

Ecology of mangrove fungi and their role in nutrient cycling: what gaps occur in our knowledge?

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Abstract

Recent investigations have increased our knowledge of the ecology of mangrove fungi. In this paper this information is reviewed with emphasis on biogeography, biodiversity, differences in the tropical and subtropical mycoflora, fungal distribution on mangrove trees, host specificity, vertical zonation and distribution with salinity. Gaps in our knowledge are discussed. There is little knowledge of the role of mangrove fungi in nutrient cycling which is also reviewed. Areas in which knowledge is deficient include quantification techniques for fungal abundance, the nature and activities of fungal extracellular enzymes and fungal modification of mangrove detritus matter, especially the dissolved form.

Introduction

Coastal wetlands are considered to be one of the most productive natural ecosystems on earth (Kohlmeyer & Volkmann-Kohlmeyer 1993a). Both in the mangal and salt marshes the mycota are considered to be extremely important in nutrient cycling. There have been numerous studies on the amount of litter production in mangrove forests (see review by Saenger & Snedaker 1993) and the role of micro-organisms in the decay of leaf litter is well documented (Fell & Master 1973; 1980; Cundell *et al.* 1979; Robertson *et al.* 1992) as is their importance in the mangrove food web (Heald 1971; Odum & Heald 1975; Fell & Master 1980; Tenore *et al.* 1982; Hutchings & Saenger 1987; Robertson *et al.* 1992). Less is known about wood production, but this is also thought to be high (Christensen, 1978; Bunt *et al.* 1979; Boto *et al.* 1984). Studies of the involvement of the fungi in the breakdown of mangrove leaves and wood have also been conducted (e.g., Hyde 1990a). This paper addresses the ecology of these fungi and their role in nutrient cycling, discussing available information and highlighting areas where knowledge is lacking.

Biogeography

Biogeographical distribution maps of marine fungi are published by Hughes (1974), Kohlmeyer (1983) and Jones (1993) and include mangrove fungi. Kohlmeyer & Kohlmeyer (1979) reviewed the literature on higher mangrove fungi and only 42 species were then known to occur on submerged parts of mangroves. Most of these were records of fungi on *Rhizophora mangle* L. in Florida, the Caribbean or central America with few records from other continents (Fig. 1). Collections of mangrove fungi have now been made throughout S.E. Asia (Hyde 1988a, 1989a,b, 1990b,c; Jones & Tan 1987; Jones *et al.* 1988; Jones & Kuthubutheen 1989; Hyde *et al.* 1990, 1993; Vrijmoed *et al.* 1994); in the Indian Ocean (Borse 1988; Hyde 1986; Hyde & Jones 1988, 1989; Jones & Hyde 1990; Chinnaraj 1993); the Pacific Ocean (Hyde, 1990d, 1992e; Kohlmeyer 1984; Kohlmeyer & Volkmann-Kohlmeyer 1987a, 1991, 1993b; Nakagiri 1993) and tropical Atlantic Ocean (Aleem 1980; Kohlmeyer, 1980, 1981; Kohlmeyer & Volkmann-Kohlmeyer 1987b, 1988) and the distribution is now better known (Fig. 1).

In this paper the distributions of four representative mangrove fungi are given, i.e. *Halosarpheia fibrosa* Kohlm. & Kohlm. (Fig. 2); *Halosarpheia marina* (Cribb & Cribb) Kohlm. (Fig. 3); *Lignincola laevis*

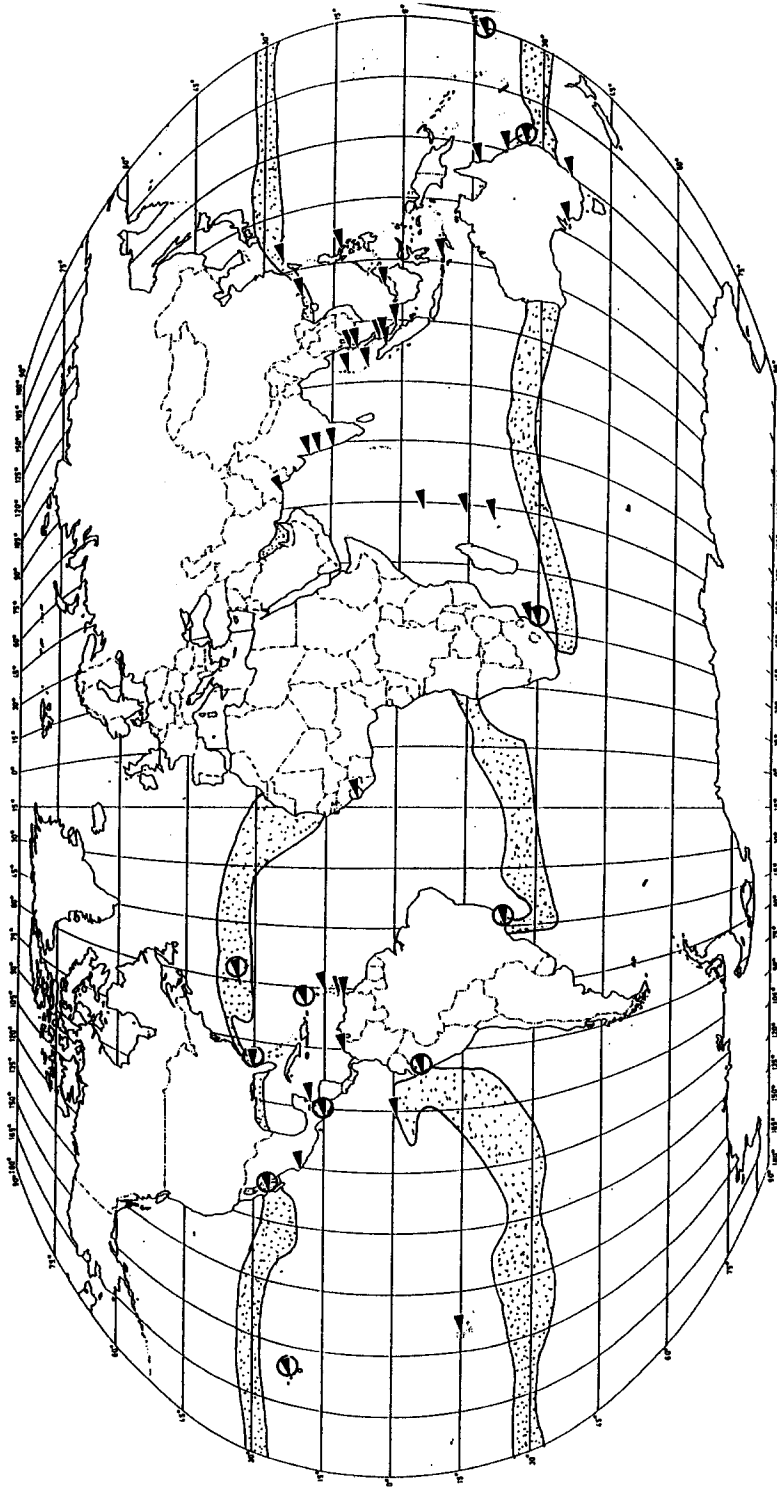


Fig. 1. Locations of reports of mangrove fungi in 1979 (o) and 1993 (<). Shaded areas are subtropical and non-shaded areas between the shaded areas are tropical.

