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BLADE ABANDONMENT/PROLIFERATION: A NOVEL MECHANISM FOR RAPID EPIPHYTE CONTROL IN MARINE MACROPHYTES

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Abstract. The strategy of blade abandonment and simultaneous rapid proliferation (via protoplasmic translocation) is unique to siphonaceous macroalgae owing to their lack of restrictive crosswalls. Siphonaceous green algae often dominate the standing stocks and productivity of Caribbean mangrove island environs and are also abundant in virtually all calm-water reef habitats. The experimental organism *Avrainvillea longicaulis* is particularly abundant in the study sites west of Carrie Bow Cay and Curlew Cay, Belize. The recycling of protoplasm out of older epiphytically impaired blades of *A. longicaulis*, and simultaneous formation of apical siphon extensions elsewhere, leads to rapid proliferation of new blades—hypothetically, at relatively low energy cost to the plant. The rapidity of siphon extension occurs at least an order of magnitude faster than that possible by photosynthetic production alone, resulting in fully formed proliferations within 3 d. At the same time, the older epiphytized blades become empty, first at the tips, then progressively toward the holdfast, appearing translucent-brown and flaccid within 3 d, followed by senescence. We hypothesize that *A. longicaulis* rapidly responds to epiphyte colonization/impairment by reallocating protoplasm for new growth through protoplasmic streaming. The alternative hypothesis, that the herbivorous crab *Thersandrus compressus* might beneficially control epiphytes on *A. longicaulis*, was falsified by its strong negative effects (i.e., decreased growth and increased host mortality). The hypothesis that allelopathic secondary chemicals may play an antifouling role also was not supported by our experiments; i.e., the consistently vigorous growth rates of the five dominant epiphyte species attached to *A. longicaulis* were not significantly less than populations of the same species attached to carbonate rock. All of the manipulative results (i.e., experimental induction of blade abandonment followed by new proliferation), as well as the populational survey findings (i.e., greater proliferation by epiphytized plants) and physiological data (i.e., photosynthetic inhibition by epiphytes), support the blade abandonment/proliferation hypothesis, thereby documenting an effective epiphyte-control strategy.

Key words: *Avrainvillea*; *Belize*; coral reefs; epiphytism; seagrass beds; siphonaceous algae; *Thersandrus compressus*.

INTRODUCTION

The effects of epiphytes on their host plants can be beneficial (e.g., Penhale and Smith 1977, Orth and Montfrans 1984), but are more often harmful (see review by Jacobs 1988), particularly at high epiphyte densities. In the case of some terrestrial vascular plants, epiphyte loads could result in detrimental breakage by increasing wind resistance and by their sheer mass. More indirect epiphyte effects on terrestrial hosts accrue from competitive overshadowing or by trapping debris and moisture, which attract bacterial, fungal, and insect pests (Johansson 1974, Kiew 1982). In terrestrial systems, the abscission of leaves during adverse conditions (e.g., in xerophytes and deciduous trees), along with the peeling away of bark during growth, might

serve the dual function of eliminating harmful epiphytes.

In the marine environment, epiphytism has not been widely studied, in contrast to the hundreds of papers on hard-surface fouling processes. Epiphytic algae are known to play an important diversifying role in marine plant (Hay 1986) and animal (Jarvis and Seed 1996) associations. When seagrasses are exposed to air, the presence of epiphytes can ameliorate the effects of desiccation (Penhale and Smith 1977), as well as possibly reduce photo-inhibition (Orth and Montfrans 1984). While fouling overgrowths have been shown to be beneficial to marine invertebrates for avoiding detection by predators (decorator crabs are a classic example, e.g., Kilar and Lou 1984), little evidence of such escapes exist for macrophyte hosts.

More often, the detrimental effects of aquatic epiphytes on host plant fitness are the case, and include increased hydrodynamic drag leading to breakage (e.g.,

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Lubchenco 1983), and smothering effects due to steeper diffusion gradients and lower light levels at host-plant surfaces (e.g., Orth and Montfrans 1984). Finely branched epiphytes outcompete their coarser hosts for nutrients and dissolved gases (e.g., Rosenberg and Ramus 1984, Short and Short 1984), potentially leading to lethal anoxic conditions following increased overall nighttime respiration (e.g., Valiela et al. 1990, Lapointe et al. 1994). Epiphytic loading has been documented to decrease the productivity (e.g., Sand-Jensen 1977) of seagrasses, as well as inhibit both subterranean (e.g., Tomasko and Lapointe 1991) and emergent (e.g., Howard and Short 1986) growth. Crustose algae that lack antifouling mechanisms are susceptible to overgrowth and may be outcompeted by epiphytes (e.g., Williams and Carpenter 1990, Littler and Littler 1997b). Since epiphytes diminish the light energy and nutrients reaching the host plant, they may indirectly influence macrophyte abundance, distribution, and productivity, as well as both sexual and vegetative reproduction (Orth and Montfrans 1984).

Epiphyte colonization processes have been shown (see Figueiredo et al. 1996) to be influenced by the interactions of host plant texture, canopy shading/abrasion, and herbivory. The important role of herbivory in eliminating harmful blooms of epiphytes from plant hosts has been demonstrated for frondose macroalgae (e.g., Lubchenco 1983, Brawley 1992), seagrasses (e.g., Howard and Short 1986, Sand-Jensen and Borum 1991, Neckles et al. 1993) and reef-building crustose coralline algae (e.g., Keats et al. 1994, Littler et al. 1995). Other approaches have been concerned with plant defense associations (e.g., Hay 1986) and with the potentially important role of chemical allelopathy (see Hay 1996 for review).

