

Citation:

Little M. M., Little D. S. & Taylor P. R. 1987. Functional similarity among isomorphic life-history phases of *Polycavernosa debilis*. *Journal of Phycology* 23: 501-505, 1 fig.

J. Phycol. 23, 501-505 (1987)

NOTE

FUNCTIONAL SIMILARITY AMONG ISOMORPHIC LIFE-HISTORY PHASES OF
POLYCAVERNOSA DEBILIS (RHODOPHYTA, GRACILARIACEAE)¹

Mark M. Littler,² Diane S. Littler

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia 20560

and

Phillip R. Taylor

Biological Oceanography Program—OCE, National Science Foundation, 1800 G Street, N.W.
Washington, District of Columbia 20550

ABSTRACT

Morphologically identical but different life-history phases of the red alga *Polycavernosa debilis* (Forsskål) Fredericq and J. Norris showed no conspicuous differences in physiological or ecological performances. The costs and

benefits of ploidy level, as measured by net photosynthesis, calorific content, structural makeup and resistance to predation, were not sufficient to result in statistically significant differences ($P > 0.05$ ANOVA) for the various reproductive phases [haploid male or female (including cystocarps) and diploid tetrasporic]. The lack of measurable functional responses leads to two hypotheses: (1) that adaptive ecological-physiological differences between life-history phases are subtle, or (2) that predominantly ge-

¹ Accepted: 1 March 1987.

² Address for reprints.

netic/reproductive factors are implicated in maintaining isomorphic life-history phases.

Key index words: calorific content; functional forms; isomorphic; *Polycavernosa debilis*; predation; primary production; Rhodophyta

In the case of algae with heteromorphic reproductive phases, there is some evidence (Littler and Littler 1980, Slocum 1980, Lubchenco and Cubitt 1980, Dethier 1981) suggesting an adaptive significance related to seasonal or habitat variations in conditions affecting growth, reproduction and mortality. For example, Littler and Littler (1983) showed for the marine brown alga *Scytosiphon lomentaria* (Lyngbye) J. Agardh that the morphologically different phases, containing specialized adaptations and two different ploidy states, represent a mechanism for spreading the risks from various sources of stress and disturbance.

However, the widespread persistence of isomorphic life history stages (i.e. *Polysiphonia*-type life history sensu Dixon 1982) among algae seems especially perplexing (see also Lubchenco and Cubitt 1980). As the stages show virtually identical forms, questions focus on whether or not there are adaptive advantages and concomitant costs associated with ploidy levels and whether these are measurable.

Most of the research on the adaptive significance of ploidy in life-history phases comes from the theoretical literature and argues convincingly for the genetic advantages of diploidy (e.g. Stebbins and Hill 1980). Some of the limited studies of algae that have compared isomorphic haploid and diploid stages (Allender 1977, Benson 1983) have corroborated this tendency, whereas others have not (Hannach and Santelices 1985). A correlation can be seen (e.g. Stebbins 1950, Stebbins and Hill 1980, Willson 1981) between plants that contain relatively low DNA levels and a tendency towards more productive, weedy-annual, opportunistic life styles (see r- and K-selection theory, Pianka 1970). Forms with high DNA content tend toward the slower-growing, perennial, environmentally resistant end of the continuum. Therefore, the advantages (Stebbins and Hill 1980) of a haploid-diploid alternation of isomorphic generations also could be related to the value of multiple metabolic options for survival in dissimilar environments. The present study was designed to test whether morphologically similar haploid and diploid individuals of the red alga *Polycavernosa debilis* (Forsskal) Fredericq and J. Norris are functionally different in regard to important physiological and ecological performances, i.e. that can be related to growth and reproduction.

One of three mutually exclusive outcomes was anticipated: (1) each phase might show different ecological/physiological benefits as well as costs, (2) a single phase might prove to be superior in all respects or (3) no discernible differences would be detected between any of the various phases. If forms

differing only in ploidy level were to exhibit ecologically meaningful differences (alternatives 1 and 2 above), then it would be essential that population biologists, community ecologists, physiologists and systematists ascertain and document ploidy levels when investigating these types of species. However, if no differences in physiological or ecological performances can be detected, then genetic/reproductive limitations would be implicated as the level of selection involved, and more subtle functional differences would have to be sought.