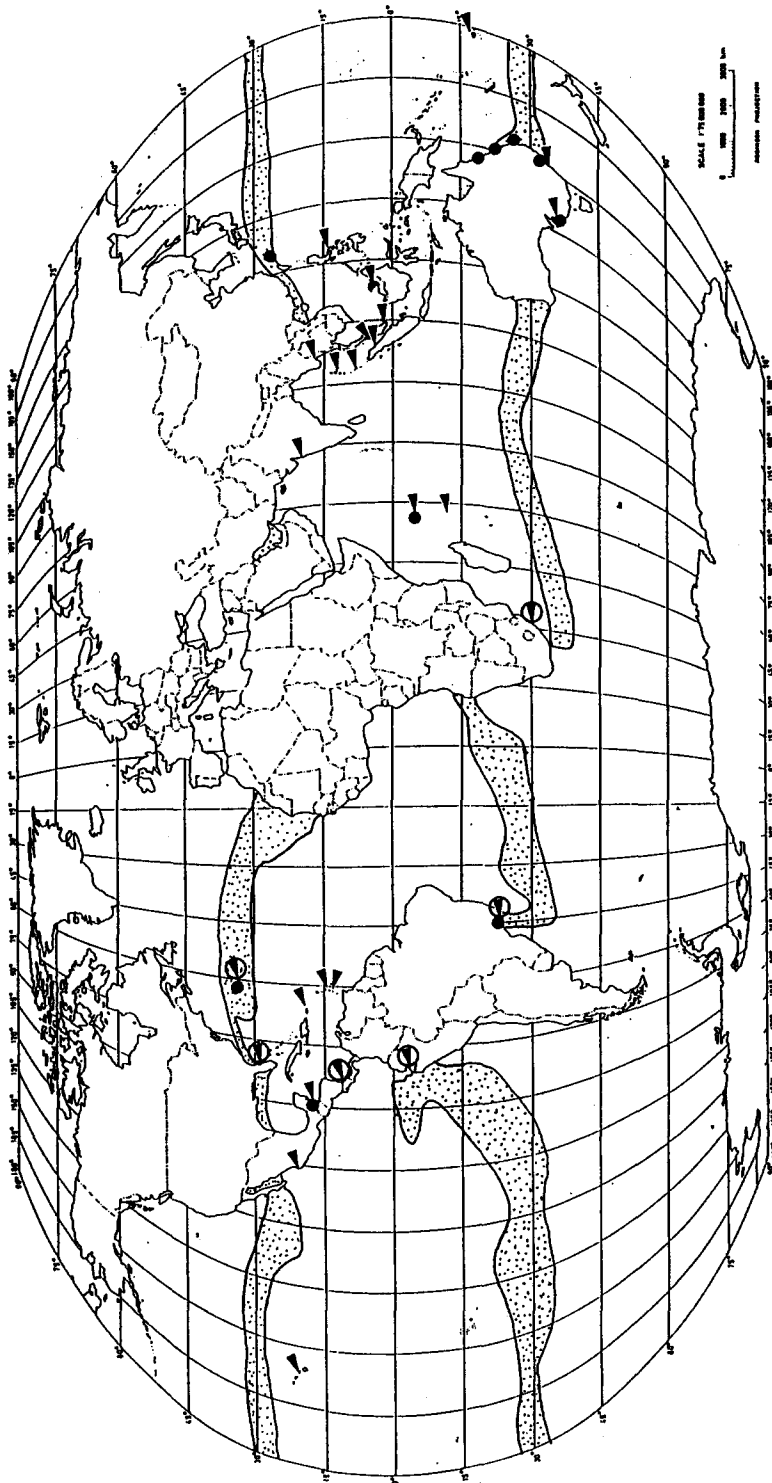


Fig. 2. World distribution of *Lulworthia grandispora* in mangroves in 1979 (o) and 1993 (<) and *Halosarpehia fibrosa* in 1993 (●).

