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Application of the functional-form model to the culture of seaweeds

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Abstract

Selecting the most appropriate species or strains is an important first step in the development of most algal cultivation systems and is usually a tedious, time-consuming, and expensive step. The functional-form model, first developed to synthesize the adaptive significance of easily assessed thallus-form attributes relative to the productivity and survival of benthic macroalgae, is applicable to the culture of seaweeds and can expedite species or strain selection. The production ecology aspects of the model are useful particularly for applications where the desired product is not species-specific, e.g., systems in which the emphasis is on algal production, such as algal biomass farms and wastewater treatment. A thallus-form with a high surface area : volume ratio is more suited for rapid production and nutrient uptake. The utility of this model to strain selection is demonstrated with the red alga *Gracilaria tikvahiae*, a species that has been considered a maricultural candidate for a number of utilizations. A continuum of surface area : volume ratios for eight clones of *G. tikvahiae* showed that this ratio decreased as morphological complexity increased and was a good predictor of both short-term photosynthesis and long-term growth rate. Clones near opposite ends of the surface area : volume ratio spectrum had significant differences for both photosynthesis and growth. Each clone of *G. tikvahiae* possesses concomitant combinations of benefits as well as costs, which should be carefully evaluated for the cultivation application of interest. Knowledge of functional-form relationships in seaweeds can significantly expedite their successful cultivation.

Introduction

Selecting the most appropriate species or strain ('screening') is an important first step in the development of most algal cultivation systems. Screening techniques for cultivated seaweeds primarily have been trial and error and usually are haphazard, tedious, time-consuming, and expensive. Although seaweeds are cultivated for a number of applications, the rates of photosynthesis

and growth are usually important considerations in seaweed mariculture. In some cases (e.g., 'biomass-farming'), sustained high rates of photosynthesis and growth are absolute requirements. Both of these attributes are important components of the functional-form model, first developed to synthesize the adaptive significance of thallus form relative to the productivity and survival of benthic macroalgae (Littler & Littler, 1980). In this paper, we apply the functional-form model

to seaweed mariculture and demonstrate how this model can be used to expedite species or strain selection.

The functional-form model

During the last decade, the functional-form model has had a major impact on understanding the ecology of marine macroalgae (e.g., Littler, 1980; Steneck & Watling, 1982; Norton *et al.*, 1982; Littler & Arnold, 1982; Gaines & Lubchenco, 1982; Littler *et al.*, 1983; Rosenberg & Ramus, 1984; Hanisak *et al.*, 1988). An important application of this model has been in macroalgal production ecology. The thallus-form/productivity relationship is applicable (Littler, 1980) over a broad range of habitats. For example, Littler (1980) found that 45 species of temperate macroalgae, in thallus-form groups from highest to lowest producer on a dry weight basis, ranked as follows: thin sheet-like forms, finely-branched forms, coarsely-branched forms, and prostrate, epilithic forms. Similarly, Odum *et al.* (1958), Kanwisher (1966), King & Schramm (1976), and Littler & Arnold (1982) noted that finely-branched forms had higher production rates than coarsely-branched species.

Species selection

The understanding of functional-form relationships can facilitate species selection for seaweed cultivation. Indeed, certain form-function relationships in certain cultivation systems have been grasped intuitively, if not always explicitly incorporated into screening programs. For example, in the screening program for high biomass production that led to the selection of the red alga *Gracilaria tikvahiae* McLachlan (Hanisak, 1987), 42 species of macroalgae were screened originally in outdoor cultures. However, this species was not the most productive one. Species of the green algal genera *Enteromorpha* and *Ulva* both were more productive than *G. tikvahiae* in short-term experiments; their high, short-term yields in cul-

ture were consistent with the functional-form model that predicts (e.g., Littler & Littler, 1980) that an alga such as *Ulva*, with its flat blade consisting of only two photosynthetic cell layers, should be among the most productive macroalgae. However, the production of these species was not sustainable for significant periods of time because they would frequently become fertile, and, as each cell of the thallus can become reproductive, entire cultures would sporulate and be lost overnight. Thus, these green algae were dropped in favor of the rapidly growing, but reproductively sterile, *G. tikvahiae* (Hanisak, 1987). The rapid growth rates and high reproductive outputs (i.e., 'r-selection', *sensu* Pianka, 1970) of these green algae also are entirely consistent with the cost versus benefits approach inherent in the functional-form concept (Littler & Littler, 1980). The cultivation of *Ulva* for biomass production and other uses in Florida proceeded (Hanisak, 1987) only with the isolation of warm-water strains that, although not completely sterile, became reproductive infrequently and, when they did, only lost small portions of their thalli.