The field portion of this study was initiated at Carrie Bow Cay, Belize (16°48' N, 88°05' W) on 1–12 April 1984 and completed during 2–24 April 1985. The Cay is one of numerous small islands that have developed on the outer margin of the Belizean barrier-reef system. Rützler and Macintyre (1982) give a thorough description of this pristine reef system (see also Littler et al. 1983).

Polycavernosa debilis is a 25-cm tall, coarsely branched, rubbery plant recently removed from the genus *Gracilaria* by Fredericq and Norris (1985). It occurs subtidally in the back-reef area at Carrie Bow Cay and is abundant in the back-reef zone of Tobacco Reef about 1.0 km to the north. Specimens from Tobacco Reef were collected at a depth of 1.0 m (in full sunlight), then quickly identified, sorted as to life-history phase under a dissecting microscope and stored in polycarbonate trays of running seawater. All of the specimens were individual thalli with no signs of anastomized branches or fusion of more than one plant, although this species exhibits such features on occasion. About 25% of the material proved to be infertile and was discarded; approximately 30% was identifiably male, 30% was tetrasporic and only 15% was female (bearing cystocarps). Voucher specimens of all three phases were preserved in 4.0% buffered Formalin, labelled and subsequently deposited in the Algal Collection of the U.S. National Herbarium, Smithsonian Institution.

Diploid tetrasporophytes and haploid male and female gametophytes were examined for their productivity, resistance to predation, calorific content and structural makeup (in reference to the predictions of the functional-form model, Littler and Littler 1980) as follows. The hypothesis we tested was that no gross-level functional differences would be evident for isomorphic forms of the same algal species differing solely in terms of sex or ploidy level. A major assumption is that structure, at some level, ultimately influences biological function and that thalli not differing in coarse-scale morphology will also not differ greatly in their ecological or physiological responses.

Measurements of net photosynthesis were made for the three life-history phases (16 replicates of each) in wide-mouth, one-liter glass jars between 0900 and 1400 h on 15 April 1985. Natural whole branches were taken from separate plants and incubated in clear polycarbonate trays under continuous stirring (using water-driven magnetic turbines) and ambient seawater temperatures (27–28° C). The natural photon flux in situ at the collection site during incubation ranged between 1000 and 2100 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of P.A.R. This is within the range of light saturation values documented for other shallow-water macroalgae (King and Schramm 1976, Lapointe et al. 1984). Dissolved oxygen was measured to within 0.01 ppm using an Orbisphere Model 2610 Oxygen Analyzer. The methods concerning selection of material, handling, incubations and oxygen analysis were within the limits recommended by Littler (1979).

Natural populations of reef fishes were used to assess the predation resistances of the three phases simultaneously. Experiments were run in the pavement-rubble channel (see fig. 5 of Rützler and Macintyre 1982) just shoreward of the reef crest during 20–24 April 1985. This zone is characterized by large schools of herbivorous parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), predominantly *Sparisoma croicensis* Bloch, *S. viride*

Bonnaterre, *S. rubripinna* (Cuvier and Valenciennes), *Acanthurus coeruleus* Bloch and Schneider and *A. bahianus* Castelnau. Fish are the dominant grazers of macroalgae at the habitat studied (e.g. Lewis and Wainwright 1985, Littler et al. 1986). The algae were cut into 7 cm-long segments and retained in running seawater for 24 h. The algal thalli were placed under elastic bands on dead coral rubble fragments and dispersed in a mechanically randomized fashion in the reef-flat channel. Thirty replicates per reproductive phase were deployed from 20–22 April 1985. We observed feeding by numerous Scaridae on the specimens, mainly by *Sparisoma viride* (stoplight parrotfish). After 48 h, the remaining thallus lengths were recorded to the nearest 0.5 cm and the percent lost to grazing was calculated. On 22–24 April 1985, predation was again assessed using the suspended line method. Seven centimeter long segments of the three life-history phases (20 replicates of each) were placed between twists of three-stranded white nylon lines (2-mm diameter) at 20-cm intervals in a mechanically randomized pattern. The lines were placed midway in the water column with each end tied to a coral head in the 1.5 m-deep rubble-pavement channel for a 48-h period. In situ observations and bite marks indicated that all losses were due to fish grazing. Thalli were quantified and percent lost to herbivory was recorded as above.