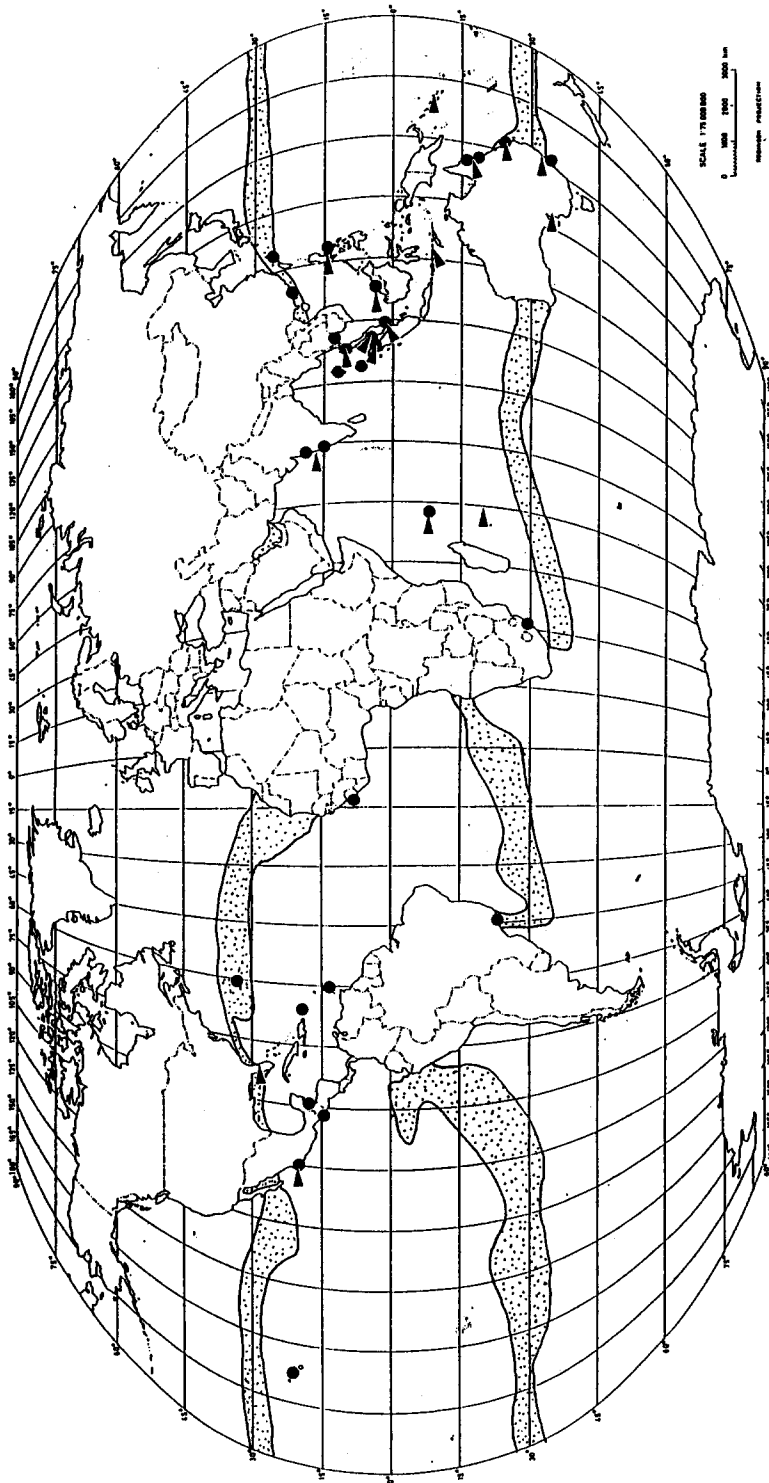


Fig. 3. World distribution of *Lignicola laevis* (●) and *Halosarpeia marina* (▷) in 1993.

Höhnk (Fig. 3) and *Lulworthia grandispora* Meyers (Fig. 2). In all cases the fungi show a pantropical distribution. This is true of most intertidal fungi, since few are host-specific and most of their hosts are pantropical in distribution (Hyde 1990a). Major gaps, however, still occur in our knowledge. There is a dearth of information from Northern and Western Australia and, considering the expanses of Australian shorelines and the potential importance of fungi in nutrient cycling to coastal ecosystems, this is a poor reflection on Australian science. Information is also lacking in the Pacific Ocean, with the exception of the Hawaiian (Oahu) and Society Islands (Moorea). Few studies have been carried out in the mangroves of South America and there is a paucity of information from African mangroves (Fig. 1).

Until recently information on mangrove fungi outside the tropics was not available. However Vrijmoed (1990), Vrijmoed *et al.* (1994) and Hyde (1990d) have published species lists for Hong Kong (subtropical) and Australia (NSW & Victoria: warm temperate) respectively. This enables a comparison with tropical mangrove mycota.

Many mangrove fungi are found in the sub-tropics and the warm temperate regions, but the species diversity in the tropics is much greater. In Brunei 100 species were identified (Hyde 1988a,c), in Hong Kong 60 species (Vrijmoed *et al.* 1994) and in Australia 60 species (Hyde 1990d, 1992a; Kohlmeyer & Volkman-Kohlmeyer 1991). This may be a reflection of mangrove species richness or the time spent on each study. In Brunei 25 mangrove tree species were examined, in Hong Kong three, while in Australia seven were examined. It may also partly be a reflection of adaptability, with fewer species being able to compete in subtropical conditions. Host specificity does not seem to be the limiting factor, as most mangrove species collected in Brunei do not appear to be host specific (Hyde 1990a). This question could be addressed by growing fungi under controlled temperature regimes.

Notable discrepancies are found in the latitudinal distribution of some mangrove fungi. *Halosarpheia fibrosa*, for example, is a rather illusive taxon described from Bermuda with very few other collections (Fig. 2). The presence of this taxon in warm temperate Australia (Hyde 1990d) may indicate a preference for subtropical as compared to tropical conditions such as those climates found in Bermuda and Southern Australia. Collections in other subtropical locations (e.g. Africa) may answer these questions of temperature selection, although the absence of this taxon from Hong

Kong is conspicuous. The collection in tropical Brunei may have been misidentified. Certainly, *H. fibrosa* is rare in the tropics and *Halosarpheia marina* is also common in the subtropics (Fig. 3), as well as in the tropics.

Further notable fungi found in Southern Australia were *Halosphaeria appendiculata* Linder and *Ceriosporopsis halima* Linder. The distribution of these taxa are normally temperate and their presence in warm temperate mangroves is interesting. Some information is now available on the mycota of subtropical mangroves, but further studies are required to establish conclusive differences with tropical mangroves. Growth studies conducted under different temperature regimes may also help us to understand the biogeography of the mangrove fungi.

Biodiversity

Kohlmeyer & Volkman-Kohlmeyer (1993b) compared the marine mycota of recently introduced *Rhizophora* species in the Pacific Ocean (Oahu and Moorea), with that of established *Rhizophora* stands in the Caribbean (Belize). Only seven and 21 species were identified in Moorea and Oahu respectively, while 43 species are known from *Rhizophora* in Belize. Reasons for the smaller number of taxa in Hawaiian mangroves were given as 1) species being rare or not fruiting on the collected material, and 2) missing species being restricted, in a broad sense, to mangroves and perhaps not yet having reached Hawaii. The even smaller number of fungi in Moorea may be accounted for by 1) the small size of the *Rhizophora* stands and trees, 2) the recent introduction of the mangrove (45 years ago) and 3) the lack of dead stems and roots in the young healthy thriving mangroves (Kohlmeyer & Volkman-Kohlmeyer, 1993b). The larger number of mangrove fungi on Oahu than on Moorea was also thought to be due to the more diversified terrestrial tree flora, providing an abundant source of driftwood for the development of these fungi. The larger number of fungi in Belize where mangroves have a longer history compared with the Pacific islands, was thought to be representative of the higher mangrove tree diversity; this was extrapolated to the western Pacific where a high diversity of the mycota can be expected from a high mangrove diversity. This appears to be true as in Thailand (Hyde *et al.* 1990) recorded 67 mangrove fungi, while Hyde (1988a, c) recorded 100 species in Brunei and Alias *et al.* (1994) have recorded 125 species in Malaysia.

In summary it seems, from the information available, that the diversity of mangrove fungi is dependent on

1. the age of the mangrove stand,
2. the diversity of the mangrove tree flora,
3. the diversity of the terrestrial tree flora, and
4. various micro-habitats in the mangrove (e.g., salinity differences, tidal range).

