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Population growth and effects of nematodes on nutrient regeneration and bacteria associated with mangrove detritus from northeastern Queensland (Australia)

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ABSTRACT: Two species of nematodes (*Monhystera* sp. and *Chromadorina* sp.) were isolated from mangal sediments from northeastern Queensland and incubated for up to 40 d in 25 cm^2 tissue culture flasks in filtered (0.20 μm Nuclepore) seawater containing fresh, 1 wk and 1 mo aged *Rhizophora stylosa* and *Avicennia marina* detritus. Populations of both nematodes decreased in flasks containing aged detritus; by Day 20 numbers of *Monhystera* sp. and *Chromadorina* sp. declined by an average of 75 and 46 %, respectively. Neither species survived for more than 3 d on fresh *R. stylosa* leaves, which had high soluble tannin contents (> 11 % dry weight). Only fresh *A. marina* leaves sustained increased nematode populations, perhaps as a result of a sufficiently high soluble nitrogen content combined with a lower tannin content (3.6 %). Concentrations of dissolved inorganic nutrients (phosphate, nitrate, nitrite, ammonia), bacterial abundance and bacterial production were not significantly different in flasks containing aged detritus plus nematodes from those in flasks lacking nematodes. Bacterial abundance and production were higher in flasks with fresh *A. marina* litter and nematodes than in those without worms, but nutrient concentrations showed no differences. A significant positive correlation between bacterial and nematode abundances occurred in flasks with fresh *A. marina* litter; no correlations between the two existed for aged detritus. It appeared that minimal population densities of worms necessary to stimulate bacterial production and increase nutrient regeneration rates were not achieved on the types of detritus tested. Results from these experiments and field observations reported from other studies suggest that nematodes may not play a major role in the cycling of organic matter in tropical mangal sediments.

INTRODUCTION

In contrast to the large number of studies of meiobenthos inhabiting temperate marine zones, ecological investigations of the meiobenthos from tropical mangrove environments are relatively few (see recent review by Alongi 1989). Just as they tend to dominate temperate meiobenthic assemblages, free-living nematodes are among the dominant taxa found in mangal habitats, where they are associated with sediments, leaf litter, wood and roots (Fell et al. 1975, Krishnamurthy et al. 1984, Alongi 1987a). Tidal inundation, desiccation, and changes in temperature and salinity (the latter often associated with monsoonal rains) have been shown to strongly affect the seasonal and spatial distribution of nematodes in mangrove-dominated estuaries (Alongi 1987a). The low species diversity of nematodes in Australian mangroves may be indicative of extreme physical stress encountered in tropical intertidal mangal habitats (Alongi 1989).

In addition to environmental changes caused by seasonal monsoons or other abiotic factors, the meiobenthos of the mangrove forest floor is exposed to extremely high inputs of organic matter via litter fall (generally estimated to be in the range of 0.5 to 3.5 gC m^{-2} d^{-1}; Bunt 1982) and to very high sediment bacterial production (0.2 to 5.2 gC m^{-2} d^{-1}; Alongi 1988).

Although it has been postulated that free-living nematodes may contribute to nutrient regeneration, carbon mineralization and microbial degradation of organic matter in the sea (Tenore et al. 1977, Gerlach 1978, Tietjen 1980, Findlay & Tenore 1982, Rieper-

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Kirchner 1989), far more is known about the role of nematodes in the cycling of organic matter in non-marine environments (Abrams & Mitchell 1980, Whitford et al. 1982, Anderson et al. 1983, Ingham et al. 1985, and references cited therein). Certainly, little is known of the role of free-living nematodes in the regeneration of inorganic nutrients from mangrove litter, and of the use of mangrove-derived detritus as a food source by nematodes.

In this paper we present results from a series of laboratory experiments in which 2 species of nematodes isolated from mangal sediments from northeastern Australia were cultured on fresh and aged detritus derived from the grey and red mangroves *Avicennia marina* and *Rhizophora stylosa*. Specific objectives of the experiments were to (1) measure the population growth rates of both nematode species on mangrove litter; (2) study the effects of the worms on regeneration of inorganic nutrients from the litter; and (3) examine the influence of nematode grazing on the abundance and production of bacteria associated with the same litter.

MATERIALS AND METHODS

Isolation of nematodes and establishment of stock cultures. Two species of nematodes were established in agnotobiotic culture from collections of mangrove litter from northeastern Queensland. Dominant mangroves in the area of collection were *Rhizophora stylosa* and *Avicennia marina*. Samples of litter and associated fauna were inoculated into 150 cm^2 plastic tissue culture flasks (Corning Glass Works, Corning, NY 14830, USA) containing filtered (0.45 μm Millipore) seawater; flasks were incubated at 25 °C on a 12 h light: 12 h dark cycle. These crude field collections were examined several times per week and, after several weeks, 2 species dominated the nematode assemblages in the flasks. These were the microlaimid *Monhystera* sp., and the chromadorid *Chromadorina* sp. The former was classed as a selective deposit feeder and the latter as an epistrate feeder according to Wieser's (1953) classification of nematode trophic types.

Successful laboratory cultures of species from both genera have been established from a variety of habitats in other parts of the world (Heip et al. 1985), and the species may belong to that group of organisms commonly referred to as 'laboratory weeds'. Nematode stock cultures were established by inoculating sufficient numbers of each species into separate 150 cm^2 tissue culture flasks containing filtered seawater and a mixture of dried leaves from several mangrove species (*Avicennia marina, Rhizophora stylosa, Brugiera gymnorhiza* and *Lumnitzera littorea*). Stock cultures were maintained at 25 °C in the dark.

