A review on frequently occurring fungi in mangroves

V.V. Sarma and Kevin D. Hyde*

Centre for Research in Fungal Diversity, Department of Ecology and Biodiversity, The University of Hong Kong, Pokfulam Road, Hong Kong; *e-mail: kdhyde@hkucc.hku.hk

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Recent studies on intertidal mangrove fungi have provided information on (a) frequency of occurrence, (b) vertical zonation, (c) host and substratum specificity, (d) succession, and (e) seasonal occurrence. Importance has been given to frequency of occurrence in many of these investigations. As with many other organisms, only a few fungi predominate on a given substratum or in a given habitat. A synopsis of frequently occurring fungi in mangroves is presented based on the literature. Although a 'core' group of fungi can be recognised from mangroves at different geographic locations, the very frequent fungi seem to differ from one site to another. The very frequent fungi however, overlap between the Pacific and Indian oceans. No data however, is available on the frequency of occurrence of mangrove fungi from the Atlantic Ocean. The number of samples examined, the dominance of the host species in the study site (availability of substrata), host specificity, vertical distribution, tissue and organ preference, temperature, salinity, succession and seasonality, appear to be some of the factors that may influence fungal communities. These factors are discussed with suggestions for methodology and future studies are made. A table, providing a synopsis of frequently occurring fungi in mangroves is also presented.

Key words: biodiversity, ecological studies, frequency of occurrence, manglicolous fungi.

Introduction

Mangroves are common to tropical or subtropical coastal regions, especially inside lagoons and at the mouths of streams and rivers, where they are protected from wave action. Mangrove trees have interesting adaptations to their aquatic habitat: some have prop roots, others have negatively geotrophic aerating roots (pneumatophores), while most possess viviparous seedlings (Chapman, 1976). The roots and fallen seedlings provide a unique habitat for fungi as the substrata are wetted daily by intertidal waters. These substrata may be submerged for as little as one hour each day, or permanently submerged except for short periods during spring tides.

Mangrove trees are fascinating study objects for the mycologist because the bases of their trunks and aerating roots are permanently or intermittently submerged, whereas the upper parts of roots and trunks rarely or never reached

Table 1. Percentage similarity between sites (can be calculated using Jaccard's coefficient or Sorensen coefficient) (Kenkel and Booth, 1992).

Sites	A	B	C	D	E	F
A	xx	xx	xx	xx	xx	xx
B		xx	xx	xx	xx	xx
C			xx	xx	xx	xx
D				xx	xx	xx
E					xx	xx
F						xx

by the salt water, although they sometime may be subjected to saline spray. Thus, terrestrial fungi and lichens occupy the upper part of the trees and marine species occupy the lower part. At the interface there is an overlap between marine and terrestrial fungi (Kohlmeyer, 1969b).

Most early studies on fungi colonizing mangroves were taxonomic and confined mainly to cataloguing fungi and describing new taxa collected in a given area (Cribb and Cribb, 1955; Kohlmeyer and Kohlmeyer, 1964-1969, 1971, 1977; Kohlmeyer, 1966, 1969a, 1981, 1984, 1985; Kohlmeyer and Schatz, 1985; Schatz, 1985). Until recently, there have been few ecological studies on manglicolous fungi. Recent studies on intertidal mangrove fungi have provided information on (a) frequency of occurrence, (b) vertical zonation, (c) host and substratum specificity, (d) succession, and (e) seasonal occurrence (Aleem, 1980; Jones *et al.*, 1988; Hyde, 1988a, 1989c, 1990b, 1991; Leong *et al.*, 1991; Poonyth *et al.*, 1999). Of these, considerable effort has been spent investigating the frequency of occurrence of manglicolous fungi (Jones and Tan, 1987; Borse, 1988; Hyde, 1988a,b, 1989a,b; Hyde and Jones, 1988; Jones *et al.*, 1988; Jones and Kuthubutheen, 1989; Tan *et al.*, 1989; Tan and Leong, 1990, 1992). Because of the importance given to frequency of occurrence of fungi, it is felt pertinent to review the literature on the very frequent fungi from different mangrove sites based on the available literature. A synopsis of frequently occurring fungi from different mangroves is presented in Table 1. The importance of such studies is discussed and recommendations for future studies are given.

History

In one of the earliest studies on the ecology of mangrove fungi Kohlmeyer (1969b) encountered three common species of marine fungi in the mangrove habitat, namely *Lulworthia* spp. (20% of all collections), *Leptosphaeria australiensis* (15%) and *Phoma* sp. (10%). Kohlmeyer (1984) also reported that *L. australiensis* was a common species of mangroves as measured by the large number of collections made. In limited forays into South

Florida's mangrove swamps, Newell (1976) found *Kallichroma tethys*, *Leptosphaeria australiensis* and *Verruculina enalia* to be very common, while Aleem (1980) reported that the ascomycetes: *Halosarpheia viscidula*, *Rosellinia* sp. (= *Halorosellinia oceanica*) and *Torpedospora radiata* were frequent on mangroves in Sierra Leone. Aleem (1980) also found that the mitosporic taxa, *Cirrenalia macrocephala*, *C. pygmea*, *C. tropicalis*, *Monodictys pelagica*, *Periconia prolifica* and *Zalerion* spp. were abundant on mangrove wood. However, with the exception of Kohlmeyer (1969b), frequency of occurrence was not discussed in any of these studies.

Quantitative data on the occurrence of tropical marine fungi have been published by Raghukumar (1973), Koch (1982), Kohlmeyer (1984), Zainal and Jones (1984, 1986) and Virjmoed *et al.* (1986a,b). However all of these reports were on driftwood in the sea, along with driftwood on the mangrove floor or panels belonging to various timbers submerged near jetties. Hyde (1986) used the following formula to calculate the percentage occurrence of fungi on a work in marine habitats including mangrove substrata, driftwood, seagrasses, angiosperm leaves and algae.

$$\text{Percentage occurrence} = \frac{\text{Number of occurrences of a particular fungus}}{\text{Total number of samples supporting sporulating fungi}}$$

In a subsequent study Hyde and Jones (1988) modified the above formula as follows:

$$\text{Percentage occurrence} = \frac{\text{Number of occurrences of a particular fungus}}{\text{Total number of samples examined}}$$

The modified formula has also been used by other workers (Leong *et al.*, 1991; Alias *et al.*, 1995).

The frequency of occurrence of fungi has been reported based on the percentage occurrence of fungi which are subsequently artificially grouped into frequency groupings (e.g. >20% = very frequent; or <20%= less frequent). Hyde (1989a) made a quantitative ecological study of fungi on mangroves of Brunei and classified the fungi as 'most common' (occurring in 10% or above of samples examined) and 'frequent' (occurring in less than 10% of samples). Leong *et al.* (1991) used the following frequency groupings: very frequent (>20%), frequent (10-20%), and infrequent (<10%).

Very frequent fungi at different mangrove sites

Early reports on new genera and new species of marine fungi were mainly from driftwood collected along the coast of the Atlantic Ocean. In the case of mangrove fungi, however, most reports available are from the Pacific and Indian Oceans. Data on frequency of occurrence of fungi is not available for the Atlantic Ocean, although several new fungi are reported from this region. A synopsis of frequently occurring fungi from different mangrove sites is provided in Table 2. *Antennospora quadricornuta*, *Dactylospora haliotrepha*, *Eutypa bathurstensis*, *Halocyphina villosa*, *Halorosellinia oceanica*, *Halosarpheia marina*, *Kallichroma tethys*, *Leptosphaeria australiensis*, *Lophiostoma mangrovei*, *Lulworthia grandispora*, *Lulworthia* sp., *Rhizophila marina*, *Savoryella longispora* and *Verruculina enalia* are the very frequently encountered fungi in the mangroves of the Indian Ocean (Table 2) in addition to several frequently recorded species. In the case of Pacific Ocean, *Caryosporella rhizophorae*, *Cirrenalia pygmea*, *Dactylospora haliotrepha*, *Halocyphina villosa*, *Halosarpheia marina*, *Lignincola laevis*, *Linocarpon appendiculatum*, *Lulworthia grandispora*, *Lulworthia* sp., *Massarina acrostichi*, *M. velatospora*, *Phomopsis* sp., *Torpedospora radiata* and *Trichocladium linderii* were reported to be very frequently recorded species. It can be found from the above list that there is an overlap of very frequently recorded species between the Indian and Pacific oceans.

