Morphological Form and Photosynthetic Performances of Marine Macroalgae: Tests of a Functional/Form Hypothesis[1]

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Abstract

Net and gross production rates were determined in the field at light intensities above 20,000 lux for 45 species of marine macroalgae from four different environments in southwestern North America. Thin sheetlike and finely branched thallus-forms showed greater rates than other forms. A morphological form more suited to efficiently utilize light energy and obtain nutrients is clearly related to the differences measured. There was a close relationship between dry weight as well as two-dimensional thallus area and photosynthetic performance for macrophytes having relatively large surface areas (*i.e.*, thin and finely branched forms). However, the productivity values for the range of coarsely-branched to encrusting forms were in closer agreement with respect to thallus area than with respect to dry weight.

Introduction

Surprisingly few productivity estimates are available for marine macrophytes although seaweeds are conspicuously abundant throughout all oceans of the world. Mann (1973) has summarized the available production data for frondose macrophytes and Littler (1973) reported on the productivity of tropical crustose coralline algae. The emerging picture suggests that reef and coastal algal communities rank among the highest primary producers on earth.

Only several studies have considered algal structure and its relationship to primary productivity. Odum, Kuenzler, and Blunt (1958) found that uptake of ^{32}P and primary productivity were correlated with the surface-to-volume ratios of seven marine benthic algae; however, the light intensity they used (450 ft-c) was probably well below natural levels. Productivity was first shown to be related to the form of an alga's thallus by Littler and Murray (1974), with later supporting data provided by King and Schramm (1976). Kanwisher (1966) conceptualized an algal frond as a population of photosynthetic cells in a structural matrix. He noted that, on a dry weight basis, massive forms containing relatively higher ratios of structural to photosynthetic components tended to have a lower photosynthetic capacity than the more delicate forms. This concept has received further elaboration by Ramus (1978) who found the relative internal light trapping capabilities of *Ulva* and *Codium* to be adaptive for high and low light intensity environments, respectively.

Traditionally, algal productivity approaches have 1) emphasized descriptions of the photosynthetic and respiratory features (usually in the field) for dominant populations (*e.g.*, Johnston 1969, Buesa 1977) or 2) involved laboratory studies on the relationships between photosynthetic performances and physical environmental factors for selected species (*e.g.*, Littler 1973, Mathieson and Norall 1975, Brinkhuis 1977). These lines of investigation, while providing much useful specific and detailed data, have not added greatly to our ability to generalize or make predictions because they provide little information on the critical selective processes that determine photosynthetic properties. Clearly, the relationships of algal morphology in respect to physiological functions (*e.g.*, productivity) under natural field conditions have adaptive implications and may reveal evolutionary "strategies" heretofore unexplored. The present research was undertaken to test the hypothesis that morphology and photosynthetic performance are related and, in so doing, begin to look at the adaptive significance of thallus form as it pertains to the productivity ecology of rocky intertidal seaweeds.