Host distribution and specificity

Kohlmeyer & Kohlmeyer (1979) discussed host specificity, and reported eight species e.g. *Didymosphaeria rhizophorae* Kohlm. & Kohlm. and *Leptosphaeria avicenniae* Kohlm. & Kohlm., that may be specific to individual host species or genera. Host specificity was also addressed by Hyde & Jones (1988), Hyde (1990a) and Hyde *et al.* (1994). The same conclusions were reached, that there is little evidence for host specificity except for a handful of species, e.g., *Trematosphaeria mangrovivis* Kohlm. has not been recorded on hosts other than *Rhizophora racemosa* Meyer, while *Hypophloeda rhizophorae* K.D. Hyde & E.B.G. Jones and *Rhizophila marina* K.D. Hyde & E.B.G. Jones appear to be confined to *Rhizophora* spp. (Hyde 1990a). The question of host specificity is therefore still unresolved and requires further study. It might be possible to grow suspected host specific fungi on different hosts in pure culture, but this would not prove host specificity since the taxa may be able to colonize other timber species in these artificial conditions. The role of endophytes in the mangrove ecosystem should also be addressed. In terrestrial ecosystems endophytic fungi present in living plants often become the saprophytic colonizers of the dead plant material due to their positional advantage (Carroll & Petrini 1983). We do not know if any marine fungi are endophytic in the roots of mangroves and become saprophytic following death. Studies need to be initiated to investigate the endophytic component of mangrove species. Despite this unanswered question the evidence so far indicates that most intertidal mangrove fungi are unspecific in their host requirements.

The question of fungal distribution on host species was investigated by Hyde (1990a). He compared the mycota of 5 intertidal mangrove tree species and found that some fungi were specific and limited to a single tree species, e.g. *Caryospora mangrovei* Kohlm.: *Xylocarpus*; *Aigialus mangrovivis* Borse and *Eutypa* sp.: *Avicennia*. Most were non-specific and developed on more than the tree species (e.g., *Hypoxylon oceanicum*

Schatz, *Leptosphaeria australiensis* (Cribb & Cribb) G.C. Hughes and *Savoryella lignicola* E.B.G. Jones & Eaton). However, dominance on each host species differed. *Passeriniella savoryellopsis* K.D. Hyde & Moozouras and *Swampomyces triseptatus* K.D. Hyde and Nakagiri were most common on *Xylocarpus* (hardwood), whereas *Hypoxylon oceanicum*, *Lulworthia* spp. and *Halosarpheia ratnagiriensis* Borse were most common on *Avicennia alba* Blume and *Sonneratia alba* J. Smith (softwood). On *Rhizophora* spp. (medium), *Cirrenalia pygmaea* Kohlm., *Caryospora rhizophorae* and *Leptosphaeria australiensis* were most common. Hyde (1990a) concluded that different taxa may be best adapted for growth on different wood types or that wood quality may provide a stimulatory effect for spore germination. By growing different taxa on different wood species under pure culture and measuring weight losses it would be possible to provide some answers to these questions. It may also be useful to compare germination rates on slivers of different wood species with spores from pure culture or field collections.

One very distinct mangrove habitat is *Nypa* palm and in a series of studies Hyde (1991a, 1992b,c, 1993), Hyde & Nakagiri (1989), Hyde & Sutton (1992) have discussed and described fungi from this habitat. The largely distinct mycota found on *Nypa* palm may be accounted for by host specificity, but salinity may also be important as *Nypa* has a somewhat narrow salinity preference (Tomlinson 1986).

Vertical zonation

Papers addressing vertical zonation of fungi in mangrove swamps have been provided by Hyde (1988b, 1989c, 1990c, 1991b). In Brunei, Hyde (1988b, 1989c) collected decaying samples of *Rhizophora apiculata* Blume from various tidal levels and found that the fungi were vertically zoned: most were limited either to the upper (e.g. *Hypoxylon oceanicum*, *Savoryella lignicola*) or lower (e.g. *Antennospora quadricornuta* (Cribb & Cribb) T.W. Johnson, *Thalassogena sphaerica* Kohlm. & Volk.-Kohlm.) levels, while only two (*Cirrenalia pygmaea* and *Lulworthia* sp.) occurred throughout the tidal range. The majority of species were collected above mean tide. In a separate study Hyde (1990c) compared fungal morphology in relation to vertical zonation, and provided the following conclusions:

1. Intertidal mangrove fungi show vertical zonation. Most are confined to a relatively small vertical range, while very few are widely distributed;
2. The greatest diversity of fungi occurs above mean tide where wood dries out superficially during low tides, but is usually inundated daily;
3. Ascomycetes with active spore release are confined to the upper intertidal, while those with passive dispersal mechanisms occur at all levels;
4. Loculoascomycetes are mostly confined to above mean tide;
5. Ascomycetes with carbonaceous ascomata walls are confined to above mean tide, while those with membranaceous walls are common throughout the tidal range;
6. Ascomycetes with superficial ascomata mostly occur above mean tide, while those with immersed ascomata occur throughout the tidal range; and
7. Ascomycetes with coloured and/or ornamented ascospores are confined to above mean tide, while those with hyaline and/or smooth-walled or sheathed ascospores are common throughout the tidal range.

The available data indicate that where there is a small tidal range, e.g., in Florida (0.8 m), this is little evidence for vertical zonation of the intertidal fungi (Kohlmeyer & Kohlmeyer, 1979). In areas where there is a large tidal range, e.g., Brunei (ca 3m) the taxa are vertically distributed. It appears that there are characteristic fungi in the lower intertidal regions where the wood is constantly submerged (e.g. *Antenno-*spora quadricornuta**), while those in the midtidal region mostly have soft structures and passive ascospore release (e.g. *Lulworthia grandispora*). Here, the wood will dry out for short periods, but the fungi will not be subjected to the harsher conditions further up the intertidal gradient. In the high intertidal a third group of fungi is evident, species with protective brittle carbonaceous ascomata and active spore release (e.g. *Hypoxylon oceanicum*). A fuzzy area between the high intertidal region and the terrestrial regions also occurs. In this region many unusual fungi sporulate, but these are unlikely to be true intertidal fungi. *Phellinus* sp, a polypore, is often found in the high intertidal on *Sonneratia grifithii* Korz in Ranong mangrove, Thailand, and Australia (Hyde *et al.* 1994; George & Kenneally 1975). It is unlikely that these fungi can grow in saline conditions, but more likely that the mycelium decays the heartwood which is not affected by salinity and sporulates on the outside surface, perhaps during neap tide periods. K.D. Hyde (unpubl. data) has seen numer-

ous terrestrial fungi sporulating on the mangrove floor in the upper intertidal region during an extreme wet spell in Ranong mangrove, Thailand, in 1988. This occurred during a neap tide period when the mangrove debris was not inundated with sea water. However, as the tidal levels rose and the decaying debris was inundated, the terrestrial fructifications collapsed within a matter of hours despite continuing heavy rainfall.

No information about vertical zonation is available for most parts of the world or most tidal ranges. It would be fascinating to examine the vertical zonation of fungi in areas with a large tidal range (e.g. the Northern Territory, Australia, 7m), although one would suspect the area of supratidal/intertidal interface, supporting "terrestrial taxa", would be much larger.

