Original papers

Escapes from herbivory in relation to the structure of mangrove island macroalgal communities

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Summary. Some shallow habitats that surround mangrove islands exhibit abruptly discontinuous macrophyte boundaries; in other regions, plant distributional patterns are less defined. Where distinct boundaries do occur, fleshy algae predominate on the roots of the red mangrove, *Rhizophora mangle*, which do not contact the bottom sediments ("hanging roots"), while calcifying algae dominate on the substratum-penetrating roots and banks (=embedded-root habitat) surrounding the mangrove thickets. Considerable natural-history and floristic information reveals that the fleshy hanging-root species are not specialists for that type of habitat. Experimental transplants showed that on banks and embedded roots where there typically are abundant macroherbivores (particularly sea urchins), most fleshy algae are eliminated.

The dominants of the hanging-root habitat (e.g., *Acanthophora spicifera, Spyridia filamentosa, Caulerpa racemosa* var. *occidentalis*) are 6–20 times more susceptible to herbivores than the dominants of the embedded-root habitat (e.g., *Halimeda opuntia* f. *triloba, H. monile*). Consequently, we suggest the former are relegated to the spatial refugia from herbivores (=non-coexistence escapes) provided by the hanging roots. Factors associated with these palatability differences include higher average calorific values (6.5 times) of the fleshy hanging-root dominants, greater proportions of organic content (2.6 times) and the general absence of calcification. The dominants of the embedded-root habitat show reduced edibility as a probable consequence of low calorific values, heavy calcification and potential herbivore-detering secondary metabolites. Correlative evidence and preliminary experimental results tentatively indicate that, in the absence of macroherbivores, the hanging-root dominants, which exhibit production rates 4.7 times greater than the dominants of the embedded-root habitat, are better competitors for space.

We suggest that variations in herbivory are responsible, in part, for maintaining greater algal diversity in mangrove systems. At a study site with abundant sea urchins, five algal species were found only in the embedded-root habitat three species were confined to the hanging roots, while three others occurred in both. At an urchin-free site, no macrophytes were found only on embedded-root substrata, while one (in trace amounts) was found only on hanging-root habitat and eight occurred in both. We predict that in the absence of herbivores, the species assemblage characteristic of the hanging-roots would exclude many of the dominants from the embedded-root habitat.

A primary goal in ecology is the elucidation of factors that influence the distributions and abundances of individual populations and the organization of communities. In many ecosystems, ecologists have observed and studied abruptly discontinuous spatial patterns, for example, the vertical zonation of montane trees and intertidal organisms, and the horizontal biotic patterns on north versus south facing slopes and across subtidal reef flats. We have learned that competitive interactions can yield distinct boundaries (Connell 1961; see recent reviews of Schoener 1983; Connell 1983; cf. Underwood and Denley 1984) which derive from the ability of an inferior competitor to maintain a population outside the region that a superior competitor can inhabit [i.e., a spatial or noncoexistence escape *sensu* Lubchenco and Gaines (1981)]. Disturbances, such as those caused by wave action (Sousa 1979) or sand scouring (Taylor and Littler 1982) along coastlines can pattern biotic communities, as can physiological constraints imposed by physical environmental factors such as substrata composition (Whittaker 1954), light (Lüning and Dring 1979), sand burial (Taylor and Littler 1982) or desiccation (Hodgson 1980). Discontinuous patterns also may result from variation in consumer activity and the relationship of this activity to the escape potentialities of prey species (see review by Lubchenco and Gaines 1981). For example, prey may develop coexistence escapes, through toxic chemistry, morphological attributes, and low energetic return, or they may utilize spatial escapes (refugia) in response to selective pressures of herbivores. While the above mechanisms may independently structure certain communities, a consideration of the potential variable interplay between species interactions (both competitive and predator-prey), and physical aspects of the environment (stress and disturbance) is needed (Hay 1981a; Taylor and Littler 1982).

The present study examines possible competitive, predatory, and physical/chemical influences on the distribution and local diversity of both plant species and plant structural/morphological types living in a Caribbean mangrove island ecosystem. By employing quantitative assessments of pattern in conjunction with experimental manipulations,

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we address the following hypotheses: (1) Most fleshy and filamentous algae are relegated to substrata that are inaccessible to grazers because the herbivores eliminate them from accessible areas; i.e., such plants must utilize spatial escapes beyond the foraging range of herbivores. In this study, the refuge habitats we have focused on are roots of the red mangrove, *Rhizophora mangle* L., that are submerged below the water line but do not penetrate the sediment (see study site description). (2) Algae in these refuge habitats are not specialists for the conditions of the refugia but are physiologically and morphologically capable of ample growth and reproduction in other regions. (3) Species confined to refuge habitats show reduced allocation to herbivore defenses in contrast to the dominant species of the habitats accessible to herbivores. Morphological and chemical mechanisms for herbivore resistance will be more developed in the latter group. We assume that in plants (terrestrial or aquatic), resources allocated to a particular metabolic process or structure usually are unavailable for, or interfere with, other potential uses. Therefore, if minimal allocation of resources to herbivore deterrence is found (e.g., in many foliose and filamentous algae), then (4) such plants should exhibit greater photosynthetic capabilities and growth rates enabling them to outgrow and competitively displace the more herbivore-resistant macrophytes in the absence of grazing. Conversely, allocation of resources to structural herbivore defense should result in reduced photosynthetic apparatus and a lower capacity for net production. Lastly, we hypothesize that (5) herbivores, in conjunction with the existence of refugia, maintain higher diversity of both macroalgal species and structural types in the mangrove system.

Study site

This study was conducted from the Smithsonian Institution's field station on Carrie Bow Cay, Belize between April 1980 and March 1983. The study sites (Fig. 1) are located on Twin Cays (16°50′ N, 80°06′ W), a mangrove island complex about 1 km long, 1 km wide and 1 km landward of the barrier reef crest. A description of Twin Cays and surrounding regions may be found in Rützler and Macintyre (1982). One habitat of the mangrove island system, here referred to as the *embedded-root habitat*, includes the prop roots of *Rhizophora mangle* that are embedded in the sediments and the more-or-less horizontal sediment base around the edge of the mangrove cays. In contrast, what we designate as the *hanging-root habitat* comprises the prop roots of *R. mangle* that are outermost in the mangrove thicket. These roots extend well below the waterline but do not reach the bottom (cf. Figs. 30a and 30b in Rützler and Macintyre 1982).

