

The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth

Aaron M. Ellison & Elizabeth J. Farnsworth¹

Department of Biological Sciences, Clapp Laboratory, Mount Holyoke College, South Hadley, Massachusetts 01075-1484, USA; Field Naturalist Program, Department of Botany, 120 Marsh Life Sciences Building, University of Vermont, Burlington, Vermont 05405-0086, USA; ¹Current address: Department of Organismic and Evolutionary Biology, Biological Laboratories, Harvard University, 16 Divinity Ave., Cambridge, MA 02138, USA

Key words: Belize, epibionts, isopods, mangroves, *Melongena*, *Rhizophora mangle*

Abstract

The aerial prop roots of the neotropical red mangrove, *Rhizophora mangle* L., begin growing well above highest high water (HHW) and often extend well below lowest low water (LLW) before rooting in the benthic substratum. In Belize, Central America, prop roots growing below LLW are colonized by diverse assemblages of organisms, including macroalgae, hydrozoans, ascidians, sponges, anemones, hard corals, and isopod crustaceans. Mangroves, root-fouling epibionts, root herbivores, and benthic predators engage in complex interactions that are major determinants of mangrove growth and production. Species richness of root epibionts increases with distance from the mainland and with proximity to the barrier reef. Species richness decreases with variability in water temperature and salinity. Ascidians and sponges transplanted from Lark Cay into the coastal Placencia Lagoon failed to survive, but anemones from Lark Cay survived in Placencia Lagoon. Reciprocal transplants survived off-shore. The gastropod predator, *Melongena melongena* L., present only in mainland estuaries, reduced local barnacle abundance and epibiont species richness in Placencia Lagoon. Isopod species richness also increases with distance from shore, but the number of roots bored by these species decreases. These isopods can reduce root relative growth rate (RGR_{root}) by 55%. On off-shore cays, sponges and ascidians ameliorate negative effects of isopods. In mainland estuaries where epibionts are less common, isopod damage to roots is more severe. Experimental studies in mangrove swamps throughout the world would clarify the importance of plant-animal interactions in these widespread tropical ecosystems.

Introduction

Epibionts are organisms that colonize and grow on virtually any living, solid, exposed surface in the marine environment (reviewed by Wahl, 1989). In mangal, littoral mangrove roots are often the only local substratum not subject to heavy sedimentation and provide ideal habitat for algal

and invertebrate epibionts (Rützler, 1969). Although epibionts may significantly impact their host (and *vice versa*; Wahl, 1989), mangrove epibionts have received only brief mention in even the most comprehensive reviews (Macnae, 1968; Chapman, 1976; Tomlinson, 1986; Wahl, 1989; but see Rützler, 1969). Except for species inventories (*e.g.* Mattox, 1949; Macnae & Kalk, 1962;

Macnae, 1968; Rützler, 1969; Hutchings & Recher, 1974; Sasekumar, 1974; Pinto & Wignarajah, 1980; Sutherland, 1980; Alvarez I., 1989), investigators have ignored epibionts (and mobile animals) because they have been thought to contribute insignificantly to direct matter and energy flow in mangrove ecosystems (*e.g.* Golley *et al.*, 1962; Odum & Heald, 1972; Lugo & Snedaker, 1974), and because the mangrove fauna is not considered host-specific (*e.g.* Macnae, 1968; Tomlinson, 1986).

Throughout the neotropics, prop roots of *R. mangle* extending below LLW are colonized by numerous algal and invertebrate epibionts (Rützler, 1969; Sutherland, 1980; Taylor *et al.*, 1986; Alvarez I., 1989; Ellison & Farnsworth, 1990). Intertidal portions of roots are often colonized by barnacles and red algae (Rützler, 1969; M. M. Littler *et al.*, 1985; Perry, 1988; D. S. Littler *et al.*, 1989). Both subtidal and intertidal roots are bored by isopod crustaceans (Sphaeromatidae and Limnoriidae; Rehm & Humm, 1973; Snedaker, 1973; Estevez & Simon, 1975; Simberloff *et al.*, 1978; Ribí, 1982; Perry, 1988; Kensley & Schotte, 1989; Ellison & Farnsworth, 1990).

Recent experimental studies have shown that epibionts directly and indirectly affect root growth and production (Perry, 1988; Ellison & Farnsworth, 1990) and total energy flow (Wada & Wowor, 1989; Rodriguez & Stoner, 1990), and that herbivorous crabs can influence mangrove zonation (Smith, 1987; Smith *et al.*, 1989). Here, we describe patterns of epibiont distribution and abundance on mangrove roots in Belize, Central America; discuss some of the apparent causes of the observed patterns; document interactions between various epibionts; and summarize the known effects of these epibionts on root and tree growth.

Study sites

Belize, located in northeastern Central America, includes the largest continuous barrier reef in the western hemisphere (Rützler & Macintyre, 1982).

Tidal amplitude throughout Belize is ≈ 30 cm (Kjerfve *et al.*, 1982). The mangroves *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn, *Laguncularia racemosa* (L.) Gaertn. f., and *Conocarpus erectus* L. (taxonomy follows Tomlinson, 1986) are found along rivers, in estuaries, and on numerous mangrove cays in the lagoon shoreward of the barrier reef (Hartshorn *et al.*, 1984; Stoddart *et al.*, 1982). All four species co-occur from HHW to mean water (MW). Below MW, *R. mangle* forms monospecific stands extending seaward to below LLW.

We studied mangrove-root epibionts at six locations in southern Belize (Fig. 1). These sites are representative of mainland estuaries (Placencia Lagoon and Big Creek), near-shore cays (Lark and Bugle Cays), and cays close to the barrier reef (Northeast Cay and Twin Cays). Detailed descriptions of these study sites are given in Ellison & Farnsworth (1990) and Farnsworth & Ellison (1991).

