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The ecology of Belizean mangrove-root fouling communities. I. Epibenthic fauna are barriers to isopod attack of red mangrove roots

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Abstract: Wood-boring isopods consume and damage aerial prop roots of mangroves that grow throughout the western Atlantic and Caribbean regions. On mangrove cays off the eastern coast of Belize, the isopod *Phycolimnoria clarkae* Kensley & Schotte attacks submerged freely hanging roots of red mangroves *Rhizophora mangle* L. At Twin Cays, these isopods reduce root relative growth rate (based on root elongation) by 55%, and do not cause an increase in lateral branching frequency relative to control roots from which isopods were experimentally excluded. These submerged roots are also colonized by a diverse array of epibionts. We demonstrate experimentally that the most common sponge and ascidian species at Twin Cays inhibit isopod colonization and hence indirectly facilitate root growth.

Key words: Belize; Isopod; Mangrove; *Phycolimnoria clarkae*; Plant–animal interaction; *Rhizophora mangle*

INTRODUCTION

Mangroves occur pantropically on all but the most exposed coasts (Chapman, 1976; Tomlinson, 1986). In the western Atlantic, prop roots of red mangroves *Rhizophora mangle* that originate well above water level and grow down into the water below LLW are often covered by a dense and diverse epibiont community (Rützler, 1969; Rützler & MacIntyre, 1982; Taylor et al., 1986). Despite centuries of research on mangrove ecosystems (reviewed by Tomlinson, 1986), studies of mangrove root epibenthic fouling communities have rarely proceeded beyond taxonomic enumeration and description (e.g., Macnae, 1968; Rützler, 1969; Sutherland, 1980). Little is known of the ecological roles of animals that live in and on submerged mangrove roots (Rehm & Humm, 1973; Simberloff et al., 1978; Taylor et al., 1986; Perry, 1988).

Intertidal root epibionts and herbivores dramatically affect primary productivity of mangroves in the eastern Pacific mangrove swamps of Costa Rica (Perry, 1988). The only faunal herbivores of mangrove roots studied to date are the sphaeromatid isopods *Sphaeroma peruvianum* of the Pacific coast of Costa Rica (Perry, 1988), and *S. terebrans*

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of the Gulf Coast of Florida (Rehm & Humm, 1973; Simberloff et al., 1978; Ribi, 1982). Isopods destroy root apices, possibly resulting in initiation of lateral buds and proliferation of lateral roots (Gill & Tomlinson, 1977; Simberloff et al., 1978). Damage to roots, and their subsequent branching, results in the characteristic red mangrove root physiognomy (Gill & Tomlinson, 1977; Simberloff et al., 1978; reviewed by Tomlinson, 1986). Rehm & Humm (1973) contended that isopods were destroying mangrove root apices more rapidly than new ones were produced, and therefore these crustaceans constituted a threat to mangrove ecosystem persistence in Florida. On the other hand, Estevez & Simon (1975), and Simberloff et al. (1978) suggested that for the same Florida mangroves, the rate of new lateral root production following isopod damage exceeded the rate of destruction of root apices by isopods. They argued, therefore, that isopods were possibly facilitating root production and were no threat to mangrove persistence. Perry (1988), working in Costa Rica, found that isopods stimulated root branching, but that overall root growth (expressed as total root length) was slowed by isopods.

Interactions between root epibionts and isopods have been studied only in the intertidal of Costa Rica's Pacific Coast (Perry, 1988). These intertidal mangrove–root animal communities are dominated by barnacles (*Balanus* and *Chthamalus* spp.; Perry, 1988; A.M. Ellison & E.J. Farnsworth, pers. obs.). However, on mangrove cays in Belize the root epibiont communities have both an intertidal and a subtidal component. Interactions between isopods and faunistically richer subtidal root epibiont communities have not been explored.

Here, we report a study that examined the null hypotheses that (a) limnoriid isopods *Phycolimnoria clarkae* have no effects on mangrove root growth or branching, and (b) that mangrove root epibionts have no significant effects on successful isopod colonization of roots. We examined effects of isopods on growth and branching of red mangrove roots using field exclosure and removal experiments, and studied interactions between root epibionts and isopods in controlled laboratory conditions.