All of the transplant experiments were conducted at the northern end of the mangrove island complex on both sides of a narrow (~20 m) channel (site A, Fig. 1, referred to as the urchin site). The seaweed assemblage on the embedded-root habitat, adjacent to dense stands of *Rhizophora mangle*, is dominated (Littler et al. 1985) by calcareous, siphonaceous green algae, primarily *Halimeda opuntia* f. *triloba* (Decaisne) Barton with lesser abundances of *H. incrassata* (Ellis) Lamouroux, *H. monile* (Ellis and Solander) Lamouroux and *Penicillus capitatus* Lamarck. *Thalassia testudinum* Banks ex König is found only in very low abundance in this area. A distinct halo virtually devoid of *T. testudinum*, like those that circumscribe many Caribbean reefs
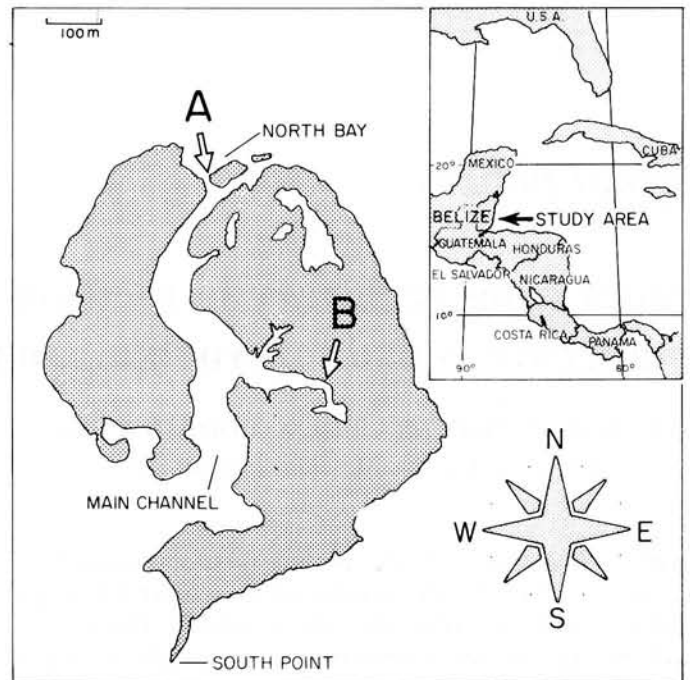

Fig. 1. Location of the study sites at Twin Cays in the Belize barrier reef/mangrove island system

(Ogden et al. 1973; Randall 1965; Earle 1972; Dahl 1973), is found on much of the submerged substrata adjoining these mangrove islands.

The hanging prop roots (those not touching the sediment) commonly provide substrata for fleshy frondose seaweeds [e.g., *Acanthophora spicifera* (Vahl) Børgesen, *Caulerpa racemosa* v. *occidentalis* (J. Agardh) Børgesen] and filamentous algae [e.g., *Spyridia filamentosa* (Wulfen) Harvey] as well as the calcified alga *Halimeda opuntia* f. *triloba*. Sponges [e.g., *Tedania ignis* (Duchassaing and Michelotti), *Ircinia felix* (Duchassaing and Michelotti) and *Lissodendoryx* sp. (Rützler and Macintyre 1982] are also common space occupiers on hanging roots.

The most conspicuous mobile animals in the mangrove habitat are sea urchins and fishes. The urchin fauna includes *Diadema antillarum* Philippi, *Lytechinus variegatus* (Lamarck), *Eucidaris tribuloides* (Lamarck), *Echinometra lucunter* (L.), *E. viridis* Agassiz and rarely, *Tripneustes ventricosa* (Lamarck). Grazing fishes are not common, and primarily consist of juvenile parrotfishes [mostly *Scarus croiserti* (Randall) generally associated with seagrass beds] and damselfishes.

The urchin-free study area (site B, Fig. 1) is also adjacent to a channel but located centrally within the more protected island group. The most striking biotic difference between the two sites is the absence of sea urchins at site B. The only common macrograzer is the crab, *Mithrax spinosissimus* Lamarck which is also common at site A. The absence of sea urchins may perhaps be a result of infrequent elevated water temperatures (>32 C). Temperature recordings taken with minimum/maximum thermometers at site B and at an open-channel site approximately 250 m south of site A have indicated maxima of 32 C and 31 C, respectively (K. Rützler, pers. comm.). While *Halimeda opuntia* is common both on the embedded-root and hanging-root substrata, fleshy and filamentous algae (*Caulerpa racemosa*, *C. mexicana* (Sonder) J. Agardh, *C. sertularioides* (Gmelin) Howe, *C. verticillata* J. Agardh, *Anadyomene stellata* (Wul-

fen) C. Agardh, *Spyridia filamentosa*) are also abundant within both habitats (see results).

Methods

Urchin densities were measured using a 1.0 m² quadrat haphazardly placed on the substratum along the penetrating roots of *Rhizophora mangle* (20 times per site). Visual counts of fishes were completed by divers to identify the common residents of both sites.

Macrophyte abundances were measured in the embedded-root habitat on and around the bases of the substratum-penetrating prop roots of *Rhizophora mangle*; (see Figs. 30a, c of Rützler and Macintyre 1982) and on the roots that do not penetrate the substratum (Rützler and Macintyre 1982, their Fig. 30b). For the cylindrical roots, cover was determined for the surface facing away from the bank and toward the open channel. In both habitats, cover was estimated using twenty 0.15 m² photo-quadrats. Color transparencies were scored in the laboratory using a ~250-dot matrix per each quadrat and two replicate scorings.

