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Review

A Review of *Gracilaria* Farming

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ABSTRACT

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Close to 5000 tonnes (t) of agar are processed annually from 25 000 to 30 000 t of *Gracilaria*, harvested mainly from the wild in Chile, Argentina, Brazil and South Africa and from fishpond culture in Taiwan, Hainan Island, China, and mainland China. Steady increases in market demand together with lack of crop management have led to overharvesting the natural stocks, to shortages of *Gracilaria*, to higher prices for the crop and, along with the increased market, to a demand for reliable crop quantity and quality. The outcome has been great interest in *Gracilaria* farming, and a diversity of farming methods has been developed.

In open waters, basically three approaches are used for planting *Gracilaria* crops: on the bottom, on nets or lines, and on floating rafts. With each approach, either vegetative material or spores can be planted. Alternatively, *Gracilaria* can be farmed in ponds, raceways or tanks. A comparative review of these methods indicates that bottom planting and line farming techniques, either from spores or from vegetative material, may provide the crops for agar and agarose production. The species so cultured yield relatively large amounts of good quality seaweed by labor-intensive means at low cost in the less-developed countries.

The future of fishpond cultivation of *Gracilaria* is difficult to predict. Perhaps the seaweed will continue to be cultivated as feed for more economically-important organisms, such as sea urchins and abalone. Production in tanks or mixed systems of pond cultivation, with or without air pumping or CO_2 addition, probably will be restricted to supplying *Gracilaria* as a luxury-priced fresh vegetable.

A variety of production ecology studies has been important in the development of the various farming methods, and increased requirements for farmed *Gracilaria* in the near future are likely to stimulate new approaches. Additional field population studies are required to increase the efficiency of wild crop management and bottom planting. Research on nutrient metabolism is crucial for tank cultivation. Understanding the environmental effects on gel production is needed to control the quality and quantity of gel produced under the various farming techniques. Farming involving the outplanting of sporelings will require further knowledge of *Gracilaria* spore biology, while biomass demands will probably stimulate new efforts in strain selection and *Gracilaria* farming methods.

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INTRODUCTION

The species of the genus *Gracilaria* are among the most important seaweeds of commerce. It is estimated (McLachlan and Bird, 1986; Moss and Doty, 1987) that close to 5000 t of agar are processed annually from *Gracilaria* crops which, on a dry weight basis, contain 15 to 20% agar. About 50% of the 25 000 to 30 000 t of dry *Gracilaria* used in agar production is harvested mainly from wild crops in the cool-temperate waters of Chile and Argentina (Mayer, 1981; Santelices and Lopehandía, 1981; Cerezo, 1986). The remainder comes mainly from fish-pond culture in Taiwan, Hainan Island, China, and mainland China (Chiang, 1981). Minor amounts are harvested in Brazil and South Africa, but the data often are not included in the international statistics.

Market demands for *Gracilaria* have increased significantly over the last ten years. For example, in Chile there was an eleven-fold increase in *Gracilaria* exports between 1967 and 1983 (Santelices and Ugarte, 1987), caused mainly by a significant increase in FOB prices which, at present, are 7.5 times the 1972 value (about US$ 1500 per dry tonne). International prices of agar (Table 1) have followed a similar pattern because the traditional market for microbiological agars has been enriched by new horticultural, entomological and genetic applications, and the market for food grade and sugar reactive agars has expanded. Demands for the agarose fraction of agar are expected to remain high due to biotechnological and biochemical needs (Renn, 1984). In addition, *Gracilaria* as food, particularly as a table vegetable, has become increasingly popular in the Caribbean and Hawaii. Retail prices in these local markets are as high as US$ 6.00 to 6.50 kg^{-1} of dry *Gracilaria* in St. Lucia Island (Smith et al., 1984) and up to US$ 3.50 to 5.00 kg^{-1} of wet weed in Hawaii.

TABLE 1

Export and FOB values for *Gracilaria* and agar from Chile, as an example of the increased market demand for these products

	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
Gracilaria harvested (dry tonne)	2200	2000	2800	3000	4700	6300	15 200	12 900	16 800	9970
Average FOB price for *Gracilaria* from Chile (US$ per tonne)	800	700	870	1150	1300	1250	1200	1250	1300	1500
Agar produced in Chile (tonne)	280	327	387	410	377	485	544	588	816	1009
FOB price for agar from Chile (US$ per tonne)	7200	9000	9000	11 000	11 000	10 800	11 000	12 850	12 500	12 500

Source: Estadísticas Pesqueras, Servicio Nacional de Pesca, Chile, 1987.