Experimental cultures and population growth studies. All experiments were conducted in triplicate using static cultures established in 25 cm^2 Corning tissue culture flasks. Leaves of *Avicennia marina* and *Rhizophora stylosa* were collected and rinsed under fresh water. After oven drying (2 to 3 d at 80 °C), fresh leaves were ground in a Wiley mill to pass a 120 μm mesh. Aged detritus was obtained by soaking leaves for 1 wk and 1 mo in a filtered (1 μm), flowing seawater bath and freeze-drying them before grinding. Subsamples of detritus were analyzed for percents carbon and nitrogen (LECO 600 C-H-N analyzer) and percent soluble tannins (Folin-Dennis method; Allen et al. 1974); all analyses were performed by the Analytical Services Section of the Australian Institute of Marine Science. In addition, nematodes were incubated on a proven source of food (Gerber's mixed cereal, Gerber Products Co., Fremont, MI 49412, USA) to compare their population growth rates and interactions with associated bacteria to results obtained from experiments using mangrove detritus.

Population growth rate studies were conducted over a period of 40 d. In all growth studies, nematodes were fed a daily ration of detritus equivalent to 25 mg N m^{-2} d^{-1}. Each flask received between 25 and 100 adult and juvenile nematodes as an initial inoculum (inocula on aged detritus were 80 or 100 worms, inocula on fresh detritus or mixed cereal were 25 or 45 worms). Numbers of worms in inocula were in the same order of magnitude as nematode abundances (17 to 138 per 10 cm^2) reported from the mid-littoral mangal sediments of several northeastern Queensland estuaries (Alongi 1987a). Numbers of worms in each flask were counted at 10 d intervals from Day 0 to Day 40. The intrinsic rate of natural increase (r) was determined using the criteria in Alongi & Tietjen (1980).

Nutrient regeneration studies. Triplicate flasks containing filtered (0.20 μm Nuclepore) seawater and mangrove detritus without nematodes were established along with each nematode experiment. Samples of water (3 ml) were taken from all flasks and immediately frozen for future measurement of dissolved ammonia, nitrate, nitrite and phosphate concentrations. Samples were taken at Days 0, 10, 20, 30 and 40; nutrient concentrations were measured using standard automated techniques at the Analytical Services Section of AIMS (Ryle et al. 1981, Ryle & Wellington 1982). A supply of the filtered seawater used in the experiments was frozen at the start and aliquots added as needed to replace water removed at sampling. Nutrient concentrations in this water did not significantly change during the 40 d period. Concentrations of nutrients in the replacement water were subtracted

from those measured in the samples to give estimates of nutrient concentrations in the experimental flasks.

Bacterial abundance and production. Effects of nematode grazing on the abundance of bacteria were examined by estimating the number of bacteria per ml of water in the flasks with and without nematodes using direct counts of acridine orange-stained cells and epifluorescence microscopy (Hobbie et al. 1977). Samples were ground for 2.5 min in a Turtex blender (Alongi 1988). Ten randomly chosen fields or at least 200 bacteria per duplicate slide were counted for each sample on a Leitz Ortholux II compound microscope with appropriate fluorescence attachments. Bacteria were enumerated on all days when nematodes were counted.

Bacterial production in replicate (n = 3 to 10) 0.5 ml aliquots of culture water and associated detritus was estimated by measuring the rate of ^{3}H-methyl thymidine incorporation into DNA, following techniques described by Moriarty (1986) and Alongi (1988). Recovery-corrected production estimates (see Alongi 1988) were determined using a conversion factor of 2.0 $\times$ 10^{18} cells dividing mol^{-1} thymidine incorporated (Moriarty & Pollard 1981) and the carbon/cell conversion factor of Rublee (1982). Thymidine incorporation was measured on the same sampling schedule given for bacterial enumeration.

RESULTS

Population growth rates of nematodes

Populations of *Monhystera* sp. and *Chromadorina* sp. declined in flasks containing 1 wk and 1 mo aged *Avicennia marina* and *Rhizophora stylosa* detritus (Fig. 1). By Day 20 the numbers of *Monhystera* sp. and *Chromadorina* sp. declined by an average of 75 and 46 %, respectively. Only on 1 wk aged *R. stylosa* detritus did the populations begin to increase again after 20 d (Fig. 1); by Day 40 populations of both species had pared their declines to about 27 %.

Although rates of decline were lowest on 1 wk aged *Rhizophora stylosa* detritus, both species of nematodes died within 3 d when incubated on fresh *R. stylosa* litter. Unfortunately, a catastrophic mortality of the *Chromadorina* sp. stock cultures prevented further experiments with this nematode. Populations of *Monhystera* sp. incubated on fresh *Avicennia marina* detritus increased; even greater increases were

