the enrichment of refractory lignocelluloses and other complex organic molecules in detritus (Raghukumar et al. 1994b, 1995; Bremer and Talbot 1995). The biochemical changes that are caused result from enzymatic degradation and utilization of various substrates, fungi-induced leaching of DOM from the detritus and fungal biomass buildup (Sect. 2.4.2).

- Fungi cultured from mangrove leaf detritus have been shown to elaborate a variety of enzymes such as cellulases, xylanase, pectinases, amylases, and proteases. Peak enzyme activity of individual enzymes depended upon the age of the detritus. For example, cellulases were most active during the initial phase of detrital degradation, while pectinases, amylases, and proteases were produced abundantly throughout decomposition. Both mycetaen fungi and the straminipilan fungi *Aurantiochytrium mangrovei* (*Schizochytrium mangrovei*) and *Halophytophthora vesicula* are capable of producing these enzymes. Another mangrove thraustochytrid, *Aurantiochytrium limacinum*, is also known to produce cellulases (Nagano et al. 2011). Total cellulolytic activity of *Kandelia obovata* leaf litter is known to peak within 6 weeks of decomposition

(Hodgkiss and Leung 1986). **Our knowledge of the enzymatic activities of fungi in detritus is still rudimentary.**

- **An important outcome of fungal degradation of complex organic molecules in detritus is release of DOM into surrounding waters and loss of weight of the particulate organic detritus.** Microbial degradation causes loss of carbohydrates, including cellulose and hemicellulose that had accumulated in the earlier phase. This process may last several weeks to months (Benner and Hodgson 1985). Among the structural carbohydrates, hemicellulose appears to be more labile, followed by cellulose, pectins, and gums. Lignin degradation may take place concomitantly with that of polysaccharides. Mycelial fungi as well as thraustochytrids inoculated onto detritus have been shown to cause rapid mass loss of mangrove leaf detritus under experimental conditions. Mass loss may depend on whether the leaves are below the low tide level and submerged or in the intertidal region. Submerged, decomposing leaves lose much of soluble organics and dry weight mass in 2–4 weeks. Leaves in the intertidal region are subject to a much slower loss.

    - Submerged leaves of *Rhizophora apiculata* in a tropical, Indian mangrove lost 30% of dry weight, as well as nearly 50% of reducing sugars and phenolics and nearly 25% of proteins within a week's time (Raghukumar et al. 1995).
    - Submerged decomposing leaves of *Rhizophora mangle* lost 40–60% of dry weight by about 3 weeks (Davis et al. 2003).
    - Submerged leaves of *Avicennia marina, Ceriops tagal,* and *Rhizophora stylosa* in an Australian mangrove lost half the initial Ash-free Dry Weight (AFDW) by 11, 27, and 39 days, respectively, while those in the intertidal region decomposed much more slowly. These showed a 50% loss of AFDW in 90, 128, and 226 days, respectively (Robertson 1988).

    These processes are significant to the food web. Leaching and release of DOM have profound implications in the "microbial loop" pathway of coastal and oceanic pelagic food web. Removal of structural polysaccharides makes the detritus more palatable to detritivores.

- **A large amount of phenolics is abiotically leached out during the initial stages.** Presence of phenolics inhibits microbial activities and deters detritivore feeding. However, some fungi that colonize early may also degrade phenolics. For example, *Halophytophthora vesicula* efficiently lowers phenolic contents in decaying mangrove leaves (Raghukumar et al. 1994b). More than 50% of the phenolics or tannins are lost within 2–3 weeks (Robertson 1988; Rajendran and Kathiresan 2007).
- **Microbial growth results in the lowering of C/N ratio.** Animals have a much higher C/N ratio compared to plant tissues. Hence, C/N ratio has generally been considered to be a good indicator of the nutritive value of detritus. Nitrogen may be lost during the early stages of decomposition, leading to a high and unsuitable C/N ratio. Subsequently, however, significant amount of nitrogen enrichment of

detritus leads to a substantial lowering of the C/N ratio. Likewise, the detritus also becomes highly enriched in P (Davis et al. 2003).

- C/N ratio of *Rhizophora mangle* leaves in subtropical mangroves declined from 90·6 to 40.7 by 70 days of decomposition (Cundell et al. 1979). C/N ratios in an Australian mangrove showed the lowest ratios by 80–160 days (Robertson 1988).
- Decomposing mangrove leaves of *Rhizophora apiculata* in a tropical Indian mangrove showed the lowest C/N ratio by 60 days of decomposition (Raghukumar et al. 1995). Despite increase in total nitrogen, total proteins in decomposed leaves may be negligible (Raghukumar et al. 1995). Total nitrogen in decomposing mangrove leaves of *Rhizophora apiculata* and *Avicennia marina* peaked by 40 days, coinciding with peak azotobacter concentrations that fix nitrogen (Rajendran and Kathiresan 2007).
- It is likely that most of the nitrogen is in the form of humic nitrogen, arising out of a complexing of microbial enzymes, carbohydrates, and phenolics with carbohydrates in the litter (Sect. 2.4.2).
- Decomposition of viviparous seedlings of *Rhizophora mangle* was accompanied by a steady increase in total nitrogen (Newell 1976).

