



## Thraustochytrid and fungal component of marine detritus. IV. Laboratory studies on decomposition of leaves of the mangrove *Rhizophora apiculata* Blume

S. Raghukumar\*, Sumita Sharma, Chandralata Raghukumar,  
Veena Sathe-Pathak, D. Chandramohan

*Biological Oceanography Division, National Institute of Oceanography, Dona Paula, Goa – 403 004, India*

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### Abstract

The role of thraustochytrid protists and fungi in detrital dynamics of leaves of the mangrove *Rhizophora apiculata* was investigated in the laboratory. Field detritus of different ages (0, 4, 7, 14, 21, 28, 46, 53 and 60 days) obtained from litter-bag experiments were inoculated individually with five fungi, *Cladosporium herbarum*, *Fusarium moniliforme*, *Cirrenalia basiminuta*, “Hyphomycete XVII” and *Halophytophthora vesicula* and one thraustochytrid, *Schizochytrium mangrovei*. Biochemical changes occurring after 1 wk in 8 ages of detritus were examined. The results suggested two phases of fungal dynamics, the first corresponding to decompositional stages of 0–21 and the second to 28–60 days. Detrital material of the first phase supported better growth of the fungi *Cladosporium herbarum*, *Fusarium moniliforme*, *Cirrenalia basiminuta* and *Halophytophthora vesicula*. Cellulase production by all the test species, in general, was greatest on such detritus. Detritus of the second phase proved to be better for the growth of the fungus “Hyphomycete XVII” and production of xylanase by all test species. Pectic enzymes, amylase and protease were produced more or less uniformly in all ages of detritus. The thraustochytrid *Schizochytrium mangrovei* grew well on both phases of detritus. The test species utilised a wide variety of substrates as sole carbon sources but differed significantly in their capabilities to elaborate the various degradative enzymes in detritus. *Fusarium moniliforme* and *Halophytophthora vesicula* caused marked increases in detrital protein, while all the test species enhanced amino acid levels. *Schizochytrium mangrovei* enhanced carbohydrate and reducing sugar contents, while *Fusarium moniliforme* and *Halophytophthora vesicula* substantially decreased the levels of the former. Growth of *Halophytophthora vesicula* in detritus caused a decline of total phenolics. The net biochemical status of detritus seems to depend upon interactions between the biochemical

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\* Corresponding author.

state of detritus, the colonising species and their biomass, and the enzymatic activities of the concerned microorganisms.

*Keywords:* Detritus; Fungi; *Rhizophora apiculata*; Thraustochytrids

## 1. Introduction

The detrital food web is of major importance in the coastal marine ecosystem (Mann, 1988; Pomeroy & Wiebe, 1988). The rates of decay processes and channelisation of energy into the various pathways of this food web are determined mainly by the chemical constitution of the particulate detritus itself (Rice, 1982). Detrital microbes and their degradative activities play a major role in altering the chemistry of the detritus. These microorganisms are, in turn, affected by the detrital chemistry (Rice, 1982; Melillo et al., 1984). Thus, abiotic leaching of soluble organics from the detritus promotes rapid, initial microbial activity (Blum & Mills, 1991; Peduzzi & Herndl, 1991). The resultant microbial colonisation and enzymatic degradation of the various compounds of detritus further accelerates the release of dissolved organic matter (DOM) and nutrient recycling (Hodson & Moran, 1989; Moran & Hodson, 1989). Biomass buildup of detrital bacteria on the particulate organic matter (POM) and DOM has often been considered a potentially significant source of organic carbon and/or nitrogen nutrition for detritivorous animals and may support food-web dynamics through both protozoans and metazoans (Lopez & Levinton, 1978; Linley & Newell, 1981; Newell & Field, 1983; Peduzzi & Herndl, 1991).

Compared to the information available on bacteria in these processes, that on fungi and the fungi-like unicellular protists, the thraustochytrids (Moss, 1986) is limited (Newell, 1976; Kohlmeyer & Kohlmeyer, 1979; Fell & Master, 1980; Fell & Newell, 1981; Cuomo et al., 1985; Raghukumar, 1990). Biomass of these two groups of organisms in detritus of marine macrophytes such as the cordgrass *Spartina alterniflora* Loisel, seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson, the brown-alga *Sargassum cinereum* J. Ag. and leaves of the mangrove *Rhizophora apiculata* Blume may reach fairly high levels (Newell et al., 1986; Sathe & Raghukumar, 1991; Sathe-Pathak et al., 1993; Raghukumar et al., 1994).

In an earlier field study on decomposition of leaves of *Rhizophora apiculata*, we observed distinct sequences of colonisation by fungal species and attainment of peak fungal and bacterial biomass by 21 and 35 days, respectively, as well as a distinct decrease in the labile organics, proteins, carbohydrates, reducing sugars and phenols and the structural compound cellulose within 21 days of decomposition (Raghukumar et al., 1994). These changes correspond to general detrital dynamics (Godschalk and Wetzel, 1978; Valiela et al., 1984) and are caused by chemical solubilisation and microbial degradation (Marinucci et al., 1981; Robertson, 1988; Moran & Hodson, 1989; Peduzzi & Herndl, 1991). However, the precise contributions of each of these processes is still incompletely understood. Our main aim behind the present work is to understand the interactions between fungal colonisation and detrital chemistry in *Rhizophora apiculata* leaf detritus, by addressing the following questions which are also of relevance to detrital microbiology in general. (1) What effects do the different decompositional

stages of detritus, representing detritus of different chemical constitutions, have on growth of microbial species? (2) In what ways do individual microbial species differ in biochemically transforming different ages of detritus, in terms of labile organics and structural compounds? (3) How do such species differ in degradative enzyme production during various stages of decomposition? These questions may be conveniently tackled by using an experimental approach with model test species, as we have done in the case of the detritus of the macroalga *Sargassum cinereum* (Sharma et al., 1994). This paper deals with the results of our study using detritus of different ages from leaves of the mangrove *Rhizophora apiculata* and five species of fungi and one thraustochytrid.