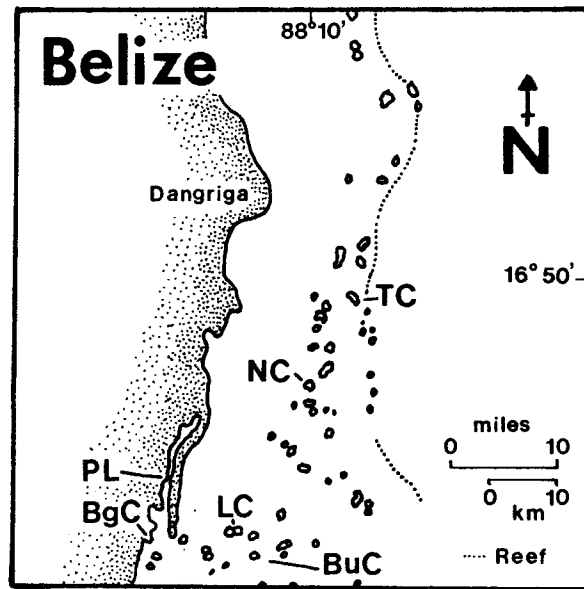


Fig. 1. Map of southern Belize, showing the six study sites. PL: Placencia Lagoon; BgC: Big Creek; LC: Lark Cay; BuC: Bugle Cay; NC: Northeast Cay; TC: Twin Cays. Names and locations follow British Survey Sheets of Belize, nos. 32 (1966), 36 (1976), and 40 (1982).

Patterns of epibiont distribution

Methods

At all six sites (Fig. 1), we sampled a minimum of 100 roots for epibionts. Roots were selected haphazardly along a 100 m transect parallel to shore. We distinguished roots as *aerial* or *ground* (rooted in the substratum). We catalogued all epibiont species encountered. At Placencia Lagoon, Lark Clay, and Twin Cays (hereafter referred to as Placencia, Lark, and Twin, respectively), we measured percent cover and vertical zonation of epibionts on roots. Percent cover was assessed by laying a transparent 5 × 20 cm sheet of acetate divided into grids of 100 1 × 1 cm squares over the seaward-facing side of the root. The number of squares under which each epibiont occurred was used as an estimate of percent cover (after correction for actual root diameter). We used additional grids to measure epibiont cover over the entire root. To assess epibiont zonation, we recorded presence of each species in 2 cm intervals along each root from 1 cm above the root cap to the upper limit of epibiont occurrence. Species occurring at the root tip (up to 1 cm above the root cap) were recorded separately.

Results

Species encountered at the six sites are listed in Table 1. Throughout, we will refer to all these species generically, except where such reference would be ambiguous. For all major taxa, species richness increased from the mainland towards the barrier reef (Table 1). Ascidians and cnidarians were absent from the Placencia estuary, and only one species in each of these two taxa was present in Big Creek. Twin and Northeast Cay, each only 4 km from the barrier reef, had the highest species richness of algae, sponges, crustaceans, and ascidians.

Epibiont species richness at Lark was much higher than at Bugle Cay, although both islands had fewer species than Twin and Northeast Cay (Table 1). Lark and Bugle Cay are both 7 km off

shore; Bugle Cay is 2 km SE of Lark. However, Lark is protected from extreme wave action by a series of cays to the east, while Bugle Cay is more wave-swept. We suspect that the low number of species present at Bugle Cay reflects increased wave exposure there. Differences in root fauna observed between Lark and Bugle Cay are comparable to differences observed between exposed and sheltered roots at Twin (A. M. Ellison & E. J. Farnsworth, pers. obs.), and we are currently exploring relationships between epibiont patterns and wave exposure.

Species composition and percent cover differed between aerial and ground roots (Fig. 2), and these patterns varied with location. Across all sites filamentous algae, fleshy algae, and balanoid barnacles were generally more abundant on aerial roots (Fig. 2B, 2C). Crustose coralline algae and chthamloid barnacles were more abundant on ground roots (Fig. 2A). At Lark, ascidians other than *Diplosoma* were more abundant on ground roots (Fig. 2B). At Twin, however, only *Didemnum conchyliatum* was found on both aerial and ground roots; all other ascidians were found only on aerial roots (Fig. 2C). Sponges were found on both aerial and ground roots at all sites. At Lark, all sponges other than *Haliclona curacaoensis* were more abundant on ground roots (Fig. 2B), but at Twin, sponges were generally equally abundant on aerial and ground roots.

At all sites, isopods attacked a much higher percentage of aerial roots than ground roots (Fig. 3). We encountered only *Sphaeroma* at Placencia and only *Phycolimnoria* at Lark. The latter species accounted for 95% of the isopod individuals found at Twin (Ellison & Farnsworth, 1990), where we also found two other sphaeromatids (Table 1).

Taken over all roots surveyed, epibiont species richness tended to be higher on aerial roots than on ground roots. At Placencia, all five epibiont species occurred on both aerial and ground roots. At Lark, 33 species were found on aerial roots, and 26 occurred on ground roots. At Twin, 47 species were found on aerial roots, while only 28 were found on ground roots. Ephemeral cnidaria (*Halocordyle*, *Halecium*, and *Sertularia*) occurred

Table 1. Taxa encountered on mangrove roots in various locations of coastal Belize (Site abbreviations as in Fig. 1).