Market demand and lack of crop management have led to overharvesting the natural stands of *Gracilaria* (Santelices and Fonck, 1979; Santelices and Lopehandía, 1981; Westermeier, 1981; Smith et al., 1984; Wang et al., 1984; Westermeier et al., 1984; Santelices and Ugarte, 1987) in several geographic areas. This has led to shortages and higher prices for *Gracilaria* and, along with the increased market, to a demand for reliable quantity and quality. The outcome has been a great interest in *Gracilaria* farming, and several serious efforts are now underway to make the farmed, rather than the wild, *Gracilaria* crops the more significant source.

As yet (1989) the *Gracilaria* farmed volume is not well known; perhaps it is 15 000 out of the 25 000 to 30 000 t of dry seaweed used annually. The principal farming areas are in the islands of Taiwan and Hainan in China (Shang, 1976; Chiang, 1981; Yang et al., 1981; Chueh and Chen, 1982), Chile (Pizarro, 1986; Santelices and Ugarte, 1987) and Hawaii. Advanced pilot farming has been completed in the U.S.A. (Hanisak and Ryther, 1986; Hanisak, 1987), St. Lucia Island in the Caribbean (Smith et al., 1984) and Brazil (Camara-Netto, 1987). Farming is being developed in Thailand (Edwards and Tam, 1984), Malaysia (Doty and Fisher, 1987), Indonesia and The Philippines (e.g. Trono, 1981). Wild crops are still an important source of the *Gracilaria* produced in Chile (Santelices and Ugarte, 1987), Brazil (Camara-Netto, 1987) and to a lesser degree in Argentina (Cerezo, 1986).

In this review we first discuss some general characteristics of the genus *Gracilaria* which are especially important to its commercial production. Then we review the management and farming practices developed for the species. Both farming and wild-crop management require production ecology information which is analyzed in this review in relation to the agronomic practice involved. Previously Hoyle (1975), Mathieson (1977), Ryther et al. (1979), Hanisak and Ryther (1984), McLachlan and Bird (1986) and Hanisak (1987) reviewed aspects of ecological responses and the approaches to farming the different species. We have not included in this review such farming possibilities as those described by Lindsay and Saunders (1980) which seem remote from reality and would result in excessively expensive crops. The present work does not intend to duplicate or replace the taxonomic, production work or usage information presented by Abbott and Norris (1985), McLachlan (1985), Armisen and Galatas (1987), Hanisak (1987) or Moss and Doty (1987). Their different approaches, largely from the capital intensive areas and the Northern Hemisphere, taken together with the present text, provide good coverage of the *Gracilaria* industry.

1. THE GENUS *GRACILARIA*

Gracilaria is classified as a red alga, but has different color manifestations. It can be black, yellow or red. Green forms and other colors are found that appear to be the result of ordinary genetic controls. The thalli can be bushy, somewhat rigid and with relatively short branches, or slender, with branches that are long in respect to their diameter. Essentially all the commercial forms are of the slender and willowy nature, with terete axes, usually less than 2 mm in diameter and not commonly over 30 cm tall.

Gracilaria spores settle after release, divide upon attaching to the substratum and form a spreading thick-centered disc from which the initial erect shoots grow. The tissues of the erect fronds are pseudoparenchymatous. There is a central tissue of large cells, and an outer surface of small cells in which the pigment is concentrated. The tetrasporangia found on the diploid thalli are cruciately divided. The carpospores are produced from round or hemispherical cystocarps 1 mm or more in diameter and are the only reproductory structures visible to the naked eye. The male structures are not always found in wild populations, but usually they are essential for describing the taxonomy of the species.