STUDY SITE

≈250 km long and 10–32 km wide, the barrier reef complex off the eastern coast of Belize is the largest continuous reef in the Caribbean Sea (Rützler & MacIntyre, 1982). Numerous mangrove cays dominated by *R. mangle* are found within the shoreward lagoon (Stoddart et al., 1982). The mangroves *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus*, and the shrub *Batis maritima* also are found occasionally on higher ground on these cays. The vegetation of all of the mangrove cays of Belize is reviewed by Stoddart et al. (1982). We worked at Twin Cays (16°48′N, 88°05′W), located in the lower third of the barrier reef complex. Twin Cays is 4 km west of Carrie Bow Cay where the Smithsonian Institution maintains a small marine laboratory (Rützler & MacIntyre, 1982; Stoddart et al., 1982). Twin Cays is an ≈ 1 km^2 group of two large and two small cays bisected by a 0.5–2 m deep "Main Channel" (site names follow convention of Rützler, 1989). Along this Main Channel, mangrove prop roots extend well below LLW. As these roots provide the only local substratum not subject to sedimentation, they are covered by epibionts (Rützler, 1969).

THE ISOPODS

Wood-boring isopods (Sphaeromatidae and Limnoriidae) are common throughout Caribbean mangrove swamps (Kensley & Schotte, 1989). In Belizean mangrove roots, we have found the sphaeromatids *Sphaeroma terebrans*, *Paracerceis caudata*, and *Dynamenella* sp., and the limnoriid *Phycolimnoria clarkae*. At Twin Cays, *P. clarkae* accounts for 95% of the isopods recovered from mangrove roots. We have never found *S. terebrans* at Twin Cays. Wood-boring isopods burrow into wood by rasping the wood fibers with the mandibles (Kensley & Schotte, 1989). Bacteria and fungi invade the wood through the wound opened by the isopods and continue the decomposition process. These fungi and bacteria form a large part of the isopods' diet (Kensley & Schotte, 1989). Although limnoriids lack cellulase-secreting gut microflora, limnoriids themselves secrete a cellulase (Boyle & Mitchell, 1978) and (unlike sphaeromatids) also consume wood (Ray, 1959).

Adult isopods burrow rapidly into wood in laboratory situations (Rehm & Humm, 1973; Estevez & Simon, 1975). Isopods leave easily seen, characteristic entry and exit holes along the root surface below mean high water (Fig. 3 of Rehm & Humm, 1973). They most commonly burrow into the soft, uncorticated root tissue within 6 cm of the root tip (Rehm & Humm, 1973; Perry, 1988), and excavate chambers several centimeters long (Estevez & Simon, 1975; A.M. Ellison & E.J. Farnsworth, in prep.). Reproduction occurs within these chambers, and the juveniles pass through all developmental stages within the roots (Rehm & Humm, 1973). Once mature, the young join the adults in burrowing behavior (Rehm & Humm, 1973).

FIELD OBSERVATIONS

METHODS

We assessed the frequency of isopod damage among roots at Twin Cays along the Main Channel, in Sponge Haven, and in Twin Bays. These sites were chosen because they have similar root epibiont communities and an abundance of freely hanging aerial roots (A.M. Ellison & E.J. Farnsworth, 1991). We sampled freely hanging young roots that extended below LLW and lacked significant ($<10\%$) epibiont cover. We sampled 135 roots ($45 \cdot \text{site}^{-1}$) in 1988 and 60 roots ($20 \cdot \text{site}^{-1}$) in 1989. The roots sampled in 1988 were a randomly chosen subset of all such roots along a 100-m transect at each site. The same percentage of young epibiont-free roots were sampled along these transects in 1989, but because there were fewer such roots, the 1989 sample size was smaller. We examined roots from all sides in situ while snorkeling.