## 2. Materials and methods

Senescent leaves (0 day detritus) as well as 4, 7, 14, 21, 28, 46, 53 and 60-day-old leaf detritus from *Rhizophora apiculata* were collected from litter-bag experiments carried out at Chorao mangroves, Goa, India: Lat.: 15° 27'–15° 38' N; Long.: 73° 42'–73° 50' E (Raghukumar et al., 1994). For this purpose, senescent yellow leaves were plucked from the trees, two of these placed in each of the seven pouches of a 1 mm mesh nylon bag and six such bags tied to a frame and immersed below the low-tide level in a mangrove creek. Water salinity during the sampling period ranged from 25 to 30 o/oo and temperature, 27–32 °C. After periodic collections, the detrital material was air-dried for 3 days followed by drying at 50 °C for one day and milled and sieved through a 200- $\mu$ m sieve. These were used for all the experiments. Six species, which were most frequently isolated from the mangrove leaves in this study (Raghukumar et al., 1994), comprising five fungi, namely *Cladosporium herbarum* (Pers.) Link ex Gray, *Fusarium moniliforme* Sheld., *Cirrenalia basiminuta* Raghukumar et Zainal, an unidentified hyphomycete termed "Hyphomycete XVII" and *Halophytophthora vesicula* (Anast. et Church.) Ho & Jong and one thraustochytrid *Schizochytrium mangrovei* Raghukumar were used as test organisms for these studies. The fungi were maintained on corn meal agar medium with 50% seawater and the thraustochytrid in seawater/pine pollen cultures (Gaertner, 1968).

### 2.1. Experimental design

The six species were grown on detrital substrates of 9 ages mentioned above. Detrital material of 250 mg dry weight was autoclaved in 100 ml seawater in 250 ml Erlenmeyer flasks and inoculated with a loopful of the thraustochytrid culture or a 5-mm disc of a 5-day-old agar culture of the fungi. Flasks inoculated with the test organisms, referred to as "inoculated detritus" in the text, were grown in shake cultures and the thraustochytrid under stationary conditions. Five replicates were maintained for each treatment. "Uninoculated control" flasks containing the same amount of autoclaved detritus in sterile seawater were maintained. After incubation for 1 wk at room temperature, the contents of the flasks were filtered separately over sterilised Whatman GF/C glassfibre filters and the culture filtrates frozen for subsequent enzyme analyses. Detritus with microbial growth from three flasks retained on the filters were used for

biochemical analyses. Those from the other two were used to estimate growth of the test organisms on detritus. Growth was estimated by analysing the ATP content (Parsons et al., 1984) using a Turner TD-20E luminometer.

## 2.2. Biochemical changes

Inoculated and control detritus, collected and processed as above, were analysed as follows: carbohydrates were estimated by the phenol-sulphuric acid method (Dawes, 1981) and reducing sugars by the dinitrosalicylic acid method of Miller (1960). Proteins were determined by the modified Lowry's method of Peterson (1977). While this method is considered more accurate than that of the original Lowry's method by extracting membrane proteolipid proteins effectively, mangrove detrital proteins that might have been complexed by the tannins might still not be estimated by this technique. Our results based on this technique, therefore, would only refer to proteins extractible thereby. Free amino acids were estimated spectrophotometrically using ninhydrin reagent (Mahadevan, 1975). Total phenols were extracted in cold methanol at 4 °C for 24 h and after centrifugation, the clear supernatant analysed using Folin-Denis reagent (Swain & Hillis, 1959). Catechol (Sigma, USA) was used as a reference standard. The results are presented as percentages of the individual biochemical constituents in dry weight detritus.

## 2.3. Enzyme estimations in culture filtrates

Cellulases, xylanase, polygalacturonase and amylase in culture filtrates were estimated by measuring reducing sugars (Miller, 1960) released from powdered microcrystalline cellulose, xylan, sodium polypectate and soluble starch as substrates using standard methods (Gessner, 1980; Suberkropp et al., 1983; Dewey et al., 1984). For all these enzymes, 1 unit corresponds to 1 µg glucose liberated per ml of culture fluid per h. Pectin lyase was estimated according to Suberkropp & Arsuffi (1984). Proteases were estimated by measuring release of amino acids from casein (Mahadevan, 1975).

Table 1

Student's *t*-test for growth (ng ATP/250 mg detritus) of test species on two age-groups of detritus from leaves of *Rhizophora apiculata*

Test species	Mean growth on 0–21-day detritus	Mean growth on 28–60-day detritus	<i>T</i> (df 7)
<i>Cladosporium herbarum</i>	266 ± 44.08	155 ± 51.0	3.5223**
<i>Schizochytrium mangrovei</i>	50.4 ± 11.93	70.3 ± 32.62	1.2764 n.s.
<i>Fusarium moniliforme</i>	4098 ± 1056	1091 ± 501	5.1942**
<i>Cirrenalia basiminuta</i>	87.7 ± 30.11	29.5 ± 7.19	3.7290**
Hyphomycete XVII	3.4 ± 1.21	76.5 ± 86.8	-1.9174*
<i>Halophytophthora vesicula</i>	427.6 ± 50.66	189.25 ± 89.06	5.0937**

Significant at: \* 5%; \*\* 1%; and \*\*\* 0.1% level. n.s. = not significant.

One unit is defined as 1  $\mu\text{g}$  of tyrosine released per ml of culture fluid per h. Four replicates were maintained for all estimations.

Peroxidase, laccase, tyrosinase and polyphenol oxidase were analysed qualitatively, following the methods of Gessner (1980).

#### 2.4. Carbon nutrition

The test organisms were grown on nine different substrates as sole carbon sources (see Table 7) at 0.25% w/v concentrations in 100 ml of a basal salts medium (Fell & Master, 1975). Growth in the presence of vanillic and ferulic acids was estimated using the basal medium with 0.25% glucose, supplemented with 0.25% of each one. One-week-old cultures were filtered over sterile GF/C glassfibre filters and growth was measured as ATP content.

### 3. Results

#### 3.1. Biomass buildup on detritus of different ages

Four of the test species, namely *Cladosporium herbarum*, *Fusarium moniliforme*, *Cirrenalia basiminuta* and *Halophytophthora vesicula* grew better on 0–21-day-old detritus (Fig. 1). Older detritus of 28–60 day age supported decreasing amounts of biomass in these fungi. Growth of “Hyphomycete XVII” and to some extent the thraustochytrid *Schizochytrium mangrovei*, was less in 0–21-day-old detritus. Maximum growth of the former occurred on 53-day-old detritus and that of the latter on 28-day-old material.