Additional samples of sorted whole plants were air dried in shaded hanging mesh bags and subsequently returned to the laboratory where they were rinsed in distilled water and dried to constant weight at 80° C. The algae then were milled to a fine powder, pelletized and five replicates ignited in a Parr Model 1241 adiabatic, semimicro, bomb calorimeter. The inorganic and organic contents of the three reproductive phases were calculated after igniting 16 replicates of dried material until constant weight at 500° C in a muffle furnace.

The diploid phase (tetrasporophyte) showed a slightly ($0.3 \text{ mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) higher net production rate than either of the haploid phases based on total dry weight of thallus (Fig. 1A), and a 0.3 and 0.5 $\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ higher rate than the female and male plants, respectively, based on thallus organic weight. However, there was no significant difference ($P > 0.05$, two-way ANOVA) between the net apparent photosynthetic rates of the three life-history phases (Fig. 1A), whether based on thallus ash-free dry weight or total dry weight.

The fish grazing data from both the rubble fragments and suspended lines (Fig. 1B) support the prediction that ecological differences among isomorphic reproductive phases are minimal. Although no significant differences ($P > 0.05$, ANOVA) between the herbivore resistances of the three phases were recorded on the rubble fragments, the tetrasporophyte thalli lost somewhat less than either the males or females (4.0% and 5.6% less, respectively). In the suspended-line feeding trials (Fig. 1B), the only significant difference ($P < 0.05$) occurred between the tetrasporophyte and the male thalli where 17.1% less was lost by the former. The tetrasporophyte thalli also lost 7.1% less than the female thalli ($P > 0.05$) when suspended.

There was no significant difference ($P > 0.05$, ANOVA) in the calorific values of the three life-history phases of *Polycavernosa debilis* (Fig. 1C), all of which averaged about 2.7 Kcal·g dry wt⁻¹ of thallus. Differences in the organic and inorganic contents also were insignificant ($P > 0.05$), with the

tetrasporophyte phase averaging about 2% lower in organic content (Fig. 1D).

No life-history phase is precisely isomorphic with respect to another since the reproductive structures are different. However, because the thalli of *Polycavernosa debilis* consist mostly of vegetative cells, our design focused on differences in ploidy level and sex, not micro-morphological differences. The parameters investigated, although limited, revealed no significant short-term ecological or physiological differences attributable to sex or ploidy level for *Polycavernosa debilis*. This result is in accordance with the functional-form model of Littler and Littler (1980) which predicts a tendency for close coupling between macro-morphological attributes and functional responses.

The three phases all showed the same calorific contents, which lie in the mid-range of values for other tropical reef macrophytes. Functional differences in calorific contents among the algae, with the exceptions of relatively low values for Corallinaceae and a tendency for high values in some ephemerals (Littler et al. 1983, Littler and Littler 1984), do not seem to have been acted upon to a large extent by selection.

The presence of natural proportions of reproductive structures and vegetative cells differing in ploidy levels do not result in statistically meaningful light-saturated photosynthetic differences in *Polycavernosa debilis*. This agrees in part with Hannach and Santelices (1985) who noted no significant differences in the growth optima of isomorphic gametophytes and tetrasporophytes of *Iridaea laminarioides* Bory or *I. ciliata* Kützting when temperature, light intensity, water movement and salinity were varied. However, their culture studies revealed different growth rates for the reproductive phases of *I. laminarioides*, but not for *I. ciliata*.