RESULTS

In 1988, 21% of the Twin Bays roots, 24% of the Sponge Haven roots, and 30% of the Main Channel roots showed evidence of isopod damage (at least one hole penetrating the root epidermis). In 1989, 27, 40, and 38% of the young roots at the same sites were damaged by isopods.

EXCLOSURE EXPERIMENTS

METHODS

To assess the effects of isopods on root growth rate and root branching frequency, in January 1988 we selected 90 freely hanging roots along the Main Channel for experimental manipulation. Isopods are known to attack primarily young, uncorticated roots (Perry, 1988). If isopod effects were to be detectable, we would expect to see such effects on young roots. We therefore chose young, uncorticated roots free of epibionts, lacking external evidence of isopod damage (i.e., holes), and that had not penetrated the water > 10 cm below LLW.

45 of these roots were enclosed in expandable black nylon bags made from nylon stockings; the other 45 were left unbagged as controls. Legs of black nylon stockings were slipped over hanging roots and attached to the roots above HHW with plastic cable ties (Edmund Scientific, Barrington, New Jersey). Because root growth may be affected by shading due to the bags, roots were assigned at random to the two treatments. All roots were either on south- or east-facing banks, and well under the mangrove canopy. Stockings were permeable to water, able to stretch as roots grew, and fouled only rarely by filamentous algae. After 6 months, all stockings were still intact. Bagged and control roots were permanently marked with 3.1-cm (inner diameter) individually numbered plastic bands (National Band and Tag, Lexington, Kentucky). None of the roots used in this or the removal experiments (see below) reached solid substratum (> 2 m below LLW) during the course of these experiments.

Following the initiation of this experiment, total root length (main root plus any new lateral roots) was measured weekly for 1 month, and remeasured 175 days later, when the bags were removed. At each sampling date, percent cover of epibionts below LLW on unbagged roots was assessed by laying a transparent 5×20-cm sheet of acetate over the seaward-facing side of the root. Acetate sheets were divided into grids of 100 1×1 cm squares, and the number of squares under which a given epibiont occurred was used as an estimate of percent cover. All roots were narrower than the 5 cm width of the acetate grid; we therefore corrected our percent cover estimates to account for root diameter as measured (± 1 mm) with vernier calipers. If roots were longer than the

($\bar{x} = 0.6 \pm 0.96$ SD) and unattacked (0.7 ± 1.04) roots. Those roots that produced laterals following isopod attack usually initiated only one lateral root.

TABLE I

Percent cover of epibionts, and number of roots attacked by isopods, after 1, 2, 3 wk, and 6 months on unbagged roots in the exclosure experiment. Values given are $\bar{x}$ ± SE (over all unbagged roots; $n = 45$), the range of percent covers, and the actual number of roots with each species of epibiont.

Species		1 wk	2 wk	3 wk	6 months
Scytonema cf.	$\bar{x}$ ± SE	6 ± 3.3	6 ± 2.3	15 ± 3.9	3 ± 1.9
polycystum	range	0–100	0–75	0–100	0–75
	n	9	7	15	2
Bostrychia spp.		0	1 ± 0.9	4 ± 1.8	9 ± 4.9
		0	0–35	0–55	0–100
		0	3	8	12
Caulerpa racemosa		0.1 ± 0.4	4 ± 1.7	7 ± 2.6	0.3 ± 0.8
		0–5	0–40	0–55	0–15
		1	5	9	1
Halimeda sp.		0	0	0.4 ± 1.3	0
		0	0	0–20	0
		0	0	1	0
Halocordyle disticha		0.4 ± 0.3	0.2 ± 0.3	2.1 ± 2.1	6 ± 3.3
		0–2	0–10	0–95	0–100
		1	1	1	4
Sertularia turbinata		0	0	0	4 ± 2.4
		0	0	0	0–100
		0	0	0	4
Didemnum conchyliatum		0	1 ± 0.6	4 ± 2.8	9 ± 3.3
		0	0–35	0–50	0–90
		0	5	7	7
Perophora formosana		0	1 ± 0.3	3 ± 1.6	7 ± 3.3
		0	0–20	0–60	0–100
		0	4	4	6
Perophora viridis		0	0	0	7 ± 3.1
		0	0	0	0–100
		0	0	0	4
Haliclona sp. 1		0	0	0.9 ± 0.9	5 ± 3.3
		0	0	0–40	0–100
		0	0	1	7
Tedania ignis		0	0.2 ± 0.2	0.2 ± 0.2	6 ± 2.9
		0	0–10	0–10	0–100
		0	1	1	4
Ulosa rutzleri		0	0.7 ± 0.7	0.8 ± 0.6	11 ± 3.1
		0	0–30	0–32	0–100
		0	1	2	4
Phycolimnoria clarkae	n	4	4	7	13