Distribution with salinity

Very few studies have investigated the effect of salinity on the mycota in mangrove forests. Most reports of intertidal fungi do not record the salinity, and studies of this sort are needed. Perhaps the only three publications that have examined salinity effect superficially are those of Hyde (1992b,c,d). Hyde (1992c) examined the fungi on *Nypa* palm collected in Tg. Api Api Brunei where the salinity is low (14-28‰). *Nypa* is a mangrove palm growing along the fringes of intertidal rivers where it is regularly flushed with river freshwater: the fungi that grow on decaying *Nypa* palm in the intertidal region are mostly different from those in higher salinity mangrove, as described above. However, many of these are unique marine species belonging to genera consistently found on terrestrial palms (Hyde 1988d; Hyde & Nakagiri 1989). Others are marine genera with species unique to *Nypa* (e.g. *Helicascus nypae* K.D. Hyde), while only a handful are found throughout mangrove ecosystems (e.g. *Lignicola laevis*). There are, however, limitations in comparing the mycota of a palm mangrove with that of other dicotyledonous mangroves since they are very different substrates. Hyde (1992d) 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 a new species *Phomatospora kandeliae* K.D. Hyde. 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. However, these are only preliminary findings and further studies should be initiated.

Succession

Only three reports discuss the succession of intertidal fungi on wood and two on the succession of fungi on mangrove leaves and seedlings. Tan *et al.* (1989) examined succession of fungi on wood of *Avicennia alba* and *A. lanata* Ridley, while Leong *et al.* (1991) examined succession on submerged *Bruguiera cylindrica* (L.) Blume and *Rhizophora apiculata*. They submerged young split stems of the tree species in Mandai mangrove and recovered samples periodically. A pattern of succession of fungi developed on the wood with *Lignicola laevis* as an early colonizer, *Verruculina enalia* (Kohlm.) Kohlm. & Volkm.-Kohlm. and *Lulworthia* sp. 1 as an intermediate colonizer and *Aigialus parvus* Schalz & Kohlm. as a late colonizer. Unfortunately this study made only brief mention of the differences in the fungi developing on bark and on the woody parts of the split stems and this should be addressed. A study of the succession of fungi on *Rhizophora apiculata* and *Xylocarpus granatum* König was carried out in Brunei by Hyde (1991b). Poles or small stems of the tree species were attached vertically across the intertidal region and recovered bimonthly. Fungal succession on these timbers differed markedly, but on both a pattern was observable. In the case of *Rhizophora* which remained bark-covered during the duration of the study *Halosarpheia minuta* Leong *et al.* was one of the earliest and most common taxa. *Lulworthia grandispora* then produced ascomata followed by *Manglicola guatemalensis* Kohlm. & Kohlm. and *Anthostomella* sp. (6 months) and *Capillatispora corticola* K.D. Hyde and *Hypophloeda rhizospora* (8 months). With *Xylocarpus granatum*, *Lulworthia* sp. was the first taxon to occur on bark on wood, along with a *Diplodia* sp. and several unidentified coelomycetes. In the later stages several fungi (i.e. *Xylomyces* sp., *Cirrenalia* spp., *Periconia prolifica* Anastasiou, *Leptosphaeria australiensis*, *Lulworthia* spp., *Halosarpheia marina*, *Calathella* sp. and *Hypoxylon oceanicum*) were common on the exposed xylem. The differences in fungi colonizing these two wood species were distinct and illustrate both fungal succession, host specificity, differences in fungi colonizing bark and wood, and resistance against fungal development due to high tannin contents in the bark.

These studies show evidence of fungal succession on submerged wood, but are a measure of the formation of ascomata rather than direct fungi colonization. It may be that some species produce fructifications more speedily than others, even though all taxa may

be present in the timber following submergence. This aspect needs further investigation as does the effect of other variables on fungal succession (e.g. salinity, wood species). For succession studies on leaves and propagules the reader should refer to Fell & Master (1973, 1980) and Newell (1986).

The role of fungi in mangrove nutrient cycling

Whereas increasing knowledge is available on the involvement of bacteria in water column and sediment productivity and nutrient cycles, virtually nothing is known about the role played by fungi in such energy pathways (Newell 1984). Even less is known on the actual involvement of fungi in mangrove nutrient cycling. Information on the role of fungi in the decay of mangrove detritus is small compared with that available for salt marsh ecosystems. Despite attention paid to gross decomposition of mangrove leaf litter, most taxonomic studies on mangrove fungi are confined to lignolytic species, which probably play an important role in the turnover of mangrove wood, an emphasis also apparent in studies of fungi-mediated decomposition in terrestrial ecosystems (Stolp 1988). Past studies on mangrove leaf litter decomposition have established that apart from some exceptions (e.g., Robertson 1986), microbial enrichment usually precedes detritivore consumption and enriched detritus is generally more attractive to detritivores (e.g., Bärlocher *et al.* 1989; Graça *et al.* 1993), probably because of the higher availability of nitrogen and the improved digestibility of detrital carbon (Lee 1989; Camilleri 1992; Lee 1993). There are also numerous reports on mangrove leaf, and to a lesser extent, wood decomposition rates. Although fungi have been isolated from decaying mangrove leaves in the past (e.g., Fell & Master 1980; Newell *et al.* 1987; Nakagiri *et al.* 1989), very little is known about the roles played by these fungi in the decomposition process, especially that of leaf litter. Reasons for this deficiency of knowledge may include: a) difficulties in quantifying fungal involvement in the decomposition process; b) lack of knowledge of fungal extracellular enzymes and their activities; c) hitherto emphasis of particulate rather than dissolved components in nutrient cycling studies.

Quantification of fungi abundance

Newell & Statzell-Tallman (1982), Newell *et al.* (1986) and Newell (1992) reviewed the methods used for quantifying fungal presence on decaying herbaceous

wetland plant tissues (mainly *Spartina*). Past methods include the estimation of volume or biomass by direct count or their converted values (e.g., Blum *et al.* 1988), but these have been criticized as inaccurate (Newell 1992). Conversion factors available for transforming direct volume counts to biomass are available, the problem being that without a knowledge of which groups of fungi are present, the conversion cannot be given much confidence. Fungi-specific molecules, e.g., glucosamine and ergosterol, have been used for the enumeration of fungi abundance. Newell & Fell (1992) attempted to measure living fungal biomass on decaying mangrove leaves and twigs using ergosterol content, a molecule characteristic of the Eumycota but not produced by vascular plants. The use of these molecules eliminates the problem of contamination from the decomposition substrate. Newell & Fell (1992) indicated that only low levels of ergosterol were detectable in decaying mangrove leaves, reflecting a small contribution from eumycotic species. The involvement of oomycetes may nevertheless be substantial, but because they do not produce ergosterol, their importance could have been overlooked (S.Y. Newell, pers. comm.). Data on fungal quantification is therefore scarce. Before techniques can be established and inter-calibration performed, relating fungal abundance to mangrove decomposition rates quantitatively will still be problematic.