Taxa	PL	BgC	LC	BuC	NC	TC
Cyanobacteria¹						
<i>Scytonema polycystum</i> Barnet & Flahault					✓	✓
Chlorophyta²						
<i>Acetabularia crenulata</i> Lamour.		✓	✓	✓		✓
<i>Caulerpa mexicana</i> (Sond.) J. Ag.					✓	✓
<i>Caulerpa racemosa</i> (Forssk.) J. Ag.			✓		✓	✓
<i>Caulerpa sertularioides</i> (S. G. Gmelin) Howe						✓
<i>Caulerpa verticillata</i> J. Ag.	✓	✓	✓			✓
<i>Derbesia osterhoutii</i> (L. & A. H. Blinks) Page			✓		✓	
<i>Halimeda</i> spp.			✓	✓	✓	✓
<i>Valonia macrophysa</i> Kütz.			✓			✓
<i>Ventricaria ventricosa</i> J. Ag.			✓			✓
Phaeophyta²						
<i>Dictyota</i> spp.		✓	✓	✓	✓	✓
<i>Lobophora variegata</i> (Lamour.) Worm.			✓	✓	✓	✓
<i>Padina sanctae-crucis</i> Børg.		✓	✓	✓	✓	✓
Rhodophyta²						
<i>Amphiroa rigida</i> var. <i>antillana</i> Børg.						✓
<i>Bostrychia</i> spp.	✓	✓	✓	✓	✓	✓
Corallinaceae			✓	✓	✓	✓
<i>Wrangelia argus</i> (Montagne) Montagne			✓		✓	✓
Porifera³						
<i>Amphimedon viridis</i> (D. & M.)		✓	✓	✓	✓	✓
<i>Chondrilla nucula</i> Schmidt				✓		
<i>Halichondria melanadocia</i> de Laubenfels						✓
<i>Haliclona implexiformis</i> (Hechtel)		✓	✓		✓	✓
<i>Haliclona curacaoensis</i> (van Soest)			✓		✓	✓
<i>Haliclona pseudomolitiba</i> de Weerd, Rützler, and Smith						✓
<i>Lissodendoryx isodictyalis</i> (Carter)			✓		✓	✓
<i>Mycale microsigmatosa</i> Arndt						✓
<i>Mycale</i> sp. 2 <i>fide</i> Rützler	✓	✓			✓	
<i>Pellina carbonaria</i> (Lamarck)	✓	✓				
<i>Tedania ignis</i> (D. & M.)		✓	✓	✓	✓	✓
<i>Ulosa ruetzleri</i> Wiedenmayer			✓	✓	✓	✓
Cnidaria¹						
<i>Aiptasia pallida</i> (Verrill)			✓	✓	✓	✓
<i>Bartholomea annulata</i> (Lesueur)					✓	✓
<i>Condylactis gigantea</i> (Weinland)			✓		✓	✓
<i>Halocordyle disticha</i> (Goldfuss)		✓	✓		✓	✓
<i>Halecium</i> spp.			✓		✓	✓
<i>Millepora alicornis</i> L.			✓	✓		
<i>Palythoa caribaea</i> D. & M.			✓	✓	✓	
<i>Sertularia turbinata</i> (Lamour.)			✓		✓	✓
Annelida						
Sabellidae			✓	✓	✓	✓
Serpulidae			✓	✓	✓	✓

Table 1. (Continued)

Taxa	PL	BgC	LC	BuC	NC	TC
Crustacea (Cirripedia) ¹						
<i>Balanus eburneus</i> Gould	✓	✓	✓	✓	✓	✓
<i>Chthamalus angustitergum thompsoni</i> (Henry)	✓	✓				
Crustacea (Isopoda) ⁴						
<i>Dynamenella</i> cf. <i>angulata</i> (Richardson)						✓
<i>Paracerceis caudata</i> Say						✓
<i>Phycolimnoria clarkae</i> Kensley & Schotte			✓			✓
<i>Sphaeroma terebrans</i> Bate	✓	✓				
Mollusca (Bivalvia) ⁵						
<i>Crassostrea rhizophorae</i> Guilding	✓				✓	✓
<i>Isognomon alatus</i> Gmelin	✓	✓	✓		✓	✓
Chordata (Tunicata) ⁶						
<i>Ascidia nigra</i> (Savigny)			✓		✓	
<i>Botrylloides nigrum</i> Herdman			✓		✓	✓
<i>Botrylloides</i> cf. <i>perspicuum</i> Herdman			✓		✓	✓
<i>Clavelina picta</i> (Verrill)					✓	
<i>Didemnum conchyliatum</i> (Sluiter)			✓		✓	✓
<i>Didemnum psammathodes</i> Sluiter						✓
<i>Diplosoma glandulosum</i> (Milne Edwards)			✓		✓	✓
<i>Distaplia corolla</i> Monniot			✓		✓	✓
<i>Ecteinascidia minuta</i> (Berrill)						✓
<i>Ecteinascidia turbinata</i> Herdman			✓		✓	✓
<i>Eudistoma olivaceum</i> (van Name)		✓	✓		✓	✓
<i>Eudistoma obscuratum</i> (van Name)						✓
<i>Perophora formosana</i> (Oka)						✓
<i>Perophora regina</i> Goodbody & Cole						✓
<i>Perophora viridis</i> (Verrill)			✓		✓	✓
<i>Styela partita</i> (Stimpson)			✓		✓	

¹ Nomenclature follows Sterrer (1986).² Nomenclature follows Littler *et al.* (1989); algae identified by D.S. Littler, Smithsonian Institution.³ Sponges identified by K. Rützler, Smithsonian Institution. *Haliclona* nomenclature follows de Weerd *et al.* (1991).⁴ Nomenclature follows Kensley & Schotte (1989); isopods identified by B. Kensley, Smithsonian Institution.⁵ Nomenclature follows McLean (1951).⁶ Tunicates identified by I. Goodbody, University of the West Indies.

only on aerial roots, while other cnidarians (*Palmyra*, *Millepora*, and *Condylactis*) occurred only on ground roots. Ascidian species richness also was much higher on aerial roots at these two sites (Lark: 5 species only on aerial roots; Twin: 11 species only on aerial roots). At Lark and Twin, isopods only attacked aerial roots.

Few clear patterns in vertical zonation of epibionts on roots were observed. Isopods were

found most commonly in the root tip ($P < 0.01$, G-test), and barnacles only occurred on the intertidal portions of the roots ($P < 0.001$, G-test). *Bostrychia* was most common at the low water line ($P < 0.05$, G-test). All of the other species occurred only below LLW, and were found with equal likelihood at all locations along the subtidal portion of the root ($P > 0.50$, G-test).