The process of shedding senescent or costly parts under adverse conditions was proposed (Littler and Littler 1980) as a potential survival strategy for long-lived marine macroalgae. Marine macrophytes that possess intercalary meristems, such as seagrasses (Sand-Jensen and Borum 1991) and kelps (i.e., Laminariales, Chapman and Craigie 1977), continuously shed epiphyte loads via the senescence of older tissues at the blade tips. Crustose coralline algae have been shown (e.g., Johnson and Mann 1986, Littler and Littler 1997b) to employ synchronous surficial sloughing to get rid of epiphytes, much in the manner of nontoxic antifouling paints. In this paper, we examine an important, yet undescribed, strategy of rapid epiphyte elimination suggested during an earlier study (Littler and Littler 1992).

Because the spongy textures of *Avrainvillea* spp. make them susceptible to epiphytic/epizoic loading, we became curious as to the reason for the conspicuous lack of epiphytes on most healthy flabella (paddle-like caps, blades). *Avrainvillea* does not produce an antifouling mucilaginous coating (Littler and Littler 1992). We posited that *Avrainvillea* spp. might have the ability

to scavenge resources (by means of protoplasmic streaming) from an older epiphytized or wounded flabellum and rapidly initiate new fronds emanating from the same rhizoidal mass. Protoplasmic streaming, unimpeded by crosswalls in siphons, leading to blade abandonment and new proliferation could also represent a uniquely rapid, heretofore-undescribed, antifouling mechanism. Such a strategy of abandonment/proliferation, hypothetically, would enable old senescent blade walls and their attached epiphyte loads to be shed at relatively low energy cost to the plant once some threshold of impairment is reached. We additionally hypothesized that the lack of epiphyte fouling could be a result, in part, of chemical allelopathy or the removal of epiphytes by grazing invertebrates (e.g., the specialist crab *Thersandrus compresus*).

All previously documented, autonomous, epiphyte-control strategies in marine macrophytes, other than mucilaginous outer coatings and proposed allelopathy, have involved species that shed senescent tissues above intercalary meristems. This study investigated a new mechanism for rapid epiphyte reduction unrelated to those previously described, which does not involve intercalary meristems. We focused on the siphonaceous green macroalga *Avrainvillea longicaulis* and examined its susceptibility to epiphytic overgrowth. To test the abandonment/proliferation hypothesis, we posited the following: (1) excessive epiphyte loading should detrimentally impact components of fitness such as photosynthetic production, (2) in experimental thalli with either natural or artificial epiphytes, abandonment of epiphytized blades and proliferation of new blades should be stimulated relative to control plants lacking epiphytes (or experimental plants maintained epiphyte-free), and (3) in natural populations, epiphytized plants should contain significantly more proliferations than epiphyte-free plants. Furthermore, (4) new proliferations should contain significantly fewer epiphytes than older primary blades, or the hypothesis obviously would be falsified (but not necessarily supported). We also examined the two alternative hypotheses that (5) *A. longicaulis* might benefit from the removal of epiphytes by the herbivorous crab *Thersandrus compresus*, and (6) that chemical allelopathy could be responsible for inhibition of epiphytic growth.

STUDY AREAS

The Belize Barrier Reef complex is the largest coral-reef tract in the Western Hemisphere (>250 km in length and from 10 to 32 km wide), consisting of an almost unbroken barrier reef containing hundreds of patch reefs, mangrove islands, and seagrass beds along its western boundary. Within the back-reef areas, assemblages of framework-building corals, algae, and seagrass beds have the same general community composition characteristic of the entire barrier reef (Burke 1982). Lagoons of the Central Province, such as those westward of Carrie Bow Cay and Curlew Cay (Fig. 1),

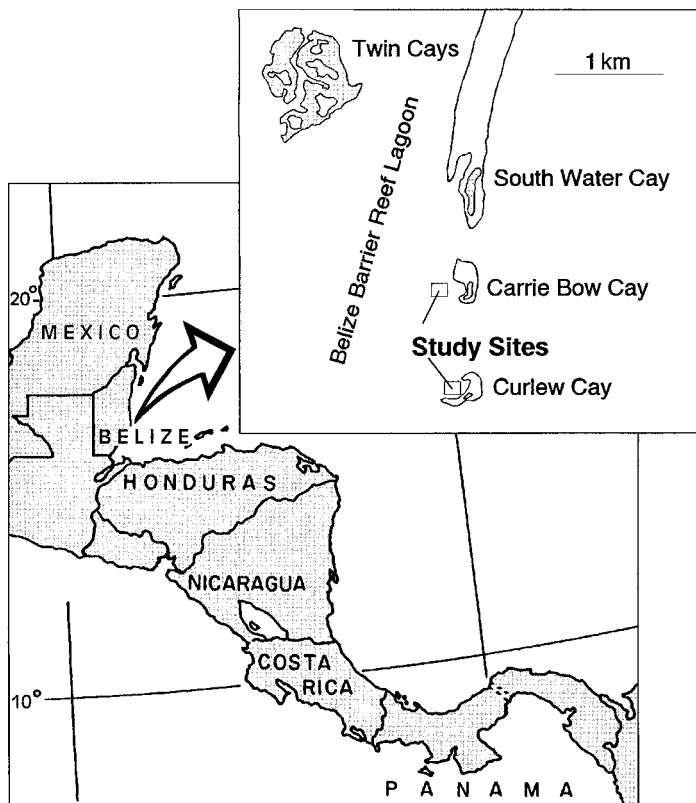


FIG. 1. Location of study sites in the Belize Barrier Reef lagoon.

are the most extensive with diverse and abundant populations of sand-dwelling macroalgae and seagrasses. These back-reef habitats comprise a well-developed lagoon system remote from major human pollutants (Lapointe et al. 1987, 1993).