A discussion on manglicolous fungi based on tropical versus temperate regions has some limitation since mangrove vegetation are mostly found in tropical regions. Mangroves in subtropical countries are less abundant and so is their fungal diversity (Hyde, 1990a). This could be attributed to substratum availability (Jones and Alias, 1997). Most of the reports on the frequency of occurrence of mangrove fungi are in the latitude range of 20° N to 20° S and longitude 80° to 120° E (Table 2).

Among the different geographical locations; South East Asia has been sampled most thoroughly (Hyde and Lee, 1995; Jones and Alias, 1997). There seem to be no discernible difference between mangrove fungi reported in the subtropics as compared to those found in tropical areas. This is also true for frequently recorded fungi. The majority of the species reported by Vrijmoed *et al.* (1994) from Hong Kong and Macau (subtropical climate) e.g. *Dactylospora haliotrepha*, *Halorosellinia oceanica*, *Kallichroma tethys*, *Leptosphaeria avicenniae* were also reported from Brunei and other tropical mangroves (Hyde and Jones, 1988; Hyde, 1989a). The marine mycota reported from warm temperate mangroves of Australia seems to be little different from those reported from tropics, for example *Halosarpheia retorquens*, *H. appendiculata* and *Tunicatispora australiensis* (Hyde, 1989c). The frequently recorded fungi

Table 2. A synopsis of frequently occurring fungi in different mangroves sites.

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
AUSTRALIA: Melbourne, Cannons Creek Coastal Reserve, Hyde, 1990c (33°38′ S, 151°23′ E)	Unidentified intertidal mangrove wood	59	*Halosarpheia marina* (18.6) *Halosarpheia fibrosa* (13.5) *Tunicatispora australiensis* (10.2)	*Aniptodera mangrovei* (6.8) *Lulworthia grandispora* (6.8) *Nais glitra* (6.8) *Dactylospora haliotrepha* (5.1)
AUSTRALIA: Sydney, Ku-Ring-Gai Chase Natinal Park, Hyde, 1990c (38°14′ S, 145°25′ E)	Unidentified intertidal mangrove wood	32	*Dactylospora haliotrepha* (12.5) *Periconia prolifica* (12.5)	*Halosarpheia fibrsoa* (9.4) *Lignincola longirostris* (9.4) *Lulworthia grandispora* (9.4) *Nais glitra* (9.4) *Aniptodera mangrovei* (6.2) *Ascocratera* cf. *manglicola* (6.2) *Halosarpheia marina* (6.2)
BRUNEI: Serasa, Hyde, 1989a (4-6° N, 114-116° E)	*Rhizophora* spp. and *Sonneratia* spp.	73	*Halocyphina villosa* (14) *Cirrenalia pygmea* (12)	*Halosarpheia marina* (10) *Leptosphaeria australiensis* (10) *Lulworthia grandispora* (8) *Lignincola laevis* (7) *Lulworthia* sp. (6) *Phoma* sp. (6)
BRUNEI: Seria, Hyde, 1989a	*Rhizophora* spp., *Avicennia* spp. and *Nypa fruticans*	60	*Lulworthia grandispora* (17) *Cirrenalia pygmea* (17)	*Halosarpheia marina* (80) *Limacospora* sp. (7) *Halosarpheia viscosa* (6)
Tungit Api Api, Hyde, 1992d	*Nypa fruticans*	250	*Linocarpon appendiculatum* (51.2) *Astrosphaeriella nypae* (49.6) *Oxydothis nypae* (32.8) *Lignincola laevis* (26.8) *Linocarpon nipae* (22) *Lulworthia grandispora* (15.6) *Halocyphina villosa* (14.4)	*Carinispora nypae* (8) *Fasciatispora nypae* (8) *Phoma* sp. (7.6) *Phialophorophoma* cf. *littoralis* (7.2) *Halosarpheia marina* (5.6)

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
(Hyde, 1989d)	*Acrostichum speciosum*	50	*Massarina acrostichi* (40) *Cirrenalia pseudomacrocephala* (21) *Aniptodera chesapeakensis* (10) *Lulworthia* sp. (spores 340-490 µm, 10)	*Trichocladium opacum*-like sp. (9) *Halosarpheia marina* (8) Unidentified hyphomycete (6)
HAWAII, Volkmann-Kohlmeyer and Kohlmeyer, 1993 (21°09′N, 156°54′W)	*Rhizophora* sp.	187	*Torpedospora radiata* (18.2) *Lulworthia* sp. (17.6) *Halosarpheia quadricornuta* (13.9) *Halosphaeria salina* (12.8) *Lignincola laevis* (12.3)	*Leptosphaeria australiensis* (9.6) *Ceriosporopsis halima* (9.6) *Kallichroma tethys* (7) *Marinosphaera mangrovei* (7) *Trichocladium alopallonellum* (6.4) *Lignincola longirostris* (5.3)
HONG KONG, Vrijmoed *et al.*, 1994 (22° N, 114° E)	*Kandelia candel*	82	*Phomopsis* sp. (18.3) *Lignincola laevis* (14.6)	*Dactylospora haliotrepha* (8.5) *Melaspilea* sp. (7.3) *Savoryella lignicola* (7.3) *Verruculina enalia* (6) *Leptosphaeria australiensis* (6) *Lulworthia* sp. (range 350 µm) (6) *Massarina velatospora* (6)
HONG KONG Poon and Hyde, 1998	*Phragmites australis*	269	*Lignincola laevis* (22.7) *Colletotrichum* sp. (21.2) *Phomopsis* sp. (19.3) *Halosarpheia phragmiticola* (15.2) *Cytoplea* sp. (11.9)	*Septoriella* sp. (8.2) *Phomatospora phragmiticola* (7.4) *Phragmitensis marina* (7.4) *Cytoplacosphaeria phragmiticola* (5.9) *Macrophomina* (5.9)
INDIA East coast, Godavari, Sarma *et al.*, 2001 (16°10′N, 82°18′E)	*Rhizophora apiculata*	1706	*Verruculina enalia* (17.1) *Cirrenalia pygmea* (11.1) *Rhizophila marina* (10.4)	*Cryptosphaeria mangrovei* (8.9) *Saccardoella rhizophorae* (6.2)
	Avicennia marina, *A. officinalis*	1294	*Verruculina enalia* (25.1) *Eutypa bathurstensis* (23.3)	*Lophiostoma mangrovei* (9.8) *Hypoxylon* sp. (5.9)

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
	(Both samples put together)	3000	*Verruculina enalia* (20.6) *Eutypa bathurstensis* (10.1)	*Lophiostoma mangrovei* (6.5) *Cirrenalia pygmea* (6.3) *Rhizophila marina* (5.9) *Cryptosphaeria mangrovei* (5.1)
Krishna, Sarma *et al.*, 2001 (15°50′N, 80°48′E)	*Rhizophora apiculata*	1283	*Verruculina enalia* (11.6) *Dactylospora haliotrepha* (11.4)	*Rhizophila marina* (9.7) *Halosarpheia abonnis* (6.2) *Lulworthia* sp. (5.5)
	Avicennia marina, *A. officinalis*	710	*Verruculina enalia* (22.7) *Eutypa bathurstensis* (22.2)	*Halocyphina villosa* (8.9) *Lulworthia* sp. (8.4)
	(Both samples put together)	2003	*Verruculina enalia* (15.5)	*Dactylospora haliotrepha* (8.7) *Eutypa bathurstensis* (7.9) *Lulworthia* sp. (6.5) *Halosarpheia abonnis* (5.4) *Halocyphina villosa* (5)
INDIA Pichavaram mangroves, Ravikumar, 1991 (11°26′N, 79°48′E)	*Rhizophora mucronata*, *R. apiculata*, *Avicennia marina*, *A. officinalis*	?	*Verruculina enalia* (27.8) *Lophiostoma mangrovei* (11.8)	*Dactylospora haliotrepha* (7.94) *Leptosphaeria australiensis* (6.68) *Aigialus grandis* (5.51)
West coast, Maharastra, Borse, 1988	*Avicennia alba*, *Sonneratia alba*, *S. apetala*, *Rhizophora mucronata*	235	-Nil-	*Massarina velatospora* (8.5) *Halocyphina villosa* (7.7) *Verruculina enalia* (6.8) *Aigialus grandis* (6.8) *Lulworthia* sp. (6) *Dactylospora haliotrepha* (5.1)