The importance of macrograzers to the algal composition of the embedded-root habitat was determined in two ways. Hanging roots ($N = 10$) with attached fleshy and filamentous algae (e.g., *Acanthophora spicifera, Caulerpa racemosa* and *Sypridia filamentosa*) were cut off and attached by cable ties to adjacent (~0.5-m distance) embedded roots to allow urchins access to the hanging-root flora. These transplants were attached so that they remained suspended above the bank sediments. Similarly, other hanging roots ($N = 10$) were removed and then reattached by cable ties to serve as controls in the assessment of handling effects. Environmental conditions other than light levels did not differ substantially between the two habitats. Distributional observations (see results) further revealed that the three algal species examined can become abundant under lower light levels such as those experienced along the embedded-root habitat. The transplanted and control roots remained intact throughout the experiments (96 h) with no deterioration that would have affected the algal epibiota. Changes in the cover of each sample (due to grazing, tissue death or growth) were quantified using the point-intercept technique on color transparencies as described previously.

While the above experiment examined whether herbivory was important to algal assemblages, the following was undertaken to differentiate between macroherbivores (primarily sea urchins) and other losses (e.g., microherbivores). Samples (~10 cm²) of 4 macrophytes (*Acanthophora spicifera, Caulerpa racemosa, Laurencia papillosa* (Forsskal) Greville and *Spyridia filamentosa*) collected from mangrove roots and nearby areas were photographed with a close-up lens. The samples were then gently placed in clothespin holders that were attached to small, dead coral fragments and transplanted to the embedded-root habitat in three treatments ($N = 6$ per species per treatment) as follows. In the cage treatment, individual samples were placed within six, $20 \times 30 \times 15$-cm aviary wire cages (~1.5-cm diameter mesh) that were fastened to the bottom among prop roots, thereby excluding macrograzers (urchins and fishes) but remaining open to micrograzers. Samples to control for cage effects were placed under six wire roofs (20×30 cm) suspended 15–20 cm above the substratum. Transplant-control samples were placed in the vicinity of cages and roofs but

not shielded by any cage material. The experimental samples were placed in groups containing one sample of each treatment. After 24–48 h, the samples were retrieved and again photographed. Changes in the cover of each sample were quantified using the point-intercept technique on the color transparencies with two replicate scorings per sample on both initial and final photosamples.

Distributional observations from our studies around the Belize barrier reef system and others, (Børgesen 1913, 1917, 1918, Taylor 1960; Earle 1972; Dahl 1973; Norris and Bucher 1982) were used to ascertain whether the fleshy frondose and filamentous macrophytes comprising the hanging-root flora might be specialized for that particular type of habitat.

We contrasted the hanging- and embedded-root floras with regard to herbivore-deterrence characteristics by measuring the organic tissue levels, calorific contents and grazer resistances of algal species. The percentage of organic tissue was determined for samples that were cleaned, dried to constant weight at 80 C and then combusted for 24 h at 500 C. Calorific values were obtained with a Parr (model 1243) semi-micro oxygen bomb calorimeter. Endothermy corrections were made for samples containing $CaCO_3$. The data are reported as $kcal \cdot g^{-1}$ dry wt determined on three replicate samples of each species.

Algal resistances to herbivory were examined using three separate methodologies (see Littler et al. 1983b). In the suspended-line method, clumps (~10 cm²; $N = 12$ per species) of each plant were secured between the twists of a three-stranded, white nylon line (2 mm) at 0.5-m intervals. Species were placed along the lines in a random arrangement. The lines were photographed then tied to rock outcrops in the water column in a 1.5 m-deep channel for a 6-h daylight period. The lines were placed in a calm-water, back reef location to minimize losses due to breakage. Also, the lines were shaken after attachment to ensure secure attachment. Any pieces that were dislodged were immediately refastened within the strands of the line at the appropriate location. Damselfish territories were avoided. This method examined the algal resistances to the entire guild of herbivorous fishes (primarily surgeonfishes and parrotfishes) and did not distinguish preferences by species. Lewis (1985), working in a nearby location, indicated the important fish grazers to be *Sparisoma rubripinne* Valenciennes, *S. chrysopterum* Bloch and Schneider, *Acanthurus bahianus* Castelnais and *A. coeruleus* Bloch and Schneider.

Resistance to general herbivory was assessed with the weighted-grid method. Species were randomly distributed (~10-cm² clumps; $N = 24$ per species) under elastic bands on four 70×70 cm weighted, plastic grids. The grids were placed on the bottom of a 1.5-m deep channel for 24 h. Control lines and grids placed in herbivore-free areas showed no losses over the duration of the experiments.

The captive-urchin method was used to assess algal resistances to herbivory by *Diadema antillarum*. Sixteen medium-sized (~3-cm mean test diameter) *D. antillarum* were placed in separate 2.0-l wide-mouth jars. Sixteen jars with urchins and 8 control jars without urchins were submerged in large, shaded seawater aquaria with flowing seawater. Paired clumps ~10-cm² of different algae were placed in each jar; one sample of each pair was *Ulva lactuca* L. which served as a basis for comparison between species throughout the experiment. Feeding trials lasted 10 h per species. In all three methods, the samples were photographed before

and after a 10-h feeding trial and the percent thallus area (two dimensional) lost to grazing for each specimen was calculated from color transparencies with the point-intercept method. Controls without urchins showed no gains or losses during the experiments and no significant reduction in the consumption of *U. lactuca* occurred over the course of the experiment.

To examine to relative competitive abilities in the absence of grazing pressure, an additional transplant experiment was performed on the dominant alga from each of the habitats studied. The hanging-root habitat was chosen as a grazer-free site for the transplants. Both *Acanthophora spicifera* and *Halimeda opuntia* (dominants of the hanging-root and embedded-root habitats, respectively) are found attached to the hanging roots around Twin Cays; both are habitat and substratum generalists (Taylor 1960). These two macrophytes were attached securely to similar, cleaned hanging roots, singly or together ($N = 10$ per treatment), with nylon cable ties during December 1980. Both species are capable of adventitious attachment of thallus parts. Quantities of the initial transplants were determined by the photographic/point-intercept methodology. After 15 mo, the roots were again sampled to determine the relative successes of each species.

