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A conceptual framework for marine agronomy*

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Abstract

Between the late 1960s and the early 1980s, several generations of phycologists in Hawaii and the Philippines, associated with M. S. Doty, contributed to developing a new approach, and to advance concepts in marine agronomy. This study reviews the approach and the main concepts contributed. Integrating these contributions with others, a basic conceptual framework for marine agronomy is presented.

Introduction

Compared to the 8 000–10 000 year history of terrestrial agronomy, marine agronomy has a short history. Less than 250 years ago, Japanese fishermen began sticking brush on the seashore to expand the grounds where *Porphyra* would settle, and less than 50 years ago, Drew (1949) provided scientific information on its life cycle that eventually allowed Japanese fishermen and farmers to artificially seed their nets, accelerating the expansion of the *Porphyra* farms.

In the 50 years following Drew's findings, close to a hundred economic seaweed taxa have been tested for their field farming potential, and nearly a dozen are being commercially cultivated today (see Ohno & Critchley, 1993 for listing). A growing body of information on the chemical structure of commercial compounds, the physiological ecology of the various species, and production technologies for different types of algae is accumulating. Furthermore, basic concepts on marine agronomy are gradually being developed, which allow the agronomic nature of seaweed to be understood and farming to be approached with greater, scientifically based, predictive capability.

Among the several scientists that have contributed to the recent development of marine agronomy, M. S. Doty played an outstanding role. Between the late 1960s and the early 1980s, Doty was able to generate a very productive scientific environment in Hawaii that attracted over 30 students and several dozen co-workers from all over the world (see Kraft, 1997 for greater details). This group contributed to the development of a new approach to marine agronomy. Such an approach led to new concepts and generalizations of widespread application in seaweed farming. This study reviews this approach and some of the most important concepts put forward by Doty and his associates. By integrating these contributions with others, a basic conceptual framework for marine agronomy is developed.

Methodological approach to farming

When Doty started his field cultivation trials (Doty, 1970), extensive seaweed farming was already being developed in Japan, China and a few other countries in south east Asia (Tseng, 1981). In addition, various laboratories in Canada (e.g. Neish & Fox, 1971; Neish et al., 1977), the U.S.A. (e.g. North, 1971; Neushul, 1972) and Europe (e.g. Pérez, 1972) were developing experimental cultivation of various types of seaweeds. Departing from the above scientific efforts, Doty and co-workers developed a product-oriented, multi-disciplinary approach to seaweed farming. Since the ultimate objective of farming was an optimization of production, potential farmers needed to know how the production function could be optimized beforehand. This involved knowing the production possibilities of the target species (e.g. biomass, carrageenan, fine

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chemical), and the pattern of temporal changes in the various products. Further, the maximum production of various compounds derived from a given species might not necessarily coincide in time, and the farmer may need to look at options in order to get the best product from farming efforts.

Since the chemical nature, quality and quantities of many seaweed products vary among different taxonomic units (Stoloff & Silva, 1957; McCandless, 1981; Jensen 1993), taxonomy is always required as an auxiliary discipline. In seaweeds, the value of 'good taxonomy' is often recognized, not only by other taxonomists but also by the commercial companies using the species as raw materials for specific applications.

To optimize production, the farmer needs to know the interactions of factors which increase production. Thus, experimental studies on production ecology are needed to understand the relationships between the target product and the abiotic environment. Once these are known, field sites with positive interactions can be identified and prepared for target species farming. Farming is thus conceived (Santelices & Doty, 1989) as any artificial expansion of the habitat, mainly resulting from increasing the area over which the desired seaweed grows naturally. Ultimately this process increases the production of the target product. Experimental testing of potentially useful farming areas, cultivation technologies and routines are needed before farms are expanded to full scale.

Productivity of an established farm depends on the quality of the genome being cultivated, on the frequency and intensity of the abiotic and biotic disturbances, and on management efficiency. Therefore genetics, community ecology and management also are considered auxiliary disciplines needed to successfully farm seaweed crops.