Belizean herbivorous fishes, as a general grazing guild, did not favor one sex or ploidy level as more palatable than another. Because large thalli of female *Polycavernosa debilis* contain easily visible red cystocarps, they might be less cryptic to large mobile fishes. This difference could account for the relative paucity of female plants in the field (only ca. 15% of the individuals collected were female). However, the 7-cm long segments that were used in the feeding trials rarely contained cystocarps and, therefore, this cue was not a factor in our experimental design. Hannach and Santelices (1985) conducted palatability studies using two species of *Iridaea* with isomorphic gametophyte and tetrasporophyte phases. No significant preferences were shown for three out of four molluscan herbivores tested. The exception was a higher consumption of gametophytic versus sporophytic specimens of *Iridaea laminarioides* by the limpet *Collisella cecilians* (Orbigny), perhaps due to unknown structural or chemical properties.

Published information on ecologically meaningful divergences between fertile isomorphic stages of algae is scarce. Our preliminary data falsify the hy-

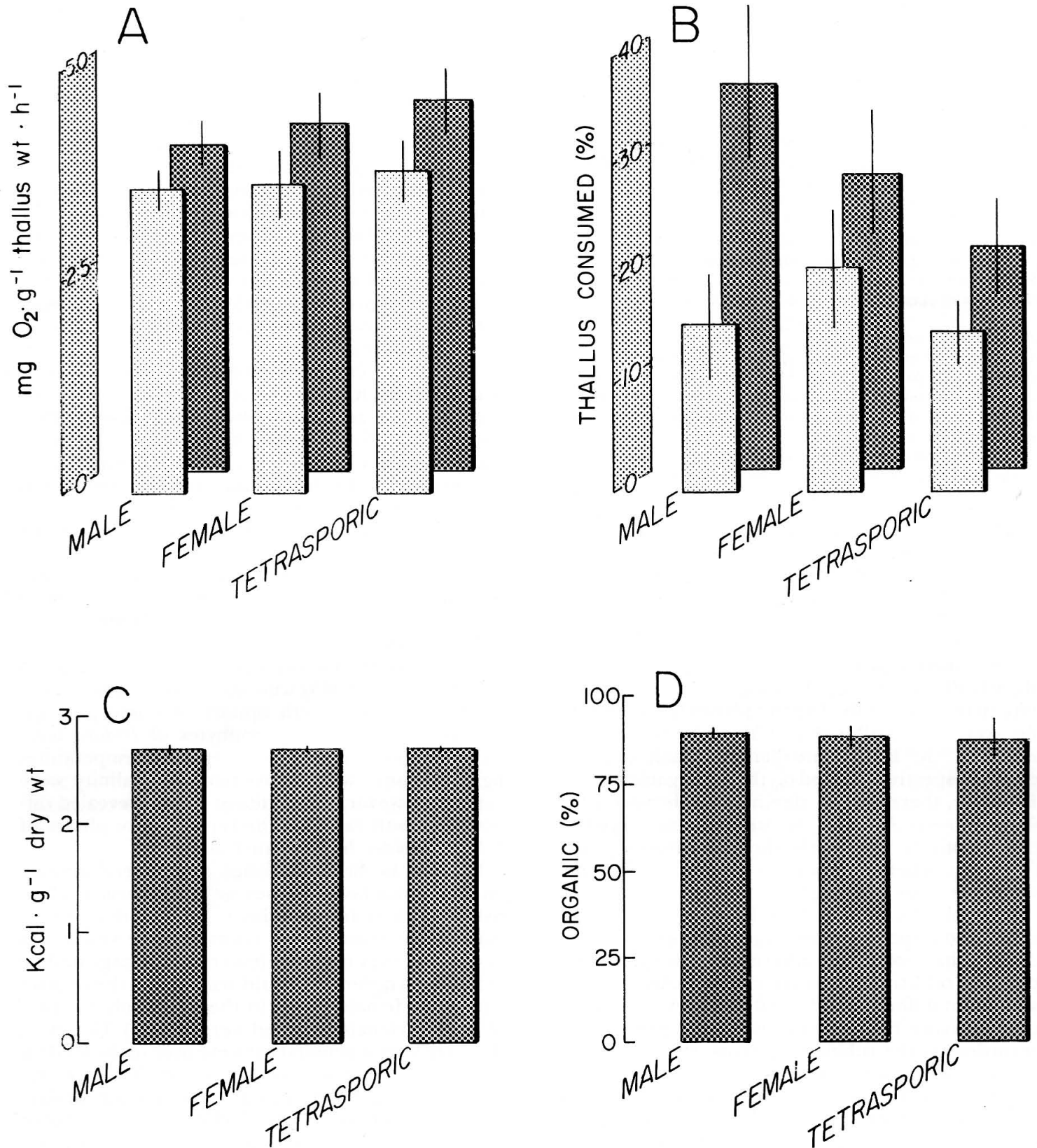


Fig. 1A–D. *Polycavernosa debilis*. A. Mean net primary productivity per thallus dry weight (light histograms in front; $n = 16$) and ash-free weight (dark, in rear; $n = 16$) for male, female and tetrasporic reproductive phases. B. Susceptibility to predation by herbivorous fishes per 48 h on coral rubble (light histograms in front; $n = 30$) and suspended lines (dark, in rear; $n = 20$). C. Dry weight calorific values ($n = 5$). D. Percent organic contents ($n = 16$). Vertical lines indicate \pm standard error.