Another example of how functional-form relationships are relevant to macroalgal culture is that of *Sargassum*. When economic analyses (i.e., models based on construction costs of large 'energy farms', rather than developed on a more biological basis) favored a floating marine biomass concept, the feasibility of developing pelagic *Sargassum* as a biomass plant was studied (Hanisak, 1987). A recent study of functional-form relationships in *S. polyceratium* Montagne (Kilar *et al.*, 1989) showed that differential allocation of resources to specialized thallus parts had important source-sink implications. *Sargassum* is a tough, morphologically complex alga, which, based on the functional-form model (e.g., Littler & Littler, 1980), would be expected to devote less energy for rapid growth and productivity in favor of increased structure and thallus longevity. Consequently, the low yields of *Sargassum* (i.e., relative to *Gracilaria* and *Ulva*), reported (e.g., Hanisak, 1987) for its experimental cultivation are consistent with the model. Whether or not these lower yields preclude the economical

cultivation of *Sargassum* remains to be seen, but it is advisable to incorporate aspects of the functional-form model in all future screening programs.

Strain selection

Often it is not species selection, but strain selection, that is of interest in macroalgal cultivation. The red alga *Gracilaria tikvahiae* has been considered (Hanisak, 1987) a prime maricultural candidate for agar extraction, bioconversion to methane, fertilizer, and sewage treatment. Recently, we used the functional-form model to interpret morphological/physiological/ecological relationships within this species (Hanisak *et al.*, 1988); these relationships also are relevant to its cultivation.

One of the advantages of *Gracilaria tikvahiae* in mariculture is that, at least under outdoor culture conditions, it has not been observed to reproduce sexually; rather, it propagates itself vegetatively, reproducing only through fragmentation of thalli (Hanisak, 1987). Such sterile cultures are useful in macroalgal cultivation because, once a desirable plant is selected, it can be maintained without genetic changes for long periods of time. As vegetative fragmentation is the principal mode of propagation for this species, its success in culture is due largely to components of growth and survival (i.e., increases in biomass, apparent photosynthesis, nutrient uptake capabilities, and predation resistance). This makes *G. tikvahiae* an appropriate choice to demonstrate the applicability of the functional-form model to macroalgal cultivation, because other long-term demographic parameters (e.g., spore production and dispersal, fertilization success, germination, recruitment, life history phases, ploidy levels, and phenology) that have proven relatively intractable in macroalgae (Dixon, 1973) do not have to be tediously measured.

In a previous publication (Hanisak *et al.*, 1988), we tested four predictions of the functional-form model along a continuum of morphotypes of *Gracilaria tikvahiae* (Fig. 1). The surface

area : volume ratios for eight clones of *G. tikvahiae* ranged from ca. 20 to 52 cm² cm⁻³ (Hanisak *et al.*, 1988). The clones fell into three distinct groups based on their surface area : volume ratios; this ratio decreased as morphological complexity increased. Clones of *G. tikvahiae* with higher surface area : volume ratios were highly branched with many smaller, finer branches; clones with lower surface area : volume ratios were thicker, more coarsely branched forms that were almost cartilaginous in texture.

These clones had significant differences in calorific content, percentage of photosynthetic tissue, net photosynthesis, and specific growth rate, all of which are a function of surface area : volume ratio (Hanisak *et al.*, 1988). These findings also demonstrate that morphological attributes can serve as indicators of potential fast-growing strains. For *Gracilaria tikvahiae*, the surface area : volume ratio was a good predictor of both photosynthesis and growth rate. For the eight clones, net photosynthetic rates varied by an order of magnitude (i.e., 1.5–12.2 mg C g⁻¹ dry wt h⁻¹ or 2.5–21.4 mg C g⁻¹ ash-free dry wt h⁻¹) for the eight clones (Hanisak *et al.*, 1988). The specific growth rates of these clones were highly correlated with their net photosynthetic rates. Specific growth rates of laboratory cultures varied by more than two-fold (0.11–0.23 biomass doublings day⁻¹). Consistent with the predictions of the functional-form model, clones near opposite ends of the surface area : volume continuum had significant differences for all of the attributes examined. Each strain of *G. tikvahiae* possesses concomitant combinations of benefits as well as costs, which should be evaluated carefully for the cultivation application of interest.