length of one acetate grid, we continued to measure epibiont percent cover over the rest of the root. Because isopods may stimulate initiation of lateral root buds, we also counted the number of lateral roots initiated on bagged and unbagged roots after 175 days.

We calculated root relative growth (elongation) rate ($\mathrm{RGR}_{\mathrm{root}}$: $\mathrm{cm} \cdot \mathrm{cm}^{-1} \cdot \mathrm{day}^{-1}$) at each sampling date after the initiation of the experiment as:

$$[\text{root length}]_{t+1}/([\text{root length}]_t \cdot [\text{days between measurements}]),$$

where t and $t+1$ are successive sampling times. $\mathrm{RGR}_{\mathrm{root}}$ is exactly equivalent to percent change in root length/day times 10^{-2}, and allows one to standardize growth rate measures for variation in initial root length. Any root subject to a *constant* elongation rate ($\approx 1\ \mathrm{mm} \cdot \mathrm{day}^{-1}$ for these young roots) should show a net decline in RGR as the denominator root length term will increase. We therefore can compare the rates of change of $\mathrm{RGR}_{\mathrm{root}}$ between treatments (bagged vs. unbagged) by calculating slopes and 95% confidence intervals (Sokal & Rohlf, 1981) for the rate of change in $\mathrm{RGR}_{\mathrm{root}}$ for each treatment. All statistics were computed using SPSS/PC+, version 2.0 (Norusis, 1988).

RESULTS

All of the unbagged roots were colonized to some degree by benthic epibionts (Table I), although the epibiont composition was very variable among roots (Tables I, II). Algae (*Scytonema* cf. *polycystum*, *Caulerpa racemosa*, *Bostrychia* spp.) and hydroids (*Halocordyle disticha*) colonized unbagged roots within 1 wk (Table I). By the second week, ascidians (*Perophora formosana* and *Didemnum conchyliatum*) and sponges (*Tedania ignis* and *Ulosa rutzleri*) had also colonized the roots at low frequencies.

After 6 months, 29% of the unbagged roots had been attacked by isopods (Table II). 15 of the unbagged roots had been colonized by the aforementioned algae (Table I), and of these 15, seven were also colonized by tunicates (*Perophora formosana* and/or *Perophora viridis*), eight were colonized by hydrozoans (*Halocordyle disticha* and *Sertularia turbinata*), and three were attacked by isopods (Table II). Of the 17 total roots colonized by ascidians (Table I), only two were also attacked by isopods (Table II). Roots colonized by the ascidians *Perophora formosana* and/or *Didemnum conchyliatum* were not attacked by isopods, but isopods did attack roots colonized by *P. viridis*. Roots colonized by the sponges *Tedania ignis*, *Ulosa rutzleri*, or *Haliclona* sp. 1 were never attacked by isopods (Table II).

Isopods had a significant negative effect on root relative growth (elongation) rate of attacked roots. As expected for roots with a roughly constant rate of elongation, $\mathrm{RGR}_{\mathrm{root}}$ declined among both bagged and control roots (Fig. 1). $\mathrm{RGR}_{\mathrm{root}}$ of roots attacked by isopods declined 55% faster ($P < 0.05$) than $\mathrm{RGR}_{\mathrm{root}}$ of bagged roots protected from isopods (Fig. 1).