pothesis that ploidy level alone results in large physiological and ecological responses; however, more subtle differences may exist. For example, a number of workers have recorded disparate distributional patterns for various algal life-history phases that are essentially isomorphic. These differences in distribution occur on geographical scales (e.g. Dixon 1960, 1965, Edwards 1973, Garbary 1976, Whittick 1978), within habitats (e.g. Barilotti 1971, Mathieson 1979, Hannach and Santelices 1985) and temporally (Hannach and Santelices 1985). Although the relative allocation of resources to structural materials was quite close in all three life-history phases examined here, biochemical differences between sporophyte and gametophyte generations have been shown for several species of Gigartineae (e.g. Pickmere et al. 1973, McCandless et al. 1975, Waaland 1975).

The lack of significant functional responses at the scale of those parameters investigated suggests that genetic/reproductive constraints may be the predominant factors involved in maintaining isomorphic reproductive phases. However, if there is adaptive value in both gametic reproduction (e.g. resource exploitation, genetic recombination) and sporic reproduction (e.g. environmental resistance, dispersal; see Willson 1981) and a single morphological form represents the "best" compromise in fitness, then isomorphic diploid and haploid phases could be maintained.

We are most grateful to D. Hanisak, J. Kilar and B. Santelices who provided thoughtful comments. Special thanks go to B. Brooks who assisted in the field and laboratory phases of the research. Field work was supported by grants from the Caribbean Coral Reef Ecosystems Program, National Museum of Natural History and Exxon Corporation. (CCRE Contribution No. 212).