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
Andaman and Nicobar islands, Chinnaraj, 1993b (6-14°N, 92-94°E)	*Avicennia marina*, *A. officinalis*, *Bruguiera gymnorrhiza*, *Rhizophora apiculata*, *R. mucronata* and *Sonneratia apetala*	606	*Verruculina enalia* (12) *Halocyphina villosa* (10.2)	*Halorosellinia oceanica* (9.6) *Lophiostoma mangrovei* (9.2) *Lulworthia grandispora* (9.2) *Ascocratera manglicola* (7.7) *Trichocladium achrasporum* (6.9) *Dactylospora haliotrepha* (6.9) *Biatriospora marina* (5.1)
Atolls of Maldives, Chinnaraj, 1993a	*Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera racemosa*	151	*Lophiostoma mangrovei* (20.7) *Verruculina enalia* (14.7)	*Dactylospora haliotrepha* (9) *Massarina thalassiae* 7.6) *Lineolata rhizophorae* (6.9)
JAPAN Irimote Island, Nakagiri, 1993 (25°20′ N, 123°90′ E)	*Rhizophora stylosa*, *Bruiguiera gymnorrhiza*	94	*Caryosporella rhizophorae* (15.9) *Dactylospora haliotrepha* (13.8) *Swampomyces triseptatus* (13.8)	*Lineolata rhizophorae* (5.3) *Verruculina enalia* (5.3)
MACAU, Vrijmoed *et al.*, 1994	*Kandelia candel*	40	*Trichocladium linderii* (35) *Phomopsis* sp. (15) *Savoryella paucispora* (12.5) *Rosellinia* sp. (10)	*Halorosellinia oceanica* (7.5) *Massarina* sp. (7.5) *Savoryella lignicola* (7.5)
MALAYSIA Pontian Besar mangrove, Tan and Leong, 1992 (1°27′N, 103°34′E)	*Rhizophora apiculata*	82 (102)	*Halosarpheia marina* (21.6) *Lulworthia* sp. (16.7) *Lignincola laevis* (11.8) *Halosarpheia retorquens* (10.8)	*Cirrenalia basiminuta* (9.8) *Bathyascus* sp. (8.8) *Aniptodera chesapeakensis* (7.8) *Antennospora quadricornuta* (7.8) *Mycosphaerella pneumatophorae* (5.9)
Sungei Gey lang, Patah, Jones and Tan, 1987 (3°10′N, 101°35′E)	*Rhizophora apiculata*	118	*Rosellinia* sp. (16.1) *Savoryella paucispora* (11)	*Halocyphina villosa* (9.3) *Trichocladium achrasporum* (8.4) *Savoryella lignicola* (7.6) *C. rhizophorae* (6.7) *Leptosphaeria australiensis* (5.9)

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
Kuala Selangor, Sementa and Port Dickson, Jones and Kuthubutheen, 1989	*Rhizophora* spp., *Avicennia* spp. and other mangrove wood	790	*Halocyphina villosa* (14)	*Kallichroma tethys* (9.6) *Lulworthia grandispora* (6.4) *Dactylospora haliotrepha* (5.7) *Halorosellinia oceanica* (5.6)
Kuala Selangor, Alias *et al.*, 1995 (3°32′ N, 101°26′ E)	*Rhizophora apiculata*, *Avicennia marina* and *Bruguiera gymnorrhiza*	259	*Halocyphina villosa* (25.3) *Leptosphaeria australiensis* (17) *Kallichroma tethys* (17) *Lulworthia grandispora* (14.8) *Marinosphaera mangrovei* (12.2) *Eutypa* sp.1 (10.2)	*Dactylospora haliotrepha* (7.9) *Lignincola longirostris* (5.2) *Ascocratera manglicola* (6.9)
Morib, Alias *et al.*, 1995 (2°72′ N, 101°50′ E)	*Avicennia marina*, *Rhizophora apiculata*, *Sonneratia apetala* and *Nypa fruticans*	258	*Leptosphaeria australiensis* (20.5) *Halocyphina villosa* (16.4) *Kallichroma tethys* (15.7) *Halorosellinia oceanica* (14.9)	*Lulworthia grandispora* (7.9) *Julella avicenniae* (7.1) *Eutypa* sp. (5.2)
Port Dickson, Alias *et al.*, 1995 (2°60′ N, 101°85′ E)	*Rhizophora apiculata*, *R. mucronata*, *Sonneratia apetala*	222	*Leptosphaeria australiensis* (16.8) *Hypoxylon oceanicum* (15.2) *Massarina ramunculicola* (15.2) *Kallichroma tethys* (13.6) *Halosarpheia ratnagiriensis* (12.4)	*Lulworthia grandispora* (7.2) *Marinosphaera mangrovei* (7.2) *Dactylospora haliotrepha* (6.8) *Massarina velatospora* (5.6) *Lignincola longirostris* (5.2)
MAURITIUS Poudre d'Or, Poonyth *et al.*, 1999 (20°03′ S, 57°41′ E)	*Rhizophora mucronata*	57 (108)	*Lulworthia* spp. (22) *Swampomyces triseptatus* (15.7) *Marinosphaera mangrovei* (11.1) *Lineolata rhizophorae* (10.2)	*Leptosphaeria australiensis* (8.3) *Halosarpheia fibrosa* (5.6)
Ile d' Amre (20°04′ S, 57°41′ E)	*R. mucronata*	85 (110)	*Lulworthia* spp. (31.8) *Lignincola laevis* (10.9) *Halosarpheia abonnis* (10)	*Acrocordiopsis patilii* (9.1) *Verruculina enalia* (9.1) *Halocyphina villosa* (8.2)

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
Beau Rivage (20° 17′ S, 57°48′ E)	*Rhizophora mucronata*, *Bruguiera gymnorrhiza*	78 (107)	*Lulworthia* spp. (26.2) *Halosarpheia* sp. (12.1) *Verruculina enalia* (12.1)	*Halosarpheia marina* (6.5) *Halocyphina villosa* (6.5)
Beau Champ (20° 17′ S, 57°48′ E)	*R. mucronata*	92 (113)	*Lulworthia* spp. (28.3) *Lignincola laevis* (17.7) *Trematosphaeria mangrovei* (21.2)	*Verruculina enalia* (8.8) *Halosarpheia viscidula* (7.1) *Halosarpheia* sp. (7.1)
Macond'e (20° 29′ S, 57° 22′ E)	*R. mucronata*	86 (140)	*Lulworthia* spp. (24.3) *Acrocordiopsis patilii* (11.4)	*Lignincola laevis* (8.6) *Verruculina enalia* (6.4) *Cytospora rhizophorae* (6.4) *Halosarpheia marina* (5.7)
MEXICO West coast, Hyde, 1992a	Unidentified intertidal mangrove wood and roots	?	*Verruculina enalia* (46) *Lulworthia grandispora* (31) *Halosarpheia marina* (20) *Trematosphaeria lineolatispora* (20) *Dactylospora haliotrepha* (20) *Aniptodera chesapeakensis* (17) *Lignincola laevis* (14) *Monodictys pelagica* (11)	*Periconia prolifica* (9) *Corollospora pulchella* (6) *Dactylospora haliotrepha* (6)
PHILIPPINES Jones *et al.*, 1988	*Rhizophora apiculata*, *Avicennia officinalis*, *Ceriops decandra*, *Excoecaria agallocha*	134	*Massarina velatospora*	*Halosarpheia marina* *Rosellinia* sp. *Savoryella lignicola* *Trichocladium achrasporum* *Zalerion varium*

