Growth rate, ultrastructure and sediment contribution of *Halimeda incrassata* and *Halimeda monile*, Nonsuch and Falmouth Bays, Antigua, W.I.

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**Abstract.** *Halimeda incrassata* and *Halimeda monile*, the two dominant rhipsalian *Halimeda*, were evaluated behind a bank barrier reef, in a fringing reef lagoon and in an open lagoon. Growth was calculated in number of segments, weight of segments and turnover rate. More than 1800 plants were stained with Alizarin Red-S dye, yielding average number of segments/plant/day and g CaCO$_3$/m$^2$/year for each of the above areas of 2.17/114, 1.43/65.7 and 1.6/56.9, respectively. Average weight CaCO$_3$/segment was 4 mg. SEM revealed ultrastructure of short and long unoriented aragonite crystals forming in new segments within 24 h and an effective holdfast system with filaments partially coated with carbonate fragments. Greatest growth occurred within thin to medium density grass beds. In Nonsuch Bay sediment production from these two species alone was 0.057 mm/year or 1$rac{1}{2}$ orders of magnitude less than estimates of the total production from all *Halimeda* species (1.0~ mm/year) over the past 6745 years.

**Introduction**

*H. incrassata* and *H. monile* are the two most common rhipsalian species of *Halimeda* occurring in Antigua. This study of their growth rate, ultrastructure and sediment production is the first for these species in the Leeward Islands.


Despite the obvious and substantial role that *Halimeda* plays in both ancient and modern reef environments, actual field studies and sediment production rates for various species of *Halimeda* in today's tropical environments are limited. This is probably due to the difficulty in measuring segment release from a plant that grows by unpredictable "spurts", varies in percentage of CaCO$_3$ with age (Hillis-Colinvaux 1980; Abel and Drew 1985), and varies in growth rate by species (Gorouau 1963; Hillis-Colinvaux 1980) and perhaps with depth (Bohn 1973). Such variables, combined with unpredictable tropical storm damage to sampling sites (Merten 1971) and patchy nature of *Halimeda* growth (Gilmartin 1960), have discouraged attempts at evaluating production rates.

Studies do indicate, however, that the low sprawling rock-bound forms such as *H. opuntia* (Drew 1983; Hudson 1985; Roberts and Phipps 1986) are faster segment producers per plant than the erect sediment-rooted rhipsalian species such as *H. incrassata* (Hillis-Colinvaux 1980; Wefer 1980). A review of the literature also shows different methodologies and duration of growth experiments, yielding a variety of results for *Halimeda* growth and CaCO$_3$ production measurements.

The Alizarin Red-S stain technique (Wefer 1980) was selected for this study because it produces a "time line" in the field with minimum damage to segments from physical handling or by attracting predators.

An SEM study of the ultrastructure of *H. incrassata* revealed sporadic infilling of interutricle areas by various sizes and shapes of aragonite needles with age. The SEM also revealed that *H. incrassata* holdfast system was made more effective by a meshwork of tiny filaments.

The contribution of *H. incrassata* and *H. monile* to the sediment package in Antigua was evaluated using both direct biologic (sediment production per plant × plants/m$^2$) and indirect stratigraphic (% of *Halimeda* in sediment × average thickness of sediment deposited/year) techniques. Both methods indicate that these two algae alone produce 1$rac{1}{2}$ orders of magnitude less than the
average annual estimated contribution from all species of *Halimeda* in Nonsuch Bay over the past 6700 years.

Antigua, one of the Leeward Islands (Fig. 1), is located along the northeastern edge of the Caribbean Sea (17°–17°10' N and 61°40'–61°55' W) and is roughly circular. The island is 22 x 17 km. Antigua represents one of many emergent crests of an Oligocene volcanic ridge with subsequent progradation of an Oligocene platform containing mixed marine/non-marine beds and reef facies (Multer et al. 1985). The island today is a mature example of the dissected “Limestone Caribbees”. Flourishing reefs (Multer and Weiss 1980; Macintyre et al. 1985) fringe all coasts except the westward leeward shores.

**Materials and methods**

After several seasons of random staining and sampling, three sites were chosen for intensive production rate studies. Criteria for selection included (1) abundance of *Halimeda* (minimum of 80 plants/m²) to insure sufficient number for periodic sampling, and (2) variety of environmental settings (Fig. 2). Final staining/sampling periods were 4/80–7/80 (site C) and 4/83–7/83 (sites A and B).

Water temperature monitored by Taylor maximum/minimum thermometers was found consistently to be 29 °C, with infrequent variations over a small temperature range (27–32 °C) throughout the year. Salinity measured with an optical refractometer remained at 35‰, with only minor fluctuations usually associated with rainy periods. Tidal changes (average daily fluctuations of 38 cm) and wind-induced currents provided water exchange.

Sites were marked at corners with PVC pipe and covered with a clear plastic (0.08 mm thick) “tent” bolted between a double rigid plastic frame held in place by anchor chain (Fig. 3). A “pocket” of dry Alizarin Red-S dye (0.19 g/liter) secured shut with a twist wire (adaptation of technique used by E.H. Gladfelter for staining coral) was released after the tent was in place, allowing dye to mix with seawater. The tent was left for 24 h and monitored for dye loss, with more added if leakage was observed. Sites were periodically visited and 8–15 different-sized plants sampled (to compensate for non-linear growth) until there were no longer any plants showing staining. Algae were then rinsed in fresh water, cleaned of epibionts and placed in 20% sodium hypochlorite (Clorox) solution which revealed white segments (new growth) above those stained. Plants were rinsed in fresh water, dried on mounting paper and secured with tape. Over 1800 plants were so mounted.

In the laboratory, plants were oven dried and segments above stain line cut off, counted and weighed to ±1 mg. Weight of segments after drying reflects both aragonite and some remaining organic material. An average of 88% CaCO₃ was found for both species by dissolving 24 samples of each species in 20% HCl.