Conceptual approach to farming

Data accumulated on seaweed farming resulted in the development of a few basic principles that, so far, seem of widespread applicability in marine agronomy. In this review, these are arranged as successive steps, leading to studies and activities needed in order to farm a previously selected target species.

Agronomic ordination of seaweeds

External morphology still appears to be the main character allowing seaweeds to be categorized. It also permits a first prediction on potential farming sites and agronomic requirements of the target species to be made.

Several types of findings support this view. The first finding indicates that external morphology integrates several algal functions and, therefore, is simultaneously related to several environmental factors (Doty, 1971; Neushul, 1972). The second, well documented by taxonomists and morphologists (e.g. Dawson, 1966), indicates that although seaweeds differ in external morphology, certain morphologies are repeated among phylogenetically different algal groups. Morphological similarities are now understood (Littler & Littler, 1980; Littler et al., 1983) as convergent adaptations to critical environmental factors, while differences between morphologies would represent divergent responses to such selection factors. Thus, environment and habitat requirements of species with convergent morphologies will be more similar than the requirement of species with divergent morphologies. Since the essence of farming is habitat expansion (Santelices & Doty, 1989), it is expected that seaweed morphology could be used as a first clue to define the type of habitat to be expanded and the type of farming to be developed.

The number of commercially farmed seaweeds (see Ohno & Critchley, 1993 for a review) is not diverse enough to provide a full agronomic classification scheme of seaweeds, but the present farming practices for different morphologies (Figure 1) suggest that this is a promising concept. Future increments in the number of farmed species would undoubtedly help to better define agronomic groups. The resulting classification scheme may or may not agree with other classification schemes based on other ecological relations (e.g. grazing; Steneck & Watling, 1982). From the agronomic point of view, some of the groups already defined in those schemes (e.g. 'corticated macrophytes' *sensu* Steneck & Watling, 1982) seem agronomically heterogeneous, while agronomically important morphologies (e.g. 'broad blades' such as *Gigartina* or *Sarcothalia)* have not been considered. Similarly, characters such as plasticity to change morphology under various water movement regimes, regeneration capacities of various plant parts and clonal versus unitary organization seem agronomically more important to classify seaweeds than the characters now used in the above classification schemes (photosynthesis, nutrient uptake, grazer susceptibility).