We also observed no difference in number of laterals produced by attacked

Table II

Distribution of epibionts and isopods on unbagged (fouled) roots in the exclosure experiment (n = 45). The numbers on the diagonal are the total number of roots colonized by each group of epibiont (A, Algae: *Scytonema* cf. *polycystum*, *Bostrychia* spp., *Caulerpa racemosa*; P, Porifera: *Tedania ignis*, *Ulosa rutzleri*, *Haliclona* sp. 1; H, Hydrozoa: *Halocordyle disticha*, *Sertularia turbinata*; T, Tunicata: *Didemnum conchyliatum*, *Perophora formosana*, *P. viridis*), or attacked by isopods (I, Isopoda: *Phycolimnoria clarkae*) after 6 months. The numbers in the off-diagonal cells are the numbers of roots with a combination of the pair of epibionts given by the row and column headings.

	A	P	H	T	I
A	15	0	8	7	3
P	–	15	0	1	0
H	–	–	8	8	0
T	–	–	–	17	2
I	–	–	–	–	13

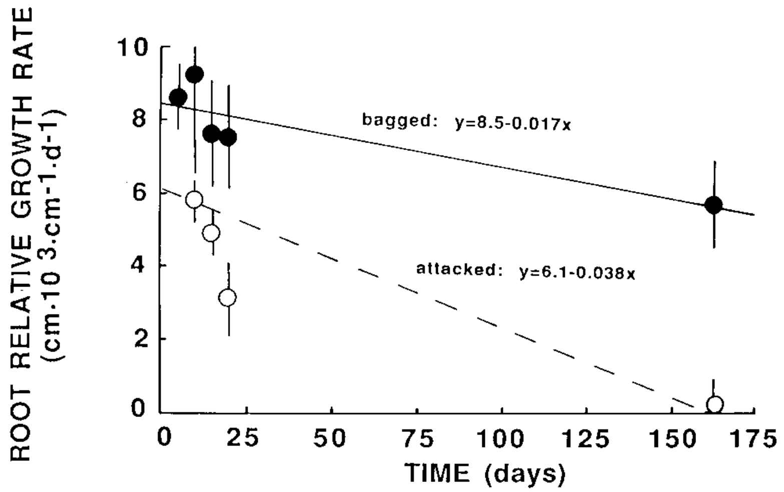

Fig. 1. $\mathrm{RGR}_{\mathrm{root}}$ of bagged roots (●) and roots attacked by isopods (○). $\mathrm{RGR}_{\mathrm{root}}$ was calculated for each sampling date by dividing total root length (including any new lateral branches) by the product of total root length at the previous date and number of days in between sampling dates. Points plotted are means ± 1 SD for each sampling date. The first point (solid symbol) is the 1-wk $\mathrm{RGR}_{\mathrm{root}}$ value for all roots (bagged and unbagged), and represents the starting condition. All other points are from after the initiation of the experiment. Slopes are significantly different from 0 ($P < 0.05$, ANOVA), and significantly differ from each other (as determined by nonoverlap of 95% confidence intervals).

Removal Experiments

METHODS

Because the distribution of epibionts among fouled roots in the exclosure experiments was disjunct (Table II), and because root growth rate and epibiont–isopod interactions may differ with root age, we examined further the effects of epibionts on isopod colonization of older (longer) mangrove roots. 30 sponge-covered freely hanging roots in Sponge Haven were chosen for experimentation. We used the sponges *Tedania ignis* and *Ulosa rutzleri* because they are the dominant epibionts (percent cover and biomass) on subtidal mangrove roots at Twin Cays (A.M. Ellison & E.J. Farnsworth, 1991). These species also were the most common sponge colonists in the exclosure experiments. Roots were chosen that extended at least 50 cm below LLW, and were completely (100%) covered (LLW to root tip) by either of these two sponges.