The topography, geology, and general biology of the Carrie Bow Cay (CBC) and Curlew Cay environs are well known due to >25 yr of study (see Ruetzler and Macintyre 1982, Littler et al. 1985, 1987, Lapointe et al. 1987, 1993, Littler and Littler 1997a). The two study sites (Fig. 1), located to the west of Carrie Bow Cay ($16^{\circ}48.209' N$, $88^{\circ}05.006' W$) and Curlew Cay ($16^{\circ}47.285' N$, $88^{\circ}04.972' W$) are typical of the back-reef regions found throughout much of the Belizean barrier tract (James et al. 1976, Burke 1982). The lagoon bottom at both study sites (3 m deep) is characterized by *Thalassia*-covered gravel and sand substrates, with scattered patchy populations of diverse siphonaeal rhizophytic macroalgae. Herbivory is very low in this habitat (see Hay 1981, Lewis and Wainwright 1985) and neither fish or sea urchin grazing nor wave shear were observed during the study (~60 person-hours of diving).

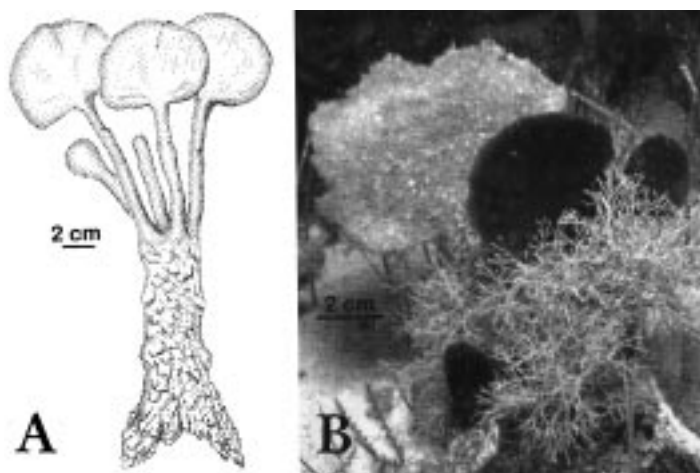
EXPERIMENTAL ORGANISM

Siphonaeal green algae often dominate the standing stocks and productivity of submerged habitats within mangrove island bays, ponds, and lakes, and occur

abundantly in virtually all calm-water reef habitats. Rhizophytes such as *Avrainvillea*, *Halimeda*, *Penicillus*, *Rhypocephalus*, *Udotea*, *Cladocephalus*, and *Caulerpa* (Chlorophyta, Bryopsidales) are among the predominant contributors to macroalgal cover and primary productivity within the vast seagrass flats throughout the tropical western Atlantic. Such "rooted" plants, by tapping the nutrient-rich interstitial pore waters (Littler and Littler 1990), can avoid many of the nutrient limitation problems experienced by other epilithic plants. The experimental organism *Avrainvillea longicaulis* (Fig. 2A, B) is particularly abundant and chemically well studied (Sun et al. 1983, Hay et al. 1990) in the Belize Barrier Reef lagoon directly west of Carrie Bow Cay and Curlew Cay (Fig. 1, 3–4 m deep).

The 1–5 blades (=flabella) of *Avrainvillea longicaulis* are broadly oval (to 10 cm high, 14 cm wide) with truncated lower margins (Fig. 2A) and are thick (>4 mm) and spongy (lacking a mucilaginous coating) with cylindrical or flattened stipes (=stalks, to 12 cm long, 13 mm diameter). The blades, stipes, and holdfast are composed of dichotomously branched, interconnected siphons entirely lacking crosswalls. The thallus is typically anchored by a massive, perennating, bulbous, rhizoidal holdfast (Fig. 2A) in open sandy or seagrass areas of shallow (to 30 m) pristine waters. Although sporic reproduction is rare (not observed in this study), where it has been reported (see Littler and

FIG. 2. (A) Typical *Avrainvillea longicaulis* illustrating the perennating subterranean holdfast (portion below 2-cm scale line), older blades (flabella), and proliferating new blades. (B) In situ photograph of +E (epiphytes added) plant with epiphytes removed from the empty, translucent, abandoned, primary blade (rear upper left), showing several newly induced proliferations (lower and right) arising from the epiphytized stalk.



Littler 1992), specialized club-shaped release structures are produced at the tips of individual flabellar siphons. We have observed perennation in *A. longicaulis* (Littler and Littler 1992), where the only remains of lost blades were scars giving rise to newly forming flabella from either the former stipes or the columnar holdfast. Species of *Avrainvillea* occur in open habitats

that do not provide large grazers protection (i.e., refugia) from their carnivorous predators. However, *A. longicaulis* is unique within the genus in being chemically defended from herbivorous reef fishes (Hay et al. 1990) by the presence of avrainvilleol, a brominated diphenylmethane derivative (Sun et al. 1983), which may reflect a predominance of escape (vs. defense) strategies in the other members of the genus. Although *A. longicaulis* is chemically resistant to fish predation, it constitutes the exclusive diet for the ascoglossan gastropod *Costasiella ocellifera* and the crab *Thersandrus compressus* (Hay et al. 1990).