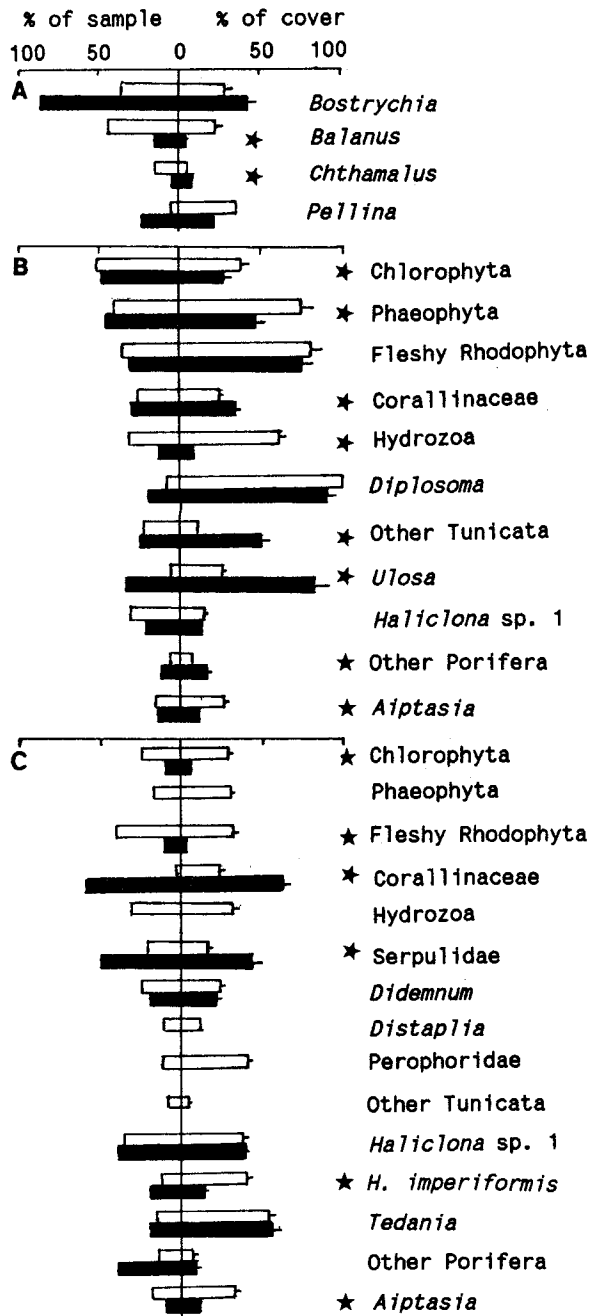


Fig. 2. Distribution and abundance of common taxa at Placencia (A), Lark (B), and Twin (C). Only taxa that occurred on at least 10% of the roots sampled (% of sample) are presented. Mean % cover (± 1 SE) of each taxa for roots on which it occurs is given for aerial (open bars) and ground (solid bars) roots. Stars indicate significant differences in % cover between aerial and ground roots ($P < 0.05$, 2-tailed t -test on angularly transformed data [Sokal & Rohlf, 1981]).

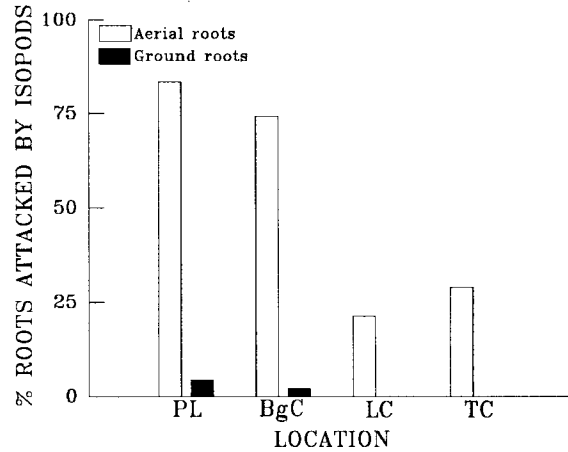


Fig. 3. Percent of aerial and ground roots attacked by isopods. Site names as in Fig. 1.

Factors affecting epibiont distribution

Methods – effects of salinity and water temperature on epibionts

Our survey revealed that several epibionts common on the cays, including the colonial ascidian *Diplosoma*, the sponge *Amphimedon*, and the anemone *Aiptasia* were absent from Placencia Lagoon. To determine if site-specific salinity and water temperature affected epibiont distribution, we reciprocally transplanted several epibionts between Lark and Placencia. On 24 November 1988, colonies of *Diplosoma*, *Amphimedon*, and *Aiptasia* were transplanted from Lark into Placencia. *Pellina*, a sponge only found in the mainland estuaries, was transplanted from Placencia to Lark. For each species, 20 replicate aerial roots with at least 50% cover of the epibiont were collected at each site. We transplanted ten of the roots *in situ* (transplant controls), and transplanted 10 to the other site. We measured percent cover of epibionts on the roots, then tied the transplants onto intact hanging roots with plastic cable ties. We transported roots in covered buckets between sites, and all roots were transplanted within 1 h of collection. Transplants were examined every 2 d for 28 d. Salinity (with a refractometer) and temperature were measured concu-

rently. After 1 month, transplanted roots had begun to decay and the experiment was terminated.

Results – effects of salinity and water temperature on epibionts

Diplosoma and *Amphimedon* died within 4 d of transplanting into Placencia. At Lark, after 28 d, 50% and 65% respectively of the *Diplosoma* and *Amphimedon* transplant controls remained (Fig. 4). *Aiptasia* from Lark survived equally well *in situ* and when transplanted into Placencia (Fig. 4). *Pellina* transplanted to Lark survived unchanged through 4 wks (Fig. 4). During the first 4 d, salinity at Placencia fluctuated between 18 and 26‰, and water temperature increased by 2 °C. Over the 4 wks of the experiment, water temperature averaged 27 °C at Lark and 28 °C at Placencia with low variance. Salinity at Lark was a constant 34‰, but at Placencia ranged from 18‰ to 31‰ (Fig. 5). Salinity at Placencia

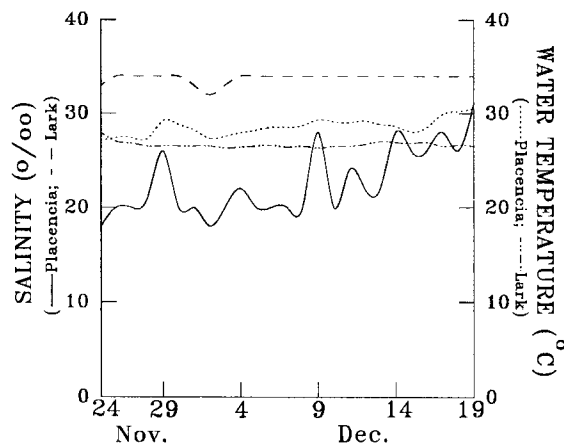


Fig. 5. Salinity (‰) and water temperature (°C) at Placencia and Lark during the transplant experiment.

changed as much as 6‰ over 48 hr, with common diurnal variation of 1–3‰ (Fig. 5).