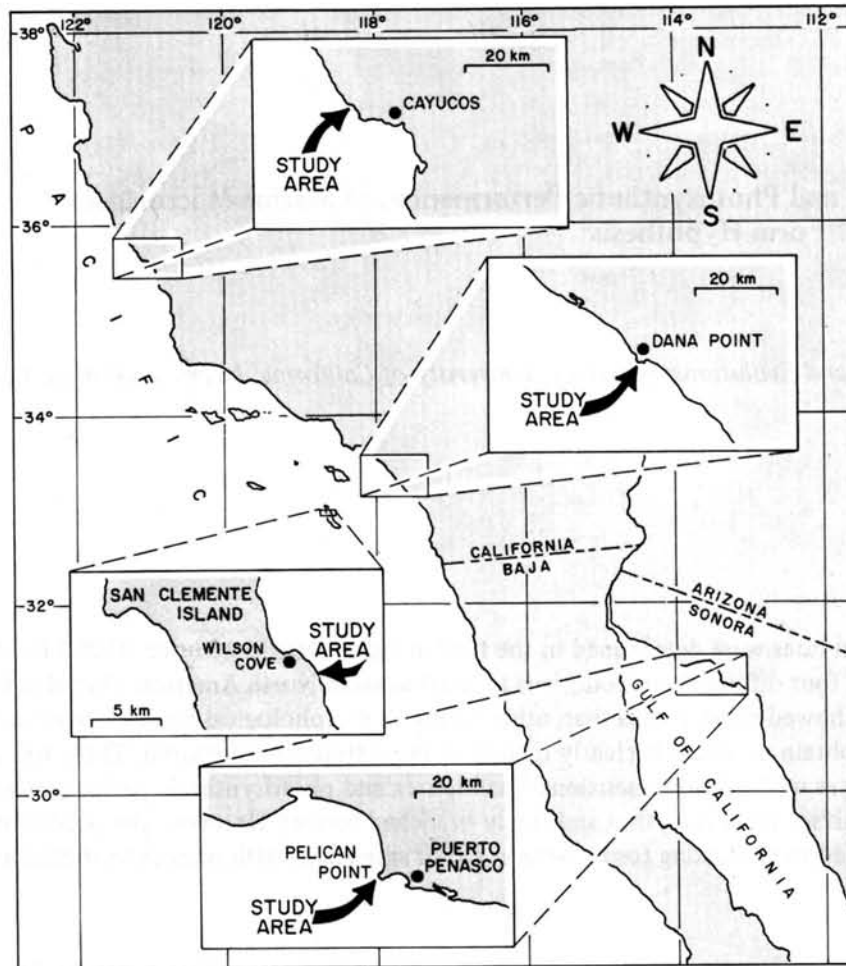[1] This paper was originally presented at the Eighth International Seaweed Symposium, 1974.

Fig. 1. Location of the four areas studied in southwestern North America.

Methods and Materials

This research was carried out at four markedly different habitats in southwestern North America with the latitudes and longitudes given in Figure 1. Photosynthetic and respiratory performances were determined at ambient water temperatures (13–16° C) for the dominant intertidal macroalgae at Cayucos on 19 February, Dana Point on 4 February, San Clemente Island on 19 and 20 May, and Puerto Peñasco on 5 March 1973, consistently under overcast skies of 20,000 to 65,000 lux. The general methods for measuring respiration and primary productivity were the same as those described by Littler and Murray (1974) with the following additional details.

Whole organisms were incubated for the smaller species [*e.g., Corallina* spp., *Gelidium pusillum* (Stackh.) Le Jol., *Gigartina canaliculata* Harv.]; however, incubations of the larger forms (*e.g., Macrocystis, Egregia, Eisenia*) were conducted on portions of representative blades or branches. Consequently, in the case of the larger forms (*i.e.*, Laminariales and Fucales), the photosynthetic performances represent overestimates because the lower producing stipe and holdfast portions of the thalli (Littler

and Arnold submitted) could not be incubated in the 300 ml bottles. Throughout the experiments, the thallus dry weights did not exceed the ratio of weight: volume: incubation time recommended by Johnston (1969). All incubations were carried out between 1000 and 1600 hrs to minimize any possible effects due to daily, endogenous photosynthetic periodicity. The incubation water was vigorously shaken before use until a stock at air saturation was obtained. All bottles were thoroughly shaken at 15 min intervals to prevent large diffusion gradients from occurring; cooling was applied by replacing the ambient seawater in the incubation trays at < 10 min intervals.