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
SEYCHELLES Hyde, 1986 (3-6° S, 53-56° E)	Mangrove drift wood	756	*Antennospora quadricornuta* (23.4)	*Halocyphina villosa* (9.7) *Leptosphaeria australiensis* (9.5) *Lulworthia grandispora* (6.6) Ascomycete sp. (6.6) *Torpedospora radiata* (6.5)
Brillant Mangrove, Hyde and Jones, 1989	*Rhizophora mucronata*	194	*Halocyphina villosa* (27.3) *Lulworthia grandispora* (22.7) Ascomycete sp. (4) (15.5) *Antennospora quadricornuta* (12.4)	*Dactylospora haliotrepha* (7.2) *Aniptodera mangrovei* (6.7) *Caryosporella rhizophorae* (0.7)
Anse boileau	*Sonneratia apetala*	135	*Halosarpheia marina* (19.3) *Halocyphina villosa* (13.3)	*Antennospora quadricornuta* (5.9) *Cirrenalia tropicalis* (5.9) *Humicola alopallonella* (5.9)
SINGAPORE Mandai mangrove, Leung *et al.*, 1991	*Avicennia alba*, *A. lanata*	414	*Halosarpheia retorquens* (32.5) *Lignincola laevis* (21.3) *Aniptodera chesapeakensis* (16) *Halosarpheia marina* (13.8) *Halosarpheia* sp.1 (13)	*Lignincola longirostris* (9) *Halosarpheia lotica* (8.5) *Marinosphaera mangrovei* (8.5) *Mycosphaerella pneumatophorae* (7.5) *Cirrenalia* sp. (6.9) *Clavarripsis bulbosa* (6.9) *Passeriniella savoryellopsis* (6.4) *Lulworthia* sp. (6.4)
SUMATRA (NORTH), INDONESIA Hyde, 1989b (3°46′N, 98°44′E)	*Avicennia* sp., *Nypa fruticans*, *Rhizophora* sp. and *Xylocarpus* sp.	150	*Halosarpheia marina* (22) *Rhizophila marina* (18.7) *Phoma sp.* (15.3) *Lulworthia* sp. (spores 340-490µm, 12.7) *Dactylospora haliotrepha* (12) *Lignincola laevis* (11.3) *Cirrenalia pygmea* (10.7)	*Aniptodera chesapeakensis* (9.3) *Lulworthia* sp. (spores 220-335 µm, 8.7) *Lulworthia grandispora* (6.7) *Aigialus grandis* (6.7) *Halosarpheia ratnagiriensis* (6) *Massarina velatospora* (6) *Halocyphina villosai* (5.3)

Table 2. (continued).

Place, publication	Main samples collected	Number samples	Very Frequent > 10%	Frequent 5-10%
THAILAND Ranong mangrove, Hyde *et al.*, 1990b	*Rhizophora apiculata*	355	*Savoryella longispora* (14)	*Aigialus grandis* (9.6) *Lulworthia grandispora* (8.5) *Phialophorophoma litoralis* (8.2) *Verruculina enalia* (7.6) *Kallichroma tethys* (7.6) *Leptosphaeria australiensis* (7.1) *Halocyphina villosa* (7.1) *Dactylospora haliotrepha* (6.8) *Marinosphaera mangrovei* (6.2) *Massarina ramunculicola* (5.6) *Phomopsis mangrovei* (5.1)
	Sonneratia griffithii	300	*Halocyphina villosa* (12.3)	*Massarina velatospora* (9.7) *Helicascus* cf. *kanaloanus* (9) *Aigialus grandis* (8.7) *Dactylospora haliotrepha* (7.7) *Savoryella lignicola* (7.3)

in this study, however, were *Dactylospora haliotrepha*, *Halosarpheia fibrosa*, *H. marina*, *Lulworthia grandispora*, *Nais glitra* and *Tunicatispora australiensis*. Further studies are needed from the subtropics to verify whether the mycota in subtropics and tropics are the same or not and whether the very frequently recorded species are the same in tropics and subtropics.

Factors affecting the frequency of occurrence of fungi

Main hosts examined/host specificity

The majority of manglicolous fungi are pantropical and occur mostly on dead cellulosic substrata. There are a few host specific fungi that are limited to one host genus or species. The frequency of occurrence of fungi depends, to a greater or lesser extent, on the host species to which the samples belong. Some fungi show specificity to a particular host (Table 3). In addition, some fungi occur more commonly on one or two hosts. The advantage with studying saprobic fungi colonizing mangrove substrata is that in most cases the host can be identified. The decomposing substrata, still attached to the host plant can easily be removed, particularly if they are at the advanced stage of decomposition. Host specificity has been addressed by Hyde and Jones (1988), Hyde (1990a) and Hyde and Lee (1995). The conclusions reached were the same, that there is little evidence for host specificity except for a few species. One very distinct mangrove host is *Nypa* palm where a largely distinct mycota is found (Table 3) (Hyde and Alias, 2000). However, the question of host specificity is still unresolved and requires further study.

The predominance of individual fungi on each host species differs as some fungi occur more commonly on certain hosts (Hyde and Lee, 1995). This has important implications in ecological studies as the percentage occurrence (in turn frequency of occurrence) may drastically change if one host is sampled more thoroughly than others (Table 2). For example Hyde *et al.* (1990a) reported the following very frequent fungi from individual hosts: *Lophiostoma* sp. and *Massarina velatospora* on *Aegiceras corniculatum*; *Savoryella longispora* on *Rhizophora apiculata*; *Halocyphina villosa* on *Sonneratia griffithii*. When all the samples from all the hosts were totalled *Savoryella longispora* was found to be a very frequent fungus (Table 2). This may be due to some fungi having a 'recurrence' on a particular host. Further examples include a survey on manglicolous fungi in Brunei, where Hyde (1989a) found that *Cirrenalia pygmea*, *Halocyphina villosa* and *Lulworthia grandispora* were very frequent fungi. The main samples collected in this study were *Rhizophora* spp., *Sonneratia griffithii* and *Avicennia* spp. In a subsequent study in Brunei conducted on *Nypa fruticans*, Hyde (1992d) reported that *Astrosphaeriella nypae*, *Lignincola laevis*,

Table 3. List of known host specific fungi on mangroves.

Host	Fungi
Acrostichum speciosum	*Massarina acrostichi*
	Phomatospora acrostichi
Avicennia marina (pneumatophores)	*Adomia avicenniae*
Avicennia spp.	*Eutypa bathurstensis*
	Eutypella naqsii
	Julella avicenniae
	Leptosphaeria avicenniae
Avicennia spp. (pneumatophores)	*Mycosphaerella pneumatophorae*
Halosarceia halocnemoides	*Cryptovalsa halosarceicola*
Nypa fruticans	*Aniptodera nypae*
	Anthostomella nypae
	A. nypensis
	Apioclypea nypicola
	Arecophila nypae
	Astrosphaeriella nypae
	A. nypicola
	Carinispora nypae
	Fasciatispora nypae
	Helicascus nypae
	Helicorhoidon nypicola
	Herpotrichia nypicola
	Leptosphaeria nypicola
	Lignincola nypae
	Linocarpon angustatum
	L. appendiculatum
	L. bipolaris
	L. nypae
	Neolinocarpon nypicola
	Nipicola carbonispora
	N. selangorensis
	Nypaella frondicola
	Oxydothis nypae
	Phomatospora nypae
	P. nypicola
	Plectophomella nypae
	Pleurophomopsis nypae
	Tirisporella beccarina
	Trichocladium nypae
	Vibrissea nypicola
Pemphis acidula	*Mangrovispora pemphi*
Rhizophora spp.	*Cytospora rhizophorae*
	Hypophloeda rhizophorae
	Rhizophila marina
Rhizophora racemosa	*Trematosphaeria mangrovei*
Xylocarpus sp.	*Coronopapilla mangrovei*

Linocarpon appendiculatum and *Oxydothis nypae* were very frequent fungi. Hyde (1989d) reported as very frequent *Cirrenalia pseudomacrocephala* and *Massarina acrostichi* on *Acrostichum speciosum* from Brunei. The foregoing examples show that the occurrence of very frequent fungi depends to a large extent on the main host samples collected (Hyde and Jones, 1988; Poonyth *et al.*, 1999; Sarma *et al.*, 2001).

