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, Spondylosa octant, 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 caloric 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 caloric 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 variations 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,
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*, 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 archin 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. montile* (Ellis and Solander) Lamouroux and *Pencillus 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 (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) Bergesen, *Caulerpa racemosa v. occidentalis* (J. Agardh) Bergesen] and filamentous algae [e.g., *Spyridia filamentosa* (Wulfen) Harvey] as well as the calcified alga *Halimeda opuntia f. triloba*. Sponges [e.g., *Tetudonia 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, *Echinochasmus 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 *Scaurus 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. serrularioides* (Gmelin) Howe, *C. verticillata* J. Agardh, *Anadyomene stellata* (Wul-