Methods – effects of predation on epibionts

We also studied the effects of the predaceous gastropod *Melongena melongena* on epibionts at Placencia. At this site, *Melongena* is the most common benthic predator, and we have observed it preying on barnacles on aerial and ground roots at Placencia. Sea urchins, thaid snails, and hermit crabs, which affect epibiont distributions in Belize and Costa Rica (Taylor *et al.*, 1986; Perry, 1988), are absent at Placencia. We randomly chose 16 small (1.0–1.5 m ht) *R. mangle* trees growing between LW and LLW for manipulation. On 1 February 1988, we constructed snail enclosure fences (1.5 × 1.5 × 1.0 m, plastic mesh cages sunk 30 cm into the mud) around 6 of these trees. Of the remaining trees, 4 were designated cage controls (cages with only two parallel sides) and six were unmanipulated. We sampled percent cover of all epibionts on all roots of each tree (>300 roots/treatment) on 2 February, 22 March, 6 November, 26 November, and 14 December 1988. At each sampling date, we counted the number of *Melongena* in a 100 × 20 m transect that included these trees within it. We simultaneously measured shell

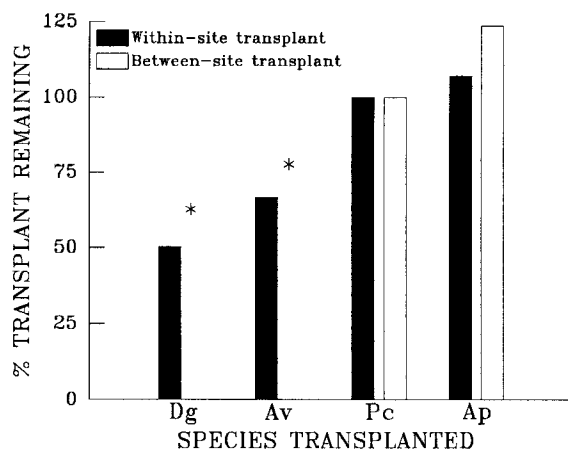
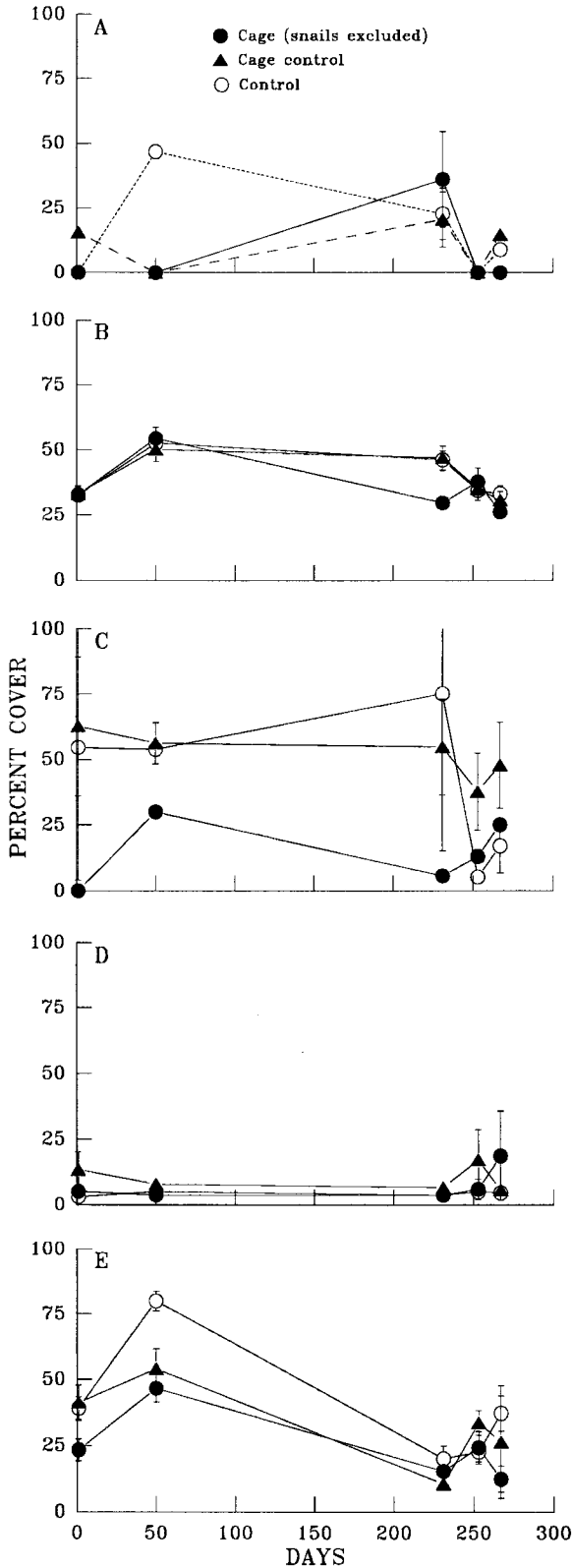


Fig. 4. Success of epibiont transplants between Placencia and Lark. *Diplosoma* (Dg), *Amphimedon* (Av), and *Aiptasia* (Ap) were transplanted from Lark to Placencia (and *in situ* at Lark). *Pellina* (Pc) was transplanted from Placencia to Lark (and *in situ* at Placencia). Bars show the mean % (cover) of the transplant remaining after 28 d when transplanted *in situ* (solid bars) or between sites (open bars). A * above a pair of bars indicates a significant difference between *in situ* and between-site transplants ($P < 0.05$, 2-tailed *t*-test on angularly transformed data).



length and width (± 1 mm) of the snails with vernier calipers.