Succession

Frequency of occurrence is affected by the stage of the decay process, as some fungi may be fruiting at the time of collection, while others may exist as mycelium. Three studies have addressed succession of intertidal fungi on mangrove wood (Hyde, 1991; Leong *et al.*, 1991; Kohlmeyer *et al.*, 1995), and two have addressed the succession of fungi on mangrove leaves and seedlings (Fell and Master, 1973; Newell, 1976). In a comprehensive study of fungal succession on seedlings of *Rhizophora mangle*, Newell (1976) recognized four overlapping stages of succession. In the initial two stages phylloplane fungi and fungi belonging to mitosporic taxa were dominant. In the final stages these fungi disappeared being replaced by facultative marine species and typical marine fungi such as *Cytospora rhizophorae*, *Lulworthia* sp., *Periconia prolifica*, *Robillarda rhizophorae* and *Zalerion varium*. It is therefore important to consider the stage of decomposition of the specimens in studying frequency of occurrence.

Leong *et al.* (1991) showed that some fungi were early colonizers on *Rhizophora apiculata*, e.g., *Lignincola laevis* and *Verruculina enalia*, while other fungi appeared later, e.g. *Dactylospora haliotrepha* and *Halorosellinia oceanica*. Hyde (1991) reported a different mycota colonizing samples of *R. apiculata* with bark. In nature prop roots seem first to be colonized by a group of bark inhabiting fungi (Hyde, 1991) and once the bark is detached, a second group of wood colonizing fungi may cause decay of wood (Leong *et al.*, 1991). Severely damaged roots however, may simultaneously be decayed by both groups of fungi. Whether this succession is an expression of the rate at which the fungi can sporulate or actual succession is yet to be established. These studies show evidence of fungal succession on submerged wood, but are a measure of the formation of fruiting bodies rather than direct fungal colonization. It may be that some species produce reproductive structures more speedily than others, even though all taxa may be present in the substrata following submergence. In some cases it depends on incubation in the laboratory (Leong *et al.*, 1991).

Spatio-temporal variation

The frequency of occurrence of a fungus may also change during different seasons. Information on seasonal occurrence of mangrove fungi is sparse. In Sierra Leone, Aleem (1980) observed that mangrove fungi display a seasonal periodicity with greater diversity and growth intensity in the wet season (May-November). Species such as *Haligena viscidula*, *Leptosphaeria australiensis*, *L. avicenniae*, *Rosellinia* sp. and *Torpedospora radiata* were found to be more frequent on mangroves towards the end of rainy season (September-October). Similar observations were made in India (Sarma and Vittal, 2001).

The same mangrove region studied at different times resulted in a different fungal species composition and frequency of occurrence. The occurrence of manglicolous fungi in Malaysian mangroves has been investigated by several workers. *Dactylospora haliotrepha*, *Halorosellinia oceanica*, *Halosarpheia marina*, *Lignincola laevis*, *Savoryella lignicola* and *Verruculina enalia* were reported to be very frequent on samples of *Rhizophora* spp. and *Avicennia* spp. and other mangrove wood from the mangroves (Jones and Kuthubutheen, 1989). Some of these fungi were either recorded infrequently or missing altogether in the study on mangrove fungi on *Rhizophora apiculata*, *Avicennia* spp. and *Bruguiera gymnorrhiza* (Alias *et al.*, 1995). Similarly, *Eutypa* sp., *Halosarpheia ratnagiriensis*, *Leptosphaeria australiensis*, *Marinosphaera mangrovei* and *Massarina ramunculicola* which were reported as very frequent (Alias *et al.*, 1995), were either infrequently recorded or rare in the study of Jones and Kuthubutheen (1989). The differences may be due to seasonal occurrence of the fungi or different host species studied, or different mangrove stands investigated within the same country (spatio-temporal variations).

However, all of these studies suffer from the lack of a good statistical experimental design. Future studies should address the problem of seasonality of mangrove fungi using a good experimental design. For example a comparative study of fungal communities during the dry season (extending up to 5 to 6 months) as compared to the wet season (extending up to 5 to 6 months) would be worthwhile (Rossman *et al.*, 1998). Collection in each season (wet or dry) should be replicated (at least 3 samplings in each season). The first replicate (sampling) should be undertaken at least one month after the beginning of the season. The idea behind this is to avoid any chances of abiotic factors being carried over from the previous season at the time of sampling. Further the seasonal study should be carried out over a minimum of 3 years or a multiple year study is more advisable (Sarma and Vittal, 2001).

Vertical distribution

The frequency of occurrence of fungi may differ depending on the level (immersed in the water to intertidal or above surface) from which the samples are collected. Kohlmeyer and Kohlmeyer (1979) and Aleem (1980) found no evidence of vertical zonation. However, Hyde and Jones (1988) observed that some fungi tend to occur consistently at certain levels (e.g. *Aigialus grandis* and *Caryosporella rhizophorae* at the mid-littoral level). They also reported that the greatest species diversity occurred at the mid-littoral level. Jones *et al.* (1988) observed that certain species were more abundant at the upper part of the intertidal zone, e.g. *Halocyphina villosa*, *Massarina velatospora* and *Rosellinia* sp. (= *Halorosellinia oceanica*). Jones and Tan (1987) reported that *Halocypina villosa* and *Halorosellinia oceanica* occurred at the upper end of the intertidal zone, while *Antennospora quadricornuta* was to be found on aerial and prop roots towards low water mark. Hyde (1988a, 1990b) investigated the vertical distribution of intertidal fungi on *Rhizophora apiculata* by defining different intertidal zones. His results indicate that intertidal fungi are vertically distributed with most fungi confined to a relatively small vertical zone (this has recently been confirmed statistically by J.P. Schmidt and C.A. Shearer, in ed.). Few fungi were widely distributed and only two were found throughout the tidal range. The greatest diversity of fungi occurred above mean tide. Hence the frequency of occurrence depends on the intertidal level from which greater number of samples are collected.

Salinity and horizontal distribution

Depending on the site from which samples of mangrove plants are collected in a horizontal plane with salinity gradient, the frequency of occurrence of fungi varies. Very few reports are available on the effect of salinity on the mycota in mangrove forests. *Rhizophora* and *Avicennia*, for instance, are able to grow in salinities ranging from full sea water (about 35‰) to fresh water. A different mycota can therefore be expected from woody substrata in salt water as compared to those in brackish water. Kohlmeyer (1969c) made preliminary observations in the Heeia Swamp on Oahu, Hawaii. Roots of mangroves in the Heeia Fishpond (salinity near 35‰) contained the marine fungi *Kallichroma tethys*, *Leptosphaeria australiensis* and *Lignincola laevis*. Further inland, between stations 4 and 5, where the salinity varied at high tide between 10 and 35‰, the marine ascomycetes *Helicascus kanaloanus* and *Verruculina enalia* were found on the dead roots of *Rhizophora*. Still further upstream, near station 1, the water salinity was almost zero. Fungi encountered in the freshwater part of the Heeia Swamp were definitely not marine species (Kohlmeyer, 1969c). Hyde (1992b) examined the mycota of

decaying intertidal *Kandelia candel* (L.) Druce where the salinity fluctuated between 3-24‰. He found that most of the fungi were typical mangrove species common in mangroves of higher salinity with the exception of *Phomatospora kandeliae*. He concluded that the distribution of fungi was probably limited by periods of higher salinity and therefore the mycota was likely to be similar throughout the salinity range of mangroves. Most reports of intertidal fungi do not record the salinity and such records are needed for any future comparisons.