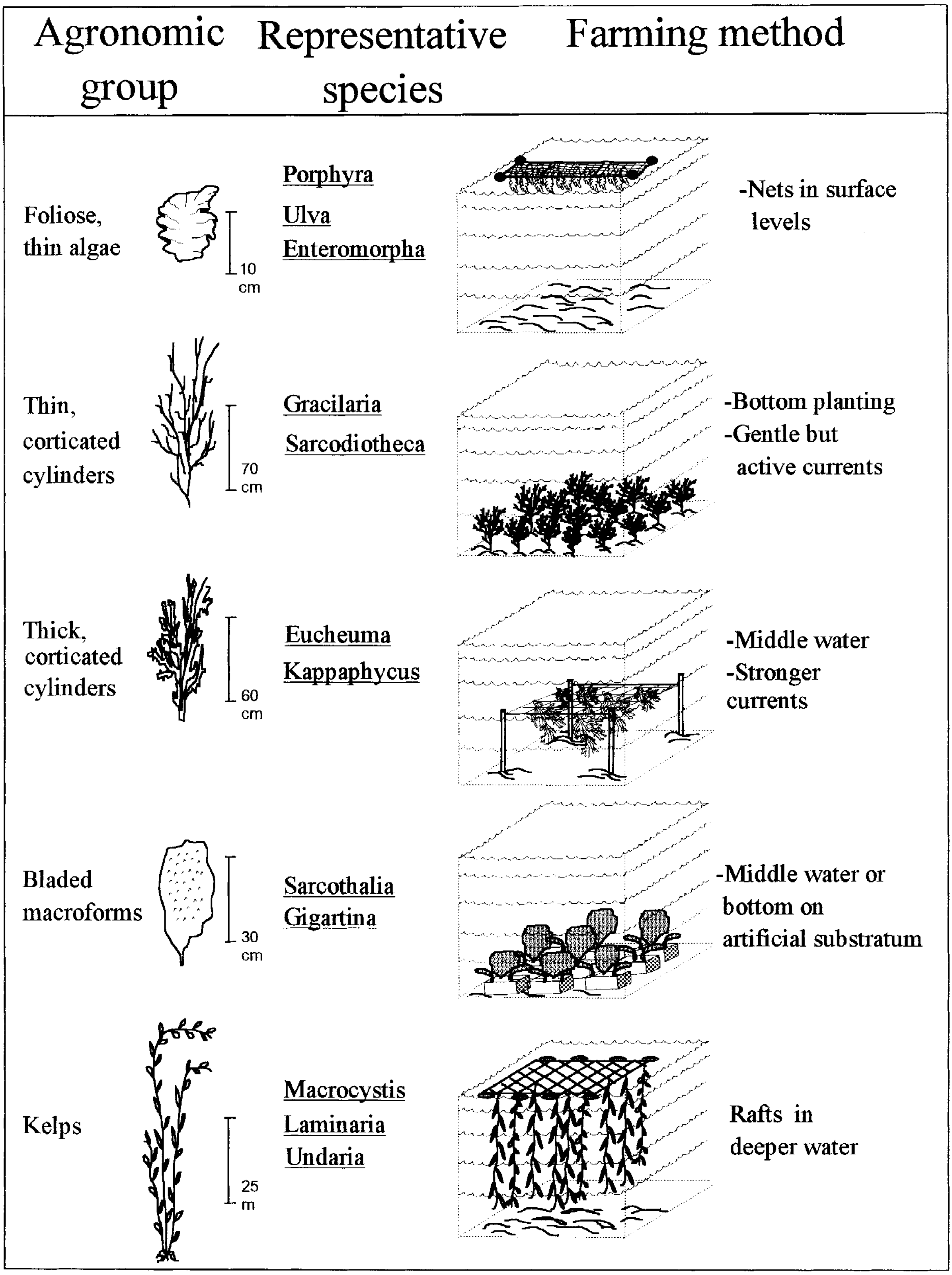

Figure 1. Agronomic classification of seaweeds, emphasizing the relations between external morphology and farming technique.

Clonal and unitary seaweeds, one-step and multi-step farming

Seaweeds can have clonal or unitary organization. Clonal seaweeds can be grown and propagated by self-replication of genetically identical units. Such units function and survive on their own if separated from one another by natural processes or injury (Santelices, 1992). Fragments of unitary seaweeds, on the other hand, cannot survive and grow, and their propagation and farming has to be started from spores.

Clonal seaweeds are best suited for one-step farming. This consists (Figure 2) of regrowing adult thalli directly from fragments. The fragment needs to have a minimum size to successfully compete in the adult environment, and in time it will regenerate the adult form.

In contrast, farming of unitary seaweeds needs to be started from spores. However, ontogenetic development of anatomically complex seaweeds may pass through various morphologies. Since the various developmental stages use the environment differently (Neushul, 1972), to be successfully farmed, each stage may require different farming practices (Figure 2). Depending on the diversity of ontogenetic forms involved, this may lead to a two-step or to a multi-step farming practice.

Early, small-size developmental stages are often farmed in nursery facilities. Depending on the life cycle of the target species, such a nursery facility may need to support the growth of the propagules and juvenile stages only or to include also the alternate, microscopic, phase of heteromorphic species. Competition with undesired microforms and early developmental stages of other macroforms is solved by pre-emption of the available substratum through enhanced recruitment of the target species. Enhanced recruitment is attained by incubation of a large number of spores. Juvenile forms may respond better when cultivated at farming facilities of species with similar habitat requirements. However, for economic reasons they are often transplanted to the adult habitat, where they may outcompete other morphologically similar taxa because of a density effect.