Mean values obtained for growth of each species in detritus of the nine different ages were segregated into two detrital age groups, namely 0–21 (five values) and 28–60 days (four values), and the difference between the means of the two groups for each species analysed individually using Student’s *t*-test (Table 1). A significant difference in growth between the two age groups was observed for all the five test fungi, corresponding to the above-mentioned observations for each species, but not for the thraustochytrid *Schizochytrium mangrovei*.

*Fusarium moniliforme* produced the highest amount of biomass on detritus, compared to the other species and “Hyphomycete XVII”, the least (Fig. 1).

#### 3.2. Biochemical changes

(1) Growth of *Fusarium moniliforme* and *Halophytophthora vesicula* resulted in a significant enhancement of protein levels of the detritus compared to the “uninoculated controls” (Fig. 2, Table 2). The other test species did not contribute significantly to the addition of proteins.

(2) Amino acid contents in “inoculated detritus” of all test species were always higher than those of uninoculated controls (Fig. 3, Table 2).

(3) The thraustochytrid *Schizochytrium mangrovei* caused a significant increase in the carbohydrate contents, while the fungi *Fusarium moniliforme* and *Halophytophthora vesicula* caused a substantial reduction (Fig. 4, Table 2).

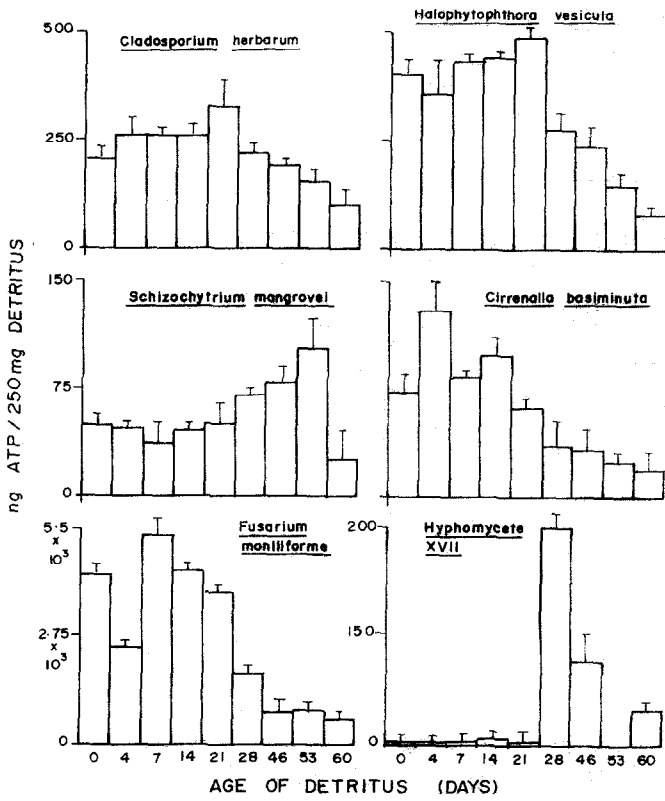


Fig. 1. Growth of the test species on different ages of *Rhizophora apiculata* leaf detritus.

Table 2

One-way analysis of variance *F* values for differences in various biochemical parameters between the two treatments: (1) Uninoculated control detritus and (2) Inoculated detritus in 9 ages of detritus for six test species (df 1,16)

Biochemical parameters	Test species					
	<i>Cladosporium herbarum</i>	<i>Shizochytrium mangrovei</i>	<i>Fusarium moniliforme</i>	<i>Cirenalia basiminuta</i>	Hyphomycete XVII	<i>Halophytophthora vesicula</i>
Proteins	1.132 n.s.	7.445*	147.429***	0.643 n.s.	0.851 n.s.	197.27***
Amino acids	468.55***	298.438***	445.785***	40.819***	89.497***	137.478***
Carbohydrates	1.29 n.s.	24.977***	160.472***	4.591*	2.591 n.s.	186.737***
Reducing sugars	0.105 n.s.	117.544***	399.72***	0.483 n.s.	5.131*	200.775***
Phenols	4.639*	7.265*	5.468*	1.519 n.s.	2.635 n.s.	22.607***

Significant at: \* 5%, and \*\*\* 0.1% level; n.s. = not significant.

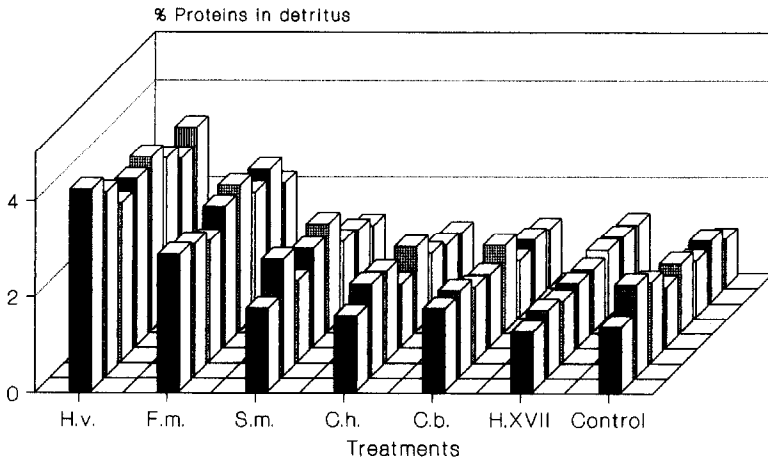


Fig. 2. Protein contents in 0, 7, 14, 21, 28, 46, 53 and 60-day-old detritus (from bottom) of *Rhizophora apiculata* leaves, inoculated with *Fusarium moniliforme* (F.m.), *Halophytophthora vesicula* (H.v.), *Cladosporium herbarum* (C.h.), *Schizochytrium mangrovei* (S.m.), *Cirrenalia basiminuta* (C.b.) and "Hyphomycete XVII" (H.XVII). Control represents uninoculated detritus. SD of triplicates in all cases,  $<0.3$ .