Results – effects of predation on epibionts

Abundance of algae (*Bostrychia* spp. and *Caulerpa verticillata*) fluctuated throughout the year on both aerial and ground roots, but there was no treatment effect on these species (Figs. 6A, 6B). Barnacles (*Balanus* and *Chthamalus*) were more abundant on aerial roots (Fig. 6C) than on ground roots (Fig. 6D) and barnacle abundance remained relatively constant until November. At the beginning of November, snail abundance increased dramatically (Fig. 7) and barnacle abundance declined on unprotected aerial roots (Fig. 6C). Simultaneously, barnacle abundance increased on ground roots of caged plants and decreased in the caged controls (Fig. 6D). The barnacle abundance data (Figs. 6C, 6D) and the snail size data (Fig. 7) both indicate possible recruitment of these species in late November. However, we have no quantitative data on recruitment in these species. Snails had no effects on *Pellina* abundance on roots in any treatment (Fig. 6E).

Effects of epibionts on mangroves

Interactions with Melongena

To determine the effects of these faunal interactions on the trees themselves, we measured tree height and stem diameter ('dbh': above the highest prop root) in the *Melongena* experiment (above). There was a trend towards increased height and 'dbh' in control and cage-control trees where snails foraged on barnacles, relative to trees

Fig. 6. Results of the snail exclusion experiment on epibiont % cover ($x \pm 1$ SE) at Placencia. A: Algae (*Bostrychia* spp. and *Caulerpa verticillata*) on aerial roots; B: Algae on ground roots; C: Barnacles (*Balanus* and *Chthamalus*) on aerial roots; D: Barnacles on ground roots; E: Sponges (*Pellina*) on ground roots. Day 0 is 1 February 1988.

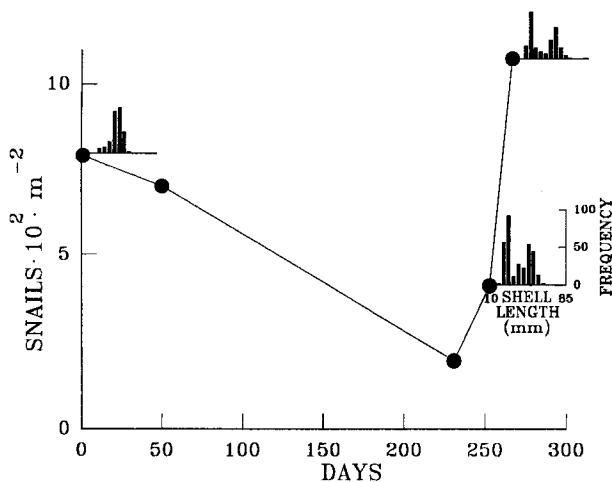


Fig. 7. Density (m^{-2}) and size distributions of *Melongena* during the snail enclosure experiment. Day 0 is 1 February 1988. The inset histograms show snail shell length distributions on 2 February, 26 November, and 14 December 1988. Shell length and width are allometrically correlated (width = $0.43 \cdot \text{length}^{1.22}$, $r^2 = 0.90$).

in snail enclosures ($P = 0.07$, Kruskal-Wallis non-parametric ANOVA). This result indicates some negative effects on tree growth by barnacles and possible amelioration of these effects by snails.

Interactions with isopods

Isopods (*S. terebrans*) were rare in these trees, but in another experiment at Placencia (Ellison & Farnsworth, in prep.), we found that *S. terebrans* reduced RGR_{root} by 60% relative to unattacked roots. At Twin Cays, Ellison & Farnsworth (1990) found that the root-boring isopod *Phycolimmoria* reduced RGR_{root} ($\text{cm cm}^{-1} \text{d}^{-1}$) of *R. mangle* by 55%. In that same study, we then asked if sponges (*Haliclona curacaoensis* and *Tedania*), ascidians (*Perophora formosana* and *Didemnum conchyliatum*), anemones (*Aiptasia*) and cyanobacteria affect isopod colonization of *R. mangle* roots. The sponges and ascidians inhibited isopod colonization, thus indirectly facilitating root growth (Ellison & Farnsworth, 1990). RGR_{root} of sponge-covered roots grew 83% faster than roots where we removed sponges *in situ* at Twin (Ellison & Farnsworth, 1990) and 50% faster than

roots from which we excluded all fauna (Ellison & Farnsworth, in prep.).

Discussion

Together, water conditions, wave exposure, root status (aerial or ground), proximity of roots to the barrier reef, and predation pressure influence epibiont distribution and diversity on Belizean mangrove roots. Epibiont species richness increases with increasing distance from the mainland (Table 1), and decreasing wave exposure and variability in water salinity and temperature (Figs. 4, 5; Bacon, 1971).

Epibiont species composition differs between aerial and ground roots. Species richness is higher on aerial roots than on ground roots. Although one might expect that ground roots would be more species-rich because of their greater age and size, we observed the opposite patterns. Ascidians and ephemeral hydrozoans are more speciose on aerial roots. These species may be outcompeted by those sponges and colonial anemones (as they are in Venezuela [Alvarez, I., 1989]) that are more abundant on older ground roots (Rützler, 1969; Sutherland, 1980). Young aerial roots may therefore serve as refugia for these weakly competitive ascidians and hydrozoans. We also observed a decline in fleshy algae abundance on ground roots relative to aerial roots. Aerial roots may provide fleshy algae an escape from herbivorous sea urchins (Taylor *et al.*, 1986). Other differences in species composition between aerial and ground roots appear to be site-specific (Fig. 2), and may reflect local variability in recruitment dynamics or epibiont succession (Sutherland, 1980; Rützler, 1987; Alvarez I., 1989).

Many root epibionts affect root growth and production directly (Perry, 1988; Ellison & Farnsworth, in prep.) and indirectly by ameliorating the negative effects of root-boring isopods (Ellison & Farnsworth, 1990). Isopods colonize only young, aerial, uncorticated roots (Rehm & Humm, 1973; Perry, 1988; Ellison & Farnsworth, 1990). At Twin, isopods significantly reduce RGR_{root} , but the presence of dense epibiont cover

prevents isopod colonization of roots (Ellison & Farnsworth, 1990). In Costa Rica, isopods (*Sphaeroma peruvianum* Richardson) also reduced root growth rate by 50% and net root production by 62% (Perry, 1988). Perry's experimental results also indicated some reduction in the effects of isopods in roots exposed to water column predators, but she was unable to identify the isopod predator.