Habitat partitioning and the abiotic environment

Even though external morphology is, without doubt, useful for characterizing the way a seaweed uses the environment, additional ecological information is required before farming. Many morphologically similar species may share a habitat, although they may differ in their fine grained responses to one or several environmental factors. To expand the niche of the species during farming, it is necessary to characterize the most important niche dimensions regulating or controlling production. This is normally done by experimentally testing the effects of key ecological factors on growth rates of the desired species. Results often give clues on the significant abiotic factors controlling growth.

Extensive laboratory and cultivation experiments with many species (see Lobban & Harrison, 1994 for a review) have suggested that growth is often regulated by a complex interaction of factors. This is the case, for example, in Gelidiales (Santelices, 1978; Frederiksen & Rueness, 1989) and Gracilariales (Hoyle, 1976, 1978), where growth is regulated by a complex interaction of irradiance, temperature, nutrients and water movement (Figure 3). For example, when light intensity or water movement are limiting, the effects of nutrients on growth are not evident. Nutrients can compensate for inadequate water movement when the latter factor is comparatively low. In turn, enhanced diffusion resulting from high water movement or nutrient additions, results in a more effective use of higher levels of irradiance and temperature, which leads to faster growth and higher pigment concentration. The above interactions indicate (Santelices, 1975) that factors very different in nature (e.g. chemical, such as nutrients, and physical, such as irradiance), may interact regulating growth of the target species and that a major decline of one factor (e.g. nutrients) could be compensated by other factors (e.g. water movement). Therefore, Liebig's law of the minimum does not appear to be directly applicable to marine agronomy.

Site fertility

Interactions, such as the above, are likely to occur in the field, but with some variations. In shallow water, where most seaweed crops are grown, environmental conditions may change very rapidly over space and time. This means that interactions are likely to be occurring at all times. In some places, water movement could, within a certain range, compensate for nutrient deficiencies. In others, variation in water movement could be compensated by adjustments in water quality, temperature and light.

The above variability could result in the occurrence, on a small scale, of places with different degrees of fertility for a given crop. Fertility represents the potential capacity of production in a given site due to its combination of favourable environmental factors

