

PRIMARY PRODUCTIVITY OF MARINE MACROALGAL FUNCTIONAL-FORM GROUPS FROM SOUTHWESTERN NORTH AMERICA¹

Mark M. Littler² and Keith E. Arnold³

Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717

ABSTRACT

New productivity data are given for 62 macroalgal species from 6 intertidal habitats spanning a latitudinal range of nearly twelve degrees on the Pacific Coast of southwestern North America. Our data, utilizing a functional-form group approach, support an hypothesis relating morphological forms to photosynthetic performances. Specifically, the Sheet-Group showed the highest productivity (mean apparent net photosynthetic performance = $5.16 \text{ mg C} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) with a reduction of ca. two-fold between each of the following four groups: Filamentous-Group (2.47), Coarsely Branched-Group (1.30), Thick Leathery-Group (0.76) and Jointed Calcareous-Group (0.45). The Crustose-Group had by far the lowest mean net productivity being only $0.07 \text{ mg C} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. The functional-form group approach is a promising tool for predicting the outcome of productivity-related ecological and evolutionary processes without being restricted temporally, geographically or taxonomically.

Key index words: macroalgae; photosynthesis; productivity; functional-form; rocky intertidal zone

Recently, increased interest has been shown (Lieberman et al. 1979, Littler 1980a, Littler and Littler 1980, 1981, Montgomery 1980a,b) in viewing marine algae from the perspective of ecologically-related groupings. These studies have used diverse viewpoints in categorizing algal species and consequently have met with varying success; all represent major improvements over the earlier "life-form" classifications (see Funk 1927, Feldmann 1938, Katada and Satomi 1975, Chapman and Chapman 1976). The latter have not been of wide usefulness because they failed to include meaningful ecological interactions and physiological attributes. What has been lacking is a predictive model for understanding the critical selective processes that determine photosynthetic properties. The functional-form approach (Littler and Littler 1980, 1981), showing that a number of hypothetically-adaptive survival strategies have been selected in various species of macroalgae, represents a major step in this direction.

The present paper presents an extension of the functional-form hypothesis proposed by Littler (1980a) who demonstrated the usefulness of a func-

tional-group viewpoint for understanding and predicting patterns of primary productivity within a diverse and previously unstudied macrophyte flora from a broad spectrum of rocky intertidal environments. Specifically, we will attempt to postulate the outcome of evolutionarily-derived morphological adaptations on productivity relationships without being constrained in time or space to a specific region, environment or phylogenetic line.

METHODS AND MATERIALS

Previously unpublished productivity data are reported herein for 62 macroalgal species⁴ (involving over 700 separate incubations) from six markedly different habitats on the Pacific Coast of southwestern North America (Fig. 1), spanning a latitudinal range of nearly twelve degrees. Net apparent photosynthesis was determined at ambient water temperatures ($13\text{--}21^\circ \text{C}$) for the dominant intertidal macroalgae at San Simeon on November 1974 and February 1979, Newport Bay (October 1974), Laguna Beach (November 1974 and June 1975), San Clemente Island (May 1975–October 1977), Punta Hipolito (February 1979) and Punta Marquez (February 1979). Incubations consistently occurred between 0900 and 1430 hours (to minimize possible daily periodicity phenomena) over a light regime of 45 000 to 95 000 lux (900 to $1900 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ P.A.R.), which was the natural light in situ and in the range of light saturation documented for intertidal macroalgae (King and Schramm 1976, Arnold and Murray 1980). Net productivity was measured by the dissolved oxygen method and calculated as milligrams carbon fixed per gram dry weight per hour assuming a photosynthetic quotient (P.Q.) of 1.00. The dry weight of calcareous species included all inorganic matter. The methods concerning the selection of material, handling, incubation and oxygen analysis followed the recommendations of Littler (1979) and Littler and Arnold (1980) and were essentially similar to those employed by Littler (1980a).

For each species, the mean of the replicates (and 95% confidence limits) were determined and ranked from highest to lowest within six functional-form groups. We used a slight modification of Littler's (1980a) seven functional groupings. These are ranked from the hypothesized highest to lowest primary productivity based on morphology, size and surface to volume ratio (see Littler and Littler, 1980, for comparative ratios for four of the groups defined here) and include: thin (one to several cells thick) tubular (often collapsed) and sheet-like (laminar) forms (herein called Sheet-Group), delicately-branched (lightly corticated) filamentous forms (Filamentous-Group), coarse branched (extensively corticated) fleshy to wiry forms (Coarsely Branched-Group), thick blades and branched leathery forms (Thick Leathery-Group), articulated upright calcareous forms (Jointed Calcareous-Group) and prostrate encrusting forms (Crustose-Group). The saccate cushion-like forms of Littler (1980a) represent special cases and have been placed into the Coarsely Branched-Group for convenience. The scheme should not be viewed as representing dis-

¹ Accepted: 26 January 1982.