The genus *Gracilaria* is widely distributed around the world. It occupies a variety of habitats, both in tropical and temperate latitudes, forming monospecific stands or multispecific vegetational assemblages. In temperate latitudes, some species can reach high-standing stocks (1 to 7 kg m^{-2}), as described for the northern Adriatic Sea and Norway (Stokke, 1957; Simonetti et al., 1970), the Atlantic coast of Canada (Bird et al., 1977a,b; Golstein, 1981), the east coast of the United States (Humm, 1944; Conover, 1958; Kim and Humm, 1965); California (Abbott, 1980; Hansen, 1984); Chile (Santelices and Fonck, 1979; Westermeier, 1981), Argentina (Mayer, 1981; Cerezo, 1986); New Zealand (Luxton, 1981) and South Africa (Isaac and Molteno, 1952). In tropical latitudes, *Gracilaria* standing stock values do not usually exceed 2 kg m^{-2} (e.g., Lawson, 1954; Raju and Thomas, 1971; Hoyle, 1978; Hay and Norris, 1984), although local specific diversity is normally higher than in temperate areas and the species often have sympatric patterns of distribution (Sotomayor and Almodovar, 1982; Hay and Norris, 1984).

1.1. Taxonomic studies

The taxonomic interpretation of the genus *Gracilaria* is currently under revision. It has been approached in recent literature by Chang and Xia (1963, 1976), Yamamoto (1978, 1984), Abbott (1980, 1983), Bird and McLachlan (1982, 1984), Sotomayor and Almodovar (1982), De Oliveira (1984) and coworkers (1983, 1984), Trono et al. (1983), Zhang and Xia (1984), Abbott and Norris (1985), and Fredericq and Norris (1985). The recently edited proceedings from a workshop on the taxonomy of economic seaweeds (Abbott and Norris, 1985) provides keys to the species and updates the basis for the taxonomy of the group, especially in regard to the Pacific species, and provides much of the basic bibliography. Since the older literature shows little consistency in the application of names to the commercial species of *Gracilaria*, the present study repeats binomial names used by the various authors, but indicates little confidence in their application. The study indicates that the names *Gracilaria verrucosa, G. confervoides, G. edulis* and *G. foliifera* may rarely be correctly applied.

The species most sought for its agar is *Gracilaria lemanaeformis*, of widespread distribution in the eastern Pacific, with closely related species such as *G. tenuifrons* (Bird and Oliveira, 1986) in the Atlantic, and *G. chilensis* (Bird et al., 1986) in the southeastern Pacific. While the form is not now of commercial importance, most authors use *G. tikvahiae* McLachlan if working in the western North Atlantic. In the western Pacific a quite different complex of species (Chang and Xia, 1963) is commonly identified as a separate genus, *Polycavernosa*, in the southwest and as *G. tenuistipitata* in the northwest.

1.2 Habitat characteristics

The large commercial crops of *Gracilaria* are found on intertidal or shallow-subtidal, wave-sheltered, horizontal or slightly inclined plane surfaces where there is unconsolidated, generally non-carbonate, sandy to muddy sediment (Fig. 1). Such fine sediments as a rule come from the breakdown of volcanic rock and are initially borne to the sea by turbulent freshwater streams and deposited where the current drops as the stream enters the sea. Where the location is protected from waves or below the sea swell levels, there is little water motion; the sediments, once deposited, remain in place and produce the mudflats found along many coasts. These usually provide the major *Gracilaria* production areas of Chile, New Zealand, Malaysia, Thailand, The Philippines, Indonesia and China. *Gracilaria* often forms monogeneric stands in these habitats where few, if any, other large red algal genera will survive. Furthermore, these mudflats show great ecological variations. *Gracilaria* must often survive frequent fresh-water dilutions, high fertilizer regimes, very low water motion, as well as high temperatures and burial in sediment. Many laboratory studies (e.g., Causey et al., 1946; Hoyle, 1978; Santelices and Fonck, 1979; Friedlander and Dawes, 1984; McLachlan and Bird, 1984; Muñoz et al., 1984; Ren et al., 1984; Bird and McLachlan, 1986) have experimentally measured the eurythermal and the euryhaline adaptability of the genus. Others (e.g. Parker, 1982, who cites much of the earlier key literature) have explored various factors influencing *Gracilaria* growth.

Major accumulations of *Gracilaria* frequently occur as free-floating populations or as combinations of free-floating and temporarily attached thalli (Causey et al., 1946; Santelices and Fonck, 1979; Mayer, 1981; Doty and Santos, 1983). Thalli may be attached to the tubes of annelid worms (Pillsbury, 1950) or to the byssal fibres of mussels (Goldstein, 1981), entangled with other algae (Bird et al., 1977a), attached to shells, small stones, pebbles or other buried

Fig. 1. Mud flat in the vicinity of Puerto Montt, southern Chile (ca. 40°S), typical habitat for *Gracilaria lemanaeformis*. (Photo by A. Larrea.)

objects (Tseng in Pillsbury, 1950; Bird et al., 1977b; Mayer, 1981; Doty and Santos, 1983) or partially buried in soft sediments due to the dynamics of the sandy bottoms (Santelices and Fonck, 1979; Mayer, 1981).