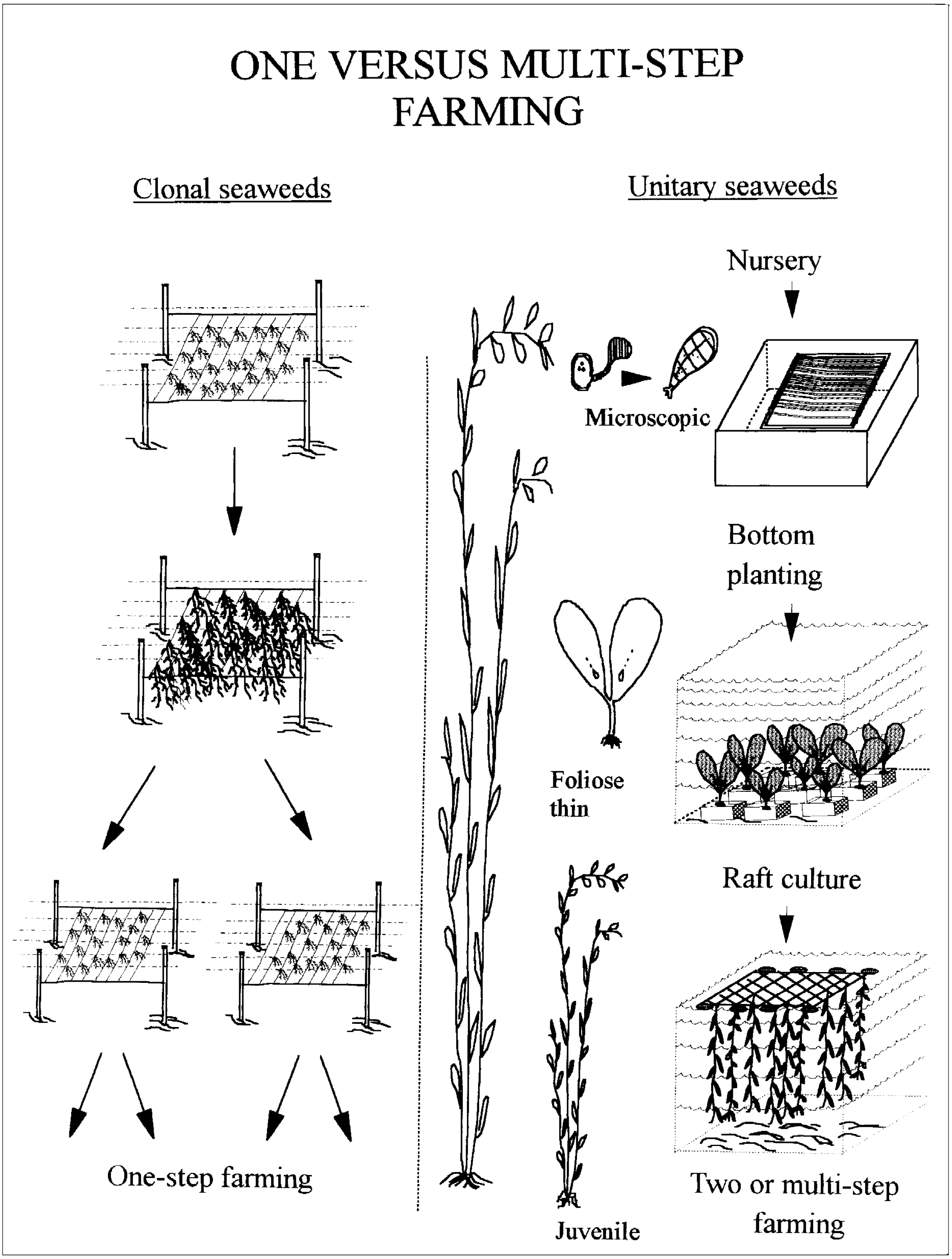

Figure 2. Relationship between seaweed organization (clones and unitary organisms) and one-step or multi-step farming.