We removed the sponges from 15 of the roots by cutting the bulk of the sponge off the root and gently removing residual sponge tissue with a toothbrush. We exercised great care in removing sponges to avoid mechanically damaging roots, as damaged roots can be attacked by fungi (Kohlmeyer, 1984). No evidence of fungal attack among our experimental roots was observed after 6 months. Roots were examined daily for 1 wk, and 6 months later, for evidence of isopod attack.

In establishing this experiment, we chose roots that appeared to be undamaged by isopods. Because of internal rot and chamber excavation, roots damaged by isopods are softer to the touch than undamaged roots. We also removed all sponges from control roots at the end of the experiment, 6 months later, to look for evidence of old isopod damage that may have occurred prior to this experiment. No evidence was found of isopod damage in control roots from which sponges were removed at the end of the experiment (save one, see below). Nor was there evidence of isopod damage in the sponge removal roots at the beginning of the experiment, immediately following sponge removals. Although it cannot be stated with complete certainty that the experimental roots had not been damaged by isopods and subsequently healed prior to our study, we are confident in our ability to detect roots undamaged by isopods.

RESULTS

Within 48 h, isopods had attacked 33% of the roots from which sponges had been removed. After 1 wk, 60% of these same roots had been attacked by isopods. 6 months later, all of these roots had been attacked by isopods. During these same 6 months, these roots also had been fouled by *Scytonema* cf. *polycystum*, *Halocordyle disticha*, and perophorid tunicates. Removal of the sponges from the control roots at the conclusion of the experiment revealed that only one had been damaged. This damage occurred to one unfouled growing tip of one root that had elongated beyond the fouling sponge. In the other 14 sponge-covered control roots, the sponges had grown at least as fast as the root itself, and no root surfaces were exposed to isopods. After 6 months, roots from which sponges were removed had increased only slightly in length ($\bar{x} = 8\% \pm 3.1\%$ SD; equivalent to a mean $\mathrm{RGR}_{\mathrm{root}}$ of $4.4 \cdot 10^{-4}\ \mathrm{cm} \cdot \mathrm{cm}^{-1} \cdot \mathrm{day}^{-1}$), while corresponding sponge-encrusted controls lengthened by $44\% \pm 6.2\%$ ($\mathrm{RGR}_{\mathrm{root}} = 2.4 \cdot 10^{-4}\ \mathrm{cm} \cdot \mathrm{cm}^{-1} \cdot \mathrm{day}^{-1}$, a more than five-fold difference ($P < 0.05$, *t* test).

ISOPOD-FEEDING EXPERIMENTS

METHODS

To investigate further the interactions between benthic epibionts and isopods, we examined the influence of selected sponges, ascidians, algae, and anemones on isopod attack frequency in paired controlled feeding trials. We used the sponge, ascidian, and algal species found most frequently on the fouled roots in the exclosure experiment (Porifera: *Tedania ignis* and *Haliclona* sp. 1; Tunicata: *Perophora formosana* and *Didemnum conchyliatum*; Cyanophyta: *Scytonema* cf. *polycystum*). Although brown anemones *Aiptasia pallida* had not colonized the fouled roots in the exclosure experiment, they are a conspicuous member of the root epibiont community and could consume isopods.

Isopods were collected from roots at Twin Cays and brought to the laboratory on Carrie Bow Cay (Rützler & MacIntyre, 1982). Isopods were placed in fine mesh boxes (4 × 4 × 8 cm) in running seawater aquaria and starved for 24 h prior to the experiments.

We collected roots with 75–100% cover of the test epibiont. In all cases, the test species covered the root tip and at least the lower 10 cm of root, the portion of the root most commonly attacked by isopods (Perry, 1988; A. M. Ellison & E. J. Farnsworth, in prep.). Roots collected from Twin Cays were transported to the laboratory in seawater buckets within 1 h of collection. Two replicate 60-l glass aquaria, continuously supplied with running seawater, were used at all times. These aquaria were each partitioned into six sections. A total of 12 paired trials, six for each of two fouling species and randomly arranged in the aquaria, were run simultaneously. In each partition, a pair of roots (one fouled, one bare) was suspended. Three isopods were introduced into each section. Roots were examined for isopod damage after 24 and 48 h. After 48 h, fouled and bare control roots were dissected to ensure that apparent isopod damage was, in fact, caused by isopod feeding, and that isopods were not present in apparently undamaged roots.