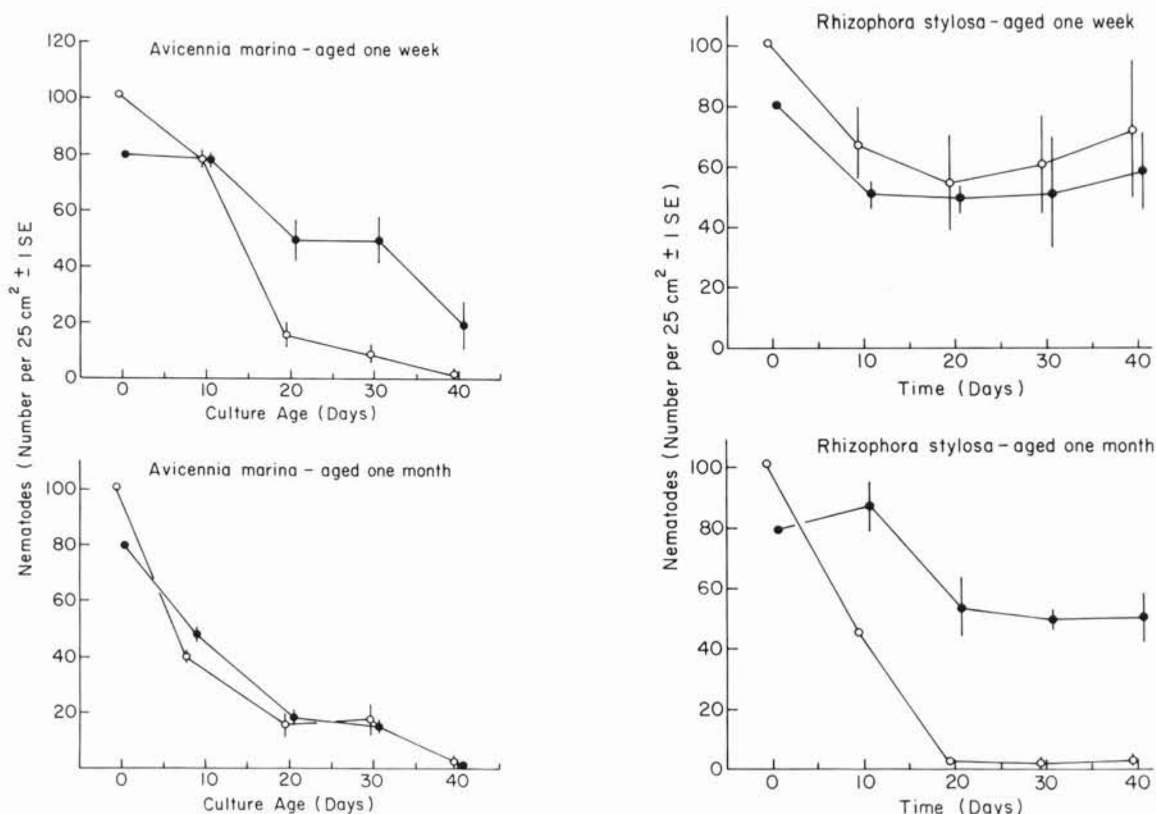

Fig. 1. Mean number of nematodes ± 1 SE (n = 3) in flasks containing aged *Rhizophora stylosa* and *Avicennia marina* detritus incubated for 40 d. (○) *Monhystera* sp.; (●) *Chromadorina* sp.

observed for populations incubated on cereal (Fig. 2). A separate experiment was conducted to see if *Monhystera* sp. would grow on a mixture of fresh *R. stylosa* and cereal; cereal was added to flasks containing nematodes that had been incubated for 1d on *R. stylosa*

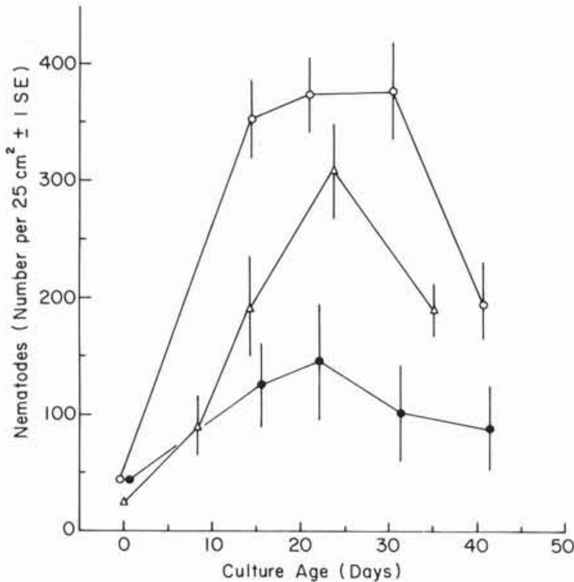

Fig. 2. *Monhystera* sp. Mean number ± 1 SE (n = 3) in flasks incubated for 40 d with fresh *Avicennia marina* detritus (●), Gerber's cereal (△) and cereal plus fresh *Rhizophora stylosa* detritus (○)

detritus and which were still alive. The total daily ration of detritus and cereal did not exceed 25 mgN m^{-2} d^{-1}. Population growth of *Monhystera* sp. on the combined diet of cereal and fresh *R. stylosa* detritus was greater than on the cereal alone (Fig. 2; Table 1).

Nutrient regeneration

Concentrations of dissolved nitrite and nitrate failed to change significantly throughout the time course of the experiment (Kruskal-Wallis test, $p > 0.05$), but phosphate and ammonia concentrations increased significantly in all flasks containing detritus or cereal (Figs. 3 & 4). In experiments using aged detritus concentrations of phosphate and ammonia increased significantly by Day 10 (Fig. 3), after which they either remained constant or varied inconsistently. The presence of nematodes exerted no short- (10 d) or longer-term (40 d) influence on concentrations of ammonia and phosphate relative to flasks without nematodes (Kruskal-Wallis test, $p > 0.05$).

Concentrations of ammonia and phosphate also increased significantly in flasks containing fresh *Avicennia marina* detritus (ammonia by Day 5, phosphate by Day 25) and in those containing cereal (Fig. 4). These experiments were terminated after 25 d. Presence of nematodes (in this case, only *Monhystera* sp.) had no influence on the concentrations of nutrients in flasks containing either fresh *A. marina* detritus or cereal.