(4) *Halophytophthora vesicula* and to a lesser extent, *Fusarium moniliforme* caused a decline in detrital reducing sugars (Fig. 5, Table 2). Growth of *Schizochytrium mangrovei*, on the contrary, caused a marked increase in reducing sugar levels.

(5) Total phenolic contents of detritus were reduced when inoculated with *Halophytophthora vesicula* (Fig. 6, Table 2). Growth of the other species did not cause a distinct change in total phenols, as compared to the controls.

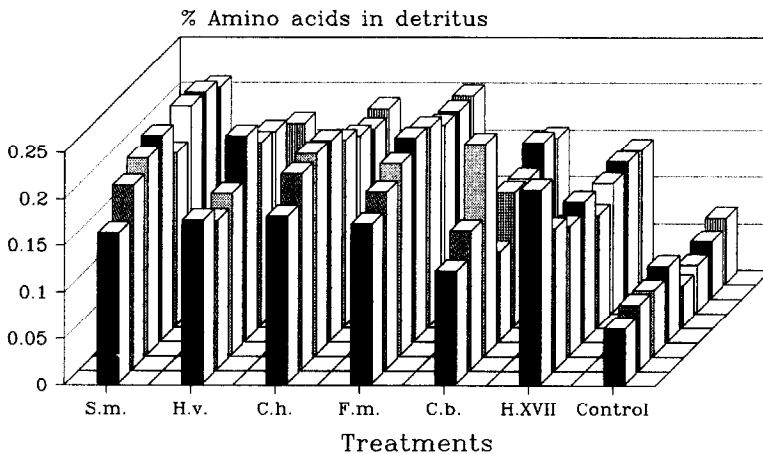


Fig. 3. Amino acid contents in 0, 7, 14, 21, 28, 46, 53 and 60-day-old detritus (from bottom) of *Rhizophora apiculata* leaves, inoculated with *Schizochytrium mangrovei* (S.m.), *Halophytophthora vesicula* (H.v.), *Cladosporium herbarum* (C.h.), *Fusarium moniliforme* (F.m.), *Cirrenalia basiminuta* (C.b.) and "Hyphomycete XVII" (H.XVII). Control represents uninoculated controls. SD of triplicates in all cases,  $<0.0125$ .

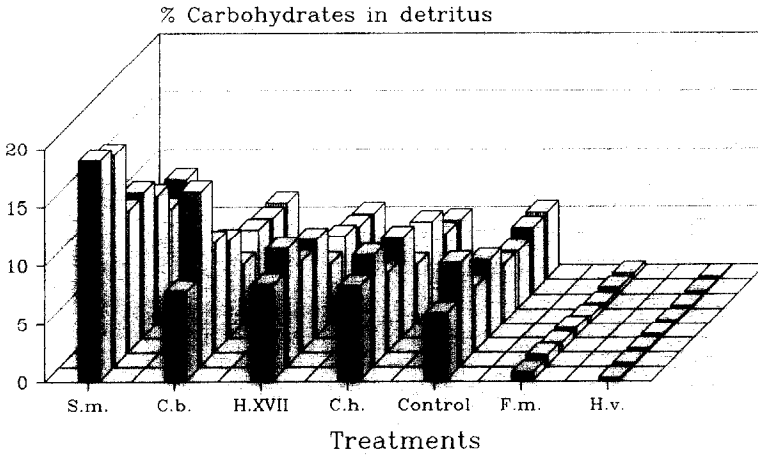


Fig. 4. Carbohydrate contents of 0, 7, 14, 21, 28, 46, 53 and 60-day-old detritus (from bottom) of *Rhizophora apiculata* leaves, inoculated with *Schizochytrium mangrovei* (S.m.), *Cirrenalia basiminuta* (C.b.), "Hyphomycete XVII" (H.XVII), *Cladosporium herbarum* (C.h.), *Fusarium moniliforme* (F.m.) and *Halophytophthora vesicula* (H.v.). Control represents uninoculated detritus. SD of triplicates in all cases, < 1.

### 3.3. Degradative enzymes

The test species differed significantly from each other in their capabilities to elaborate the various enzymes (Tables 3–6). In general, *Fusarium moniliforme* produced the highest amounts of polygalacturonase and protease in detritus (Tables 3 and 4). Another pectolytic enzyme, pectin lyase was elaborated best by *Halophytophthora vesicula* (Table 3). Proteases were not detected in the hyphomycetes *Cirrenalia basiminuta* and

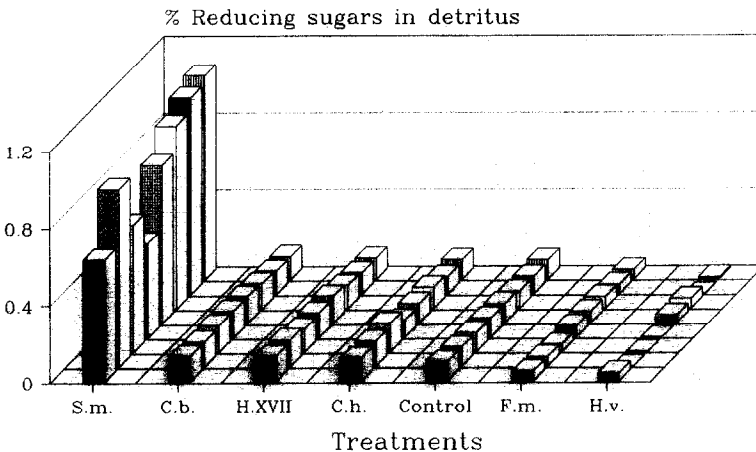


Fig. 5. Reducing sugar contents of 0, 7, 14, 21, 28, 46, 53 and 60-day-old detritus (from bottom) of *Rhizophora apiculata* leaves, inoculated with *Schizochytrium mangrovei* (S.m.), *Cirrenalia basiminuta* (C.b.), "Hyphomycete XVII" (H.XVII), *Cladosporium herbarum* (C.h.), *Fusarium moniliforme* (F.m.) and *Halophytophthora vesicula* (H.v.). Control represents uninoculated controls. SD of triplicates in all cases, < 0.06.