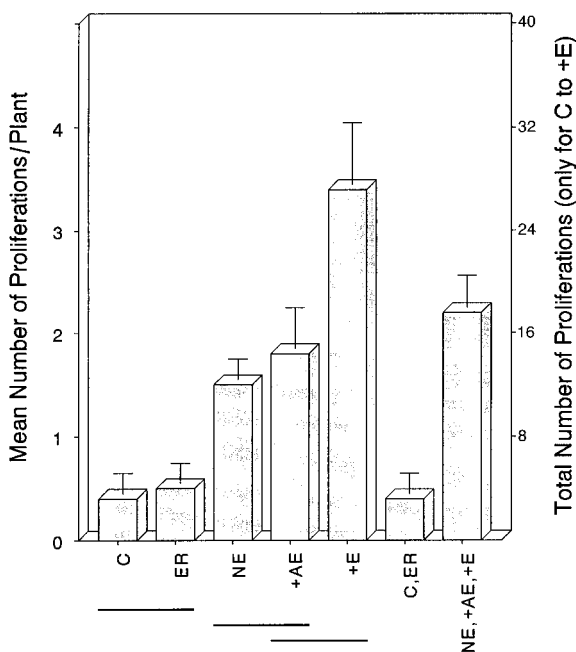


FIG. 3. Results of 12-d experimental manipulation of epiphyte loads on *Avrainvillea longicaulis* showing mean numbers of proliferations per plant (left axis) and total number of proliferations per treatment (right axis). C = control, ER = epiphytes removed, NE = natural epiphytes, +AE = artificial epiphytes, and +E = epiphytes added ($N = 8$). "C, ER" = no epiphytes ($N = 16$); "NE, +AE, +E" = epiphytized ($N = 24$). Error bars represent $+1$ SE. Lines below figure connect groups that do not differ significantly ($P > 0.05$, Bonferroni).

In the past, studies of western Atlantic species of *Avrainvillea* have been hampered by the lack of an adequate taxonomy. A major obstacle to understanding the ecological role of siphonalean algae is the high biodiversity of taxonomically problematical genera. For example, five species of *Avrainvillea* are abundantly represented in the interior ponds of nearby Twin Cays (Fig. 1). Using previous treatments (e.g., Gepp and Gepp 1911, Taylor 1960, Olsen-Stojkovich 1985), it would be possible to identify only a small fraction of the taxa actually present. *Avrainvillea longicaulis* and the similar-appearing *A. mazei* co-occur in both of the lagoon habitats studied here and require precise discrimination. The monograph on Caribbean *Avrainvillea* (Littler and Littler 1992) alleviated the taxonomic problem and suggested this study.

METHODS AND MATERIALS

On 25 April 1997, we simulated epiphyte loading on experimental (vs. control) thalli of *Avrainvillea longicaulis* by artificially attaching natural epiphyte populations as well as by placing fine-mesh nylon cloth over the flabella and measuring the times and abundances of new proliferations. An unmanipulated, naturally epiphytized group was also tagged and monitored. Proliferations were predicted to be significantly greater in these experimental thalli relative to epiphyte-

free thalli. Simultaneously, we physically removed epiphytes on an experimental group and identified an unmanipulated, epiphyte-free, control group of tagged plants and then recorded any new proliferations, which, in both cases, were predicted to be statistically lower than in the three epiphytized experimental groups detailed below. Data were tested statistically using analysis of variance followed by the Bonferroni (Dunn), a posteriori, multiple classification test (SAS 1985). All percent data were arcsine transformed prior to analysis.

Forty thalli were selected at the Curlew Cay site (3 m in depth) in consecutive order of their being encountered without bias as to size or other factors, assigned randomly to treatments ($N = 8$) and labeled nearby with weighted and numbered strips of yellow surveyor's tape. None of the plants contained crabs or other mesofauna. Microorganisms such as blue-green algae, diatoms, and bacteria were not observed to form more than trace discontinuous coverages when examined microscopically. All 40 plants were consecutively macrophotographed and macrovideotaped, and the proliferations were counted in situ and recorded on waterproof paper.

Epiphytes were gently hand-removed by pinching or crushing (without pulling) them off at the base from all treatments except natural epiphytes (NE). Controls (C) were exceptional in being selected as epiphyte-free thalli. The experimental thalli with epiphytes added (+E) had natural proportions (see below) of the five predominant epiphytic macroalgae attached by a single thin (1 mm thick \times 9 cm long), dull-beige, rubber band that did not contact the host plant. This technique gently held the epiphytes in place without distorting or constricting the flabellum in any way. The dominant epiphytes, and their natural cover proportions (digitized from stop-action quadrats of the macrovideo transects, see populational survey below), were the macrophytes *Amphiroa fragilissima* (mean \pm 1 SE = $28 \pm 5\%$), *Dictyota pulchella* ($27 \pm 3\%$), *Spyridia complanata* ($19 \pm 4\%$), *Laurencia intricata* ($15 \pm 4\%$) and *Acanthophora spicifera* ($11 \pm 3\%$). White nylon mesh panels (0.62-mm strand diameter, 1.55-mm hole diameter, 37% light attenuation) were placed over all artificial-epiphyte treatments (+AE), with each lightly held in place by a single thin rubber band. The epiphyte-removal treatment (ER) involved the daily gentle removal of all epiphytes by hand pinching. Twelve days later, on 7 May, epiphytes and the nylon mesh panels were macrophotographed and then removed prior to recording to enhance visibility. The 40 tagged thalli were then photographed again and video-recorded; new proliferations also were counted in situ.

To test the hypothesis that rapid proliferation, simultaneous with blade abandonment, was due mainly to re-allocation and not new production, we used daily macrovideo recording and stop-action digitization between 25 April and 10 May to follow the progression of dense green protoplasm out of the epiphytized blades

as they emptied during senescence. Ten blades from independent plants containing natural epiphytes that had just become translucent at the tips were monitored. Laboratory observations confirmed that this process involved downward cytoplasmic streaming toward the stipe and holdfast in all 10 samples. The evacuation of blades as a function of distance from the former growing tips was then quantified over time. Simultaneously, the length of 20 independent new proliferations were measured and areal increases of proliferating blades quantified by stop-action digitization. Laboratory observations again confirmed that the siphon tips of all rapidly proliferating blades were being formed by upward cytoplasmic streaming.