In addition, the net production capabilities of the dominant macrophytes were used as an index of growth and competitive abilities. Primary production rates are directly correlated (e.g., Wassman and Ramus 1973; Brinkhuis 1977) with the potentials of algae to grow rapidly and, presumably, to exploit space, nutrient and light resources. Measurements of net photosynthesis were made by incubating samples ($N > 4$ per species) in 0.5-m deep water on the shallow reef flat in a current channel. Incubations were conducted between 0900 and 1500 h under light levels averaging 1,500 $\mu E \cdot m^{-2} \cdot s^{-1}$ P.A.R. Net photosynthesis was calculated as mg carbon $\cdot g^{-1}$ dry algal wt $\cdot h^{-1}$. See Littler (1979) for details on methods.

Results

Sea urchins represent a conspicuous component of the fauna at and around the site A location at Twin Cays. Total urchin density assessed during April 1982 averaged 4.4 urchins $\cdot m^{-2}$ in the embedded-root habitat. *Echinometra viridis*, *E. lucunter* and *Lytechinus variegatus* dominated the sea urchin assemblage (Table 1); *Diadema antillarum* and *Eucidaris tribuloides* were less than 5% and 2% of the total urchin densities, respectively. The sea urchin *Tripneustes ventricosa* was present but not recorded in quadrats. The densities of urchins did not change noticeably over the period of our herbivory studies. During approximately 20 person-hours of searching, no urchins were encountered at site B.

Fish diversity at the study sites was not high (Table 2); 13 taxa were recorded at site A, and 10 at site B. The most common species were snappers, grunts, parrotfishes and damselfishes. Densities were low relative to nearby reef habitats. There appear to be no major differences between the fish faunas at the two sites.

Halimeda opuntia was consistently the most abundant plant of the embedded-root habitat (Table 3); it was equally abundant at sites A and B during April 1982 and in March 1983 ($P > 0.05$, Mann-Whitney U-Test). The second most common species on the embedded-root habitat at the urchin

Table 1. Mean densities of sea urchin species at Site A (± 1 standard error). $N = 20$

Species	Density (number $\cdot m^{-2}$)
Echinometra viridis	1.60 ± 0.60
E. lucunter	1.30 ± 0.60
Lytechinus variegatus	1.20 ± 0.30
Diadema antillarum	0.20 ± 0.08
Eucidaris tribuloides	0.05 ± 0.05
Total densities	4.40 ± 1.00

Table 2. Fish taxa occurring at the Twin Cays study sites during a survey on 23 April 1985. A + indicates the taxon was encountered at the site during our fish survey

Taxa (common name)	Site A	Site B
Strongylura notata (redfin needlefish)	+	+
Sphyraena barracuda (great barracuda) juvenile	+	+
Caranx sp. (jack) juvenile		+
Gerres cinereus (yellowfin majorra)	+	+
Ocyurus chrysurus (yellowtail snapper) juvenile	+	+
Lutjanus apodus (schoolmaster snapper) juvenile	+	+
Lutjanus jocu (dog snapper) juvenile	+	+
Haemulon spp. (grunts)	+	+
Chaetodon capistratus (foureye butterfly fish)	+	+
Eupomacentrus sp. (damselfish)	+	+
Abudefduf saxatilis (sergeant major)	+	
Thalassoma bifasciatum (bluehead wrasse)	+	
Scarus croicensis (striped parrotfish)	+	
Sparisoma radians (bucktooth parrotfish)	+	

site (site A) was *H. incrassata* (Table 3) while the more common taxa from the urchin-free embedded-root habitat (site B) included filamentous diatoms, *Spyridia filamentosa*, *Caulerpa racemosa*, *C. mexicana* and *C. verticillata*. In the hanging-root habitat at site A (Table 3), the most common species was *C. racemosa* (16.4% mean cover) followed by *Acanthophora spicifera* (11.4%) and filamentous diatoms (4.3%). Filamentous diatoms (34.6%) dominated the hanging roots at site B, followed by *Halimeda opuntia* [20.6%, contrary to predictions of our competition hypothesis]), *Spyridia filamentosa* (12.8%) and *Anadyomene stellata* (7.7%).

At the urchin site, five algal species were found exclusively in the embedded-root standing stock samples (Fig. 2), while three species were exclusive to the hanging-root samples. At the urchin-free site, three species were found solely in the embedded-root samples, one (in trace amounts) was specific to hanging-root substrata and eight were found on both.

We have divided the macrophytes into two broad structural groups (Fig. 3): (1) the calcifying group including *Halimeda* spp. (three species), *Penicillus capitatus* Lamarck and *Amphiroa rigida* var. *antillana* Børgesen; and (2) the noncalcareous group, which includes filamentous (*Spyridia filamentosa* and diatoms), saccate (*Valonia ventricosa* J. Agardh), sheet-like (*Anadyomene stellata*) and coarsely-branched (*Caulerpa* spp., *Acanthophora spicifera*) algae. The two groups are functionally different in respect to their palatability to grazers (and other features, see below) with

Table 3. Habitat distribution and abundance (% cover) of marine macrophyte species. Values represent mean percentage cover ±1 standard error; site A, with urchins; site B, urchin free (see text for site descriptions); TR (trace), ≤0.1% cover