Recurrence on different substrata/tissue specificity (wood, twigs, pneumatophores, seedlings, leaves or roots)

Some fungi occur more frequently on certain tissues or organs than others. Hence, the frequency of occurrence differs depending on the number of samples collected belonging to individual substrata (organs) viz., wood, seedlings, pneumatophores, prop roots, leaves or roots. Kohlmeyer (1969b) observed that among large collections, several fungi were encountered only in roots and stems of living *Avicennia* or *Rhizophora* and appear to be host specific. Hyde *et al.* (1990a) investigated the distribution of fungi on *Sonneratia griffithii* and showed that some fungi were more common on pneumatophores, e.g., *Aigialus grandis* and *Massarina velatospora*, while others were common on twigs, e.g., *Saccardoella mangrovei* and *Savoryella longispora*.

Ravikumar and Vittal (1996) reported on the fungi colonizing different substrata of *Rhizophora apiculata* and *R. mucronata* from Pichavaram mangroves of Tamil Nadu, East coast of India and concluded that different substrata of the same host plant are colonized by different frequently occurring fungi. Not only greatest diversity and numbers of fungi were found on prop roots when compared to seedlings and wood, but also each substratum had its own very frequent, frequent and infrequent fungi. *Cirrenalia pygmea* common on prop roots and seedlings was absent on wood. Similarly, *Aigialus grandis* common on seedlings was only frequent on prop roots and occasional on wood. *Halocyphina villosa*, which was common to seedlings, was occasional on prop roots and wood. *Dactylospora haliotrepha*, which was frequently recorded on wood and prop roots, was occasional on seedlings. Similar findings were observed on *Rhizophora apiculata* and *Avicennia* spp. (Sarma and Vittal, 2001). The fungi on different parts of palm fronds (i.e. leaves and petioles) were found to support different fungi (Yanna *et al.*, 2001). According to Hyde *et al.* (1990b), bark was an important factor in determining the mycota present on *Rhizophora apiculata* particularly when small diameter roots were examined. Young roots surrounded by bark were invariably colonized by

Leptosphaeria sp., *Lulworthia grandispora*, *Massarina ramunculicola*, *Phomopsis* sp. and *Rhizophila marina*. Young roots lacking bark were colonized by a different group of fungi (*Dactylospora haliotrepha*, *Halocyphina villosa*, *Kallichroma tethys*, *Marinosphaera mangrovei*, *Phialophorophoma* cf. *litoralis*, *Savoryella lignicola*, *Verruculina enalia*, *Leptosphaeria australiensis*, *Xylomyces* sp.).

It is evident that samples with or without bark may influence the frequency of occurrence of fungi. This indicates that some fungi may preferentially develop on certain tissue types. In frequency of occurrence studies it is therefore important to examine different plant structures, as they appear to support different frequently occurring fungi.

Incubation

The common practice of incubating samples in moist chambers also affects the percentage occurrence of fungi and in turn the frequency of occurrence of fungi. Incubation time is therefore a further parameter that must be considered when studying ecology of marine fungi (Hyde, 1992c). Prasannarai and Sridhar (1997) observed that the percentage and frequency of occurrence of fungi varied at different incubation periods. In their study they found that six months incubation of driftwood yielded about 70% of the total marine fungi encountered when compared to 2, 12 or 18 months of incubation. Incubation of wood in the laboratory will also favour the presence of certain fungi, particularly the mitosporic fungi, and may not reflect the situation in the nature (Hyde and Jones, 1988). Perhaps future studies should adopt a standard incubation period, or more practically, samples should be examined as soon as possible and then at regular intervals (Hyde, 1992c).

Different techniques

Particular techniques may also have a role in determining the frequently occurring fungi. Jones and Kuthubutheen (1989) made a comparison between two techniques and found that examination of intertidal drift or attached wood yields a much greater number of species than those on submerged test blocks. The advantage of baiting with test blocks enables the investigator to follow the sequence of colonization by fungi with supporting information on data of submergence, origin of the substratum and the physical parameters of the test site (Jones and Hyde, 1988; Alias and Jones, 2000). The procedure however, is often limited in that only a narrow range of timber species can be tested and the period of exposure is often restricted. Examination of driftwood has limitations in that no information is available on the length of exposure, the origin and the identification of the substratum. Examination of driftwood does however,

provide a broad picture of the organisms involved in the colonization of substrata in the mangrove ecosystem.

Differences have been observed in the species composition and frequency of occurrence of fungi between natural samples and pre-sterilized panels submerged in waters for succession studies (Jones, 1968, 1971; Curran, 1975; Vrijmoed *et al.*, 1986a; Leong *et al.*, 1991). With longer periods of submersion, there was some degree of rotting of the wood caused by initial colonisers and this would precondition the wood blocks and pave the way for other fungi to settle. Such preconditioning of wood is also known to favour the settlement of marine fouling organisms (Kohlmeyer, 1984; Vrijmoed *et al.*, 1986b). At the final stage of exposure Leong *et al.* (1991) observed that wood blocks were heavily infested with fouling organisms. These formed a physical barrier to the settlement and growth of marine fungi and many have hindered the appearance of more species towards the end of exposure period. Jones *et al.* (1972) and Vrijmoed *et al.* (1986b) previously reported that fewer fungal species were observed on wood heavily infested with fouling organisms compared to wood free of such organisms.

Tan *et al.* (1989) reported that the data obtained with wood baits differed markedly from those sampled randomly in mangroves. The samples submerged as test panels yielded a greatest number of very frequent species (six for *Avicennia alba*, five for *A. lanata*, and two from random sampling). Of these, only *Lignincola laevis* was common to both methods of sampling. *Halosarpheia* sp. and *H. retorquens* were frequent or very frequent in random collections but either absent or infrequent on test panels. Tan *et al.* (1989) suggested that factors like timber dimensions, position on the shore and degree of exposure and drying out of timber on fungal communities need to be studied.

Studies by Kohlmeyer (1984), Zainal and Jones (1984, 1986), Hyde and Jones (1988) and Tan *et al.* (1989) have demonstrated the presence of a distinctive mycota for wood exposed in mangroves and sawn wood submerged in the open sea as test panels.

Other factors

Kohlmeyer *et al.* (1995) have attributed the differences in mycota between Man-of-War and Twin Cays to differences in the nutrient content of the seawater, although there is also some difference in wave action, the Man-of-War site being clearly more exposed. This may also positively affect fungal colonization because of increased oxygen supply. Typical mangrove-inhabiting species such as *Ascocratera manglicola*, *Caryosporella rhizophorae* and *Lophiostoma mangrovei* common on Man-of-War and Twin Cays, could not be

detected, i.e. did not fruit on the experimental stakes. All three have large, hard-walled ascomata and apparently need a long time to fruit, probably over 2 years as evident by these experiments. Though these fungi were absent from the experimental stakes, in their natural habitat they always occur high up in the intertidal zone.

According to Volkmann-Kohlmeyer and Kohlmeyer (1993) it is difficult, for the following reasons, to determine the frequencies of marine fungi. (a) It has to be kept in mind that we are able to count only those fungi that can be identified from their fruiting stage, not those that are possibly present in the substratum in the vegetative (hyphal) state (This problem can be overcome partly by dividing into different pieces horizontally and incubated to allow sporulation). (b) substrata (driftwood, intertidal wood, mangrove roots and branches) are usually not uniform, consisting of uneven lengths and diameters of wood, with and without bark. Meyers and Reynolds (1958) suggested that for controlled experiments wood samples of equal sizes and identical origin need to be exposed for predetermined periods of time. However the collection of a variety of natural substrata has the advantage of providing a larger number of fungal species (Kohlmeyer and Kohlmeyer, 1979).

There was little difference between fungi colonizing samples of small diameter (less than 2.5 cm) when compared to samples of large diameter (large trunks of 30-50 cm in diameter) (exceptions being influenced by bark presence) (Hyde *et al.*, 1990b). Further investigations are needed to establish whether differences in the diameter of the samples has any affect on the species composition and frequency of occurrence.