All of the O_2 values were converted to mg C fixed/g dry wt/h and to g C fixed/m^2 of thallus/h by assuming a photosynthetic quotient of 1.20 (Strickland 1960). For each species the two replicate measurements of respiration were averaged and added to the four values of the light replicates, and the mean ± 90 % confidence intervals were determined, to obtain estimates of gross productivity. These were then arranged in thallus form categories (Figs. 2 and 3) roughly corresponding to decreasing surface area to volume ratios.
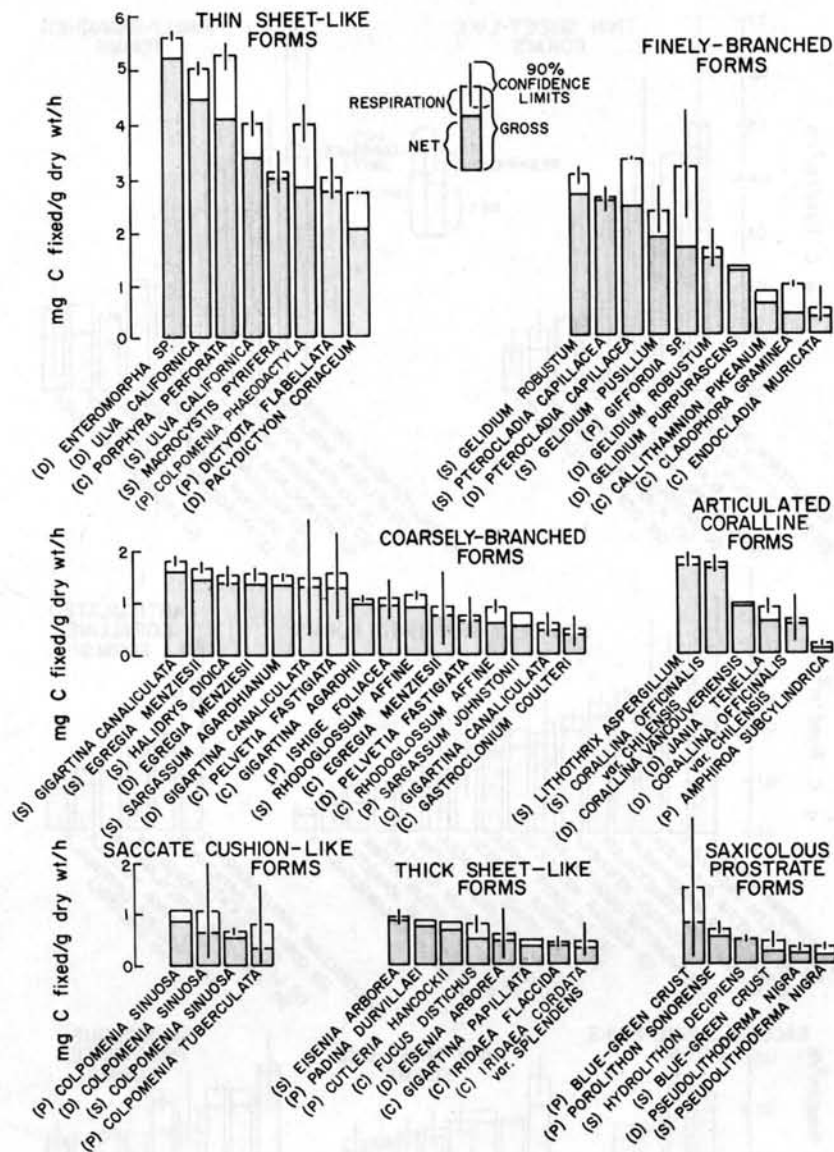
Fig. 2. The net and gross primary productivity (mg C/g dry weight/h) of seven thallus-form groups of macroalgae measured at Dana Point (D), Cayucos (C), Puerto Peñasco (P) and San Clemente Island (S). Where 90% confidence limits are lacking they are greater than + or − the mean.

Results and Discussion

The macrophytes have been ranked (Fig. 2) in thallus-form groups from highest to lowest net producer on a dry-weight basis. At light intensities above 20,000 lux, the thin sheet-like forms were by far the greatest producers per unit of biomass followed by finely-branched forms, with saxicolous prostrate forms producing somewhat less than any of the other macrophytes. Finely-branched forms produced more than coarsely-branched forms, in agreement with the findings of Kanwisher (1966) and Odum et al. (1958). A thallus-form more suited to utilizing light energy and obtaining nutrients would seem, as a working hypothesis, to explain the differences measured. In partial support, *Ulva* has been shown (Ramus 1978) to have a morphology especially adaptive to high light regimes. Also, Odum et al. (1958) found that the uptake of ^{32}P was more rapid in algae having relatively high surface to volume ratios. *Entero-*

morpha sp., *Ulva californica* Wille and *Porphyra perforata* (L.) C. Ag. comprise a group with considerably higher apparent photosynthetic performances than other algae measured. The extremely thin construction of these three minimizes self-shading; also, they have larger cells than most other macroalgae resulting in relatively little internal self-shading by non-photosynthetic wall components.