Table 1. Intrinsic rates of natural increase (after 20 d) of nematodes incubated on mangrove detritus and also on Gerber's mixed cereal

Food type	Nematode species	
	Chromadorina sp.	*Monhystera* sp.
Avicennia marina		
Fresh	–[a]	0.054
Aged, 1 wk	−0.022	−0.088
Aged, 1 mo	−0.071	−0.088
Rhizophora stylosa		
Fresh	–[b]	–[b]
Aged, 1 wk	−0.021	−0.029
Aged, 1 mo	−0.019	−0.187
Fresh, cereal added	–[a]	0.120
Gerber's cereal	–[a]	0.101

[a] No data
[b] Nematodes died within 2 to 5 d

Bacterial abundance and production

For each type of detritus, no significant differences in bacterial abundance related to the presence of nematodes occurred from Day 10 to the end of the experiment (Kruskal-Wallis test, $p > 0.05$). Bacterial abundance was lowest in flasks containing 1 mo old *Avicennia marina* litter and greatest in flasks containing *Rhizophora stylosa* detritus (Table 2). In contrast, in flasks containing fresh *A. marina* litter, bacterial abundance was significantly greater in those with nematodes than in those lacking nematodes, whereas the reverse was true for flasks containing nematodes incubated on cereal (Mann-Whitney U test, $p < 0.05$). Duration of the experiments with fresh detritus was 30 d (Table 2). A pooling of all data from flasks containing nematodes incubated with aged detritus revealed no significant correlation (Spearman rank order) between nematode and bacterial abundance ($r = -0.218$, $p > 0.05$, $df = 62$); the same was true for the cereal flasks ($r = 0.45$, $p > 0.05$, $df = 13$). However, a significant positive correlation between bacterial and nematode abundance did occur in flasks containing worms and fresh *A. marina* litter ($r = 0.94$, $p < 0.05$, $df = 13$).

Production of bacteria was not significantly affected by the presence of nematodes in any experiment employing aged detritus (Table 3). Production was less in flasks with *Rhizophora stylosa* litter than in those

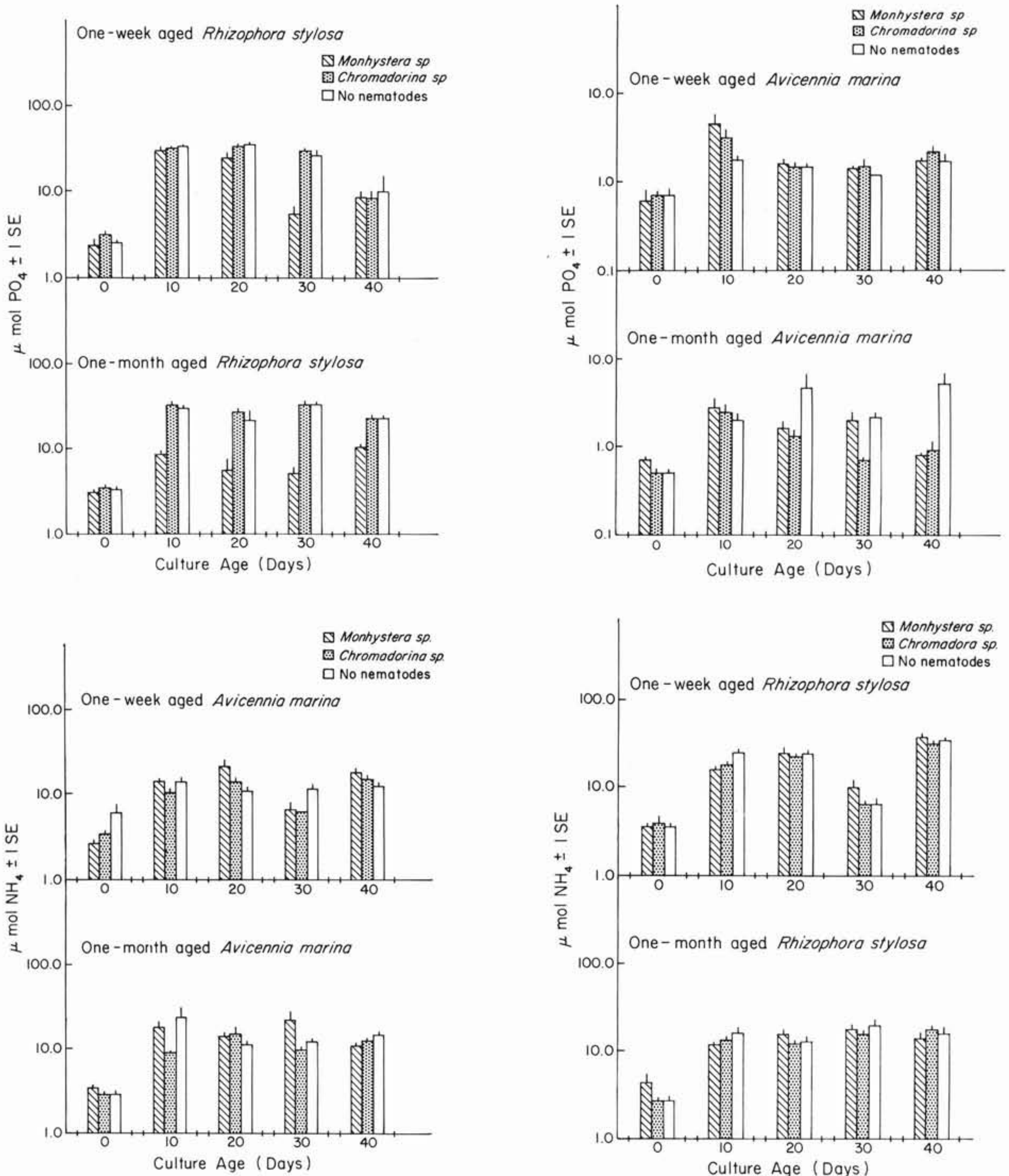

Fig. 3. Mean concentration of dissolved inorganic phosphate and ammonia (± 1 SE) in flasks containing aged *Rhizophora stylosa* and *Avicennia marina* detritus incubated for 40 d (n = 3). Flasks contained detritus plus *Monhystera* sp., *Chromadorina* sp. or no nematodes