Importance of frequency of occurrence studies

Frequency of occurrence studies will help us to establish the most common fungi in an area. Of the hundreds of species present in a community, relatively few exert a major controlling influence by virtue of their size, numbers, or activities (Krebs, 1985). Dominant species are those that are highly successful ecologically and determine to a considerable extent the conditions under which the associated species must grow (Krebs, 1989). In communities that are extremely species rich, most species are likely to be sparsely distributed (Rabinowitz, 1981). Typically only a few fungi will dominate a given area, while the other fungi will be rarely encountered (Cooke and Rayner, 1984). Future studies should elucidate that if a particular group of fungi occur frequently in a given area or on a particular host it has to be tested whether these are the fungi responsible for shaping the fungal community structure of the given site/habitat. However it should be remembered that studies on fungal frequency are different from those of other organisms.

Fungi are known to produce a battery of enzymes (Subramanian, 1983). Our knowledge of enzyme production by marine/mangrove fungi is still in its infancy. It will be interesting to study a fungus that is very frequent in a particular area, infrequent at another area and rare in the third area, to establish whether there are any differences in their enzymatic capabilities/composition. If a particular fungus collected from a particular type of environment is not growing well or is not producing all the enzymes than an isolate from other locations then a comparison/correlation should be made between enzymatic capabilities and frequency of occurrence of that fungus collected from different regions. Though this assumption seems to be speculative some attention may be given for future studies in this direction. Alternatively it may also be possible that a very frequent fungus may not be able to produce all the enzymes but has the ability to succeed by virtue of its genetic composition.

Some mangrove fungi have to tolerate great variation in salinity with respect to seasonal conditions; others tolerate desiccation, and salinity variation in the intertidal zone e.g. arenicolous spores (Jones and Jensen, 1999). It would be interesting to conduct physiological studies of the very frequent fungi at different concentrations/regimes of salinity, temperature, pH and other factors in the laboratory and correlate these with the results obtained in the field. A correlation between the factors affecting the frequency of occurrence of fungi discussed so far and the dominance (frequent occurrence) of certain fungi cannot be established if they are not accompanied by the verification of these factors under *in vitro* conditions. Isolates collected from different places, show different responses to temperature. Fungi of the same species vary greatly in the extracellular enzymes they produce even from one stream to another (Yuen *et al.*, 1998). These species may have geographical races, which are adapted to the conditions prevailing at their site of collection (Yuen *et al.*, 1998). Panebianco (1994) investigated marine fungi and found that the temperature requirements for growth of marine fungi are related to their geographical distribution. Tropical and temperate fungi have an optimum growth at 20-25 C. Tropical freshwater fungi do not grow well at low temperatures and so are absent in temperate regions (Yuen *et al.*, 1998). Although temperate species grow best at 25 C, they are not able to grow as rapidly as tropical species and this probably accounts for their absence in tropical streams (Yuen *et al.*, 1998; Zare-Maivan and Shearer, 1988). It would be interesting to conduct similar studies on marine fungi and correlate the results with frequency of occurrence of the fungi tested.

Recommendations and protocols

Most of the studies on the ecology of marine/mangrove fungi have suffered from a lack of statistical analysis. There have been various approaches in the way samples are collected, the number of samples collected and examination methods. This has been largely due to the desire by marine mycologists to identify the large numbers of taxa that were new to science. It is now likely that most marine fungi have been described (or at least collected) and updated keys are available (Kohlmeyer and Volkmann-Kohlmeyer, 1991; Hyde and Sarma, 2000). The sufficient taxonomic information now available and the latest keys to mangrove fungi should form the basis for sound ecological studies of marine fungi (Pointing and Hyde, 2000).

Diversity most simply can be expressed as species richness, that is, the number of species (Magurran, 1988). However, since richness increases in direct relation to number of individuals, area and variety of habitats sampled, differences in sampling methods may introduce statistical and ecological bias into comparisons of diversity among different localities. As more individuals are included, the probability of discovering rare species increases (Schluter and Ricklefs, 1993). The relationship between the diversity and sample size depends on the probability of distribution of taxa among abundance classes (Schluter and Ricklefs, 1993). These distributions have been described by a variety of mathematical relationships each of which predicts a somewhat different relationship between diversity and sample size and suggests a different approach to normalizing diversity with respect to the number of individuals sampled (Magurran, 1988).

In comparative studies, either sampling should be consistent with respect to number of individuals, or species counts should be normalized with respect to sample size (Simberloff, 1979). Ecological variation over the temporal and spatial dimensions of the sample may augment diversity because of the increased number of areas, habitats or seasons included (Schluter and Ricklefs, 1993).

A related problem involves the ecological importance of common and rare species. A simple count gives equal weight to all taxa, whether they occur repeatedly in a sample or are represented by a single individual. Ecologists have devised diversity indices that weigh the contribution of species according to their abundance usually discounting rare species to some degree (Whittaker, 1972; Pielou, 1977). However, because the abundance of species within samples tend to exhibit regular patterns of distribution (Whittaker, 1972; May, 1975), sample size, species richness, and variation indices of species diversity are generally interrelated. Therefore, species richness, preferably normalized

with respect to sample size, is a suitable measure for most broad scale comparisons of diversity (Schluter and Ricklefs, 1993).

Before future ecological studies are undertaken, it is necessary to establish the objectives. Once these are decided it is important that standard protocols are adopted. Since in most cases availability of time and funds are limiting factors there needs to be a balance in achieving the objective of establishing the species diversity of a given mangrove site and at the same time finding out the frequency of occurrence of fungi using standard sample numbers. Initial surveys will help us to establish the expected number of fungi from a given number of samples in a mangrove site. An attempt is made here to propose a protocol/experimental design keeping in mind different objectives such as species diversity, frequency of occurrence, vertical distribution and seasonal occurrence. These experimental designs can be modified following future studies.

Protocol

In a mangrove all of the dominant mangrove trees (dominant in % occurrence and cover) should be sampled by collecting equal numbers of samples. A protocol is given as an example to study the diversity of mangrove on 4 dominant tree species, during 3 seasons at 3 vertical zones. This protocol could be completed by an experienced mycologist, but a student would have problems handling these sample numbers. Since biodiversity is being investigated, different substrate types (prop roots, branches) would need to be randomly collected.

1) *Rhizophora* spp. (10 replicates) are collected at 3 vertical zones, from 3 salinity zones, during 3 seasons (= 270 samples).
2) *Avicennia* spp. (10 replicates) are collected at 3 vertical zones, from 3 salinity zones, during 3 seasons (= 270 samples).
3) *Sonneratia apetala* (10 replicates) are collected at 3 vertical zones, from 3 salinity zones, during 3 seasons (= 270 samples).
4) *Xylocarpus granatum* (10 replicates) are collected at 3 vertical zones, from 3 salinity zones, during 3 seasons (= 270 samples).

Total samples for one season (270 × 4) = 1080
Total over two years = 2160

The results would provide overall data on fungal diversity and the frequent species present. Statistical differences in fungal communities on different hosts, at different seasons, and at different vertical zonations could

also be tested using ordination techniques. It is unlikely however, that all rare species in a mangrove could be established, due to inadequate sampling and the fact that not all plant species would be examined.

Remarks and limitations

In previous studies on the frequency of occurrence of fungi in mangroves there have been differences in the number of samples collected and examined (Table 2). A study with more samples will give a different picture of percentage occurrence than a study with few samples. We advise that the minimum number of samples that should be collected and examined should be between 540-1060 for one season or 1000-2000 for 2 seasons (wet and dry), but this does depend on the objectives of the study. In this way there can be a consensus on the number of samples collected in future studies by marine mycologists.

It should however, be mentioned that the number of samples collected will depend on the availability of substrata and numerous other factors. In addition to the number, care should also be taken to collect samples from different individual plants, to avoid pseudoreplication. A uniform sample size (preferably length and if possible its diameter) should be maintained.