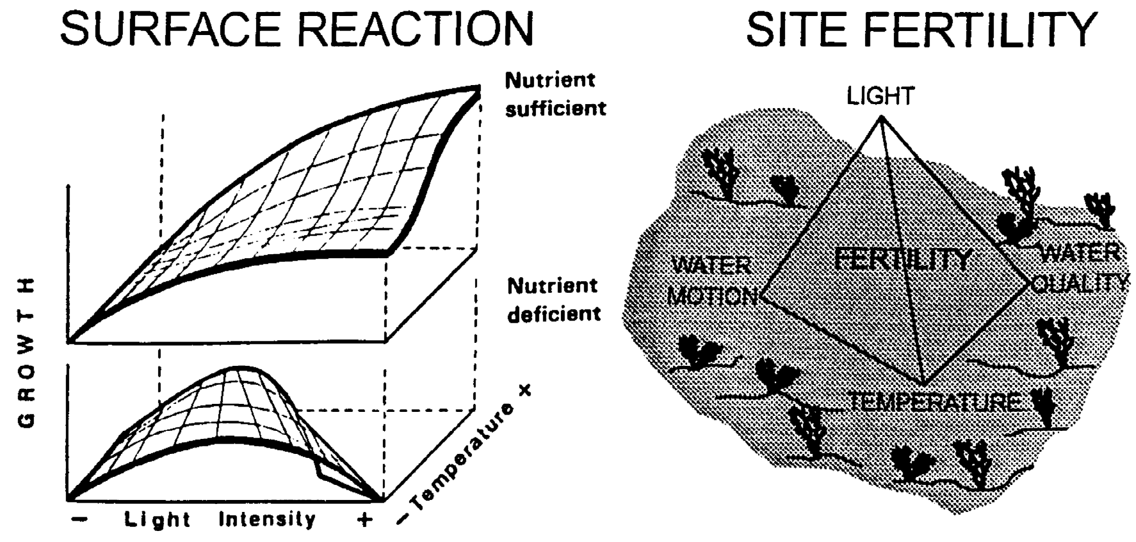

Figure 3. Comparison of diagrammatic representation of interacting factors. Left, surface reaction from laboratory experiments. Right, fertility site concept, applied to field situations.

(Doty, 1979). This can be estimated from observations of standing crop or measured by growth rates or production rates.

The site fertility concept was represented (Doty, 1979) by a tetrahedron (Figure 3). Each axis of the tetrahedron corresponds to one of the four ecologically important factors determining algal growth (irradiance, temperature, water movement, water quality), while the resulting volume represents the fertility of the given site. Any change in the physical environment modifying the above factors would change the position of the respective vertex in the tetrahedron. However, the volume representing fertility may or may not change, depending on the occurrence of compensatory changes in the other factors.

After its original formulation, Doty (1979) recognized that many more than only four environmental variables should be considered when explaining algal growth. However, for simplicity, the hypothesis included only these four components. Others could be added later if experimental and empirical results recommended their inclusion.

The site fertility hypothesis has the merit of conceptually explaining the short-term, almost random changes in standing crop and production potential often found in natural habitats. It anticipates that seaweed production will be heterogeneous in any given habitat due to the natural variations of the abiotic components. In addition, the concept allows controlled laboratory results on the effects of environmental factors on growth to be contrasted with the variability often found in the field. Many laboratory data are of limited use because they consider factor ranges which are totally unrealistic compared to field variation. Also, laboratory experiments normally maintain the different levels of a given factor constant, while in the field they may vary significantly through time. It should be noted that careful characterization of the abiotic environment determining fertility is lacking for most seaweed crops, including some of those which are currently being farmed. How to measure these factors, and what kind of statistical method to apply in order to have realistic results, are among the most complex problems facing marine farming today.

The essence of farming

The site fertility concept easily leads to an understanding of the essence of farming. If the site is fertile, the main activity will be to harvest and manage the crop, re-populating areas that might become less productive due to extensive harvest. If there is an abundance of fertile sites for the target species, but they are being occupied by a different crop, selective harvesting of the competitor, especially at times of the year when the competitor's recruitment is reduced (Santelices, 1990,

1996) would allow habitat expansion of the target species. If there is a fertile site which lacks the adequate substratum (e.g. fertile sites on sandy beaches), provision of the right substratum would allow the horizontal expansion of the habitat of the target species. Similarly, if any one of the key interacting factors determining the fertility of the site is found to be sub-optimal, that factor might be modified to increase fertility. Thus, farming always involves the introduction of artificialities that expand the area over which the desired crop will grow beyond where it would grow naturally. A successful expansion will result in a monoculture of the target species, freed from its natural community components, and at production costs that would compete with the production of the wild crop or with other farms producing the same seaweed elsewhere.

Although the site fertility hypothesis may, in theory, suggest the possibility of manipulating all abiotic factors, the situation in the sea is quite limiting. Farm enlargement to real scale is done horizontally to obtain cost-free sunlight. At a price, a farmer can attempt to control water quality. Handling of water movement and quantities in field farming is extremely difficult. Generally the farmer requires site testing to determine if water movement will allow growth of the target species. Similarly, there is little a farmer can do about sea water temperature. Due to the specific heat of water, it takes large amounts of energy to change and maintain the temperature of the water in which seaweeds grow. Thus, if the temperature is not right at a given site, moving a farm to where sea water temperatures are adequate to the crop is usually all a farmer can do to stay productive. All the above constraints emphasize the need to adequately select a site, to know how the environment varies from one place to another, how the different abiotic elements are interrelated and how their individual variabilities and compensatory effects modify crop growth.