RESULTS

In these laboratory trials, isopods preferred bare roots to those covered by the colonial ascidians and sponges (Table III). Isopods attacked unfouled roots and roots fouled by blue-green algae and anemones with equal likelihood (Table III). Isopods appeared to swim freely among filaments of blue-green algae and in between anemones, colonies of which do not completely obscure root surfaces. We recovered 69% (74 of 108) of the isopods used in all of the experiments. These isopods had burrowed into the roots (normally within 5 mm of the root tip) and had begun excavating chambers.

TABLE III

Results of isopod feeding experiments. Total number of monospecifically fouled and bare (control) roots attacked are presented. For each pair, there were 6 fouled and 6 control roots.

Epibiont	Fouled		Control
Scytonema cf. *polycystum*	6	NS	4
Perophora formosana	0	*	6
Didemnum conchyliatum	1	*	5
Haliclona sp. 1	0	*	6
Tedania ignis	0	*	5
Aiptasia pallida	2	NS	4

NS, no significant difference. *$P < 0.05$, sign test.

INTERACTIONS BETWEEN ANEMONES AND ISOPODS

METHODS

We had hypothesized that the brown anemone *A. pallida* growing on mangrove roots would prey on isopods and thereby prevent them from colonizing roots. Although we had expected to see a significant effect of anemones on isopod attack frequency in the isopod-feeding experiments, no effect was observed (Table III). Unlike the filter-feeding sponges and anemones, *A. pallida* may prey directly on animals the size of wood-boring isopods. The results of the isopod-feeding experiments (Table III), however, suggested that *A. pallida* does not prey on *Phycolimnoria clarkae*. To investigate possible interactions between these anemones and the isopods, in July 1989 we randomly collected 50 *A. pallida* individuals, and dissected them within 1 h of collection to determine if isopods were present in gastrovascular cavities of the anemones. We also attempted to feed isopods to anemones. Anemones (n = 10) were placed individually into 50-ml finger bowls containing fresh seawater and allowed to acclimate for 15 min, by which time tentacles were fully extended. Two isopods were placed into each finger bowl. Anemones and isopods were observed for 1 h to determine if the anemones would sting and ingest the isopods.

RESULTS

We found no traces of isopods in gastrovascular cavities of dissected *A. pallida* individuals, although many amphipods as large as or larger than *Phycolimnoria* were recovered. Anemones rejected isopods in controlled feeding trials. Within 15 min, all isopods had been stung and killed; however, anemones did not consume the isopods, they dropped them. Anemones regurgitated isopods that were pipetted directly into the gastrovascular cavities of the anemones.

DISCUSSION

Our sampling of submerged young, freely hanging red mangrove roots across Twin Cays indicates that a substantial fraction of these roots are attacked by isopods. Perry (1988) found that isopods preferentially attack young roots; they either can not or will not colonize heavily corticated roots that are firmly rooted in the substratum. Significant secondary thickening and cortication of mangrove roots does not occur until after roots are firmly anchored in benthic substratum (Gill & Tomlinson, 1977). If destruction of root meristems by isopods results in a net increase in number of laterals relative to undamaged controls, or if these laterals together grow more rapidly than a single unattacked root, then it could be argued that isopods enhance mangrove root growth (Simberloff et al., 1978; Perry, 1988). No difference in the number of lateral roots initiated by young roots following isopod attack was found. We further observed that RGR_{root} of young roots attacked by isopods declined more rapidly than RGR_{root} of roots protected from isopods (Fig. 1). These results do not support the hypothesis that isopods enhance root growth.