Using a populational survey approach on 30 April, we quantified the proportion of proliferating new thalli on epiphytized vs. nonepiphytized primary blades of *Avrainvillea longicaulis* from the two back-reef study sites at Curlew Cay and Carrie Bow Cay ($N = 123$). In addition, we characterized the cover and growth of epiphytes on older thalli of the same individual plants by scoring point-intercept transects (Littler and Littler 1985) across close-up, macrovideo, stop-action samples. If either (1) new proliferations did not contain significantly fewer epiphytes than older primary blades, or (2) epiphytized plants did not show significantly more proliferations than epiphyte-free plants, then the abandonment/proliferation hypothesis would be rejected.

To test the hypothesis that production alone could account for any new proliferations, we measured the photosynthetic rates of *Avrainvillea* assimilators on 4–5 June under ambient environmental conditions (30° – 31° C, 36‰ salinity, 1500 – $2100 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, using the same methods detailed in Littler et al. (1987). We incubated healthy *Avrainvillea* containing moderate levels of natural epiphytes from 3–4 m deep, leeward of CBC, and the same blades with the epiphytes carefully removed by pinching, as well as the epiphytes incubated separately ($N = 6$ for all treatments), to examine the hypothesis that epiphytes may interfere with primary productivity. Cleaned blades were also incubated at 50% ambient light (under neutral-density screening) to simulate the effects of epiphyte shading. We chose photosynthetic production as an indicator of fitness, since growth is a relatively intractable parameter due to the inaccessibility of the massive holdfast. As mentioned earlier (Littler and Littler 1992), reproductive material is quite rare in *Avrainvillea*.

On 28 April, we initiated an experiment to test the alternative hypothesis that the herbivorous crab associate *Thersandrus compressus*, by removing harmful epiphytes, might benefit the host plant *Avrainvillea longicaulis*, in a manner similar to the chiton/coralline algal association on the nearby reef crest (Littler et al. 1995). Neither the Curlew Cay nor the Carrie Bow Cay populations of *A. longicaulis* were observed by us to contain the conspicuous ascoglossan *Costasiella ocell-*

TABLE 1. Populational survey data for epiphytized vs. epiphyte-free *Avrainvillea longicaulis* sampled at Carrie Bow Cay and Curlew Cay study sites.

Number of flabella	Epiphytized thalli (<i>N</i> = 82 plants, 132 flabella)				Epiphyte-free thalli (<i>N</i> = 41 plants, 105 flabella)	
	Young proliferations (<i>N</i> = 41 plants, 62 flabella)		Old blades (<i>N</i> = 41 plants, 70 flabella)		Young proliferations E	Old blades F
	With epiphytes A	Without epiphytes B	With epiphytes C	Without epiphytes D		
0	33	13	1	37	31	0
1	6	12	20	4	8	12
2	2	10	15	0	2	15
3	0	4	4	0	0	13
4	0	2	1	0	0	3
Total flabella	10	52	66	4	12	93
% of total flabella	16	84	94	6	11	89

Note: The following differences were significant ($P < 0.05$, Bonferroni): B > A, C > D, A + B > E, F > E, F > D.

lifera studied by Hay et al. (1990), but ~10% of the plants did contain the cryptic crab *T. compressus*. Twenty, whole, crab-free *A. longicaulis* plants were transplanted from the Carrie Bow Cay site to the Curlew Cay site and arranged in two parallel rows 3.0 m apart, oriented east to west. The thalli were placed in holes wedged open in the sandy substrate by titanium crowbars at 1.0-m intervals. Thalli in the north row had a single crab per thallus added ($N = 10$) and replaced thereafter when lost, whereas those in the south row were monitored as crab-free controls ($N = 10$). The plants were photographed at the time of initial setup and 12 d later at termination on 10 May. The macrophotographic samples were scored for areal coverage in the laboratory (Littler and Littler 1985).

The alternative hypothesis that chemical allelopathy (e.g., the unique compound avrainvilleol) might be responsible for inhibition of epiphytic growth (cf. Schmitt et al. 1995) also was investigated by macrovideo sampling concurrent with the other manipulative studies. During 25 April to 7 May, we contrasted changes in cover of 50 populations ($N = 10$ per species) of five of the dominant epiphytes (listed above) attached to *Avrainvillea longicaulis* with 50 comparable populations attached to dead carbonate rock ($N = 10$ per species) in the same habitat at Curlew Cay.

RESULTS

At the end of the 12-d experimental period, the eight +E replicates had significantly more ($P < 0.05$, Bonferroni) new proliferations (27 total proliferations, Fig. 3) than any of the other treatments except those with artificial epiphytes (+AE, 14 proliferations). The rapidity of siphon extension was impressive, resulting in many centimeters of "new growth" at the blade margins within several days. At the same time, new basal proliferations had begun to appear while the older epiphytized blades emptied, becoming translucent-brown

and flaccid (Fig. 2B). The +E samples had ninefold more proliferations (27 total) after 12 d than the controls (C, 3 proliferations), whereas the proliferations on thalli with artificial epiphytes (+AE, 14 proliferations) were fivefold greater, and the samples with natural epiphytes (NE, 12 proliferations) were fourfold greater (all significant at $P < 0.05$, Bonferroni). The plants with epiphytes continuously removed (ER) had only 4 total proliferations (Fig. 3) and were not significantly different ($P > 0.05$, Bonferroni) from the controls (C, 3 proliferations), but showed significantly fewer proliferations than the three groups with epiphytes (+E, +AE, and NE). When all samples subjected to epiphyte loading combined (+E, +AE, and NE, $N = 24$) were contrasted with all epiphyte-free specimens combined (ER and C, $N = 16$), the former group averaged 5.5-fold more (2.2 vs. 0.4) proliferations per plant than the latter (significant at $P < 0.05$, Fig. 3).