Concluding remarks

Successful mariculture requires a comprehensive understanding of the fundamental biology of the organism in culture. The functional-form model, particularly as it relates to production ecology, can be used as a basis for decision making in seaweed mariculture. Minimally, a great deal of

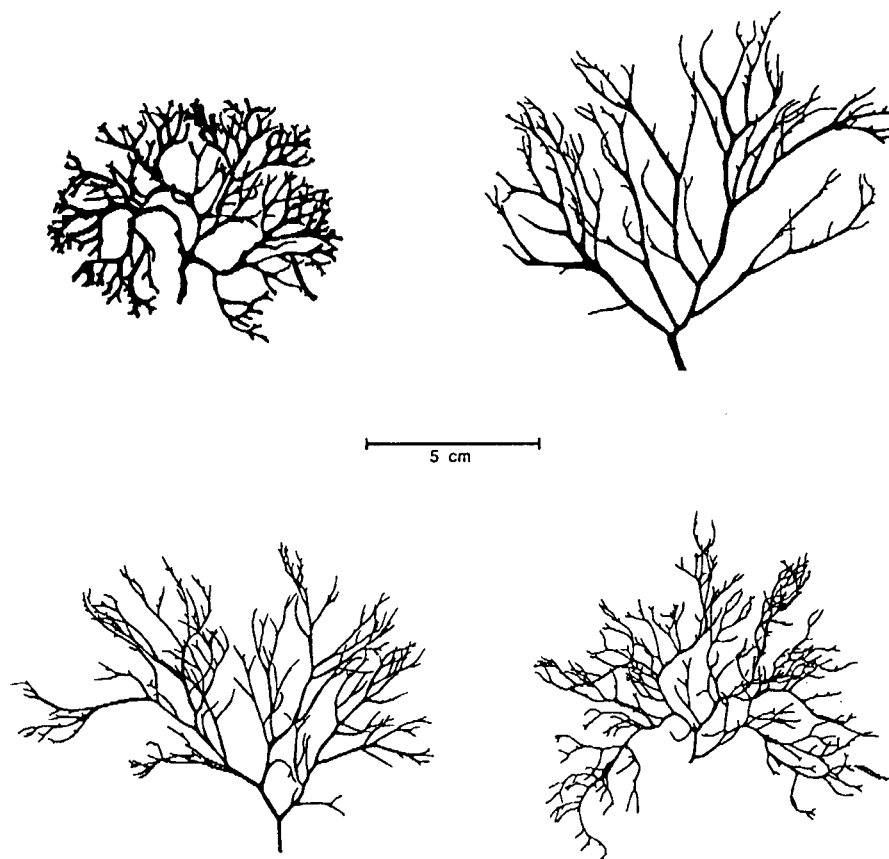


Fig. 1. Drawings of selected clones of *Gracilaria tikvahiae* from outdoor tank cultures that demonstrate its range of morphological variability. Surface area : volume ratio, productivity, and growth rate increase from top to bottom and from left to right. For these clones, surface area : volume ratio ranges between 20 and 52 $\text{cm}^2 \cdot \text{cm}^{-3}$; productivity ranges between 6 and 12 $\text{mg C} \cdot \text{g}^{-1}$ dry weight $\cdot \text{h}^{-1}$; growth rate ranges between 0.14 and 0.23 doublings $\cdot \text{d}^{-1}$ (data from Hanisak *et al.*, 1988).

time and money could be saved by utilizing the model, at least as a first step in the selection of potential candidate species for a particular application. Applications of the functional-form relationship could be in elucidating: (1) potentially fast-growing morphotypes within a species, (2) the fastest-growing stages in the development of differentiated algae, (3) the fastest-growing alternates of heteromorphic life-histories, or (4) the more useful portions of differentiated plant thalli, as well as (5) the tradeoffs between environmental resistances and rapid growth for evaluating a given form's outplanting potential.

One problem with relying primarily on morphological features as a measure of 'form' is the integration of these features into a meaningful,

quantifiable value that can be measured easily for all species. Surface area : volume ratio, which is the result of numerous morphological features of algae, has been shown (Hanisak *et al.*, 1988) to provide an integrative measure of morphological complexity that has functional significance. Fundamentally, this ratio relates the potential for the exchange of energy and nutrients (as determined by surface area) to the volume (i.e., biomass) of an organism (Hanisak *et al.*, 1988). With few exceptions (Rosenberg & Ramus, 1984), attempts to correlate absorption with surface area (e.g., Odum *et al.*, 1958; Gutknecht, 1961) have received little attention during recent investigations of nutrient uptake by macroalgae.

Surface area : volume ratio has significance to

macroalgae in a cultivation system as well as in natural ones. This is particularly true for applications where the desired product is not species-specific, e.g., systems in which the emphasis is on algal production, such as algal biomass farms and wastewater treatment. A thallus-form with a high surface area:volume ratio is more suited to obtaining light energy for conversion to biomass (e.g., 'energy farm' applications). Moreover, because nutrient uptake is a metabolic process by which algae actively transport compounds across membrane surfaces, it is reasonable to assume that the rate of uptake is dependent upon the relative amount of surface area available for such transport; thus, a thallus-form with a high surface area: volume ratio also is more suited for rapid nutrient uptake (e.g., wastewater treatment applications). At present, the functional form model has not been applied to other agronomically desirable characters, such as epiphyte resistance or gel production, but they should be explored.

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