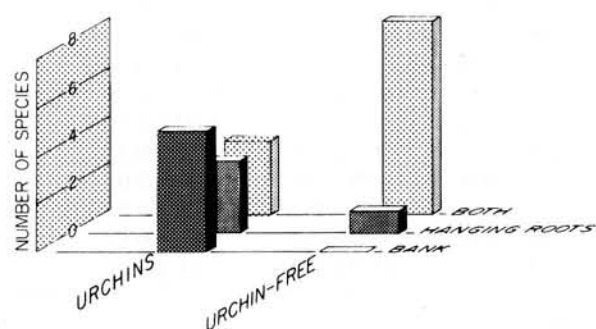| Macrophyte species	Embedded-root habitat 1982		1983		Hanging-root habitat 1983	
	Site A	Site B	Site A	Site B	Site A	Site B
Halimeda opuntia f. triloba	46.4±4.8	35.3±5.1	20.3±4.4	25.0±6.8	TR	20.6±8.1
H. incrassata	3.6±1.8	–	0.6±0.4	–	–	–
H. monile	0.9±0.5	–	0.2±0.2	–	–	–
Penicillus capitatus	0.9±0.4	–	TR	–	–	–
Valonia ventricosa	–	–	TR	–	–	–
Caulerpa sertularioides	–	–	–	TR	–	0.5±0.3
C. racemosa var. occidentalis	–	7.2±2.4	–	2.1±0.8	16.4±4.8	5.3±2.6
C. mexicana	–	–	–	1.8±1.4	–	1.6±1.6
C. verticillata	TR	TR	TR	1.9±0.9	TR	0.2±0.2
C. peltata	–	–	–	–	–	TR
Anadyomene stellata	–	–	–	TR	–	7.7±6.1
Acanthophora spicifera	–	–	–	–	11.4±3.9	–
Spyridia filamentosa	–	3.5±1.7	–	–	2.1±2.1	12.8±7.4
Amphiroa rigida var. antillana	–	–	TR	–	–	–
Filamentous diatoms	0.6±0.3	8.7±2.5	TR	19.5±4.0	4.3±2.4	34.6±11.1
N (quadrats)	21	17	18	15	16	10

Fig. 2. Richness of macroalgal species exclusively in embedded-root habitat (front, darkly-shaded histograms), hanging-root habitat (middle, medium shading) or on both habitats (rear, lightly shaded) from 20 0.15-m^{-2} quadrat samples at both the sea-urchin and urchin-free sites
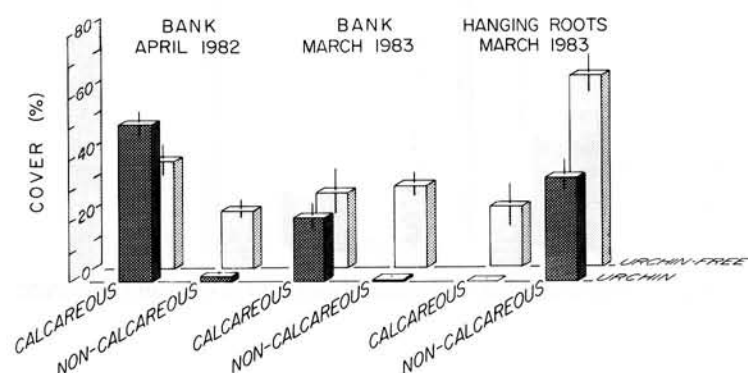

Fig. 3. Distributions and percentage cover (±1 standard error) of the calcareous and non-calcareous seaweed structural groups in the Twin Cays system at the urchin (front, darkly-shaded histograms) and urchin-free (rear, lightly shaded histograms) sites

the calcareous forms showing significantly greater herbivore resistances.

Comparisons of macrophyte abundances in the embedded-root habitat show no differences for calcareous algae at the two sites (April 1982: site A = 51.8%; site B = 35.3%;

$P > 0.05$, March 1983: site A = 21.4%, site B = 26.8%; $P > 0.1$, Mann-Whitney U-Tests), while the urchin-free site (site B) supported significantly more non-calcareous macrophytes than the urchin site (April 1982: site A = 1.4%, site B = 19.4%; March 1983: site A = 0.1%, site B = 27.3%; $P < 0.002$. On hanging roots, both calcareous and non-calcareous macrophytes were more abundant at site B (calcareous seaweeds: site A, 0.03%; site B, 20.2%; $P < 0.002$; non-calcareous: site A, 34.4%; site B, 62.9%; $P < 0.02$), suggesting that macrophyte population variation is affected by factors in addition to variation in macrograzers.

The results of the first series of experimental transplants support the hypothesis that herbivores influence the habitat distribution of macrophytes in the mangrove island system. Following 96 h of exposure to grazers on the embedded-root habitat, all transplanted roots had lost >99% of their attached algae; two of these had sea urchins (*Diadema antillarum*) grazing on their surfaces when collected. Controls showed no discernible changes in algal abundance during the same period.

The second manipulative experiment (Table 4) corroborates previous evidence that herbivory can influence macrophyte distribution and further shows that the larger herbivores (i.e., those excluded by the aviary wire cage) are of considerable importance. All species exhibited significantly greater losses [Table 4; $P < 0.05$, Friedman's test (Zar 1974)] when exposed to macroherbivores than when access was prevented by the cages. In every case, the two treatments with exposure to herbivores (the cage controls and controls) were statistically similar (Table 4). These results indicate, however, that macrograzer activity is not solely responsible for the biomass lost in the experiment. Micrograzer activity (i.e., grazers capable of entering the 1.5 cm mesh in the wire cages) is probably also important. L. Coen (pers. comm.), working in the same mangrove island system, has found abundant populations of herbivorous amphipods and small crabs.

We have listed (Table 5) quantitative attributes of the macrophytes which, hypothetically, relate to their abilities

Table 4. Percentage ($\pm$1 standard error) of seaweed cover removed by herbivores in embedded-root habitats. The P-values are listed for pairwise comparisons (Friedman's test) of treatments (X, caged = protected from herbivores; CC, cage control; C, control = exposed to herbivores)

Species	Date	Treatments			N	P-values of statistical comparisons		
		Cage (X)	Cage control (CC)	Control (C)		X-CC	X-C	C-CC
Acanthophora spicifera	4/80	3.4 ± 2.1	49.9 ± 15.0	50.5 ± 15.0	6	<0.02	<0.02	>0.10
Spyridia filamentosa	4/80	27.2 ± 14.0	67.9 ± 14.1	79.7 ± 8.5	6	<0.026	<0.002	>0.41
C. racemosa var. occidentalis	4/80	63.3 ± 11.9	91.0 ± 4.9	92.6 ± 6.3	6	<0.01	<0.01	>0.26
Acanthophora spicifera	12/80	40.9 ± 12.7	82.6 ± 6.2	85.8 ± 8.7	11	<0.02	<0.02	>0.47
Laurencia papillosa	12/80	0.9 ± 0.9	28.2 ± 11.1	47.8 ± 16.9	6	<0.05	<0.03	>0.20