Fungal extracellular enzymes

Both bacteria and fungi process the detritus substrates by the digestive activities of extracellular enzymes. The taxonomy and activities of bacterial extracellular enzymes, unlike those of the fungi, are fairly well known (e.g., Chaloupka & Krumphanzl 1987). Chaloupka & Krumphanzl (1987), for example, make no mention of the type and activities of the enzymes secreted by fungi. The scanty information available on fungal enzymes is largely for terrestrial species. This disparity probably originates from the lack of knowledge on the fungal taxa involved in the mangrove decomposition process. In addition to being a potential indicator of fungal biomass (Newell 1992), extracellular enzyme assays will help understand the kinetics and mechanism of the decomposition process. Recently, Wu (1993) identified 25 genera (42 strains) of fungi from mangroves in the Tansui Estuary near Taipei, Taiwan, and found that most of the ascomycetes were able to secrete a wide range of enzymes potentially capable of decomposing mangrove litter. Other

reports on the activities of mangrove fungi in southeast Asia are, however, almost non-existent.

Fungi-mediated production of DOM

It is increasingly recognized that much of the nutrient cycling in aquatic ecosystems takes place in the dissolved form (Wetzel 1984), an aspect largely overlooked in previous trophic studies of mangrove ecosystems (Robertson 1987). Although in some ecosystems some macrodetritivores (e.g., crabs, amphipods) are capable of processing large quantities of mangrove leaf litter per unit time (Robertson 1986; Poovachiranon *et al.* 1986; Lee 1989; Robertson & Daniel 1989), microbes (of which fungi are an important component) are the ubiquitous and constant decomposers of leaf and, in particular, wood litter in the mangal. A large proportion of the end product of fungal processing of mangrove litter is, however, likely to be dissolved rather than particulate. Given the complex nature of the dissolved organic matter in aquatic systems (Wetzel 1984), nothing is known about the type and quantity of DOM which may be derived from fungi-mediated mangrove decomposition.

Another poorly known aspect of the decomposition process is the extent of enrichment possible with fungal colonization of mangrove detritus. Significant increases in the nitrogen content of decaying detritus resulting in decrease in the C:N ratio are common (e.g. Lee 1989). Most detritivores tend to prefer enriched to fresh detritus unless environmental constraints limit the availability, e.g. in tidal forests where mangrove leaf litter export is high (e.g. Robertson 1986). To what extent fungi are responsible for this enrichment is, however, unknown. This enrichment has largely been attributed to the microbial community as a whole and the relative importance of the bacteria and the fungi in the time dimension and the mobilization of different components of the detritus have rarely been investigated.

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References

- Aleem, A. A., 1980. Distribution and ecology of marine fungi in Sierra Leone (Tropical West Africa). *Bot. Mar.* 23: 679–688.
- Alias, A. & E. B. G. Jones, 1994. Biodiversity of fungi in tropical mangroves. In *Fifth International Mycological Congress, Abstracts*.
- Bärlocher, F., S. Y. Newell & T. L. Arsuffi, 1989. Digestion of *Spartina alterniflora* Loisel material with and without fungal constituents by the periwinkle *Littorina irrorata* Say (Mollusca: Gastropoda). *J. exp. mar. Biol. Ecol.* 130: 45–53.
- Blum, L. K., A. L. Mills, J. C. Ziemann & R. T. Ziemann, 1988. Abundance of bacteria and fungi in seagrass and mangrove detritus. *Mar. Ecol. Prog. Ser.* 42: 73–78.
- Borse, B. D., 1988. Frequency of occurrence of marine fungi from Maharashtra Coast, India. *Indian J. Mar. Sci.* 17: 165–167.
- Boto, K. G., J. S. Bunt & J. T. Wellington, 1984. Variations in mangrove forest productivity in Northern Australia and Papua New Guinea. *Estuarine, coastal and Shelf Science* 19: 321–329.
- Bunt, J. S., K. G. Boto & G. Boto, 1979. A survey method for estimating potential levels of mangrove forest primary production. *Mar. Biol.* 52: 123–128.
- Camilleri, J. C. 1992. Leaf-litter processing by invertebrates in a mangrove forest in Queensland. *Mar. Biol.* 114: 139–145.
- Carroll, G. C. & O. Petrini, 1983. Patterns of substrate utilization by some fungal endophytes from coniferous foliage. *Mycologia* 75: 53–63.
- Chaloupka, J. & V. Krumphanz, 1987. Extracellular enzymes of microorganisms. Plenum Press, New York. 216 pp.
- Chinnaraj, S., 1993. Higher marine fungi from mangroves of Andaman and Nicobar Islands. *Sydowia* 45: 109–115.
- Christensen, B., 1978. Biomass and primary productivity of *Rhizophora apiculata* Bl. mangrove in Southern Thailand. *Aq. Bot.* 4: 43–52.