with *Avicennia marina* throughout the experiment. Bacterial production on all aged litter was highest from Day 10 to Day 30 and decreased significantly between Days 30 and 40 (Mann-Whitney U test, $p < 0.05$). In flasks containing fresh *A. marina* litter, bacterial production increased from Day 0 to Day 40, and although production at Day 30 was greater in flasks with worms than in those without worms, no differences related to

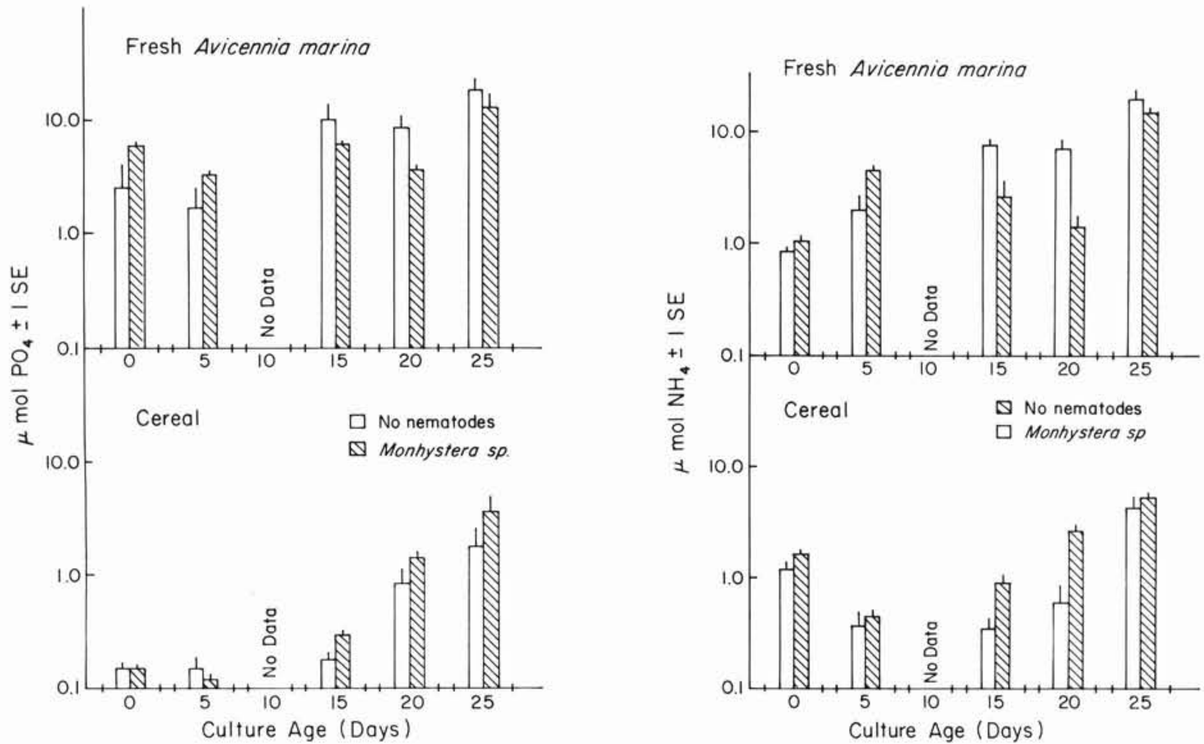

Fig. 4. Mean concentration of dissolved inorganic phosphate and ammonia ± 1 SE (n = 3) in flasks containing fresh *Avicennia marina* detritus or Gerber's cereal incubated for 25 d with *Monhystera* sp. or without nematodes

Table 2. Average abundance of bacteria (cells $ml^{-1} \times 10^7 \pm 1$ SE; n = 3) in culture flasks with and without nematodes. *Aa*: fresh *Avicennia marina*; *Avc*: 1 wk aged *A. marina*; *An*: 1 mo aged *A. marina*; *Rhz*: 1 wk aged *Rhizophora stylosa*; *Ro*: 1 mo aged *R. stylosa*; *Ce*: Gerber's cereal. *M*: flasks with *Monhystera* sp.; *C*: flasks with *Chromadorina* sp.; Bl: flasks without nematodes