1.3 Life history and fertility

Laboratory studies of *Gracilaria* have revealed (Ogata et al., 1972; Bird et al., 1977c; McLachlan and Edelstein, 1977) a typical "*Polysiphonia* type" of life cycle (Fig. 2) for several species. Therefore, diploid carpospores and haploid tetraspores are expected to be produced, but farmed populations often remain sterile. In field populations female thalli are recognizable without the aid of a microscope as the cystocarps, which bear the carpospores, are hemispherical lumps readily visible to the naked eye. Thus, most experimental work involving spores is done with carpospores. Field populations comprising both free-floating and attached thalli can show gametophytic differentiation in the attached population, while the free-floating thalli are either sterile (Causey et al., 1946; Santelices and Fonck, 1979; Pizarro, 1986) or tetrasporophytic (Bird et al., 1977b). The sterile fronds grow indefinitely and propagate naturally or can be vegetatively propagated merely by fragmentation. This method is used

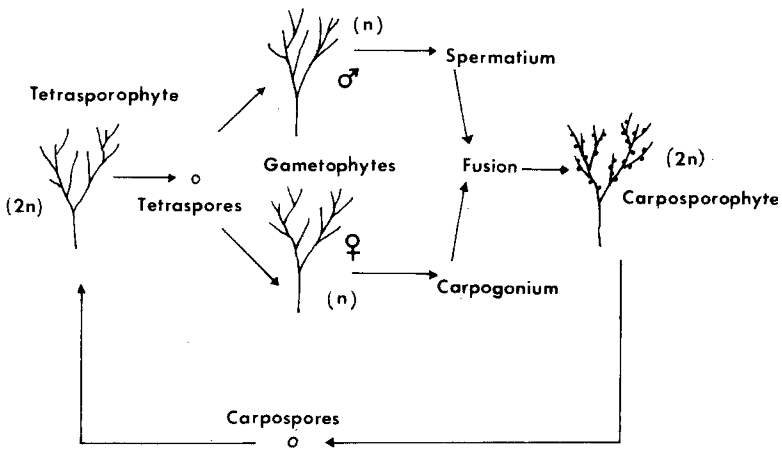

Fig. 2. Life history diagram for *Gracilaria*. In general the gametophytes and tetrasporophytes are macroscopically identical. The carpospores are embedded in macroscopic hemispherical swellings on the female gametophytes (cystocarps).

currently to produce most of the wild and farmed crops in the West Indies, Hawaii, Chile and China.

A sterile *Gracilaria* population cannot be identified as an academically recognized species, as taxonomy requires knowledge of the reproductive structures. It is not surprising then that the taxonomy of many of the commercially important *Gracilaria* crops remains poorly understood. Industry often refers to its *Gracilaria* resources by their areas of origin rather than by a scientific species name (Stancioff, 1981).

Differences in productivity, both of biomass and gel quantities, are reported from karyologically different phases of some species of *Gracilaria* (Edelstein, 1977; Hoyle, 1978; Kim and Henriquez, 1979; Ren and Chen, 1986). McLachlan and Bird (1986) commented that these differences remain unclear and are assumed to be insignificant. However, since the two phases may have different modes of living, it is not surprising that such differences in productivity may exist.

1.4 Agar production

The principal product of *Gracilaria* is agar. The various national and international standards appear to recognize only one kind, but there are numerous grades of agar, depending on a number of tabulated qualities. For example, industrial applications are dominated by three quality grades; (a) *sugar reactive agar*, whose gels are consistently stronger as a function of sugar concentration, (b) *"standard agar"* having the temperature and other requisites for microbiological purposes, and (c) *food-grade agar* which is any agar not meeting the standards for (a) or (b). The sugar gel agar of international commerce is obtained largely from *Gracilaria lemaneiformis*. This is one of the few situations where the taxonomic application of the name is fairly consistent. The microbiological grade agar is produced largely by other genera such as *Gelidium* and *Pterocladia*, aside from the small amount of *Gracilaria* agar that meets the standards for particular blends. Food-grade agar is extracted from a wide variety of seaweeds but largely from *Gracilaria* species other than *G. lemaneiformis*.