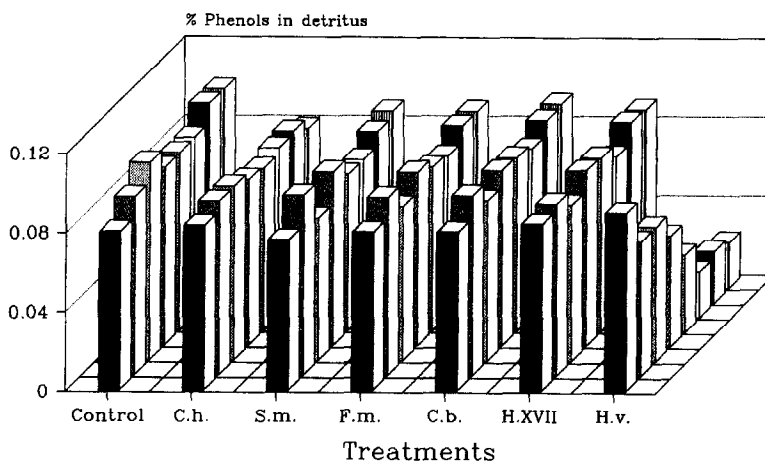


Fig. 6. Total phenolic contents of 0, 7, 14, 21, 28, 46, 53 and 60-day-old detritus (from bottom) of *Rhizophora apiculata* leaves, inoculated with *Cladosporium herbarum* (C.h.), *Schizochytrium mangrovei* (S.m.), *Fusarium moniliforme* (F.m.), *Cirrenalia basiminuta* (C.b.), “Hyphomycete XVII” (H.XVII) and *Halophytophthora vesicula* (H.v.). Control represents uninoculated detritus. SD of triplicates in all cases, <0.006.

“Hyphomycete XVII” (Table 4) and pectin lyase was not found in *Cladosporium herbarum*, *Fusarium moniliforme* and *Cirrenalia basiminuta* (Table 3). *Cladosporium herbarum* and “Hyphomycete XVII” produced higher amounts of xylanase than the others (Table 5). Amylase and cellulases were secreted best by the thraustochytrid *Schizochytrium mangrovei* (Tables 4 and 5).

Any given species produced more or less uniform amounts of polygalacturonase, pectin lyase, proteases and amylase in detritus of different decompositional stages (Tables 3, 4 and 6). However, cellulases and xylanases were generally secreted in larger amounts in 0–21- and 28–60-day-old detritus, respectively (Tables 5 and 6).

None of the test species produced peroxidases. Only “Hyphomycete XVII” elaborated laccase, while tyrosinase was detected in this species and *Fusarium moniliforme*.

### 3.4. Growth on various carbon sources

The thraustochytrid *Schizochytrium mangrovei* and the fungus *Fusarium moniliforme* were the most versatile, producing better growth than the others on six of the 11 substrates tested, namely glucose, starch, pectin, gelatin, casein, tributyrin and vanillic acid (Table 7). *Cirrenalia basiminuta* was the most fastidious, growing poorly on 6 of the 11 substrates tested. Best growth on Tween-20 was produced by *Fusarium moniliforme*, on ferulic acid by “Hyphomycete XVII” and on xylan by *Cladosporium herbarum*. The six species preferred different carbon sources for best growth. *Cladosporium herbarum* preferred xylan, *Schizochytrium mangrovei* – starch, *Fusarium moniliforme* – cellulose and Tween-20, “Hyphomycete XVII” – glucose supplemented with ferulic acid, *Halophytophthora vesicula* – cellulose and *Cirrenalia basiminuta* – pectin and xylan.

Table 3  
Production (units ml culture fluid) of polygalacturonase and pectin lyase by test species on different ages of detritus from leaves of *Rhizophora apiculata*

Test species	Age of detritus (days)							
	0	7	14	21	28	46	53	60
<b>Polygalacturonase</b>								
<i>Cladosporium herbarum</i>	46.6 ± 1.12	36.1 ± 1.01	27.7 ± 1.43	24.1 ± 0.85	43.8 ± 1.69	38.3 ± 0.17	19.6 ± 0.46	40.3 ± 1.19
<i>Schizochytrium mangrovei</i>	19.2 ± 0.34	54.6 ± 1.81	28.5 ± 2.39	40.6 ± 1.58	45.8 ± 0.79	29.6 ± 1.28	26.2 ± 0.59	33.3 ± 0.91
<i>Fusarium moniliforme</i>	45.3 ± 0.83	62.5 ± 0.67	71.2 ± 0.46	49.0 ± 4.2	66.7 ± 1.32	63.2 ± 1.02	40.8 ± 5.61	36.2 ± 1.53
<i>Cirrenalia basiminuta</i>	35.9 ± 0.98	41.0 ± 0.67	25.8 ± 1.76	24.1 ± 2.99	26.6 ± 0.22	21.0 ± 0.56	22.8 ± 0.91	57.2 ± 2.05
Hypomycete XVII	15.4 ± 0.4	25.7 ± 0.8	16.5 ± 0.75	22.9 ± 1.2	16.3 ± 0.61	26.0 ± 0.95	38.2 ± 1.7	32.4 ± 2.4
<i>Halophytophthora vesicula</i>	42.33 ± 1.85	38.0 ± 0.68	30.43 ± 2.31	29.05 ± 1.25	36.8 ± 3.42	34.4 ± 2.56	25.75 ± 1.35	30.78 ± 4.5
<b>Pectin lyase</b>								
<i>Cladosporium herbarum</i>	0	0	0	0	0	0	0	0
<i>Schizochytrium mangrovei</i>	1.1 ± 0.01	0.1 ± 0.03	0.8 ± 0.01	0.7 ± 0.01	0.7 ± 0.09	0.8 ± 0.01	0.6 ± 0.01	0.8 ± 0.06
<i>Fusarium moniliforme</i>	0	0	0	0	0	0	0	0
<i>Cirrenalia basiminuta</i>	0	0	0	0	0	0	0	0
Hypomycete XVII	0.9 ± 0.11	1.0 ± 0.06	0.7 ± 0.05	0.9 ± 0.06	0.9 ± 0.04	0.6 ± 0.04	0.8 ± 0.04	0.8 ± 0.04
<i>Halophytophthora vesicula</i>	3.93 ± 0.62	4.1 ± 0.23	2.85 ± 0.11	2.83 ± 0.08	2.86 ± 0.04	2.62 ± 0.15	3.62 ± 0.6	1.99 ± 0.8