Table 5. Comparative morphological/functional attributes of the marine seaweeds.[a] Variation about the means is expressed as $\pm$1 standard error. NA indicates the values are not available

Species	Suspended lines (% eaten)	Weighted grids (% eaten)	Captive Diadema (% eaten)	Calories (Kcal·dry g^{-1})	% Organic tissue	Productivity (mg C·g^{-1}·h^{-1})
Caulerpa mexicana	86.8 ± 5.8	NA	NA	3.52 ± 0.04	24.3 ± 0.2	0.51 ± 0.11
C. racemosa	81.9 ± 5.5	100.0 ± 0.0	NA	2.56 ± 0.05	50.1 ± 1.7	0.89 ± 0.09
C. sertularioides	64.4 ± 5.7	NA	NA	3.18 ± 0.02	32.5 ± 0.4	1.13 ± 0.56
C. verticillata	90.0 ± 6.9	NA	NA	4.06 ± 0.02	37.5 ± 0.3	0.66 ± 0.07
C. peltata	97.1 ± 1.3	NA	NA	2.16 ± 0.04	49.9 ± 2.3	1.04 ± 0.28
Acanthophora spicifera	99.6 ± 0.5	37.3 ± 5.3	79.7 ± 9.6	1.62 ± 0.03	42.1 ± 0.3	1.25 ± 0.13
Spyridia filamentosa	NA	93.3 ± 3.3	NA	0.72 ± 0.02	37.7 ± 1.6	2.92 ± 0.70
Anadyomene stellata	99.6 ± 0.2	NA	NA	NA	56.7 ± 0.6	1.20 ± 0.24
Halimeda monile	4.8 ± 2.1	17.7 ± 7.1	7.7 ± 2.6	0.51 ± 0.03	12.9 ± 0.9	0.20 ± 0.05
H. opuntia f. triloba	NA	NA	NA	NA	10.1 ± 0.8	0.21 ± 0.13
Penicillus capitatus	NA	0.0 ± 0.0	NA	0.69 ± 0.02	33.7 ± 2.2	0.56 ± 0.07
Amphiroa rigida var. antillana	57.9 ± 9.1	2.1 ± 2.1	1.6 ± 1.6	0.11 ± 0.02	11.3 ± 0.2	0.11 ± 0.01

[a] Some of these data have been extracted from Littler et al. (1983a) and Littler et al. (1983b)
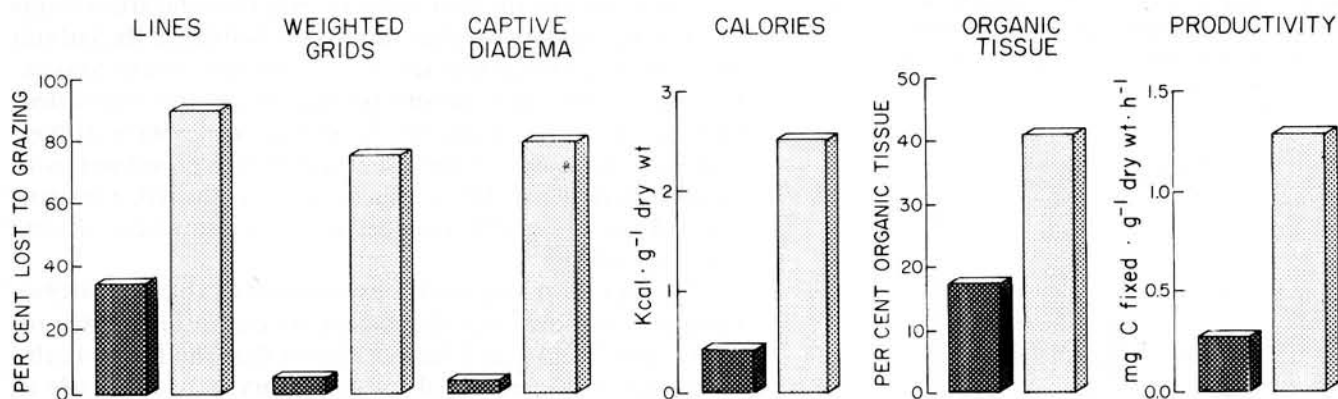

Fig. 4. Comparative morphological/functional attributes of the calcareous (dark histograms) and non-calcareous (light histograms) seaweed groups from the Twin Cays system

to deter or discourage herbivory (Littler and Littler 1980; Littler et al. 1983a). The non-calcareous forms (Fig. 4) are more susceptible to grazers than the calcareous algae (average loss on lines, 88% vs. 14%, respectively; on weighted grids, 77% vs. 7%; with captive *Diadema antillarum,* 80% vs. 4%). The non-calcareous group also exhibits higher calorific values than the calcareous group (average 2.6 kcal·g dry wt^{-1} vs. 0.4) and greater percentages of organic tissues (36% vs. 14%).

With regard to the net photosynthetic rates for the individual macrophyte species (Table 5) and the two structural-group averages (Fig. 4), the non-calcareous species exhibited a 5-fold greater mean apparent production rate (1.28 mg C·g dry wt^{-1}·h^{-1}) as compared with the calcareous algae (0.27 mg C).