The standards for agar are qualitative, non-chemical in nature and of no interest to the large users, who are much more concerned with the physical and chemical functioning of the agar as a raw material in a particular application. However, from the chemist's point of view (Yaphe, 1984), seven kinds of *Gracilaria* agar may be recognized. They may be separated into three major categories: Group (1) high gel-strength agar due to a major fraction being non-ionic agarose; Group (2) gel strength lower than Group 1 and with the agarose ionic due to pyruvate and sulfate; and Group (3) low gel-strength agars that may be more highly sulfated. The three groups differ in their adsorption on DEAE-Sephadex A-50 and their elutability from it, as follows: Group 1, may be eluted with water; Group 2, eluted with water plus 0.5 *M* sodium chloride, and Group 3, strongly bound to the Sephadex so as to be only partially eluted by 2.5 *M* sodium chloride. The amounts of pyruvate, sulfate and methoxyl groups are associated with agar melting point, gel strength, ionic nature of the agarose and other attributes of subgroups of these three major groups.

It has been known for some time that variations in agar yield and quality do exist among different species, different populations and, as already mentioned, different life history phases within a given population (Yaphe and Duckworth, 1971; Penniman, 1977; Whyte and Englar, 1978, 1979, 1981; Kim and Henriquez, 1979; Usov et al., 1979; Asare, 1980; Bird et al., 1981; Whyte et al., 1981; Yang et al., 1981; Tam and Edwards, 1982; Shi et al., 1983, 1984; Craigie et al., 1984). Genetic differences probably are of primary importance and, indeed, some morphological mutants of *Gracilaria tikvahiae* have shown gel strengths greatly surpassing their wild types (Patwary and Van der Meer, 1983c). Seasonality also plays a role, as several authors (Asare, 1980; Wang and Yang, 1980; Whyte et al., 1981; Yang et al., 1981; Friedlander and Zelikovitch, 1984) have found gel yield and quality inversely related to the seaweed densities, which peak in spring or summer. Experimental incubations of *Gracilaria* show that nitrogen content of the thallus, temperature, and tissue age are important factors. Outdoor cultivation experiments (De Boer, 1979; Bird et al., 1981) have indicated that agar content is highest in thalli receiving unenriched or slightly nitrogen-enriched seawater, and decreases exponentially with further nitrogen enrichment. This seems to be an extension of the Neish effect found in *Chondrus* (Neish and Shacklock, 1971). However in *G. tikvahiae* the nitrogen concentration range for maximum biomass production and highest phycocolloid content coincided; agar strength improved as the nitrogen content of the thallus increased (Craigie et al., 1984). Elevated galactose and low anhydrogalactose levels are common in nitrogen-deficient individuals while 4-0-methyl-L-galactose content of the agar declines as nitrogen content increases. In these studies, Craigie et al. (1984) found that in the more nitrogen-deficient thalli, the agar contained more sulfate, less anhydrogalactose, and had lower gel strengths than in nitrogen-sufficient thalli.

Thallus age and growth temperature also have a role. Yield of native agars was 9 to 11% in young parts of *Gracilaria tikvahiae* and 19 to 23% from the most mature parts (Craigie and Wen, 1984). Agar with maximum gel strength and 3,6-anhydro-L-galactose content, and minimum sulfate and 4-0-methyl-L-galactose content was produced at low temperature by apical segments of young lateral branches. The poorest quality agar was obtained from mature segments of the thalli, especially when grown at high temperatures. Agars prepared from mature parts of the thalli were greatly enriched in 4-0-methyl-L-galactose, which reached 8.8% of the weight of the agar at 27°C. These results may explain why the agar from pond-grown *Gracilaria* in subtropical areas such as Taiwan and Hainan has lower gel strengths (Wang and Yang, 1980; G.-Z. Ren, pers. commun., 1986) than that from the wild crops.

The agars of *Gracilaria* have received considerable attention for they have several commercially desirable features not otherwise readily obtainable. For example, their hysteresis is such that their melting and gelling points are often widely separated, depending on the species. Melting points from 45 to over 110°C have been recorded. Higher gelling points are often correlated with methylation (Guiseley, 1970). The presence of pyruvic acid or of high sulfate content (e.g. 10 to 13%) is generally related to low gel strength. The viewpoint that agar consists of two major fractions, agaro-pectin and agarose is an oversimplification, but still a useful concept, for agarose has proven to be a very desirable commercial product of agar.