² Present address: Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

³ Present address: Department of Biological Sciences, California State Polytechnic University, Pomona, California 91768.

⁴ See Abbott and Hollenberg (1976) for authors of species mentioned in this paper.

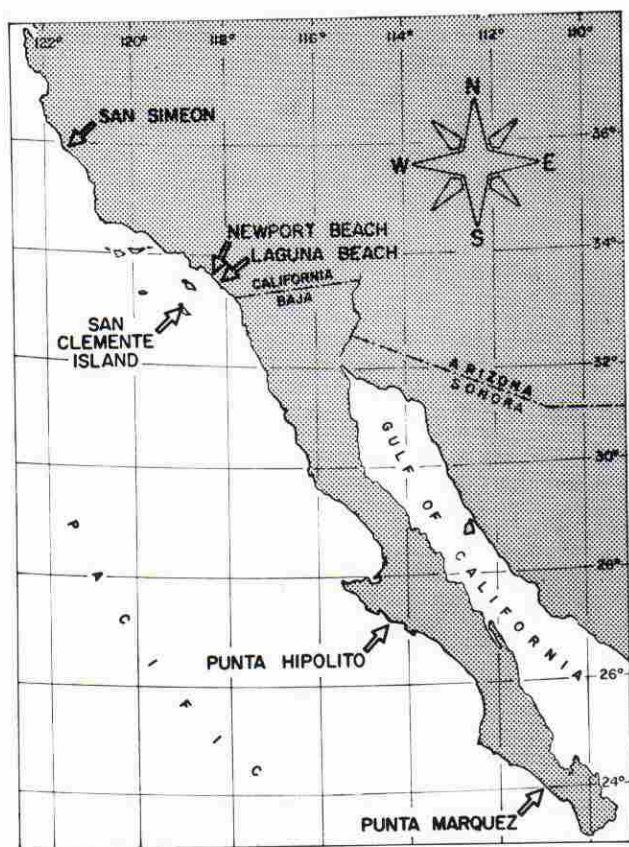


FIG. 1. Location of the six study sites on the Pacific Coast of southwestern North America.

crete differences between groups, but as mid-points along a continuous gradient of possible thallus types. We appreciate that algae, which reproduce by spores or gametes develop initially as microscopic germlings and may pass through several functional groups (Neushul 1972, Littler and Littler 1980) before reaching maturity; however, we will deal only with mature plants in this paper.

RESULTS

The taxa have been ranked (Fig. 2) in functional-form groups from highest to lowest producer. The ranking of means for groups fits the predicted pattern with about a factor of two in reduction of net photosynthesis between each of the first five groups (i.e. Sheet-Group = $5.16 \text{ mgC} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, Filamentous-Group = 2.47 , Coarsely Branched-Group = 1.30 , Thick Leathery-Group = 0.76 , Jointed Calcareous-Group = 0.45); whereas, the Crustose-Group was dramatically lower than any other group (almost 7 times lower than the Jointed Calcareous-Group) with a mean net productivity of only $0.07 \text{ mgC} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. This ordering of groups was remarkably consistent within each study area, irrespective of geographic location (Fig. 2). There was greater than two orders of magnitude difference between the photosynthetic rates of the highest (*Ulva taeniata*) and lowest (*Pseudolithoderma nigra*) producers measured. Several species in each group consis-

tently had productivity values below the mean of the next lower group, but only one or two species in the next lower group were higher than the mean of the preceding group. An exception to this overlap is the array of encrusting species (Fig. 2) which were clearly separated from all other forms by their exceptionally low net photosynthetic rates.

There were no significant differences ($P > 0.05$, Eberhardt 1968) in productivity between sets of any of the eight species from the different geographic regions (Fig. 2). Furthermore, no taxonomically-related patterns in primary productivity were discerned because both brown and red algal divisions had species that ranked among the lowest and highest producers. Green algal representatives of the relatively unproductive Thick Leathery-Group, Jointed Calcareous-Group and Crustose-Group were not available and, consequently, green algae artificially ranked among the highest producers except for *Codium fragile* from Punta Hipolito ($0.57 \text{ mgC} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$).