Culture flask	Day 0	10	20	30	40
Aa M[a]	0.35 ± 0.02	3.51 ± 0.81	2.81 ± 0.72	3.39 ± 0.52	No data
Aa Bl	0.22 ± 0.02	1.50 ± 0.44	1.06 ± 0.23	2.48 ± 0.05	No data
Avc M[b]	0.42 ± 0.02	1.80 ± 0.40	4.90 ± 1.25	11.60 ± 2.81	2.60 ± 1.01
Avc C	0.41 ± 0.04	1.50 ± 0.39	1.10 ± 1.19	2.20 ± 0.51	1.60 ± 0.41
Avc Bl	0.40 ± 0.04	0.25 ± 0.05	1.70 ± 1.16	2.40 ± 0.91	1.83 ± 0.43
An M[b]	0.75 ± 0.22	1.41 ± 0.45	1.03 ± 0.13	0.78 ± 0.07	0.30 ± 0.04
An C	0.34 ± 0.09	0.47 ± 0.02	1.09 ± 0.17	0.75 ± 0.11	0.08 ± 0.00
An Bl	0.30 ± 0.10	0.07 ± 0.01	0.25 ± 0.03	0.21 ± 0.05	1.13 ± 0.10
Rhz M[b]	2.20 ± 0.33	1.63 ± 0.62	5.01 ± 0.24	7.34 ± 1.67	8.93 ± 1.99
Rhz C	1.40 ± 0.40	0.42 ± 0.09	1.39 ± 0.35	4.04 ± 0.47	6.83 ± 0.34
Rhz Bl	0.70 ± 0.02	0.43 ± 0.03	0.49 ± 0.10	3.73 ± 0.13	4.54 ± 0.48
Ro M[b]	2.38 ± 0.37	3.79 ± 0.92	8.40 ± 2.20	5.61 ± 0.28	3.48 ± 0.42
Ro C	0.71 ± 0.16	1.31 ± 0.82	3.63 ± 0.50	8.30 ± 0.45	8.42 ± 0.41
Ro Bl	0.42 ± 0.01	0.31 ± 0.08	3.21 ± 0.43	4.13 ± 0.62	4.48 ± 0.69
Ce M[c]	1.21 ± 0.32	0.86 ± 0.15	1.06 ± 0.34	1.18 ± 0.19	No data
Ce Bl	0.31 ± 0.01	1.94 ± 0.55	1.34 ± 0.30	1.89 ± 0.01	No data

[a] Bacterial abundance significantly greater in flasks with nematodes
[b] No significant differences in bacterial abundance among flasks
[c] Bacterial abundance significantly greater in flasks without nematodes

Table 3. Average production rates (cells ml^{-1} d^{-1} $\times 10^7 \pm 1$ SE; n = 3) in culture flasks with and without nematodes. Abbreviations as in Table 2

Culture flask	Day 0	10	20	30	40
Aa M	•	•	0.62 ± 0.20	4.90 ± 0.96	1.07 ± 0.07
Aa Bl	•	•	0.11 ± 0.01	0.49 ± 0.10	1.60 ± 0.29
Avc M	2.16 ± 1.21	2.43 ± 0.26	2.40 ± 0.26	3.07 ± 0.26	1.35 ± 0.20
Avc C	4.13 ± 0.91	2.53 ± 0.41	2.27 ± 0.08	2.87 ± 0.18	1.17 ± 0.23
Avc Bl	1.29 ± 0.54	2.83 ± 0.22	1.90 ± 0.33	2.27 ± 0.15	1.16 ± 0.10
An M	1.27 ± 0.51	2.07 ± 0.41	1.63 ± 0.14	1.43 ± 0.09	0.84 ± 0.03
An C	1.74 ± 1.02	2.43 ± 0.14	1.93 ± 0.32	1.83 ± 0.12	0.68 ± 0.03
An Bl	1.44 ± 0.54	2.77 ± 0.09	1.80 ± 0.14	1.77 ± 0.14	0.82 ± 0.01
Rhz M	0.15 ± 0.00	0.44 ± 0.03	0.39 ± 0.01	0.88 ± 0.03	0.23 ± 0.01
Rhz C	0.15 ± 0.00	0.44 ± 0.03	0.39 ± 0.01	0.88 ± 0.03	0.23 ± 0.01
Rhz Bl	0.14 ± 0.00	0.53 ± 0.05	0.26 ± 0.03	0.69 ± 0.03	0.25 ± 0.05
Ro M	0.19 ± 0.04	0.65 ± 0.03	0.47 ± 0.04	0.49 ± 0.04	0.30 ± 0.01
Ro C	0.22 ± 0.06	0.47 ± 0.01	0.49 ± 0.02	0.64 ± 0.03	0.30 ± 0.02
Ro Bl	0.18 ± 0.01	0.59 ± 0.04	0.56 ± 0.02	0.44 ± 0.08	0.24 ± 0.02
Ce M	•	0.31 ± 0.01	0.71 ± 0.08	1.23 ± 0.07	0.74 ± 0.03
Ce Bl	•	0.48 ± 0.24	0.79 ± 0.09	1.47 ± 0.17	1.12 ± 0.08

• No detectable uptake of thymidine

nematode presence was evident at Day 40 (Table 3). For the cereal flasks, no differences in production related to nematode presence were observed.

DISCUSSION

Population growth of nematodes on mangrove detritus

Despite the high rates of organic input and sediment bacterial production associated with tropical mangrove estuaries (Bunt 1982, Alongi 1988), the abundance of nematodes in northeastern Australian mangal sediments is generally lower than that found in comparable temperate environments (salt marshes, sheltered intertidal sediments, etc.; Alongi 1987a). Tropical mangal sediments are exposed to great salinity changes caused by seasonal monsoons; the ensuing freshwater runoff from heavy rains can also affect grain size distribution, organic content of the sediments, dissolved nutrients and leaching of mangrove-derived soluble tannins into the sediments (Alongi 1989).