The fleshy species, *Acanthophora spicifera,* showed higher cover than the calcified *Halimeda opuntia* on the roots containing transplanted thalli of both. The experimental results, however, are not conclusive, as the ability of *H. opuntia* to be successfully transplanted was not well established. Roots that initially had an average *Halimeda* planar cover of 455 cm^2 ($N=7$) and 108 cm^2 of *A. spicifera*
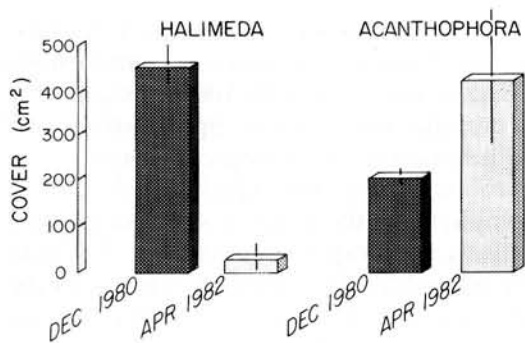
Fig. 5. Percent cover (±1 standard error) of macrophytes experimentally transplanted to cleaned, hanging roots of *Rhizophora mangle* during December 1980 and 16 months later (April 1982)

(Fig. 5), completed the 15-mo experiment with the following biotic abundances: *A. spicifera*, 432 cm²; *H. opuntia*, 38 cm²; *Spyridia filamentosa*, 36 cm²; filamentous Rhodophyta, 7 cm². The last two taxa were not experimentally transplanted, but are fleshy algae that recruited onto the hanging roots during the experiment. Three of the 10 transplant roots were lost, six of the seven remaining replicates experienced 100% mortality of the *H. opuntia*, while four showed increases in *A. spicifera*. Overall, *A. spicifera* increased by 402%, while *H. opuntia* exhibited a 92% decrease (Fig. 5). Of the 20 single species (control) transplants, 7 of the 10 roots with transplanted *A. spicifera* and 6 of the 10 *H. opuntia* controls were lost. All of the remaining exhibited less than one percent cover of algae at the termination of the experiment.

Discussion

At site A, sea urchins are present and abundant and the boundaries between the embedded-root habitat and the hanging roots are distinct, coinciding with the steeply-sloped or undercut edges of the mangrove island. Seaweeds are partitioned with respect to these boundaries (Table 3), resulting in an overall greater number of species and morphological types. The causes of such distinct boundaries in communities have been attributed to (1) specialization in response to physical conditions and resultant physiological constraints leading to resource partitioning (Klopfer 1959; Williams 1964; Terborgh 1971; Taylor 1982), (2) competitive interactions (Connell 1961; Daubenmire 1966; Grant 1972; Colwell 1973; see Schoener 1983; Connell 1983 for reviews) and (3) the activity and selectivity of consumers (Harper 1969; Connell 1971; Paine 1974; Lubchenco 1978; Hay 1981a). All of these factors have been implicated as mechanisms that may enhance the species richness (within- or between-habitats, MacArthur 1965) of natural communities. In the mangrove system studied, both competition and consumers may act independently and in concert to differentially influence plant distributions and diversity.

A survey of the literature concerning distributions of the species comprising the hanging-root flora (e.g., *Acanthophora spicifera*, *Spyridia filamentosa*, *Caulerpa racemosa*), in conjunction with the findings reported herein, support our contention that they are not specialists for hanging-root substrata. These algae, in the absence of herbivores, utilize many habitats (roots, shells, coral fragments) for attachment and on rare occasions can be found growing on the embedded-root habitat at site A. *Acantho-*

phora spicifera is a habitat generalist in shallow waters (Taylor 1960) and is common on both mangrove roots and exposed localities (Børgesen 1918). It has been reported (Doty 1961; Russell 1981) as an invasive "weed-species" introduced to Hawaiian reefs from Guam. In the barrier reef system around Twin Cays, *A. spicifera* is common (Norris and Bucher 1982) on sandy-rubble substrata in shallow back-reef locations having low levels of herbivory (Hay 1981b). This alga also extends into deeper waters where herbivory is low; for example, it is commonly found on sand-plains below 20 m in the Virgin Islands (Earle 1972), Puerto Rico (Dahl 1973) and Panama (Hay 1981a).

Spyridia filamentosa also is a habitat generalist, found commonly around Twin Cays on mangrove roots and dead coral fragments on sandy substrata (Norris and Bucher 1982). This species is characterized (Børgesen 1917) as being morphologically variable, common on mangrove roots, lagoon bottoms, white sandy regions and reefs; it also occurs in deeper, lower-light, sand-plain habitats (below 20 m, Earle 1972).

The *Caulerpa* species found on the hanging roots at Twin Cays similarly are not restricted to such substrata, nor are they even limited to hard surfaces. *Caulerpa mexicana* is common near mangroves, both on the sandy/muddy bottoms and on roots (Taylor 1960); it is also found in *Thalassia* beds (Norris and Bucher 1982), in large sandy areas within *Thalassia* beds around Carrie Bow Cay, and in deeper sand plains (Dahl 1973). Børgesen (1913) reported *C. sertularioides* from both sheltered and exposed coastal areas in the Virgin Islands. *Caulerpa racemosa* is also common on the soft bottoms in the channels of Twin Cays. While *A. spicifera*, *S. filamentosa* and *Caulerpa* sp. are habitat generalists, these species occupy the embedded-root habitat of mangroves (Table 3) only when macrograzers are rare.

The flora of the embedded-root habitat at the urchin site (site A) is more restricted in terms of physical environmental requirements. The siphonaceous seaweeds *Halimeda incrassata*, *H. monile* and *Penicillus capitatus* have a well-developed, basal mass of rhizoids that serves to anchor the thallus in soft substrata (i.e., sand or mud). As a consequence, these taxa are not well-suited for attachment to harder substrata such as mangrove roots, coral fragments, etc., thus partially explaining their distributional patterns. *Halimeda opuntia*, *Amphiroa rigida* and other calcified species are not similarly restricted but can occupy a diversity of habitats on both hard and soft substrata. The former is found on the hanging roots at both study sites (Table 3); abundantly at site B. The success of *H. opuntia* is contrary to our competition-based predictions (hypothesis 4). We initially predicted that the herbivore escape adaptations of the embedded-root dominants at site A would exist at the expense of competitive ability and thus, in the absence of grazing pressure, the hanging-root flora should supplant them. Our experimental transplants were at best weakly supportive of this hypothesis; the distributional pattern of *H. opuntia* was contrary to it. *Halimeda opuntia* was a dominant both of the embedded-root habitat at the urchin site and the two habitats at the non-urchin site. Either competitive abilities are not sacrificed significantly to herbivore defenses in this species or perhaps variations in other factors (e.g., micrograzers, physical factors) are affecting the observed pattern.