A ranking of net production rates on the basis of thallus area is given in Figure 3. The same patterns are generally recognizable, from highest to lowest producer, as were evident on the basis of dry weight (Fig. 2). It is apparent that thin and finely-branched seaweeds show higher production rates per unit area than coarsely-branched forms, which in turn are higher than either saccate forms, prostrate forms, or thick sheet-like forms.

For the thin sheet-like and finely-branched forms, net productivity was closely correlated with both dry weight
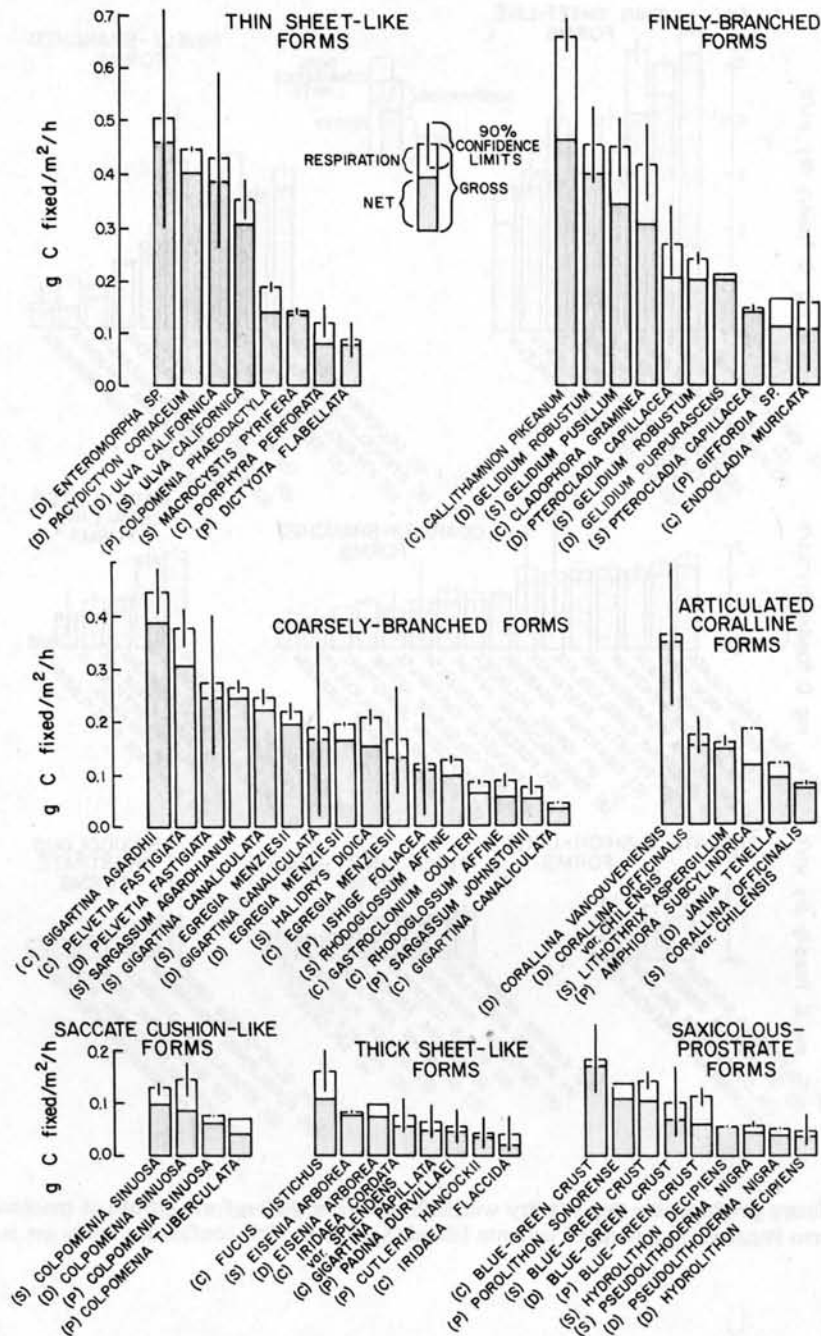
Fig. 3. The net and gross primary productivity in grams carbon fixed per hour per square meter of two-dimensional (*i.e.*, normal to the light path) thallus area of seven thallus-form groups of macroalgae measured at Dana Point (D), Cayucos (C), Puerto Peñasco (P) and San Clemente Island (S). Where 90 % confidence limits are lacking they are greater than + or − the mean.