- Allender, B. M. 1977. Ecological experimentation with the generations of *Padina japonica* Yamada (Dictyotales: Phaeophyta). *J. Exp. Mar. Biol. Ecol.* 26:225-34.
- Barilotti, D. C. 1971. Ecological implications of haploidy and diploidy for the isomorphic brown alga *Zonaria farlowii* Setch. et Gardn. *J. Phycol.* 7(suppl.):4.
- Benson, M. R. 1983. An ecological study of isomorphism in *Dictyopterus undulata*. *Western Soc. Natur.* Abstr., p. 11.
- Dethier, M. N. 1981. Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. *Oecologia (Berl.)* 49:333-9.
- Dixon, P. S. 1960. Studies on marine algae of the British Isles: *Ceramium shuttleworthianum* (Kütz.) Silva. *J. Mar. Biol. Assoc. U.K.* 39:375-90.
- 1965. Perennation, vegetative propagation and algal life histories, with special reference to *Asparagopsis* and other Rhodophyta. *Bot. Goth.* 3:67-74.
- 1982. Life histories in the Florideophyceae with particular reference to the Nemaliales *sensu lato*. *Bot. Mar.* 25:611-21.
- Edwards, P. 1973. Life history studies of selected British *Ceramium* species. *J. Phycol.* 9:181-4.
- Fredericq, S. & Norris, J. N. 1985. Morphological studies on some tropical species of *Gracilaria* Grev. (Gracilariaceae, Rhodophyta): taxonomic concepts based on reproductive morphology. In Abbott, I. A. & Norris, J. N. [Eds.] *Taxonomy of Economic Seaweeds*. California Sea Grant College Program, University of California, La Jolla, pp. 137-55.
- Garbary, D. 1976. Life-forms of algae and their distribution. *Bot. Mar.* 19:97-106.
- Hannach, G. & Santelices, B. 1985. Ecological differences between the isomorphic reproductive phases of two species of *Iridaea* (Rhodophyta: Gigartinales). *Mar. Ecol. Prog. Ser.* 22: 291-303.
- King, R. J. & Schramm, W. 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. *Mar. Biol. (Berl.)* 37:215-22.
- Lapointe, B. E., Rice, D. L. & Lawrence, J. M. 1984. Responses of photosynthesis, respiration, growth and cellular constituents to hypo-osmotic shock in the red alga *Gracilaria tikvahiae*. *Comp. Biochem. Physiol.* 77:127-32.
- Lewis, S. M. & Wainwright, P. C. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *J. Exp. Mar. Biol. Ecol.* 87:215-28.
- Littler, M. M. 1979. The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. *Aquat. Bot.* 7:21-34.
- Littler, M. M. & Littler, D. S. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.* 116:25-44.
- 1983. Heteromorphic life-history strategies in the brown alga *Scytosiphon lomentaria* (Lyngb.) Link. *J. Phycol.* 19:425-31.
- 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *J. Exp. Mar. Biol. Ecol.* 74:13-34.
- Littler, M. M., Littler, D. S. & Taylor, P. R. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J. Phycol.* 19:229-37.
- Littler, M. M., Taylor, P. R. & Littler, D. S. 1986. Plant defense associations in the marine environment. *Coral Reefs* 5:63-71.
- Lubchenko, J. & Cubitt, J. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676-87.
- Mathieson, A. C. 1979. Vertical distribution and longevity of subtidal seaweeds in northern New England, U.S.A. *Bot. Mar.* 30:511-20.
- McCandless, E. L., Craigie, J. S. & Hansen, J. W. 1975. Carrageenans of gametangial and tetrasporangial stages of *Iridaea cordata* (Gigartineae). *Can. J. Bot.* 53:2315-8.
- Pianka, E. R. 1970. On r- and K-selection. *Am. Nat.* 104:592-7.
- Pickmere, E. S., Parsons, M. & Bailey, R. W. 1973. Composition of *Gigartina* carrageenan in relation to sporophyte and gametophyte stages of the life cycle. *Phytochemistry* 12:2441-4.
- Rützler, R. & Macintyre, I. G. 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. In Rützler, R. & Macintyre, I. G. [Eds.] *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities*. Smithsonian Contributions to the Marine Sciences, No. 12. Smithsonian Institution Press, Washington, D.C., pp. 9-45.
- Slocum, C. J. 1980. Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. *J. Exp. Mar. Biol. Ecol.* 46:99-110.
- Stebbins, G. L., Jr. 1950. *Variation and Evolution in Plants*. Columbia University Press, New York, 662 pp.
- Stebbins, G. L. & Hill, G. J. 1980. Did multicellular plants invade the land? *Am. Nat.* 115:342-53.
- Waaland, J. R. 1975. Difference in carrageenan in gametophytes and tetrasporophytes of red algae. *Phytochemistry* 14:1359-62.
- Whittick, A. 1978. The life history and phenology of *Callithamnion corymbosum* (Rhodophyta: Ceramiaceae) in Newfoundland. *Can. J. Bot.* 56:2497-9.
- Willson, M. J. 1981. On the evolution of complex life cycles in plants: a review and an ecological perspective. *Ann. Missouri Bot. Gard.* 68:275-300.