Hydrolyzable tannins are thought to interfere with herbivorous feeding by imparting a noxious taste or increasing the acidity of plant material. They may also precipitate plant proteins and gastrointestinal enzymes, thereby reducing protein digestion (Zucker 1983, Robbins et al. 1987). The latter authors have shown that available protein in plants, a factor of demonstrated importance to marine herbivores and detritivores (Tenore 1981, Findlay 1982), is reduced by protein-precipitating tannins, which can remain soluble even when plant leaves become dry.

For detritus rich in soluble tannins and other polyphenols, it has been shown that tannin content and available nitrogen may act as hierarchical feeding cues, with the latter perhaps being more important. Valiella et al. (1984) found that the marsh gastropod *Melampus bidentatus* preferred younger to older *Spartina alterniflora* litter even though the former was richer in tannins and poorer in total nitrogen; in older litter soluble nitrogen may be bound to lignins and thus be unavailable to consumers.

Weight percents of hydrolyzable tannins in the *Rhizophora stylosa* used in the present study were about 3 times greater than in *Avicennia marina*; in both species tannins decreased with increasing age of detritus (Table 4). Percent total nitrogen increased with age in *R. stylosa* litter, but fresh *A. marina* detritus had as much nitrogen as 1 mo old litter. The results of the present study suggest that complex relationships may exist between tannin content, nitrogen content and age that determine the utilization of mangrove litter by nematodes. The only detrital source on which nematodes grew was fresh *A. marina*, which had a tannin content (3.6 %) similar to 1 mo aged *R. stylosa*, and a nitrogen content of 1.98 % (similar to the nitrogen content of 1 mo old detritus). While there is no information on the 'available' vs 'non-available' nitrogen con-

Table 4. Carbon, nitrogen and soluble tannin contents (all percent dry weight) of mangrove detritus used in nematode experiments. Carbon and nitrogen values are means of duplicate, soluble tannins means of triplicate, analyses

Detrital type	Percent dry weight		
	Carbon	Nitrogen	Soluble tannins
Rhizophora stylosa			
Fresh	40.15	1.04	11.45
Aged, 1 wk	41.47	1.28	8.23
Aged, 1 mo	43.95	1.63	3.43
Avicennia marina			
Fresh	40.97	1.98	3.55
Aged, 1 wk	45.80	1.43	2.37
Aged, 1 mo	48.18	1.84	0.98

tent of the detritus used in this study, the possibility exists that the nitrogen in fresh *A. marina* and *R. stylosa* litter is more 'available' to the nematodes than the nitrogen in older litter (similar to the observations of Valiella et al. 1984 for *Spartina alterniflora*). This would make fresh litter a more desirable food, assuming a sufficiently low tannin content. For *R. stylosa*, however, the high tannin content of fresh litter (> 11 %) was probably sufficient to either render the material unattractive for consumption or to actually precipitate the protein-digesting enzymes of the worms and cause death by starvation.

Thus the only litter with a sufficiently low tannin content and high enough available nitrogen content to probably be useful to the nematodes was fresh *Avicennia marina*. The intrinsic rate of natural increase of another nematode isolated from Australian mangroves (*Terschellingia longicaudata*) grown on fresh *A. marina* litter was 0.054 (Alongi 1987b), very similar to that of *Monhystera* sp. (Table 1). Alongi also observed that *T. longicaudata* failed to grow on fresh *Rhizophora stylosa* detritus; the same was true for nematodes used in the present study.

It has been shown that the caloric content of aging mangrove detritus may decrease until there is sufficient accumulation of bacterial biomass (Cundell et al. 1979); caloric content (sensu available calories; Tenore 1981) might also be a factor rendering fresh *Avicennia marina* more utilizable than aged detritus. For example, Findlay (1982) found that the available caloric and nitrogen contents of detritus significantly affected the carrying capacity of *Diplolaimella chitwoodi*, a nematode closely related to *Monhystera* sp.

Growth of *Monhystera* sp. on cereal was in agreement with previous studies that have shown cereal's suitability as food for nematodes (Alongi & Tietjen 1980, Findlay 1982, Alongi 1987b). However, the fact that the growth of *Monhystera* sp. populations was greatest on a combined diet of cereal and tannin-rich *Rhizophora stylosa* detritus suggests that further experiments are necessary to identify the exact cause of the failure of worms to grow on aged detritus alone. If the tannins were killing the worms outright, why did the worms not die in flasks containing fresh *R. stylosa* leaves regardless of the presence of cereal?

The mixture of the cereal and mangrove detritus made analysis of the former for tannins impossible, so the extent of absorption (or adsorption) of tannins by the cereal particles is unknown, as is the capability of the cereal to in some way render the protein binding property of tannins harmless to the nematodes. We obviously do not know if the nematodes were eating only the cereal flakes in the mixture, or if the cereal somehow made the fresh litter now palatable (and in fact, more nutritious). It is possible that the high nitrogen content of the cereal (5.0 %; Findlay 1982) more than compensated for the high tannin content of the litter in the cereal-litter mixture, and that *Monhystera* sp. was following feeding cues in the same manner as Valiella et al. (1984) observed for *Melampus bidentatus*.

It should be acknowledged that batch culture conditions such as those employed in the present study often influence experimental results relative to those obtained using flow-through conditions. In addition to accumulation of tannins in the flasks (already cited), another factor that was potentially inhibitory to nematode population growth in the flasks was ammonia. While the average concentration of NH_4 in flasks that failed to support worm growth was higher after 10 d (15 µM in aged *Rhizophora stylosa* flasks, 12.8 µM in aged *Avicennia marina* flasks; Fig. 3) than after 15 d in flasks where growth was better (6.7 µM in fresh *A. marina*, 0.9 µM in cereal flasks; Fig. 4), NH_4 concentrations in naturally occurring mangal soils are normally in the same range as those measured in our flasks (Boto & Wellington 1984). We therefore consider it unlikely that the concentration of NH_4 in flasks containing aged detritus was the primary reason for poor nematode growth in these flasks.