and with surface area. This trend would seem to be due to the fact that nearly all of the biomass in the thin and finely-branched forms is photosynthetic, which results in a close functional relationship between primary production and total thallus dry weight.

This was not the case for the other five thallus-form groups where confidence limits were wider in terms of dry weight (Fig. 2) than in terms of surface area (Fig. 3); that is, 14 % wider for coarsely-branched forms, 73 % for articulated corallines, 143 % for saccate cushion-like forms, 21 % for thick sheet like forms, and 5 % for prostrate forms. These five groups have relatively more of their biomass made up of structural and other non-photosynthetic components; therefore, one might

predict that dry weight would not be so closely related to primary productivity as would the surface area actually intercepting the light energy.

Because only two replicates per species were used in the respiration studies (Figs. 2 and 3), it is not possible to detect any consistent patterns except that the forms with relatively higher proportions of photosynthetic tissue (*e.g.*, thin and finely-branched forms) tended to have higher absolute rates of respiration. The greater proportions of structural tissues in the larger coarse species did not result in proportionately greater ratios of respiration to photosynthesis, indicating that much of the structural material is non-metabolic. The exceptionally low absolute respiration values shown by

most of the coralline algae on a weight basis (Fig. 2) would seem to support this interpretation.

Many of the highly-productive sheet-like forms (with the exception of the blade portions of *Macrocystis*) have been noted (Bokenham and Stephenson 1938, Northcraft 1948, Fahey 1953, Murray and Littler 1978) as very early colonizers of disturbed rocky-intertidal substrates. Connell's (1975) successional hypothesis states that disturbed patches will most likely be recolonized first by species with high reproductive output (*i.e.*, long reproductive seasons and large numbers of propagules). Littler and Murray (1975) extended the characteristics. of this pioneer (opportunistic) group of algae to include features such as rapid growth rates, high productivity, and simple thalli with high surface to volume ratios. It would appear from our data (Figs. 2 and 3) that selection in disturbed or fluctuating environments has favored opportunistic species (*e.g.*, *Enteromorpha*, *Ulva*, *Porphyra*) having high net productivity, while the large conspicuous species (*e.g.*, calcareous forms, thick forms, prostrate crusts) able to predominate in less stress-ful predictable habitats do so at the cost of lower photo-synthetic rates. This is no doubt due to the allocation of energy and materials to structural components in the latter, which then become unavailable for photosynthesis and reproduction.

This study has supported the prediction that morpho-logical form and physiological function are intimately related in the macroalgae. Furthermore, since the thallus-form/productivity relationship was applicable over a broad latitudinal range including different habitats, it would appear that selection pressure for small thallus-forms with rapid growth and high reproductive output as well as selection for large morphological forms con-taining considerable structural tissue are widespread evolutionary forces among the macroalgae. A major limitation in the currently-proposed life-form classific-ation schemes (Katada and Satomi 1975, Chapman and Chapman 1976) is the failure to include considerations of ecological interactions or metabolic functions; these must be treated before a realistic and utilitarian synthesis of "forms" in the algae can be forthcoming.

Acknowledgments

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