Unconditioned mangrove detritus contains a large amount of refractory compounds such as lignocelluloses (Lee 1995). **Microbial enrichment and modification of detritus may be a prerequisite for many detritivores to feed on them**. Fungi and bacteria thus play a key role in the trophic web through the detrital pathway. A large variety of detritivorous animals such as crabs, crustaceans, gastropods, and fish consume mangrove leaf detritus.

- Sesarmid crabs drag enormous quantities, often up to 80% of the decomposing leaves into their burrows, where they are shred and consumed. The crab *Sesarma meinerti* is estimated to consume nearly 43% of leaf fall from *Avicennia marina* (Forsk.) Vierh. in a south African mangrove (Emmerson and McGynne 1992). Crabs assimilate around 10% of the consumed detritus and excrete most of it. The excreted, modified detritus may again serve as a source of microbial activity (Hutchinson et al. 2014). Thus, *Sesarma brockii* from an Indian mangrove preferred to consume 40-day decomposed *Avicennia marina* leaves. This aged detritus promoted growth, survival, and molting frequency of the crabs (Ravichandran et al. 2006).
- Detritivorous fish belonging to *Mugil* spp. (mullets) play an important in the trophic dynamics of the Sundarban mangrove ecosystem in India (Ray and Straškraba 2001). Other important leaf detritus consumers are the mangrove snails. Smaller invertebrates such as amphipods and isopods also shred and consume detritus.
- Mangrove detritus is abundant in mangrove tidal creeks and contributes to the nutrition of juvenile prawns belonging to *Penaeus merguiensis* de Man. They assimilate the detritus with an efficiency of about 13% (Newell et al. 1995).

- Fungi in mangrove detritus may provide detritivores with essential nutrients. Thraustochytrrids are rich in ω3 (omega-3) polyunsaturated fatty acids (PUFAs), which are essential in the nutrition of marine crustaceans and fish. These PUFAs reached a maximum by 2 weeks of decomposition in decaying mangrove leaves of *Kandelia candel* and in late stages of decaying *Bruguiera gymnorrhiza*, indicating their enrichment in terms of these essential nutrients (Mfilinge et al. 2003).

Several fungi live in commensalistic association with mangrove animals or as saprotrophs in animal substrates. Eighty four yeasts were isolated from three bivalve molluscs and four crab species in mangroves at Rio de Janeiro, Brazil, of which more than 44 were novel species. *Kluyveromyces aestuarii* predominated the yeast communities of 2 detritus feeding crabs, *Sesarma rectum* and *Uca* spp., (de Araujo et al. 1995; Kutty and Philip 2008). *Halophytophthora* has been found to grow in dead and live pupae of the biting midge *Culicoides subimmaculatus* in the upper intertidal region of Australian coastal waters (Stephen and Kurtböke 2011).

5.3 Fungi in Mangrove Sediments and Waters

Mangrove sediments are rich in organic matter. DOM and POM derived from mangrove detritus enrich mangrove soils and provide abundant nutrition for microorganisms residing therein. Mangrove sediments even just a few centimeters below the surface are anoxic. **Mycetaen fungi can be cultured from anaerobic mangrove sediments.** Most of these marine-derived fungi belong to terrestrial genera (Rai et al. 1969; Nayak et al. 2011).

Chytrids and labyrinthulomycetes are common in mangrove sediments and waters (Ulken 1983a, b). Brackish water habitats with low salinities have been found to harbor Chytridiomycetes and Blastocladiomycetes. *Phlycochytrium mangrovis* Ulken is a common inhabitant in the mangroves of Cananeia, Brazil; Hawaii, USA; and Veracruz, Mexico. Others include *Olpidium* sp., *Rhizophydium* sp., *Chytridium proliferum* Karling, *Chytriomyces multi-operculatus* Sparrow and Dogma, and *Catenaria anguillulae* Sorokin. Waters of higher salinities have been observed to contain more straminipilan fungi, comprising *Thraustochytrium multirudimentale, T. pachydermum*, *Schizochytrium* sp., and *Ulkenia visurgensis*.