Approximately $20 \pm 8\%$ (mean ± 1 SD) of the total thallus length became empty after ~24 h following detection of incipient abandonment in 10 independent blades that had been naturally colonized by epiphytes. These blades showed an average of $\sim 50 \pm 14\%$ of the distance from their distal margins becoming translucent after ~48 h, with dense protoplasm remaining mostly in the proximal flabellar stipe regions after ~72 h. Concomitantly, 20 proliferating incipient blades increased at a rate of several centimeters per day at their margins to produce new flabella averaging 47.1 ± 10.0 cm² in area within 72 h.

Our investigations of the epiphyte/proliferation status of natural populations of *Avrainvillea longicaulis* (Table 1) revealed that heavily epiphytized plants had 4.3 times more proliferations than epiphyte-free plants (47% new proliferations vs. 11%, significant at $P < 0.05$, Bonferroni), as well as 30 times fewer old blades (3% old blades vs. 89%, $P < 0.05$), in conformity with

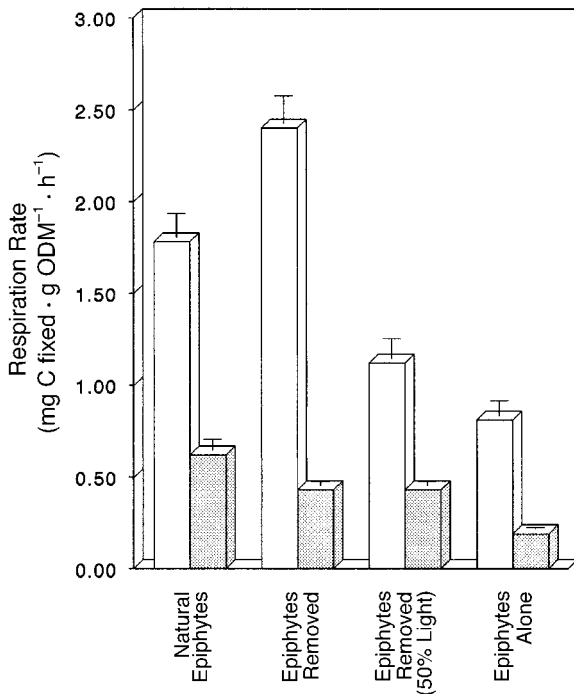


FIG. 4. Photosynthetic (unshaded) and dark respiration (shaded) rates of *Avrainvillea longicaulis* and its natural epiphytes, combined and separate ($N = 6$). Error bars represent $+1$ SD.

the data in Fig. 3. There were five times more young blades without epiphytes than with epiphytes (16% vs. 84%, $P < 0.05$, Table 1), and 16 times more old blades with epiphytes than without epiphytes (94% vs. 6%, $P < 0.05$).

Epiphyte-free *Avrainvillea longicaulis* blades showed a maximum net photosynthetic rate of 2.40 ± 0.15 mg C fixed per gram of organic dry mass (ODM) per hour, with a dark respiration rate of 0.43 ± 0.02 mg C consumed · g ODM⁻¹ · h⁻¹ (Fig. 4). The presence of epiphytes caused a 25% reduction in the photosynthetic production of *A. longicaulis* (significant at $P < 0.05$, Bonferroni), while increasing dark respiration by 31% (Fig. 4). Since the production of the epiphytes alone was conservatively measured (owing to wounding during removal) at 0.81 ± 0.08 mg C · g ODM⁻¹ · h⁻¹ (Fig. 4), then the production of epiphytized *Avrainvillea* alone may have been as low as 0.97 mg C · g ODM⁻¹ · h⁻¹, suggesting a 60% epiphyte-induced decrease. Reduction of light energy by half resulted in lowering production of cleaned blades by 54% ($P < 0.05$) to 1.12 ± 0.11 mg C · g ODM⁻¹ · h⁻¹, a value not significantly different ($P > 0.05$) from that calculated for the blades containing epiphytes above (i.e., 0.97 mg C · g ODM⁻¹ · h⁻¹).

The 20 newly formed blades (mean area = 47.1 cm²) contained an average of 12 ± 2 mg ODM/cm² (28.3% C), which converts to 3.4 ± 0.6 mg C/cm² of proliferating blade. Given the photosynthetic production of 0.97 mg C · g ODM⁻¹ · h⁻¹ determined above (with the

normal inhibitory effects of epiphytes), and erring on the high side by assuming that this rate could be sustained for 10 h/d, with dark respiration at 0.43 mg C consumed · g ODM⁻¹ · h⁻¹ for 14 h (not including respiration of the massive holdfast), we arrive at a net rate of 3.7 mg C · g ODM⁻¹ · d⁻¹. The mature assimilators incubated averaged 0.51 ± 0.12 g ODM, and therefore could have produced only 1.9 mg C · plant⁻¹ · d⁻¹ at most. Consequently, photosynthetic production alone (for epiphytized blades) could only account for 0.6 cm² of new thallus growth per day (or 1.8 cm²/3 d), a theoretical rate conservatively slower than that exhibited during epiphyte-induced proliferation by a factor of ~ 26 .

Although transplantation shock was shown by the initial faded appearance of all 20 thalli, 80% of those with crabs added (Fig. 5) experienced cover losses leading to mortality of the emergent (water-column) portions. In contrast, the crab-free controls only had 30% of the thalli undergoing cover losses (significantly less at $P < 0.05$, Bonferroni). Seventy percent of the crab-free transplants showed new growth and recovery, vs. none (0%) for those with crabs present ($P < 0.05$, Fig. 5).