DISCUSSION

The ranking of functional groups (Fig. 2) supports the functional-form hypothesis of Littler (1980a) and Littler and Littler (1980). The data for the first three groups are also in agreement with those of Odum et al. (1958), Kanwisher (1966), Littler and Murray (1974), King and Schramm (1976) and Arnold and Murray (1980), in that forms with higher surface area to volume ratios outproduced species with lower ratios (see p. 38 of Littler and Littler 1980 for representative ratios). However, as pointed out by Littler (1980b), clumped (turf) forms of some filamentous algae with high surface to volume ratios have been shown (Dawes et al. 1978, Littler and Arnold 1980) to be exceptions to this pattern. It is likely that selection for resistance to predation, desiccation or thermal stress has led to the tightly clumped habits of some filamentous turf algae (Hay 1981), resulting in self-shading and intraspecific competition for nutrients and thereby reducing photosynthetic capacity.

The relative abilities of the various morphologies to utilize light and obtain nutrients would appear to account for the differences among groups. Odum et al. (1958) also noted that uptake of ^{32}P and primary productivity below saturating light intensities were correlated with the surface to volume ratios of seven marine macrophytes. The thin tubular and sheet-like forms (Fig. 2) have considerably higher apparent photosynthetic rates than the other algae measured. Littler (1980a) attributed this to their extremely thin construction which minimizes self shading; also, they have thinner-walled cells than most other coarser forms, thus relatively less internal shading of the photosynthetic apparatus. The light-utilization capabilities of three groups of macroalgae were examined by Raven et al. (1979) in terms of cell size. These were giant-celled stress-tolerant

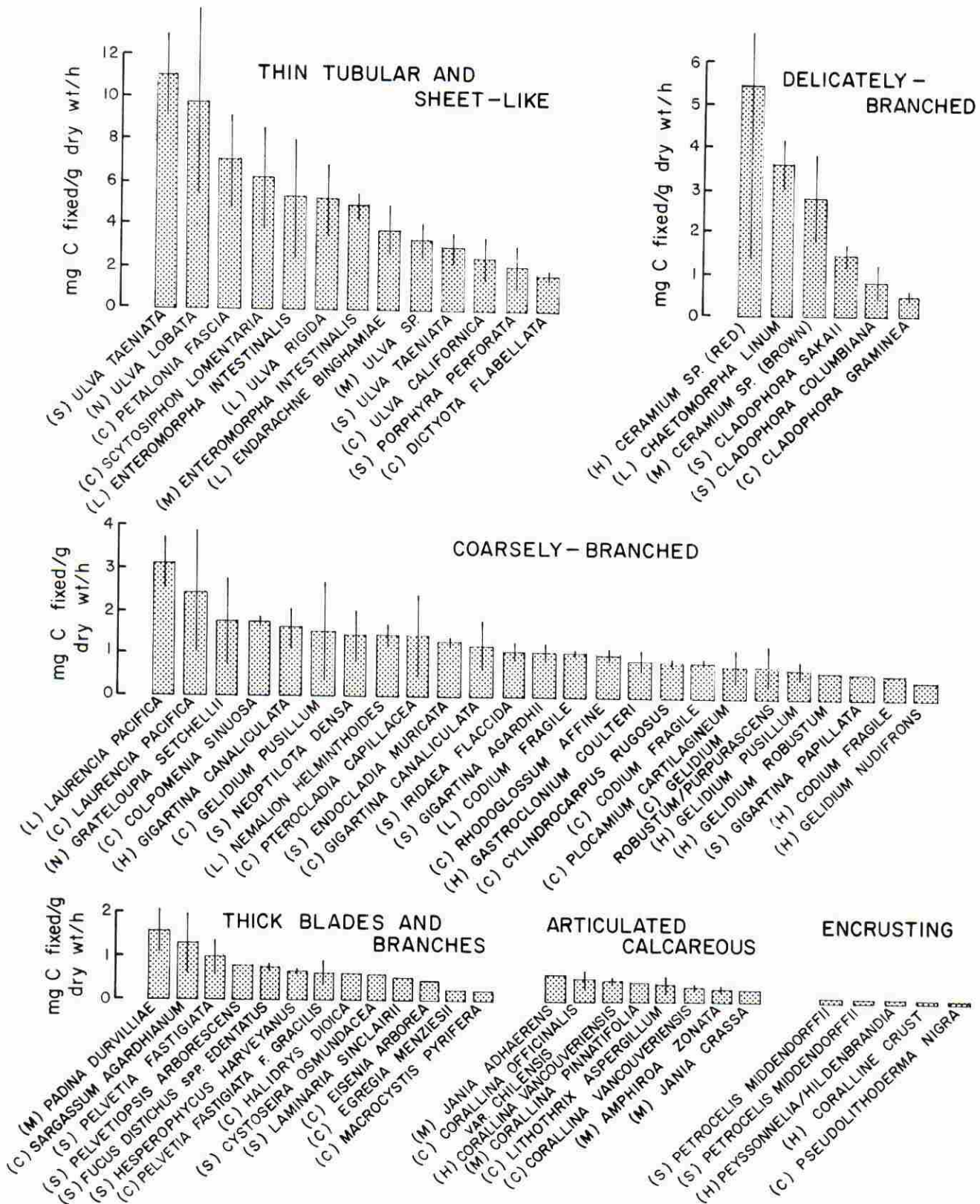


FIG. 2. Net apparent photosynthetic performances ($\pm 95\%$ CI) of the six functional-form groups measured at San Simeon (S), Newport Beach (N), Laguna Beach (L), San Clemente Island (C), Punta Hipolito (H) and Punta Marquez (M).