- Cundell, A. M., M. S. Brown, R. Stafford & R. Mitchell, 1979. Microbial degradation of *Rhizophora mangle* leaves immersed in the sea. *Estuarine and Coastal Marine Science* 9: 281–286.
- Fell, J. W. & I. M. Master, 1973. Fungi associated with the degradation of mangrove (*Rhizophora mangle* L.) leaves in South Florida. In L. H. Stevenson & R. R. Colwell (eds), *Estuarine Microbial Ecology*. University of South Carolina Press, Columbia: 455–466.
- Fell, J. W. & I. M. Master, 1980. The association and potential role of fungi in mangrove detrital systems. *Bot. Mar.* 23: 257–263.
- George, A. S. & K. F. Kenneally, 1975. The flora of the Prince Regent river reserve, north-western Kimberley, Western Australia: A biological survey of the Prince Regent river reserve, North-West Kimberley, Western Australia in August, 1974. *Widl. Res. Bull. West. Aust.* 3: 1–116.
- Graça, M. A. S., L. Maltby & P. Calow., 1993. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I: feeding strategies. *Oecologia* 93: 139–144.
- Heald, E. J. 1971. The production of organic detritus in a South Florida estuary. University of Miami Sea Grant Technical Bulletin. No. 6.
- Hughes, G. C. 1974. Geographical distribution of the higher marine fungi. *Veröff. Inst. Meeresforsch. Bremen. Suppl.* 5:419–441.
- Hutchings, P. & P. Saenger, 1987. *Ecology of mangroves*. University of Queensland Press, St. Lucia.
- Hyde, K. D., 1986. Frequency of occurrence of lignicolous marine fungi in the tropics. In S. T. Moss (ed), *The Biology of Marine Fungi*. Cambridge University Press, Cambridge: 311–322.
- Hyde, K. D., 1988a. Studies on the tropical marine fungi of Brunei. *Bot. J. Linn. Soc.* 98: 135–51.
- Hyde, K. D., 1988b. Observations on the vertical distribution of marine fungi on *Rhizophora* spp., at Kampong Danau mangrove, Brunei. *Asian Mar. Biol.* 5: 77–81.
- Hyde, K. D., 1988c. Studies on the tropical marine fungi of Brunei II. Notes on five interesting species. *Trans. Mycol. Soc. Japan* 29: 161–171.
- Hyde, K. D., 1988d. The genus *Linocarpon* from the mangrove palm *Nypa fruticans*. *Trans. Mycol. Soc. Japan* 29: 339–350.
- Hyde, K. D., 1989a. Ecology of tropical marine fungi. *Hydrobiologia* 178: 199–208.
- Hyde, K. D., 1989b. Intertidal mangrove fungi from North Sumatra. *Can. J. Bot.* 67:3078–3082.
- Hyde, K. D., 1989c. Vertical zonation of intertidal mangrove fungi. In T. Hattori, Y. Ishida, R. Maryama, R. Mortia & A. Uchida (eds), *Recent Advances in Microbial Ecology*. Japan Scientific Societies Press, Tokyo: 302–306.
- Hyde, K. D., 1990a. A comparison of the intertidal mycota of five mangrove tree species. *Asian Mar. Biol.* 7: 93–107.
- Hyde, K. D., 1990b. *Caryospora mangrovei* sp. nov. and notes on marine fungi from Thailand. *Trans. Mycol. Soc. Japan* 30: 333–342.
- Hyde, K. D., 1990c. A study of the vertical zonation of intertidal fungi on *Rhizophora apiculata* at Kampong Kapok Mangrove, Brunei. *Aq. Bot.* 36: 255–62.
- Hyde, K. D., 1990d. Intertidal fungi from warm temperate mangroves of Australia, including *Tunicatispora australiensis* gen. et sp. nov. *Aust. Syst. Bot.* 3: 711–718.
- Hyde, K. D., 1991a. A new Amphisphaeriaceae fungus from intertidal fronds of *Nypa fruticans*. *Trans. Mycol. Soc. Japan* 31: 265–271.
- Hyde, K. D., 1991b. Fungal colonization of *Rhizophora apiculata* and *Xylocarpus granatum* poles in Kampong Kapok mangrove, Brunei. *Sydowia* 43: 31–38.
- Hyde, K. D., 1992a. *Julella avicenniae* Borse comb. nov. (Thelenelaceae) from intertidal mangrove wood and miscellaneous fungi form the NE coast of Queensland. *Mycol. Res.* 96: 939–942.
- Hyde, K. D., 1992b. Fungi from *Nypa fruticans*: *Nipicola carbospora* gen. et sp. nov. (Ascomycotina) *Crypt. Bot.* 2: 330–332.
- Hyde, K. D., 1992c. Fungi from decaying intertidal fronds of *Nypa fruticans*, including three new genera and four new species. *Bot. J. Linn. Soc.* 110: 95–110.
- Hyde, K. D., 1992d. Intertidal fungi from *Kandelia candel* including *Phomatospora kandellii* sp. nov. *Trans. Mycol. Soc. Japan* 33: 313–316.
- Hyde, K. D., 1992e. Intertidal mangrove fungi from the west coast of Mexico, including one new genus and two new species. *Mycol. Res.* 96: 25–30.
- Hyde, K. D., 1993. Fungi from palms. V. *Phomatospora nypae* and notes on intertidal fungi from *Nypa fruticans* in Malaysia. *Sydowia* 45: 199–203.
- Hyde, K. D. & E. B. G. Jones, 1988. Marine mangrove fungi. *Mar. Ecol. (Berlin)* 9: 15–33.
- Hyde, K. D. & E. B. G. Jones, 1989. Ecological observations on marine fungi from the Seychelles. *Bot. J. Linn. Soc.* 100: 237–254.
- Hyde, K. D. & A. Nakagiri, 1989. A new species of *Oxydothis* from the mangrove palm, *Nypa fruticans*. *Trans. Mycol. Soc. Japan* 30: 69–76.
- Hyde, K. D. & B. C. Sutton, 1992. *Nypaella frondicola* gen. et sp. nov., *Plectrophomella nypae* sp. nov. and *Pleurophomopsis nypae* sp. nov. (Coelomycetes) from intertidal fronds of *Nypa fruticans*. *Mycol. Res.* 96: 210–214.