Farming productivity

At present, close to a dozen seaweed species are commercially cultivated (see Ohno & Critchley, 1993 for review). However, only a few authors (Doty, 1981, 1986; Pizarro & Barrales, 1986; Santelices & Doty, 1989; Westermeier et al., 1993; Pizarro & Santelices, 1993; Santelices, 1996) have discussed the interaction of some of the factors determining farm productivity. Data suggest productivity would depend (Figure 4) on the fertility of the farming site, already discussed, the algal genome being cultivated, the frequency and intensity of biotic and abiotic disturbances, and the agronomic diligence.

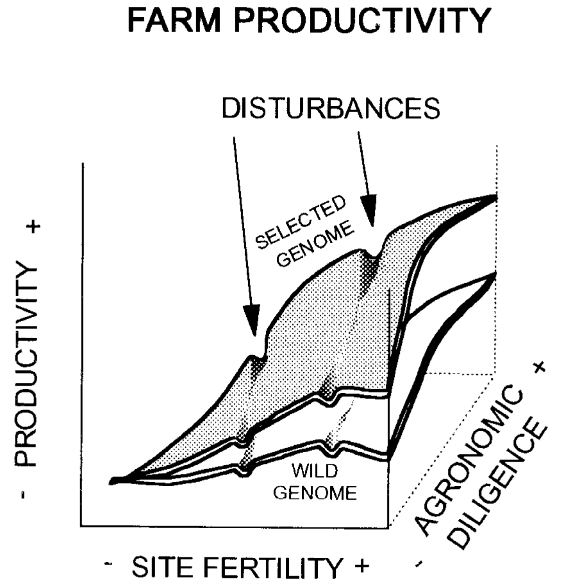

Figure 4. Interacting effects of site fertility, genome, agronomic diligence and disturbance in farm productivity.

Genetic improvement and breeding of new strains have been successful in some commercial crops such as *Laminaria* (Wu & Lin, 1987) and *Porphyra* (Miura, 1975, 1976; Ohme et al., 1986; Shin & Miura, 1990). Other crops, although characterized in terms of qualitative or quantitative genetics (see Patwary & van der Meer, 1992 for review), have not been genetically improved. Recent studies with clonal species (Santelices et al., 1995) are revealing additional sources of variability, which are likely to influence and complicate traditional strain selection practices.

Physical and biological disturbances are an unavoidable part of farming (Santelices, 1996). The habitat expansion done in farming always involves invading the natural habitat of other species, some of which may later return to the farm as competitors. On the other hand, the more distant the expanded area is from the original habitat of the target species in terms of abiotic environment, the higher the probabilities of processes that, while being normal in that habitat, would constitute disturbances for the growth of the target species. Long-term monitoring of catastrophes and major disturbances (e.g. Pizarro & Santelices, 1993) is required in all farming programmes and specially so in those involving extensive habitat modifications.

Agronomic diligence refers to the farmer's capacity to influence the other three factors determining farm productivity. Through simple selection practices the farmer can help in cultivar selection. Through farm manipulation, he can modify, to some extent, the fertility of the farming site, and through selective removal of competitors and grazers, the farmer may anticipate and reduce the negative effects of pests, consumers and other natural enemies.

The very different nature of the four types of factors determining farm productivity does not easily allow quantifications and comparisons in a single figure. Their joint inclusion (Figure 4) is intended to simultaneously outline the effects of these four factors and to call attention to the need to look at all of them if a successful farming operation is intended.

Conclusion

Farming activities with seaweeds have encouraged the development of various approaches and farming methods. As human populations and markets continue growing a larger number of seaweed species will probably be farmed in the future. It is expected that the basic concepts outlined here would help in such developments. At the same time, those new developments should serve as testing grounds for these ideas, as well as sources of new conceptual components for marine agronomy.

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