All 50 populations of the dominant epiphytic algal species growing on *Avrainvillea longicaulis* (Fig. 6) remained robust and increased in coverage (mean cover increase = 12%, range = 4.9–20.0%). Also, there were no significant differences ($P > 0.05$, Bonferroni) when the growth of epiphytic populations was contrasted with the growth of 50 comparable control populations attached to dead carbonate substrates (mean cover in-

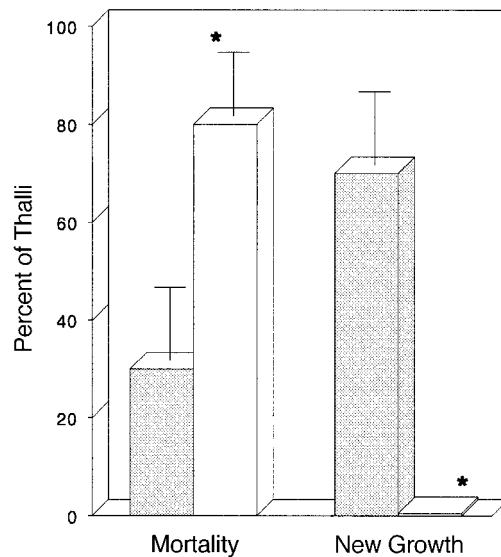


FIG. 5. Percentage of transplanted *Avrainvillea longicaulis* plants experiencing mortality or new growth, with (unshaded) and without (shaded) the crab *Thersandrus compressus* ($N = 10$), over a 12-d experimental period. Error bars represent $+1$ SE; asterisks indicate significant differences ($P < 0.05$, Bonferroni).

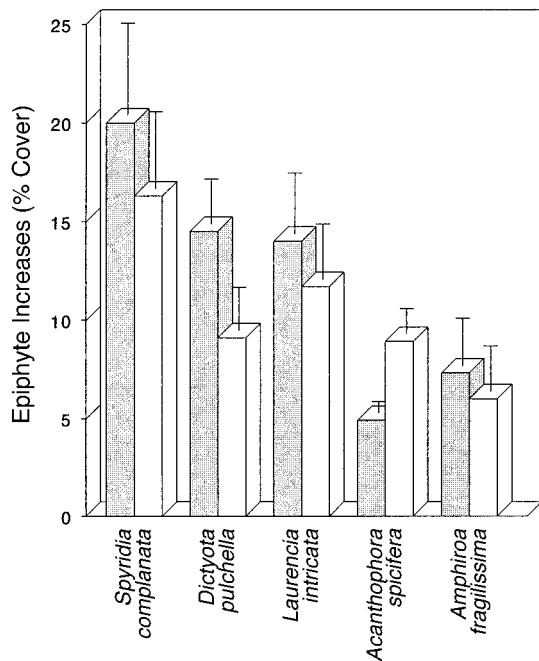


FIG. 6. Changes in cover of the five dominant epiphyte species attached to *Avrainvillea longicaulis* blades (shaded) or dead calcareous rock (unshaded) over a 12-d experimental period ($N = 10$ per species, error bars represent $+1$ SE). No significant differences between the two substrates were recorded ($P > 0.05$, Bonferroni).

crease = 10%, range = 6.0–16.3%, Fig. 6). It is interesting that four of the five species showed greater growth on *Avrainvillea* than when attached to rock.

DISCUSSION

The typically detrimental effects of aquatic epiphytes on host plant fitness have been well documented and include increased hydrodynamic drag leading to breakage (e.g., Lubchenco 1983), and smothering effects due to steeper diffusion gradients and lower light levels at host-plant surfaces (e.g., Orth and Montfrans 1984). Productivity (Sand-Jensen 1977) as well as both subterranean (e.g., Tomasko and Lapointe 1991) and emergent (e.g., Howard and Short 1986) growth of seagrasses is inhibited under epiphyte loading. In agreement, our physiological data (Fig. 4) showed that epiphyte loading significantly reduced the photosynthetic production of *Avrainvillea longicaulis* by ~60%. Since epiphytes diminish the light energy and nutrients reaching the host plant, they may indirectly influence macrophyte abundance, distribution, and productivity, as well as both sexual and vegetative reproduction (Orth and Montfrans 1984).

All previously documented, autonomous, epiphyte-control strategies in marine macrophytes, other than mucilaginous outer coatings and allelopathy (Hay 1996), have involved species with intercalary meristems. Such species (e.g., corallines [Littler and Littler

1997b], seagrasses [Sand-Jensen and Borum 1991], and laminarialean kelps [Chapman and Craigie 1977]) erode away at the older apical regions taking a “conveyor-belt” series of epiphytic successional stages with them. This study reveals a new mechanism unrelated to those previously described, which does not involve the aforementioned shedding of senescent tissues above intercalary meristems. The replicates subjected to epiphyte loading showed significantly more proliferation than the epiphyte-free samples (Fig. 3), in strong support of the abandonment/proliferation hypothesis. The +E manipulation, where experimentally added, living epiphytes completely covered the blade surfaces, resulted in the induction of higher numbers of proliferations (Fig. 3) than occurred on the treatment with sparser, natural levels of epiphytes (NE).

Further support for the hypothesis was provided by the populational survey (Table 1), which confirmed the prediction that epiphytized plants would show significantly more proliferations than epiphyte-free plants. Also, the postulate that “if older blades were to contain significantly less epiphytes than younger proliferations, then the hypothesis would be falsified” was not supported. The reason for this finding is not profound, i.e., colonization was not instantaneous and fewer epiphytes on young blades probably resulted from insufficient time for colonization. However, if colonization had been rapid on newly forming flabella, it would have negated any hypothetical advantage for proliferation as an effective epiphyte-control mechanism.