- Hyde, K. D., A. Chalermpongse & T. Boonthavikoon, 1990. Ecology of intertidal fungi at Ranong mangrove, Thailand. *Trans. Mycol. Soc. Japan* 31: 17–28.
- Hyde, K. D., A. Chalermpongse, & T. Boonthavikoon, 1993. The distribution of intertidal fungi on *Rhizophora apiculata*. In: B. Morton (ed), *The Marine Biology of the South China Sea. Proceedings of the First International Conference on the Marine Biology of Hong Kong and the South China Sea*, Hong Kong 1990. University of Hong Kong Press, Hong Kong: 643–652.
- Jones, E. B. G. 1993. Tropical marine fungi. In S. Issac, J. C. Frankland, R. Watling & J. S. Whatley (eds.), *Aspects of Tropical Mycology*. Cambridge University Press, Cambridge: 73–89.
- Jones, E. B. G. & K. D. Hyde, 1990. Observations on poorly known mangrove fungi and a nomenclatural correction. *Mycotaxon* 37: 197–201.
- Jones, E. B. G. & A. J. Kuthubutheen, 1989. Malaysian Mangrove Fungi. *Sydowia* 41: 160–169.
- Jones, E. B. G. & T. K. Tan, 1987. Observations on manglicolous fungi from Malaysia. *Trans. Brit. Mycol. Soc.* 89: 390–392.
- Jones, E. B. G., F. R. Uyenco & M. P. Folosco, 1988. Fungi on driftwood collected in the intertidal zone from the Philippines. *Asian Mar. Biol.* 5: 103–106.
- Kohlmeyer, J., 1980. Tropical and subtropical filamentous fungi of the Western Atlantic Ocean. *Bot. Mar.* 23: 529–544.
- Kohlmeyer, J., 1981. Marine fungi from Martinique. *Can. J. Bot.* 59: 1314–1321.
- Kohlmeyer, J., 1983. Geography of marine fungi. *Aust. J. Bot. Suppl. Ser.* 10: 67–76.
- Kohlmeyer, J., 1984. Tropical marine fungi. *Mar. Ecol. (Berlin)* 5: 329–378.
- Kohlmeyer, J. & E. Kohlmeyer, 1979. *Marine Mycology. The Higher Fungi*. Academic Press, New York.
- Kohlmeyer, J. & B. Volkmann-Kohlmeyer, 1987a. Marine fungi from Aidabra, the Galapagos, and other tropical islands. *Can. J. Bot.* 65: 571–582.
- Kohlmeyer, J. & B. Volkmann-Kohlmeyer, 1987b. Marine fungi from Belize with a description of two new genera of ascomycetes. *Bot. Mar.* 30: 195–204.
- Kohlmeyer, J. & B. Volkmann-Kohlmeyer, 1988. *Ophiodeira* gen. nov. (Halosphaeriales) and a survey of higher marine fungi from Saint Croix (Virgin Islands). *Can. J. Bot.* 66: 2062–2067.
- Kohlmeyer, J. & B. Volkmann-Kohlmeyer, 1991. Marine fungi from Queensland, Australia. *Aust. J. Mar. Freshw. Res.* 42: 91–99.
- Kohlmeyer, J. & B. Volkmann-Kohlmeyer, 1993a. Two new genera of Ascomycotina from saltmarsh *Juncus*. *Systema Ascomycem* 11: 95–106.
- Kohlmeyer, J. & B. Volkmann-Kohlmeyer, 1993b. Biogeographic observations on Pacific marine fungi. *Mycologia* 85: 337–346.
- Lee, S. Y., 1989. The importance of Sesarminae crabs *Chiromanthes* spp. and inundation frequency on the decomposition of mangrove (*Kandelia candel* (L.) Druce) leaf litter in a Hong Kong tidal shrimp pond. *J. exp. mar. Biol. Ecol.* 131: 23–43.
- Lee, S. Y. 1993. Leaf choice of the sesarminae crabs *Chiromanthes bidens* and *C. maipoensis* in a Hong Kong mangal. In B. Morton, (ed.), *Marine Biology of the South China Sea: Proceedings of the First International Conference on the Marine Biology of Hong Kong and the South China Sea*, Hong Kong, 1990. Hong Kong University Press, Hong Kong: 597–604.
- Leong, W. F., T. K. Tan & E. B. G. Jones, 1991. Fungal colonization of submerged *Bruguiera cylindrica* and *Rhizophora apiculata* wood. *Bot. Mar.* 34: 69–76.
- Nakagiri, A., 1993. Intertidal mangrove fungi from Iriomote Island. *IFO Res. Commun.* 16: 24–62.
- Nakagiri, A., S. Tokumasu, H. Araki *et al.* 1989. Succession of fungi in decomposing mangrove leaves in Japan. *Proc. Int. Symp. Micro. Ecol.* 5: 297–301.
- Newell, S. Y. 1984. Bacterial and fungal productivity in the marine environment: a contrastive overview. *Colloques Int. Cent. Natn. Rech. Scient.* 331: 133–139.
- Newell, S. Y. 1986. Mangrove fungi: the succession in the mycoflora of red mangrove (*Rhizophora mangle*) seedlings. In E. B. G. Jones (ed), *Recent Advances in Aquatic Mycology*. *Elek Science*: 5: 1–91.
- Newell, S. Y. 1992. Estimating fungal biomass and productivity in decomposing litter. In G. C. Carroll, & D. T. Wicklow (eds), *The fungal community. Its organization and role in the ecosystem*. Marcel Dekker, Inc., New York: 521–561.
- Newell, S. Y., R. D. Fallon & J. D. Miller, 1986. Measuring fungal-biomass dynamics in standing-dead leaves of a salt-marsh vascular plant. In S. T. Moss, (ed), *Biology of Marine Fungi*, Cambridge University Press, Cambridge: 19–25.
- Newell, S. Y. & J. W. Fell, 1992. Ergosterol content of living and submerged, decaying leaves and twigs of red mangrove. *Can. J. Microbiol.* 38: 979–982.
- Newell, S. Y., J. D. Miller & J. W. Fell, 1987. Rapid and pervasive occupation of fallen mangrove leaves by a marine zoosporic fungus. *Appl. Environ. Microbiol.* 53: 2464–2469.
- Newell, S. Y. & A. Statzell-Tallman, 1982. Factors for conversion of fungal biovolume to biomass, carbon and nitrogen: variation with mycelial ages, growth conditions, and strains of fungi from a salt marsh. *Oikos* 39: 261–268.
- Odum, W. E. & E. J. Heald, 1975. The detritus food web of an estuarine mangrove community. In L. E. Cronin (ed), *Estuarine Research. Vol. I*. Academic Press, New York: 265–286.
- Poovichiranon, S., K. G. Boto, & N. C. Duke, 1986. Food preference studies and ingestion rate measurements of the mangrove amphipod *Parhyale hawaiiensis* (Dana). *J. exp. mar. Biol. Ecol.* 98: 129–140.
- Robertson, A. I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *J. exp. mar. Biol. Ecol.* 102: 237–248.
- Robertson, A. I., 1987. The determination of tropic relationships in mangrove dominated systems: areas of darkness. In C. D. Field & A. J. Dartnall (eds), *Mangrove ecosystems of Asia and the Pacific: status, exploitation and management*. Australian Institute of Marine Science, Australia: 292–304.
- Robertson, A. I. & P. A. Daniel, 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* 78: 191–198.
- Robertson, A. I., D. M. Alongi & K. G. Boto, 1992. Food chains and carbon fluxes. In A. I. Robertson & D. M. Alongi (eds), *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington D.C.: 293–326.
- Saenger, P. & S. C. Snedaker, 1993. Pantropical trends in mangrove above-ground biomass and annual litter fall. *Oecologia* 96: 293–299.
- Stolp, H., 1988. *Microbial ecology: organisms, habitats, activities*. Cambridge University Press, Cambridge. 308 pp.
- Tan, T. K., W. F. Leong & E. B. G. 1989. Succession of fungi on wood of *Avicennia alba* and *A. lanata* in Singapore. *Can. J. Bot.* 67: 2686–2691.
- Tenore, K. R., J. C. Cammen, S. E. G. Findlay & N. Phillips, 1982. Perspectives of research of detritus: do factors controlling the availability of detritus to macroconsumers depend on this source? *J. Mar. Res.* 40: 473–490.
- Tomlinson, P. B. 1986. *The botany of mangroves*. Cambridge University Press, Cambridge. 413 pp.

- Vrijmoed, L. L. P. 1990. Preliminary observations of lignicolous marine fungi from mangroves in Hong Kong. In B. Morton (ed), Proceedings of the Second International Marine Biological Workshop: the marine flora and fauna of Hong Kong and southern China, Hong Kong, 1986, Hong Kong University Press, Hong Kong: 701–706.
- Vrijmoed, L. L. P., K. D. Hyde & E. B. G. Jones, 1994. *Diaporthe salsuginea* sp. nov. and *Aniptodera* sp. nov. from Hong Kong and Macau mangroves. Mycol. Res. 96: 699–704.
- Wetzel, R. G., 1984. Detrital dissolved and particulate organic carbon functions in aquatic ecosystems. Bull. mar. Sci. 35: 503–509.
- Wu, R. Y., 1993. Studies on the microbial ecology of the Tansui Estuary. Bot. Bull. Acad. Sin. 34: 13–30.