If isopods colonize roots before sponges and ascidians then these epibionts will not prevent isopod attack. Rützler (1969) and Sutherland (1980) described successional patterns of epibionts on recently submerged mangrove roots. These successional sequences begin with filamentous blue-green algae, which are followed by macroalgae, hydroids, and bryozoans, and culminate with ascidians, sponges, and/or anemones. However, we observed that some members of all of these taxa colonize roots at any time within 6 months of submergence (Table I). This result suggests that root epibionts recruit onto available roots more as a consequence of larval abundance and space availability, rather than following a strict successional sequence. Therefore, sponge and ascidian recruitment may precede, and prevent, isopod attack.

The results of the sponge removal experiment suggest that at least some sponges inhibit isopod colonization by providing a physical or unpalatable chemical barrier to isopods. When the root extension rate exceeds that of the sponges, as it did in one of the control roots in Sponge Haven, the exposed root tip was attacked.

The results from the controlled isopod feeding trials also support our hypothesis that certain root epibionts present a barrier to isopods (Table III). Isopods did not colonize roots encrusted with the ascidians *Perophora formosana* or *Didemnum conchyliatum*, or the sponges *Tedania ignis* or *Haliclona* sp. 1, but did colonize those roots covered by only filamentous blue-green algae or incompletely by brown anemones.

These sponges and ascidians may act as a simple physical barrier to isopod colonization if isopods are unable to bore through these epibionts, or they may render mangrove roots cryptic to isopods. Oysters (Feifarek, 1987) and clams (Vance, 1978) covered with epibionts are less frequently preyed upon than are unfouled bivalves, and these authors have proposed that epibenthic fauna increase the crypsis of their host. Epibionts may similarly deter isopods from colonizing mangrove roots.

Alternatively, these sponges and ascidians may be unpalatable to isopod crustaceans.

Many sponges (including species of *Tedania* and *Haliclona*) and some ascidians are known to produce a wide variety of structural defenses (Meylan, 1988) and allelochemicals (e.g., Bakus & Green, 1974; Jackson & Buss, 1975; Bakus, 1981; reviewed by Russell, 1984) that are toxic to fish, crustaceans, and other marine organisms.

Our experiments did not distinguish whether sponges and ascidians provide roots with structural or chemical defenses. However, in the sponge removal experiments described above, the only sponge-covered root colonized by isopods was one whose root tip was not covered by sponge tissue. This result suggests that if the sponges possess allelochemicals, their protective function does not extend to unfouled portions of the root (i.e., the hypothesized allelochemicals are not diffusing over long distances and must be sampled by the isopods to be effective). Further experimental work and chemical assays are needed to determine the mechanism(s) of isopod deterrence by these sponges and ascidians.

We had also hypothesized that predaceous anemones would consume isopods, thereby preventing them from attacking mangrove roots. However, isopods were not found in guts of anemones, and the anemones rejected isopods in controlled feeding trials. Isopods did not discriminate between bare roots and roots fouled by anemones (Table III). We therefore cannot support our initial hypothesis that brown anemones protect roots from isopod attack.

Common encrusting epibionts prevent negative effects of isopod crustaceans on young mangrove roots in the western Atlantic. These epibionts appear to present physical or chemical barriers to isopod colonization. Along the eastern Pacific coast, predators reduce isopod colonization of young mangrove roots (Perry, 1988). We and Perry (1988) have demonstrated that isopods do not enhance mangrove root growth as expressed by total root length. While Perry (1988) and Simberloff et al. (1978) found that damage by isopods increased root branching, we found that damage by isopods did not increase lateral roots production. This difference between our results and those of Perry (1988) and Simberloff et al. (1978) may simply result from our having used different isopods.

In contrast, where epibionts and/or predators are not abundant, isopods appear to have greater effects on mangrove roots. In coastal estuaries in southern Belize *Sphaeroma terebrans* damages nearly 100% of aerial mangrove roots and causes an increase in lateral root production (A.M. Ellison & E.J. Farnsworth, in prep.). Mangroves in these estuaries lack epibenthic fauna, and isopod predators are uncommon. Complex biotic interactions between epibionts and herbivores therefore appear to be important determinants of the structure and persistence of mangrove ecosystems.

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