The strategy of simultaneous abandonment/proliferation is unique to siphonaceous macroalgae owing to their lack of restrictive crosswalls. Leaf/blade senescence following epiphyte colonization is a common plant response and not unique in this strategy; however, the mobilization of protoplasm out of older, epiphytically impaired blades and concomitant reallocation to form new siphon extensions elsewhere is novel. The older epiphytized blades emptied out from the tips downward within several days, appearing as translucent-brown and flaccid cellulosic shells (Fig. 2B), prior to disintegration. Simultaneously, upward cytoplasmic streaming in new regions resulted in fully developed photosynthetically competent proliferations within 3 d (mean areal increases of 47 cm²). We posit that such recycling (salvaging) of existing protoplasm by translocation is more efficient than synthesizing new protoplasm from scratch and could lead to rapid blade proliferation at relatively lower energetic costs compared to the photosynthetic production of entirely new growth. As calculated above for epiphytized blades, photosynthetic production alone would be 26 times too slow to account for the rapidity of blade proliferation.

The strong negative effects (e.g., reduced host growth and increased mortality, Fig. 5) falsified the hypothesis that herbivory by the specialist crab *Therapsandrus compressus* might beneficially control epiphytes in *Avrainvillea longicaulis*. Such detrimental

effects are in marked contrast to the positive interactions shown by a herbivorous chiton (*Choneplax lata*) and coralline algal (*Porolithon pachydermum*) mutualistic association in the nearby Belize Barrier Reef crest-system (Littler et al. 1995). In this association, the herbivorous chiton grazes the principal prey, *Porolithon*, but in so doing reduces the colonization by epiphytes, which results in increased biomass of the host alga. Transplantation shocked the growth of *A. longicaulis*, as indicated earlier, but the presence of *T. compressus* clearly hastened the demise of the transplants and prevented the recovery evidenced by the crab-free control group (Fig. 5).

Because intense competition occurs on most solid marine substrates (see Jackson 1977), chemically mediated allelopathic interactions have been predicted (Hay 1996) to be common. However, few marine studies (e.g., Schmitt et al. 1995) have adequately investigated the role of chemical allelopathy. There are three requirements (Hay 1996) that must be fulfilled to demonstrate that potential hosts are chemically resistant to epiphytic organisms: (1) unusual host resistance to fouling, (2) a secondary compound with an effect on colonizers, and (3) the presence of the secondary compound on host surfaces. Since the first two of these requisites was not met by our observations (Fig. 6, Table 1), the hypothesis that allelopathic secondary chemicals may play an antifouling role (see Hay 1996) could not be supported. We not only recorded widespread epiphytism on *Avrainvillea longicaulis* (Table 1), but consistently healthy growth for all 50 populations of the five dominant epiphyte species after attachment and intimate siphon contact (Fig. 6), as well as for nine other minor epiphytic algae. Four of the five species showed greater growth on *Avrainvillea* than when attached to rock. In some cases, robust epiphytic thalli of *Acanthophora* and *Laurencia* penetrated through and out the other side of the *A. longicaulis* blades.

Conversely, all of the populational survey data (e.g., greater proliferation by epiphytized plants, abundant epiphyte loads on older blades, Table 1), physiological findings (e.g., photosynthetic inhibition by epiphytes, Fig. 4) and manipulative results (e.g., experimental induction of blade abandonment followed by rapid proliferation, Fig. 3) strongly supported the abandonment/proliferation hypothesis, thereby documenting a unique epiphyte-control strategy for siphonaceous macroalgae. Few counterparts to this strategy are present in terrestrial systems, except perhaps the dropping of leaves under the inhibitory effects of epiphyte overshadowing (e.g., Kiew 1982, Jacobs 1988). We predict that further studies will show blade abandonment/proliferation to be widespread among the order Bryopsidales, as we have observed what appears to be the same phenomenon in some species of *Caulerpa*, *Halimeda*, and *Udotea*.

Furthermore, we postulate that the stipes and blades

of *Avrainvillea longicaulis* serve as expendable assimilators, with a major function of building a massive perennating/storage organ, the columnar holdfast (Fig. 2A), which can comprise the bulk of the thallus biomass (Olsen-Stojkovich 1985). Unlike the other genera of Bryopsidales, *Avrainvillea* is long lived (see Littler and Littler 1992) and does not undergo mass synchronous spawning (Clifton 1997) followed by death and disintegration of the entire thallus (holocarp). Physical disturbances (such as storms and herbivory), as well as physiological stresses (such as epiphyte loading), result in disproportionate losses of the relatively delicate exposed assimilators, which can be replaced by perennation from the subterranean holdfast during more favorable conditions. A further marine example of this phenomenon is demonstrated by the seagrass *Thalassia testudinum* (Heck and Valentine 1995), which is able to compensate for short-term sea urchin grazing losses on emergent shoots by mobilizing stored carbohydrates from the rhizomes (see Tomasko and Dawes 1989). Selection for this strategy is also amply represented in terrestrial environments, as shown by the multitude of vascular plants that crown-sprout after physical forces such as severe storms, fires, freezes, or overgrazing have removed the aboveground canopies.

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ERRATA

In the article by C. E. Cáceres (1998) entitled “Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs,” *Ecology* **79**(5):1699–1710, a transcription error was made when converting the raw emergence data to number emerging per square meter. All reported values for daphniid emergence (e.g., Fig. 7, and “Direct estimate” in Table 2) should be multiplied by a factor of 7.7. This does not include the “indirect” estimates for emergence reported in Table 2. This error affects only the values for emergence rates; the conclusions of the paper are unaffected.