Table 4  
Production (units/ml culture fluid) of amylase and proteases by test species on different ages of detritus from leaves of *Rhizophora apiculata*

Test species	Age of detritus (days)							
	0	7	14	21	28	46	53	60
<b>Amylase</b>								
<i>Cladosporium herbarum</i>	9.7 ± 1.21	26.7 ± 0.11	28.2 ± 0.56	20.8 ± 0.32	9.2 ± 0.34	11.7 ± 0.51	40.0 ± 0.30	21.0 ± 0.29
<i>Schizochytrium mangrovei</i>	60.8 ± 1.70	61.7 ± 0.90	49.9 ± 0.79	59.4 ± 0.81	48.2 ± 0.34	45.6 ± 0.34	47.9 ± 0.69	49.2 ± 0.52
<i>Fusarium moniliforme</i>	25.4 ± 0.22	13.4 ± 0.13	26.4 ± 0.34	33.0 ± 0.22	60.6 ± 0.59	30.7 ± 0.03	74.5 ± 0.67	23.3 ± 0.22
<i>Cirrenalia basiminuta</i>	22.9 ± 1.23	19.4 ± 0.34	20.2 ± 0.34	33.5 ± 0.44	19.8 ± 0.47	25.1 ± 0.34	20.6 ± 0.34	23.7 ± 0.34
Hyphomycete XVII	0	0	0	0	0	3.0 ± 0.45	2.6 ± 0.06	0
<i>Halophytophthora vesicula</i>	38.15 ± 0.13	34.67 ± 1.68	32.5 ± 2.34	29.09 ± 1.85	44.73 ± 2.56	41.16 ± 3.4	44.81 ± 1.8	30.61 ± 3.64
<b>Protease</b>								
<i>Cladosporium herbarum</i>	12.1 ± 0.16	10.0 ± 0.23	10.8 ± 0.09	16.7 ± 0.25	8.1 ± 0.18	5.3 ± 0.27	12.5 ± 0.17	12.7 ± 0.23
<i>Schizochytrium mangrovei</i>	16.0 ± 0.18	17.1 ± 0.27	16.6 ± 0.25	18.5 ± 0.29	9.5 ± 0.16	22.9 ± 0.11	21.0 ± 0.13	18.7 ± 0.09
<i>Fusarium moniliforme</i>	21.3 ± 0.01	23.3 ± 0.05	24.2 ± 0.04	24.2 ± 0.09	22.4 ± 2.4	22.4 ± 0.02	22.0 ± 0.04	23.5 ± 0.01
<i>Cirrenalia basiminuta</i>	0	0	0	0	0	0	0	0
Hyphomycete XVII	0	0	0	0	0	0	0	0
<i>Halophytophthora vesicula</i>	14.28 ± 1.23	1.8 ± 0.08	2.28 ± 0.45	3.48 ± 0.89	0.36 ± 0.03	4.68 ± 0.65	0.94 ± 0.02	1.56 ± 0.58

Table 5  
Production (units/ml culture fluid) of cellulases and xylanase by test species on different ages of detritus of leaves of *Rhizophora apiculata*

Test species	Age of detritus (days)									
	0	7	14	21	28	46	53	60		
<b>Cellulases</b>										
<i>Cladosporium herbarum</i>	16.7 ± 1.24	27.1 ± 0.45	7.8 ± 0.22	3.7 ± 0.12	9.3 ± 0.26	0.6 ± 0.34	0	4.9 ± 0.34		
<i>Schizochytrium mangrovei</i>	39.5 ± 0.39	40.2 ± 0.59	43.6 ± 0.12	37.6 ± 0.87	40.8 ± 0.34	41.8 ± 1.03	43.6 ± 0.68	36.5 ± 0.47		
<i>Fusarium moniliforme</i>	37.1 ± 1.5	25.0 ± 2.86	34.37 ± 4.51	28.9 ± 2.3	12.9 ± 1.25	20.31 ± 2.56	17.57 ± 3.4	8.98 ± 2.5		
<i>Cirrenalia basiminata</i>	25.78 ± 0.18	13.28 ± 1.3	6.64 ± 0.89	3.51 ± 0.65	10.15 ± 1.25	7.42 ± 1.16	8.2 ± 0.93	9.37 ± 0.86		
Hypomycete XVII	3.4 ± 0.85	27.1 ± 0.22	19.9 ± 0.9	24.0 ± 1.4	0	3.0 ± 0.01	2.6 ± 0.24	0		
<i>Halophytophthora vesicula</i>	40.62 ± 2.4	12.1 ± 0.34	10.15 ± 1.01	10.15 ± 0.22	5.46 ± 0.32	5.07 ± 0.05	6.24 ± 0.29	5.46 ± 0.02		
<b>Xylanase</b>										
<i>Cladosporium herbarum</i>	81.8 ± 0.94	28.7 ± 0.52	21.8 ± 3.13	74.9 ± 1.92	112.8 ± 1.43	170.2 ± 1.58	155.7 ± 4.96	133.2 ± 0.98		
<i>Schizochytrium mangrovei</i>	1.62	8.66	1.91	1.58	1.67	2.4	2.61	1.3		
<i>Fusarium moniliforme</i>	8.27 ± 0.02	14.06 ± 0.35	22.72 ± 0.09	19.34 ± 0.11	48.48 ± 0.1	62.86 ± 0.25	53.95 ± 0.09	31.51 ± 0.09		
<i>Cirrenalia basiminata</i>	21.55 ± 0.12	4.29 ± 0.98	17.25 ± 0.11	53.4 ± 2.99	48.48 ± 0.1	62.86 ± 0.25	53.95 ± 0.09	31.51 ± 0.09		
Hypomycete XVII	14.52 ± 2.63	22.65 ± 4.31	45.76 ± 2.34	67.78 ± 6.85	148.87 ± 10.56	169.9 ± 18.23	161.37 ± 6.51	161.59 ± 9.3		
<i>Halophytophthora vesicula</i>	8.66 ± 1.25	1.17 ± 0.35	2.73 ± 0.09	2.55 ± 0.12	3.55 ± 1.03	3.87 ± 0.34	3.56 ± 1.24	4.17 ± 0.25		

Table 6

Two-way ANOVA *F* values to test for differences in the production of degradative enzymes between (a) nine different ages of detritus and (b) six different test species

Treatments	Polygalacturonase	Pectin lyase	Protease	Amylase	Cellulases	Xylanase
Between ages of detritus (df 8.40)	1.032 (n.s.)	0.807 (n.s.)	1.270 (n.s.)	1.195 (n.s.)	4.018*	4.539**
Between test species (df 5.40)	6.673**	143.7**	109.3**	25.7**	16.37**	14.66**

n.s. = Not significant at 5% level; \* Significant 1% level; \*\* Significant at 0.1% level.