To explain distributional patterns in the flora at site

A, we conclude that herbivores, not physiological or morphological constraints, restrict the fleshy plants to refugia on the hanging roots. Comparisons between the dominant seaweeds of the embedded- and hanging-root habitats showed significant differences with regard to attributes (e.g., energy content, inclusion of non-nutritive structural tissues and the possible production of anti-herbivore chemistry) that affect the probability of being eaten (Littler and Littler 1980; Lubchenco and Gaines 1981; Paul and Fenical 1983; Littler et al. 1983b). Experimental manipulations of macroherbivore access demonstrated that they are responsible in part for the general paucity of the hanging-root flora in the embedded-root habitat.

The predominant macrophytes of the embedded- and hanging-root habitats at site A fall into two broad structural categories (Fig. 3), calcified and noncalcified groups, respectively. The dominants of the hanging-root habitat allocate significantly less to characteristics that reduce the effectiveness of herbivores, both as individual species (Table 5) and as a functional assemblage (non-calcareous group, Fig. 4). All of the dominants of the embedded-root habitat are calcified, a feature considered to be an effective structural herbivore deterrent (Paine and Vadas 1969). Of the hanging-root flora, only *Halimeda opuntia* contains $CaCO_3$. Calcification not only poses an impediment to ingestion (and possibly digestion), but also reduces the energetic value (on a mass basis) of an alga to herbivores. All of these factors are important in the differential palatabilities (Table 5, Fig. 4) between the embedded-root and hanging-root floras.

Deterrence of herbivory by plant chemistry (Feeny 1975; Fenical 1975; Rhoades and Cates 1976; Lubchenco and Gaines 1981) is not known well enough to permit conclusive comparisons between the two groups. Numerous species of *Caulerpa* found in the vicinity of Twin Cays, exhibited unusual secondary metabolic compounds (Norris and Fenical 1982) that may have anti-herbivore activity. For example, *C. sertularioides* and *C. verticillata* contain the compound caulerpin (Aguilar-Santos 1970) and *Caulerpa*, *Penicillus* and *Halimeda* produce terpenoids (Norris and Fenical 1982). The substance halimedatrial in some *Halimeda* has been suggested (Paul and Fenical 1983) as a strong herbivore inhibitor. While the above-mentioned compounds and various substances in other taxa (e.g., *Stypopodium zonale* (Lamouroux) Papenfuss; Gerwick and Fenical 1981) have been suggested to deter herbivorous fishes, the toxins contained in these macrophytes may be of less consequence in restricting herbivory by sea urchins (Littler et al. 1983b), the major macroherbivores in the system studied.

Previous reports on the palatability to herbivores of many of the algae examined here indicate a general low preference for members of the embedded-root flora (at site A) and similar taxa. The urchins *Echinometra lucunter* and *Lytechinus variegatus* avoid eating *Halimeda* (Lawrence 1975); *Diadema antillarum* showed low preference for *Penicillus* (Ogden 1976) and *Halimeda* (Littler et al. 1983b). Both Earle (1972) and Mathieson et al. (1975) indicated that *Penicillus* was rarely eaten in fish-feeding trials, however, preferences by fishes for *Halimeda* showed considerable variation. *Caulerpa* was also a low preference among urchins (Lawrence 1975) and fishes (Earle 1972; Mathieson et al. 1975). Reports on the loss of algal biomass to a general array of reef herbivores indicated (Hay 1981b; Hay and Goertemiller 1983; Lewis and Wainwright, 1985) low edibil-

ity for *Halimeda* spp. (0–18% losses over a 24 h period), and high preferences for *Spyridia filamentosa, Acanthophora spicifera* and *Caulerpa sertularioides* (90–100% losses).

The correlative evidence discussed in support of the hypothesis of grazer limitation of these tropical marine plant distributions is corroborated by our experimental studies. The dominant macrophytes of the hanging-root flora, other than *Halimeda opuntia*, are rapidly consumed (Table 4) when placed in the embedded-root habitat. This is likely due to micrograzers as well as the sea urchins. The relative paucity of herbivorous fishes leads us to believe that they are of minor importance. As in the case of seagrass beds adjacent to reefs (Randall 1965; Ogden et al. 1973) and algae on sand plains (Hay 1981a), the distributional limits of these tropical seaweeds are controlled by herbivores.

Our results support the hypothesis that herbivores exert important influences on the spatial distribution of marine algal taxa and morphological groups within a mangrove system. The hanging-root dominants (*Acanthophora spicifera, Caulerpa racemosa, Spyridia filamentosa*) are relegated to the predictable spatial refugia of the inaccessible hanging roots because of their low allocation of resources to herbivore deterrence and consequent higher preference by the mangrove-associated herbivores. The dominants of the embedded-root habitat at site A (*Halimeda opuntia, H. incrassata, H. monile, Penicillus capitatus*) persist because of their coexistence escape adaptations (calcification, low calorific values and perhaps supplemental toxicity) which greatly reduce their probability of being consumed.

Above, we have outlined the macrophytic populational variation that exists in a mangrove system with respect to the probability of herbivore/plant encounters and plant escape mechanisms. This variation influences plant distributional patterns and also has an important effect on overall diversity within this community. One set of species (Fig. 2) survives primarily in non-coexistence refugia, spatially isolated from the dominant herbivores; another set persists among herbivores by virtue of coexistence mechanisms that greatly reduce their probability of being consumed. The inability of herbivores to gain access to all habitats within the system thus enhances the diversity of both the plant species and structural types by allowing the fleshy frondose and filamentous (non-calcified) species to persist. We further predict that the activity of herbivores in the embedded-root habitat may prove to be important in the augmentation of biotic diversity in this system by preventing the competitive exclusion of some of the less productive (Table 4), slower growing, but herbivore-resistant macrophytes.

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