Our experiments suggest that nematode populations do not grow well on single sources of aged mangrove detritus. Despite these results, however, population densities approximating those that were achieved on fresh *Avicennia marina* detritus, and on fresh *Rhizophora stylosa* leaves plus cereal, are normally found in nature (Alongi 1987a). If naturally occurring populations are using foods other than mangrove detritus, it is unknown to us what these foods might be. Diatoms and other benthic microalgae are, by themselves, normally excellent sources of food for nematodes (Alongi & Tietjen 1980, Tietjen 1980), but production by such microorganisms in northeastern

Queensland mangal sediments is severely limited by low light intensity under the dense mangrove canopy (Alongi 1988). It thus appears likely that nematodes utilize a larger suite of nutritionally poor mangrove-derived foods than did the 2 species employed in this study to sustain themselves at the low population levels generally observed. An indication of this is that abundances of nematodes in our stock cultures (where 4 sources of mangrove detritus were used) were more representative (ca 50 worms per 10 cm^2) of those occurring in nature (Alongi 1987a) than those achieved on either species of aged mangrove detritus alone.

Influence of nematodes on bacterial abundance and production

Bacterial abundance and production were unaffected by the presence of nematodes in all experiments involving aged detritus (Tables 2 & 3), which is not surprising considering the failure of nematodes to grow on aged detritus. For fresh *Avicennia marina* litter, bacterial abundance was significantly greater in flasks containing nematodes than in those lacking worms, whereas the reverse was true for flasks containing cereal. As for production, no long-term (40 d) effects associated with worm presence were observed for either fresh *A. marina* litter or cereal.

Few experiments have been conducted that describe the effects of meiofaunal grazing on bacterial abundance and production. Alongi (1985) observed no effects of the nematode *Diplolaimella chitwoodi* on the population dynamics of bacteria incubated in dishes containing cereal, and Moriarty et al. (1985) found that abundance and production of bacteria at Davies Reef (Australia) was enhanced by the presence of meiofauna only when the latter's population densities were double naturally occurring ones. More work has been done to study the effects of nematodes on bacteria in non-marine environments; results of these studies have varied. In sewage sludge microcosms bacterial abundance was greater in the presence of nematodes (Abrams & Mitchell 1980), while in desert systems elevated abundances of nematodes led to reductions in bacterial abundance and significantly slower litter decomposition rates (Whitford et al. 1982). Anderson et al. (1983) found that while the terrestrial nematode *Mesodiplogaster lheritieri* initially stimulated bacterial growth, bacterial numbers eventually decreased as a result of higher nematode feeding rates. Ingham et al. (1985) observed that low densities of the terrestrial bacteriovore *Acrobeloides* sp. failed to affect bacterial numbers in microcosms using blue grama grass as a substrate, but that elevated nematode densities were accompanied by increased bacterial abundance.

Alongi (1988) has reported that bacterial abundance and production in northeastern Australian mangrove sediments are higher than in most other benthic environments; in contrast, meiofaunal populations are lower than those reported from similar habitats (Alongi 1987a). Low populations of nematodes will obviously have little simulatory influence on bacterial production (as was the case in our experiments with aged detritus), but it appears that natural populations of bacteria in Queensland mangal sediments are in little need of stimulation by nematodes and other meiofauna. In such sediments, the rapid processing of mangrove litter by large populations of crabs can greatly facilitate bacterial production (Robertson & Daniel 1988). Where nematode growth was relatively good, as on fresh *Avicennia marina* litter, grazing activities may have stimulated increases in bacterial production and abundance, at least for 30 d (Table 3). Highly elevated nematode densities (as in flasks containing cereal) may have increased grazing activity to the point that bacterial abundance was actually less in flasks containing nematodes (Table 2).

Nutrient regeneration

The lack of statistical differences in the concentrations of dissolved ammonia and phosphate between flasks with and without nematodes was no doubt related to the relatively low numbers of nematodes in the flasks, even where growth was positive (as on fresh *Avicennia marina* detritus). Findlay & Tenore (1982) observed that the ability of the nematode *Diplolaimella chitwoodi* to enhance carbon remineralization was a direct function of both nematode abundance and detrital type: mineralization of vascular detritus (*Spartina*) was much less influenced by worm presence than was seaweed detritus (*Gracilaria*). Tannin-rich litter such as mangrove detritus decomposes slowly (Zucker 1983); nematodes contributed little to nutrient regeneration in the experimental flasks because the small quantities of ammonia and phosphate released by the low numbers of worms were insufficient to raise concentrations above those resulting from leaching and bacterial decomposition alone.

The failure of the nematodes employed in this study to grow on any mangrove detrital type tested but fresh *Avicennia marina* may indicate some type of substrate limitation (at least as fas as *A. marina* and *Rhizophora stylosa* are concerned). The poor nutritional quality of mangrove litter (high tannins, low nitrogen content) may be one of the reasons for the low abundance of nematodes observed in tropical Queensland mangal sediments (Alongi 1987a). The low abundances of nematodes, other meiofauna and macroinfauna (Alongi

1989) may indicate that in tropical mangrove estuaries large, motile organisms like amphipods and crabs are the dominant animals influencing rates of litter decomposition (Robertson & Daniel 1988, Alongi 1989).

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