#### 4. Discussion

A comparison of field (Raghukumar et al., 1994) and the present experimental data suggests that there are two distinct phases of fungal dynamics in the mangrove leaf detritus, with respect to biomass as well as enzyme production (Table 8). These are (1) 0–21 days, and (2) 28–60 days. The former apparently corresponds to the rapid microbial decompositional phase which overlaps the initial leaching period of a few hours to a few days and lasts for a few weeks and the latter to the recalcitrant phase of longer duration (Godschalk & Wetzel, 1978; Valiela et al., 1984).

##### 4.1. Dynamics during the first phase (0–21 days)

The fungi *Cladosporium herbarum*, *Fusarium moniliforme*, *Cirrenalia basiminuta* and *Halophytophthora vesicula*, which preferred to grow in the initial phase of decomposition, as well as the thraustochytrid *Schizochytrium mangrovei*, which grew well on such detritus (Fig. 1), may be capable of tolerating the higher amounts of phenolics present at this stage (Raghukumar et al., 1994), that could inhibit microbial growth (Cundell et al., 1979; Gonzalez-Farias & Mee, 1988). The low values of phenolics reported by

Table 7

Growth of the test organisms (ng ATP/ml) on various carbon sources

Carbon source	<i>Cladosporium herbarum</i>	<i>Schizochytrium mangrovei</i>	<i>Fusarium moniliforme</i>	<i>Cirrenalia basiminuta</i>	Hyphomycete XVII	<i>Halophytophthora vesicula</i>
Glucose	1.5	109.1	26.3	0.2	11.5	12.1
Gelatin	2.1	47.0	47.0	ND	9.3	0.2
Casein	0.1	54.0	6.2	ND	6.9	1.4
Starch	0.4	122.3	26.0	0.1	15.4	13.1
Tributyryn	0.1	15.0	0.2	ND	ND	ND
Cellulose	0.2	63.2	73.9	ND	48.0	68.6
Pectin	1.5	26.8	45.6	0.7	34.7	15.9
Tween-20	0.06	27.9	73.9	ND	0.03	ND
Vanillic acid	0.4	93.2	15.3	0.2	13.1	0.6
Ferulic acid	0.1	1.8	2.7	0.03	72.5	1.6
Xylan	4.2	1.0	0.06	0.7	0.3	1.5

Table 8

Summary of events during decomposition of leaves of *Rhizophora apiculata*

Events	First decomposition phase: 0–21 days	Second decomposition phase: 28–60 days
Growth of fungal species	Maximum growth of "initial coloniser" fungi; good growth of thraustochytrids	Maximum growth of "late coloniser" fungi; increased growth of thraustochytrids
Degradation of cellulose	Greater cumulative degradation	Diminished cumulative degradation
Degradation of xylan	Diminished cumulative degradation	Greater cumulative degradation
Degradation of pectin	Steady degradation	
Protein buildup	Substantial increase by some species	
Amino acids buildup	Substantial increase by all species	

us in 0-day-old detritus are probably underestimates, resulting from incomplete extractions of phenolics that had complexed with other compounds during autoclaving of the detritus for experiments. Some fungi such as *Halophytophthora vesicula* may themselves reduce the phenolic levels of detritus (Fig. 6). The above fungi grew well on 0 day detritus, suggesting that similar to bacteria (Kenworthy et al., 1989; Blum & Mills, 1991; Peduzzi & Herndl, 1991), they might be important during the initial leaching period.

Thraustochytrids and *Halophytophthora vesicula*, for instance, rapidly colonise dead mangrove leaves as soon as they fall into the water (Newell et al., 1987; Raghukumar et al., 1994). Such species, colonising the initial phase of decomposition, may degrade a wide variety of organic compounds, as suggested by their capability to grow on any of several carbon sources (Table 7). Species of this phase could also be important in contributing to the peak fungal biomass obtained by 21 days in the field (Raghukumar et al., 1994).

All the test species also produced greater amounts of cellulases in 0–21-day-old detritus (Tables 5, 6 and 8). This suggests that cumulative microbial degradation of cellulose may take place mostly in the initial 2–3 wk. We have observed that cellulose decreases rapidly during the first 21 days of decomposition in the field (Raghukumar et al., 1994). Results of Moran & Hodson (1989) on decomposition of *Spartina* ligno-cellulose also indicated a more rapid bacterial utilisation of this substrate in the initial period of 2 wk.

#### 4.2. Dynamics during the second phase (28–60 days)

The fungus "Hyphomycete XVII" preferred to grow in detritus older than 21 days (Fig. 1, Table 1), although it could utilise a wide variety of carbon sources (Table 7). Therefore, it may not be the nutritional fastidiousness or competition from other microorganisms, the experiments having been conducted under axenic conditions, but susceptibility to inhibitory substances such as phenolics present in early stages of decomposition, which may determine biomass buildup of such species. The thraustochytrid *Schizochytrium mangrovei* also grew well on such detritus (Fig. 1, Table 1). Field observations also indicated that these two species occurred in higher densities

during later stages of decomposition (Raghukumar et al., 1994). Removal of phenolics in nature by abiotic leaching, as well as microbial action by fungi such as *Halophytophthora vesicula* could pave way for the growth of microorganisms susceptible to such inhibitory compounds, as suggested by Harrison & Chan (1980) for bacteria in eelgrass detritus. Later stage detritus is characterised by low amounts of labile organics and relative high contents of recalcitrant compounds such as cellulose and lignin. The substantial growth of the above organisms on older detritus implicates them in degradation of recalcitrant structural compounds of mangrove detritus, such as lignin, cellulose and xylan. Correspondingly, the thraustochytrid produced high amounts of cellulases in detritus and “Hyphomycete XVII”, xylanases. The latter also elaborated laccase and tyrosinase, which might be involved in lignin degradation. The high production of cellulases by *Schizochytrium mangrovei* is interesting since thraustochytrid protists have been thought to be incapable of utilising cellulose (Bahnweg, 1979). Further work on these protists, which are common in marine macrophytic detritus (Miller & Jones, 1983; Sathe-Pathak et al., 1993; Raghukumar et al., 1994) is warranted to find out their role in degradation of recalcitrant detrital compounds.