strategists (sensu Grime 1977; e.g. *Chaetomorpha darwinii*) found to be shade plants, smaller-celled fugitive algae (e.g. *Enteromorpha intestinalis*, *Chaetomorpha linum*) classified as sun plants, and small-celled canopy forms (e.g. *Laminaria digitata*) which are sun tolerant. In agreement, Ramus (1978) found the internal light trapping abilities of giant-celled *Codium* and relatively smaller-celled *Ulva* to be adaptive for low and high light environments, respectively. Littler and Littler (1980a) showed that, on an area basis, large forms (i.e. the lower producing groups in Fig. 2) contain significantly greater proportions of structural vs. photosynthetic tissue, much of which exhibits low metabolic rates (Kanwisher 1966, Littler 1980a, Kremer 1980), and this results in lower net production rates based on dry weight.

There is no relationship between primary productivity and phylogenetic affinity in agreement with the findings of Littler and Murray (1974), Buesa (1977) and Littler (1980a). This is in marked contrast to the interpretation of Johnston (1969), who noted that brown algae were considerably more productive than green and red algae. Johnston's (1969) data are most easily interpretable in light of the functional-form hypothesis, since he compared a relatively small spectrum of species and forms. Even within widely differing phylogenetic lines (Divisions), there exists a repetition of forms illustrating convergent evolution in response to factors that regulate fitness, and our data, along with those of Littler and Murray (1974), Littler (1980a) and Arnold and Murray (1980), show that photosynthetic performances are clearly and consistently related to these functional-form groups.

The point has been raised (King and Schramm 1976) that higher intertidal algae produce more than lower intertidal species. Again, this is more closely related to functional form than to tidal height. Because there is more stress and disturbance higher on the shore, there tend to be more opportunistic species in that habitat. As shown by Littler and Littler (1980, 1981), the opportunists incorporate such features as rapid growth rates, high reproductive output and simple, small thalli with high surface to volume ratios and high photosynthetic capabilities. Selection in disturbed or fluctuating environments (Littler and Littler 1981) has led to opportunistic or ephemeral forms such as *Ulva*, *Petalonia*, *Scytosiphon*, *Enteromorpha*, *Ceramium* and *Chaetomorpha*, while the coarser and tougher conspicuous species such as thick forms, calcareous and encrusting species persist in less stressful, more biologically-accommodated habitats at the cost of markedly lower photosynthetic rates.

This difference is doubtless due to the allocation of energy and resources to structural components in the persistent species, that are consequently unavailable for photosynthesis and reproduction. The evolution of environmental resistance (hardiness), defenses against predation or interference com-

petition include costs due to (1) an energetic commitment or (2) a material commitment that results in reduced potential for photosynthesis and, hence, slower growth and lower reproduction; as well as (3) the possible incompatibility of such systems with essential metabolic processes. For a given feature to be selected, the benefits resulting from the investment of resources must be greater than the costs plus the competing alternative investments that are possible given the organism's genetic constraints.

This study further supports the prediction that morphological form and physiological function are co-evolved in the macroalgae. Although exceptions to the patterns described here exist and more will likely appear, the functional-form group approach is a promising tool for interpreting physiological and morphological co-evolved interrelationships. Specifically, it demonstrates considerable credibility in predicting the outcome of productivity-related ecological processes without being bound to a particular geographic region or phylogenetic line. For this reason, the functional-form group approach should prove more utilitarian in lieu of the "life-form" (Feldmann 1938), life history (Lieberman et al. 1979) or phylogenetic (Montgomery 1980a,b) classification schemes. As an "applied" example, the functional-form relationship could reasonably be used to identify potentially highly-productive species, or in fingerprinting the most productive portions of differentiated algal thalli, to be used in biomass-energy conversion programs (Jackson 1980). The importance of seaweeds in fixing energy in coastal waters has been well documented (Blinks 1955, Kanwisher 1966, Mann 1973, Littler 1973, Littler et al. 1979); however, because of the descriptive nature of much of the previous research, new viewpoints, such as the one presented here, are needed to lead to accurate predictions or to realistically interpret macroalgal metabolic functions and ecological-evolutionary interactions.

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