In Belize, predation may also ameliorate potentially negative effects of epibionts on tree growth. In the mainland estuary at Placencia, *Melongena* predation reduces barnacle cover on both aerial and ground roots (Fig. 6). Those trees on which *Melongena* reduced barnacle cover grew more rapidly than trees with heavy barnacle cover. In the only other study of the effects of barnacles on mangrove roots, Perry (1988) found that *Balanus* spp. reduced *R. mangle* root growth rate (cm month^{-1}) by 30% and net root production ($\text{g root}^{-1} \text{month}^{-1}$) by 52% along the Pacific coast of Costa Rica. Perry (1988) found that barnacles were preyed upon by snails (*Thais kiosquiformis* Ducloux and *Morula lugubris* Adams) and hermit crabs (*Clibanarius panamensis* Stimpson) and proposed that predators indirectly facilitate tree growth.

Epibionts are found world-wide on mangrove roots (Mattox, 1949; Macnae & Kalk, 1962; Macnae, 1968; Rützler, 1969; Hutchings & Recher, 1974; Sasekumar, 1974; Pinto & Wignarajah, 1980; Sutherland, 1980; Alvarez I., 1989), but studies of their roles in the mangal have only just begun (Perry, 1988; Wada & Wowor, 1989; Ellison & Farnsworth, 1990; Rodriguez & Stoner, 1990). Historically, ecological studies of mangroves have emphasized floristic inventories (reviewed in Chapman, 1976; Tomlinson, 1986) and descriptions of energy flow and nutrient cycling (Golley *et al.*, 1962; Odum & Heald, 1972; Lugo & Snedaker, 1974). Although an oft-stated goal of faunistic studies in mangal is the determination of the trophic structure and energy budget of a given mangrove swamp (Sasekumar, 1984), this goal can not be achieved without detailed experimental studies. Intensive manipulative experiments in the marine rocky intertidal have revealed

trophic complexity and determinants of community structure not predicted by observation alone (*e.g.* Connell, 1961; Connell, 1975; Paine, 1966; Paine, 1988; Menge *et al.*, 1986; Menge & Sutherland, 1987). Similar studies in temperature zone salt marshes have documented major effects of benthic invertebrates on plant production (Bertness, 1984; Bertness, 1985). In mangrove swamps, recent studies have uncovered unexpected interactions between herbivorous crabs and plant zonation (Smith, 1987; Smith *et al.*, 1989), and between epibionts and root production (Perry, 1988; Ellison & Farnsworth, 1990; Rodriguez & Stoner, 1990). Long-term experimental studies on plant-animal interactions in mangroves throughout the world would likely yield new insights into community structure, functioning, and complexity.

Acknowledgements

EARTHWATCH (Center for Field Research), the National Geographic Society, and the Smithsonian Institution NMNH (with additional support from EXXON) supported this research. We thank six teams of dedicated EARTHWATCH volunteers for field assistance, and Chris, Skip, Jessica, and Meredith White for friendship and logistical support at Lark and Placencia. Meredith White collected the salinity data at Placencia. This is contribution no. 303, Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution, and paper 2 in the series 'The ecology of Belizean mangrove-root fouling communities'.

References

- Alvarez, I. A., 1989. Establecimiento, desarrollo y mantenimiento de una comunidad epibentónica tropical. Ph.D. Thesis, Universidad Central de Venezuela, Facultad de Ciencias. 150 pp.
- Bacon, P. R., 1971. The maintenance of a resident population of *Balanus eburneus* (Gould) in relation to salinity fluctuations in a Trinidad mangrove swamp. *J. exp. mar. Biol. Ecol.* 6: 187-198.
- Bertness, M. D., 1984. Ribbed mussels and *Spartina*