Formulas

$$\text{Percentage colonization} = \frac{\text{Number samples supporting fungi}}{\text{Number of samples examined}} \times 100$$

$$\text{Percentage occurrence of Species A} = \frac{\text{Number of collections of Species A}}{\text{Number of samples examined}} \times 100$$

$$\text{Average number of fungi per sample} = \frac{\text{Number of taxa identified}}{\text{Number of samples examined}} \times 100$$

Frequency of occurrence of fungi can be tabulated using the following frequency groupings:

Very frequent ≥ 10%	Infrequent = 1-5%
Frequent = 5 to 10%	Rare ≤ 1%

Marine mycogeography

Marine mycogeography (the study of geographical distribution of marine fungi) is a relatively recent field. Pirozynski (1968) reviewed the geographical distribution of fungi and discussed the merits and demerits of methods to study fungal distribution. Hughes (1974) has divided the oceans into five biogeographic temperature determined regions, namely arctic, temperate, subtropical, tropical and antarctic. Distribution maps for selected species were provided by Kohlmeyer (1983, 1987), Hyde and Lee (1995) and Jones and Alias (1997). In addition to the distribution maps comparisons of mycota among different mangrove sites within a country or major geographical region can also be made using similarity indices.

Percentage similarities of species composition between sites may be calculated using Jaccard and Sorensen coefficient based on binary data (presence or absence). Cluster analysis can then be computed using Jaccard and Sorensen similarity coefficient (Kenkel and Booth, 1992).

$$\text{Jaccard coefficient: } J = \frac{c}{a + b + c}$$

$$\text{Sorensen coefficient : } C = \frac{2c}{2c + a + b}$$

a = Number of species occurring in 'a' alone
b = Number of species occurring in 'b' alone
c = Number of co-occurrence of species

Seasonal occurrence

Various ecological indices have been developed based on information theory (Shannon-Weaver index and Simpson index). These indices have been used to measure the community diversity and its relation to community properties such as productivity and stability or to the environmental conditions at different seasons to which the community is exposed (Atlas, 1984). These indices have been applied to study various communities such as bacteria (Griffith and Lovitt, 1980; Bianchi and Bianchi, 1982), phytoplankton (Lakkis and Novel-Lakkis, 1981; Pollingher, 1981) and seaweeds (Lapointe *et al.*, 1981). However, seasonal occurrence of fungal communities colonizing mangrove wood have not been seriously investigated. The seasonal occurrence of mangrove fungi can be studied in the warm/wet season and dry/cold seasons by maintaining the uniformity in the number of samples collected and

examined. We recommend a multiple-year study for seasonality of mangrove fungi.

The following equations may be used to calculate the different ecological studies viz., species diversity, seasonal occurrence (Magurran, 1988).

Species Dominance

Simpson Index $= \sum Pi^2$

Species Diversity

Shannon-Weaver Index (H') $= - \sum Pi^2$

$$Pi = \frac{ni}{N}$$

N = Total numbers of individuals (records)

ni = Number of individuals of i1, i2, i3, i4, i5, ...ix

Replication

Biological non-independence is widespread in mycological studies and careful experimental design is necessary to avoid this problem. Replicates must be independent and when samples with different treatments are considered in the experiments, their distribution should be randomized (Pointing *et al.*, 2000). For guidelines on avoiding pseudoreplication the following texts are recommended (Hurlbert, 1984; Underwood, 1997).

Pilot study

A prerequisite for most of the objectives mentioned above is to find out the leveling off or the sufficiency of sample number which should be determined by plotting the log normal distribution curve or species area curve (Magurran, 1988). Unfortunately, species-area curves have rarely been generated prior to sampling for fungal community analyses (Zak and Rabatin, 1997). When determining species-area relationships, samples should be taken from the same contiguous area. If subsamples are collected from scattered areas across a habitat, the species area curve will bow out the line and will have a steeper slope due to sampling artifact (Rosenzweig, 1995). While it may take more number of samples to reach an asymptote it is suggested that 80% cut off mark is advisable. An initial pilot study will help to find out the minimum number of samples needed to examine (Fig. 1).

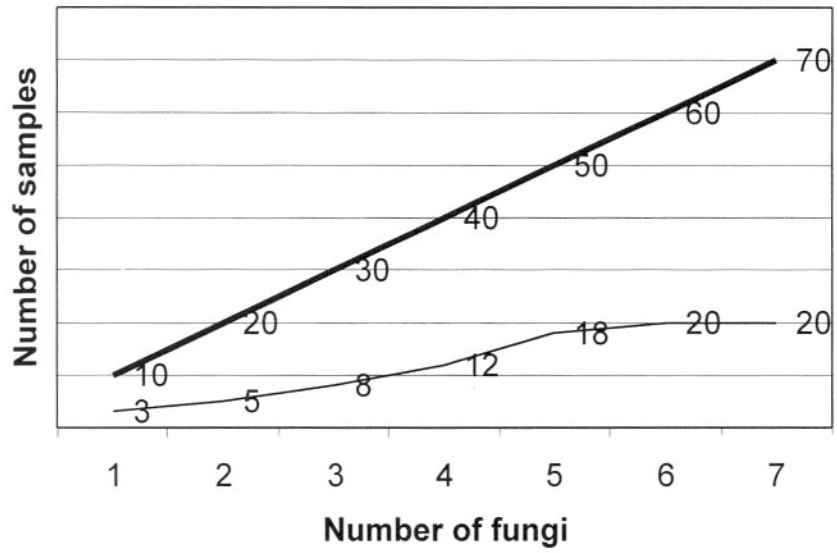

Fig. 1. Species area curve. It is likely that most fungi have been identified in the lower curve.

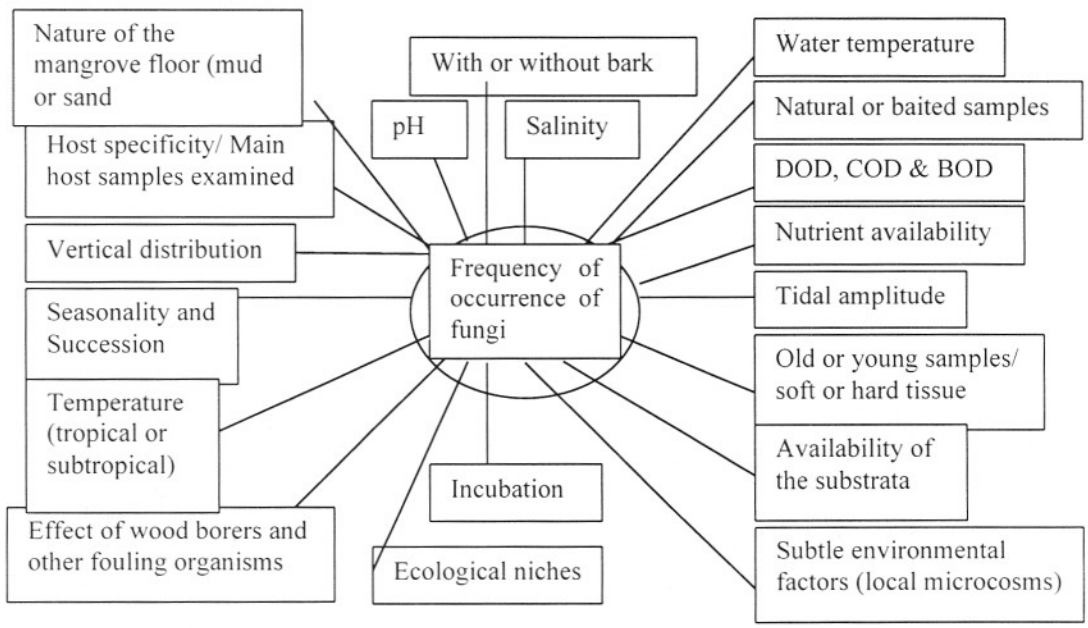

Fig. 2. Parameters to be considered for discussing frequency of occurrence.

Conclusion

Some fungi certainly occur more frequently than others. A range of fungi occur frequently in the mangrove ecosystem, although these differ as to their location.

Many factors will have an effect on species/frequency of occurrence either individually or synergistically. We have traced the factors affecting the frequency of occurrence of fungi in the mangroves in the foregoing account. Future studies should take into consideration all the factors listed in Fig. 2 and should try to elucidate the effects of these factors in the laboratory. Collections may include different tree species, old or young samples with or without bark, samples from high up or low down in the intertidal region, soft or hard tissue, during wet or dry season and variations in sampling procedures.

We have made an attempt to provide a protocol for future studies based on experience. While this is not still exhaustive we feel that these recommendations should be used to standardize the techniques. They may be improvised following further suggestions or amendments.

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