The second phase may be characterised by a more rapid degradation of xylan compared to the first, the test species generally elaborating greater amounts of xylanase during this period (Tables 5 and 6). Even *Cladosporium herbarum* which did not grow well in this phase, elaborated higher amounts of the enzyme in such detritus (Table 5). This is similar to the production of cellulases by “Hyphomycete XVII”, where higher production of the enzyme was observed in the first phase, even when growth was poor (Table 5). In such cases, the metabolic activities of the species could remain high, even if their conversion efficiency to form cell biomass happened to be low.

Pectin, starch and proteins may be degraded at steady rates throughout decomposition, since the amounts of the corresponding enzymes, polygalacturonase, pectin lyase, amylase and proteases, elaborated in the two phases of decomposition did not differ significantly (Table 3, 4 and 6). Production of these enzymes, therefore, does not appear to be correlated to the biomass of the concerned species.

#### 4.3. Biochemical changes caused in detritus

(1) While 2 of the 6 test fungi, *Halophytophthora vesicula* and *Fusarium moniliforme* were capable of enriching detritus in terms of proteins, all six substantially increased amino acid levels (Figs. 2 and 3). Such increases apparently take place through “nitrogen immobilisation” (see Fell & Master, 1980). Our results support the view of Biddanda & Riemann (1993) that detrital microorganisms may play a vital role in contributing free amino acids to detritus by nitrogen immobilisation, which are probably retained in detritus by adsorption to microbial cells. In nature, such a buildup of proteins and amino acids may, to a certain extent, offset losses of these components by leaching, although net values only decrease with time, probably because microbial biomass is not allowed to develop to a sufficient level (Melillo et al., 1984; Rice & Hanson, 1984).

(2) Detrital carbohydrate levels may be reduced by fungi such as *Fusarium moniliforme*, *Halophytophthora vesicula* (Fig. 4), through enzymatic degradation. Interestingly,

*Schizochytrium mangrovei* caused an increase in detrital carbohydrates, similar to our results on other thraustochytrids in detritus of the brown alga *Sargassum cinereum* (Sharma et al., 1994). It is likely that *Schizochytrium mangrovei*, which produced high amounts of cellulases, degraded the corresponding substrate and converted the fibre content into more soluble forms. This thraustochytrid also caused a marked increase in reducing sugars. This could have resulted from the high production of cellulases and amylases by this protist (Tables 4 and 5), release of reducing sugars as byproducts and a loose hydrolysis-uptake coupling, resulting in “sloppy feeding” (Moran & Hodson 1989; Peduzzi & Herndl 1991). Another possibility is the copious production of extracellular polysaccharides by the thraustochytrid. *Fusarium moniliforme*, *Schizochytrium mangrovei* and *Halophytophthora vesicula* were the most successful organisms in biochemically transforming detritus.

Our results cannot be quantitatively extrapolated to the process in nature since autoclaving the detritus, necessitated by experiments under axenic conditions, could have modified the substrate to an unknown extent. Nevertheless, our studies indicate that different fungi and thraustochytrids in mangrove leaf detritus respond varyingly to the different ages of detritus in terms of biomass and enzyme production. Individual species, in turn, could affect the biochemical nature of detritus in various ways. The net biochemical status of detritus in nature would depend upon the biomass of the concerned organisms and their metabolic activities, as well as the extent of abiotic leaching (Fig. 7).

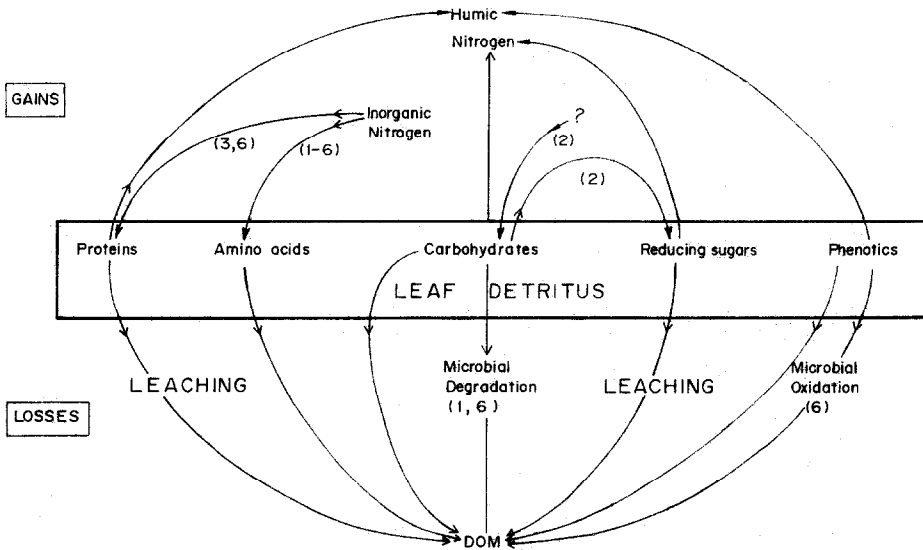


Fig. 7. Schematic diagram on the possible involvement of (1) *Cladosporium herbarum*; (2) *Schizochytrium mangrovei*; (3) *Fusarium moniliforme*; (4) *Cirrenalia basiminuta*; (5) “Hyphomycete XVII” and (6) *Halophytophthora vesicula* in the biochemical transformation of *Rhizophora apiculata* leaf detritus.



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