Dense populations of thraustochytrids and labyrinthulids, amounting up to 65700 cells per liter of sediments, have been reported from sediments of mangroves in the Red Sea and Malaysian coasts (Ulken 1986). These numbers are apparently underestimates since the quantification was based on a culture method using the Most Probable Number technique and not direct cell counts. *Thraustochytrium aureum, T. aggregatum, T. kinnei, T. pachydermum, Schizochytrium aggregatum,* and *Labyrinthula* sp. have been found in these environments.

Anaerobic sulfate reduction is usually considered as the most important respiration process in these layers. Fungi are mostly aerobic organisms, and their activity in the anoxic sediments is expected to be poor. However, **fungal hyphae have been detected in anoxic sediments using Calcofluor staining and epifluorescence microscopy, suggesting that fungi may be active in anaerobic sediments**. A study on mycetaen fungi in anoxic mangrove sediments using 454 pyrosequencing of the nuclear ribosomal internal transcribed spacer 1 and 2 (ITS-1 and ITS-2) revealed a high diversity, Agaricomycetes of the Basidiomycota being dominant (Arfi et al. 2012). It is possible that some marine fungi are capable of tolerating low oxygen tensions and play an important role in turnover of the enormous amount of lignocellulosic organic matter in mangrove sediments compared to bacteria (Pointing and Hyde 2000).

Yeasts too are abundant in mangrove sediments. *Candida taylori, Kluyveromyces aestuarii, and Lachancea meyersii* have been reported from mangrove swamps in Florida, Bahamas, and Brazil. Some species such as *Kwoniella mangroviensis, Candida sharkiensis, C. rhizophoriensis, Cryptococcus mangaliensis,* and *Rhodosporidium paludigenum* appear to be specifically associated with mangrove habitats (Statzell-Tallman et al. 2008; Fell 2012; Jones and Fell 2012). Four marine basidiomycetous species, belonging to *Rhodosporidium fluviale, R. diobovatum, R. paludigenum,* and *R. sphaerocarpum*, have been isolated from sea water in mangrove habitats.

- Decaying leaves of *Rhizophora mangle*, *R. apiculata*, *Avicennia marina*, and other mangrove trees, as well as viviparous seedlings of *Rhizophora mangle*, have been extensively studied for fungi.
- Mangrove leaves follow the three typical, initial, intermediate, and final phases of decomposition.
- Mycosere, microbial biomass buildup, and biochemical changes are the important events of detrital formation.
- Fungi existing as endophytes and those that colonize fallen dead leaves and seedlings from surrounding waters carry out their decomposition.
- The initial leaching from detritus encourages colonization by r-strategy bacteria and fungi which utilize the soluble organics.
- The oomycete *Halophytophthora* is an extremely common fungus in mangrove leaves. This fungus shows a number of adaptive features that has made it highly successful in colonizing mangrove detritus.
- Members of labyrinthulids and thraustochytrids are abundant in mangrove detritus. *Aurantiochytrium mangrovei and A. limacinum* are two of the commonest thraustochytrids in most mangroves.
- Dead mangrove leaves are rapidly colonied by obligate and facultative marine fungi.

(continued)

- Fungal abundance and biomass peak during the intermediate phase of decomposition of mangrove leaves.
- Growth and enzymatic degradation by fungi alter the biochemistry of the intermediate phase detritus.
- Fungal and bacterial growth results in mass loss of detritus, biochemical changes, a decrease in C/N ratio, a decline in recalcitrant lignocelluloses, and a persistent microbial biomass. Biotic and abiotic processes result in shredding and fragmentation of the detritus into finer particles.
- Fungal biomass in leaf detritus reaches up to 1.7% of detrital dry weight.
- Microbial enrichment and modification of detritus may be a prerequisite for many detritivores to feed on them.
- Mycetaen fungi can be cultured from anaerobic mangrove sediments.
- Chytrids and labyrinthulomycetes are common in mangrove sediments and waters.
- Fungal hyphae have been detected in anoxic sediments.

Future Directions

1. Diversity of fungi in mangrove leaf detritus in many parts of the world has been poorly studied.
2. Our knowledge of fungal biomass in mangrove leaf detritus is still rudimentary. Total fungal biomass, including mycetaen and straminipilan fungi, has not been elucidated so far.
3. A large amount of mangrove detritus is "outwelled" to nearby coastal waters. Microbial biomass thus transported out of the mangroves into surrounding coastal waters and buried in coastal sediments has not been quantified. Biochemical and molecular markers for fungi will help understand this.
4. Finer aspects on the role of fungi in detrital dynamics have not been addressed. For example, what is the role of fungi in DOM release and nitrogen enhancement in mangrove leaf detritus?
5. Diversity and activity of fungi in mangrove sediments and waters has not been studied in detail. Do anaerobic fungi inhabit mangrove soils?
6. Are fungi important in nutrition of mangrove detritivores? If so, in what manner?