1.5 Genetic improvement and breeding of new strains

The basic Mendelian genetics of *Gracilaria* has been studied, revealing (Van der Meer and Bird, 1977; Van der Meer, 1977, 1978, 1979; Van der Meer and Todd, 1977) complete and incomplete dominance patterns. Some cultivated strains have better growth responses (Van der Meer and Patwary, 1983; Patwary and Van der Meer, 1982, 1983a,b) or produce better quality agars (Patwary and Van der Meer, 1983c) than their wild types, and several mutants have been isolated and cultivated in the laboratory. Yet little genetic selection is practised today; management of wild and farmed stocks is just beginning.

2. WILD CROP HARVESTING AND THE TRANSITION TO FARMING

2.1 Harvesting with and without management

Harvesting practices for wild crops appear to be dictated more by the crop prices offered than by planned productivity optimization of a site. Thus, harvesting of the wild crop in southeast Asia and its continentally related island groups can best be described as opportunistic rather than managed. As is characteristic of opportunistic practices, in the absence of appropriate management, excesses may occur. Thus, the opportunity may be lost for a stable business or for realizing an optimal sustained yield.

With management of the wild crop or its logical successor, a farmed crop, both stability and sustained higher yields may appear. The need is recognized for positive management that will encourage both increased and more stable production, use of ecological information and, ultimately, the development of farming. Positive management must include learning and applying the production ecology of *Gracilaria*. Determining the conditions that maximize wild crop yields eventually should lead to the optimization of conditions for farming yields.

2.2 Ecological determinants

Gracilaria monocultures are found in various geographic areas, yet in only a few places have they been used as renewable resources. In still fewer places have the results of production ecology studies been used to develop management policies. The quantitative effects of ecological determinants observed in laboratory incubations of a few thalli (reviewed by Hoyle, 1975; Mathieson, 1977; McLachlan and Bird, 1986) have not always had predictive value nor have they led toward understanding the dynamic changes of the wild populations of *Gracilaria*. For example, the highly productive *Gracilaria* beds of Coquimbo, central Chile (ca. 30°S), showed a seasonal cycle of growth correlated with seasonal changes in light intensity and surface water temperature (Santelices and Fonck, 1979). This seasonal growth cycle is interrupted by storms. Thus, a decrease in biomass is found at times during summer (February) and early fall (April), months in which storm frequency is increased. In these particular localities, storm frequency is also high during winter; however, its effects on biomass removal are less evident then, due to the reduced winter standing crops.

Information on *Gracilaria* productivity at other latitudes indicates that other patterns of response may be expected as well. In Concepción, Chile, storms are highly seasonal, starting early in the fall and correlated with a cycle of abrupt biomass decline, followed by an increase in standing crop in spring and summer (Romo et al., 1979; Westermeier, 1981). Even in the far western tropical Pacific or the southeastern Asian tropics, but especially in areas where storms are not very frequent, the cyclic variation in standing crop has been correlated with seasonal or monsoonal changes in light intensity, temperature or salinity. Ryther et al. (1984) and Bird (1984) report *Gracilaria* as growing half as fast in Florida during the part of the year with lower temperature.

In eastern Canada, Edelstein (1977) found production of *Gracilaria* to be limited to a single period: spring and early summer. In Massachusetts, Conover (1958) described a seasonal cycle of *Gracilaria* growth strongly correlated with maximum radiation. Also, on the west coast of Canada, at 49°N where the annual temperature varies little and there are enough nutrients in the seawater (Lindsay and Saunders, 1980), production was closely correlated with radiation in the period of May through October. Throughout the rest of the year Lindsay and Saunders found that production was negligible because of light limitation. It should be noted, however, that in a study performed in Great Bay Estuary, New Hampshire, the growth of *Gracilaria tikvahiae* correlated neither with seasonal light variations nor with dissolved inorganic nutrients (Penniman et al., 1986). This was felt to be true because seasonal variations in the more significant factor, water temperature, lagged behind those of light. The lack of correlation between growth and the usual water nitrogen concentration was explained by Penniman et al. (1986) by the capacity of *Gracilaria* to rapidly assimilate and store enough nitrogen for 2 weeks' growth.

The importance of sediment for the establishment and maintenance of *Gracilaria* beds is often overlooked. There has been a tendency to stress *Gracilaria*'s tolerance to being covered by sand (Wood, 1945) or being able to grow through a layer of sediment. However, the relationship between *Gracilaria* thalli and unconsolidated sedimentary bottoms seems to be more complex than that.