- alterniflora* production in a New England salt marsh. *Ecology* 65: 1794–1807.
- Bertness, M. D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* 66: 1042–1055.
- Chapman, V. J., 1976. Mangrove vegetation. J. Cramer, Vaduz, Lichtenstein, 447 pp.
- Connell, J. H., 1961. Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31: 61–104.
- Connell, J. H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In M. L. Cody & J. Diamond (eds), *Ecology and evolution of communities*. Belknap, Cambridge, MA, USA: 460–490.
- Ellison, A. M. & E. J. Farnsworth, 1990. The ecology of Belizean mangrove-root fouling communities: I. Epibenthic fauna are barriers to isopod attach of red mangrove roots. *J. exp. mar. Biol. Ecol.* 142: 91–104.
- Estevez, E. D. & J. L. Simon, 1975. Systematics and ecology of *Sphaeroma* (Crustacea: Isopoda) in the mangrove habitats of Florida. In C. Walsh, S. Snedaker & H. Teas (eds), *Proceedings of international symposium on biology and management of mangroves*. University of Florida, Gainesville, FL: 286–304.
- Farnsworth, E. J. & A. M. Ellison, 1991. Patterns of herbivory in Belizean mangrove swamps. *Biotropica* 23: 555–567.
- Golley, F., H. T. Odum & R. F. Wilson, 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* 43: 9–19.
- Hartshorn, G., L. Nicolait, L. Hartshorn, G. Bevier, R. Brightman, J. Cal, A. Cawich, W. Davidson, R. DuBois, C. Dyer, J. Gibson, W. Hawley, J. Leonard, R. Nicolait, D. Weyer, H. White & C. Wright, 1984. Belize country environmental profile. Trejos Hnos Sucs. S.A., San Jose, Costa Rica, 152 pp.
- Hutchings, P. A. & H. F. Recher, 1974. The fauna of Careel Bay with comments on the ecology of mangrove and seagrass communities. *Aust. Zool.* 18: 99–128.
- Kensley, B. & M. Schotte, 1989. Guide to the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington, D.C., 308 pp.
- Kjerfve, B., K. Rützler & G. H. Kierspe, 1982. Tides at Carrie Bow Cay, Belize. In K. Rützler & I. G. Macintyre (eds), *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities*. Smithsonian Inst. Press, Washington, D.C.: 47–51.
- Littler, D. S., M. M. Littler, K. E. Bucher & J. E. Norris, 1989. Marine plants of the Caribbean: a field guide from Florida to Brazil. Smithsonian Inst. Press, Washington, D.C., 263 pp.
- Littler, M. M., P. R. Taylor, D. S. Littler, R. H. Sims & J. N. Norris, 1985. The distribution, abundance, and primary productivity of submerged macrophytes in a Belize barrier-reef mangrove system. *Atoll Res. Bull.* 282: 1–18.
- Lugo, A. E. & S. C. Snedaker, 1974. The ecology of mangroves. *Ann. Rev. Ecol. Syst.* 5: 39–64.
- Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Adv. mar. Biol.* 6: 73–270.
- Macnae, W. & M. Kalk, 1962. The ecology of the mangrove swamps at Inhaca island, Mozambique. *J. Ecol.* 50: 19–34.
- Mattox, N. T., 1949. Studies on the biology of the edible oyster, *Ostrea rhizophorae* Guilding in Puerto Rico. *Ecol. Mono.* 19: 339–356.
- McLean, R. A., 1951. The Pelecypoda or bivalve mollusks of Porto Rico and the Virgin Islands. In *Scientific survey of Porto Rico and the Virgin Islands*. N.Y. Acad. Sci. 17: 1–183.
- Menge, B. A., J. Lubchenco, S. D. Gaines & L. R. Ashkenas, 1986. A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. *Oecologia (Berl.)* 71: 75–89.
- Menge, B. A. & J. P. Sutherland, 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130: 730–757.
- Odum, W. E. & E. J. Held, 1972. Trophic analyses of an estuarine mangrove community. *Bull. mar. Sci.* 22: 671–738.
- Paine, R. T., 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65–75.
- Paine, R. T., 1988. Food webs: road maps of interactions or grist for theoretical development. *Ecology* 69: 1648–1654.
- Perry, D. M., 1988. Effects of associated fauna on growth and productivity in the red mangrove. *Ecology* 69: 1064–1075.
- Pinto, L. & S. Wignarajah, 1980. Some ecological aspects of the edible oyster *Crassostrea cucullata* (Born) occurring in association with mangroves in Negombo lagoon, Sri Lanka. *Hydrobiologia* 69: 11–19.
- Rehm, A. & H. J. Humm, 1973. *Sphaeroma terebrans*: a threat to the mangroves of southwestern Florida. *Science* 182: 173–174.
- Ribi, G., 1982. Does the wood-boring isopod *Sphaeroma terebrans* benefit red mangroves (*Rhizophora mangle*)? *Bull. mar. Sci.* 31: 925–928.
- Rodriguez, C. & A. W. Stoner, 1990. The epiphyte community of mangrove roots in a tropical estuary: distribution and biomass. *Aquat. Bot.* 36: 117–126.
- Rützler, K., 1969. The mangrove community, aspects of its structure, faunistics and ecology. In *Lagunas Costeras, un Simposio*. UNAM-UNESCO, Mexico: 515–535.
- Rützler, K., 1987. Recruitment of sponges and their space competitors to settling plates in Twin Cay mangrove habitats. In K. Rützler (ed.), *Caribbean Coral Reef Ecosystems: progress report 1987*. National Museum of Natural History (Dept. of Echinoderms & Lower Invertebrates), Smithsonian Inst., Washington, D.C.: 23–24.
- Rützler, K. & I. G. Macintyre (eds), 1982. *The Atlantic bar-*

- rier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithsonian Institution Press, Washington, D.C., 539 pp.
- Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. *J. anim. Ecol.* 43: 51–69.
- Sasekumar, A., 1984. Methods for the study of mangrove fauna. In S. C. Snedaker & J. G. Snedaker (eds), *The mangrove ecosystem: research methods*. UNESCO, Paris, France: 145–161.
- Simberloff, D., B. J. Brown & S. Lowrie, 1978. Isopod and insect root borers may benefit Florida mangroves. *Science* 201: 630–632.
- Smith, T. J. III, 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology* 68: 266–273.
- Smith, T. J. III, H. T. Chan, C. C. McIvor & M. B. Robblee, 1989. Comparisons of seed predation in tropical tidal forests from three continents. *Ecology* 70: 146–151.
- Snedaker, S. C., 1973. Mangroves, isopods, and the ecosystem. *Science* 183: 1036–1037.
- Sokal, R. R. & F. J. Rohlf, 1981. *Biometry*, second edition. W. H. Freeman & Co., New York, N.Y., 859 pp.
- Sterrer, W. (ed.), 1986. *Marine fauna and flora of Bermuda*. John Wiley & Sons, New York, N.Y., 742 pp.
- Stoddart, D. R., F. R. Fosberg & D. L. Spellman, 1982. Cays of the Belize barrier reef and lagoon. *Atoll Res. Bull.* 256: 1–76.
- Sutherland, J. P., 1980. Dynamics of the epibenthic community on roots of the mangrove *Rhizophora mangle* at Bahia de Buche, Venezuela. *Mar. Biol.* 58: 75–84.
- Taylor, P. R., M. M. Littler & D. S. Littler, 1986. Escapes from herbivory in relation to the structure of mangrove island macroalgal communities. *Oecologia (Berl.)* 69: 481–490.
- Tomlinson, P. B., 1986. *The botany of mangroves*. Cambridge University Press, Cambridge, U.K., 413 pp.
- Wada, K. & D. Wowor, 1989. Foraging on mangrove pneumatophores by ocypodid crabs. *J. exp. mar. Biol. Ecol.* 134: 89–100.
- Wahl, M., 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar. Ecol. Prog. Ser.* 58: 175–189.
- Weerdt, W. H. de, K. Rützler & K. P. Smith, 1991. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters. *Proc. Biol. Soc. Wash.* 104: 189–205.