Gracilaria beds of Chile normally contain numerous *Gracilaria* fragments able to survive even when buried in sediment for up to 6 months (Santelices et al., 1984). There, the sandy or muddy bottom relief changes due to water movement, and some of these thallus fragments become uncovered and start growing (Fig. 3). They will grow and branch until their size and shape lead to such increases in frictional drag that portions of the thallus are removed by water movement. A part of the materials so removed will be washed ashore and provide the crop fishermen gather. Another fraction of the material later sinks, eventually becomes covered by sand and produces a further crop from the buried fraction. Therefore it is the soft, unconsolidated nature of the sediments, together with the ability of *Gracilaria* to withstand burial, that promotes the vegetative propagation and growth of the species in this region. In turn, as *Gracilaria* beds become consolidated, the groups of thalli act as sediment traps, further modifying the nature of the bottoms. When over-exploited, *Gracilaria* beds may lose this uppermost layer of sediment because of the decreased thallus density and size which provide the sediment trap function. In artificial plantings, Pizarro (1986) has shown experimentally the effects of inter-thallus

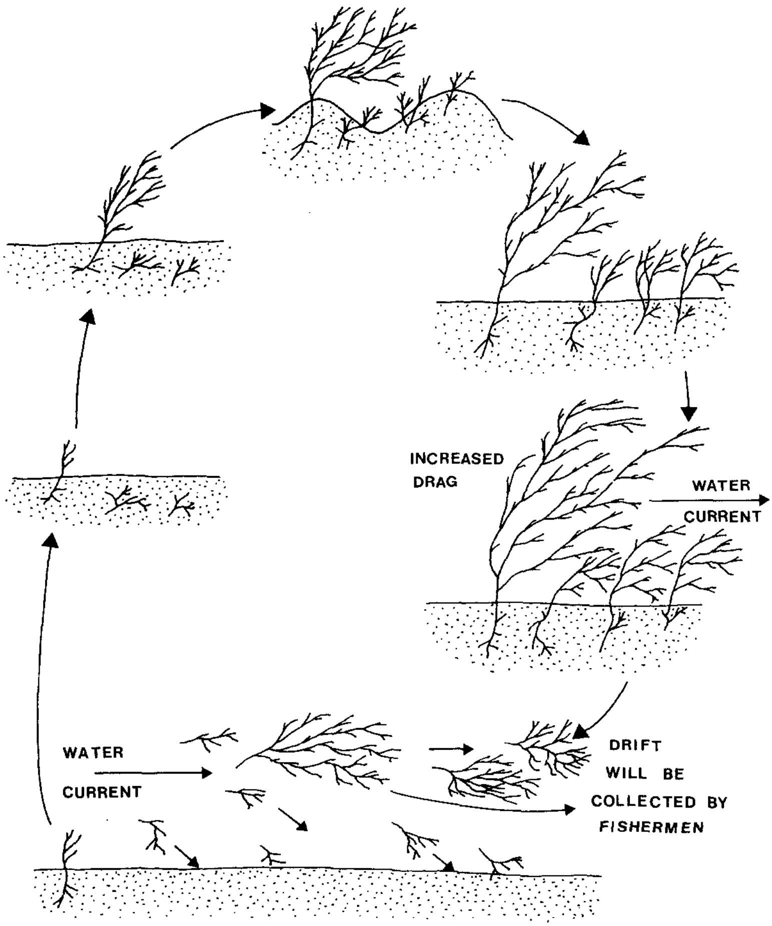

Fig. 3. Diagram of the natural sediment habitat of *Gracilaria* showing the dynamics of underground and emerging thalli. As underground thalli are exposed to light, they start growing. They will grow and branch until their size and shape lead to increases in frictional drag. Portions of these plants are removed by water movement. A fraction of these materials will sink, eventually becoming covered by sand and giving rise to more underground thalli.

distance on sand accumulation. Sand or mud flats appropriate to the growth of *Gracilaria* are formed by deposition of fines from other sources besides freshwater streams. In New Zealand, as a result of the daily tertiary treatment of about 300 000 m^3 of domestic sewage, some mud flats in Manukau Bay have become intertidal due to sediment accumulation. Over 130 ha of these flats now bear *Gracilaria secundata* (Luxton, 1981) with mean standing crops of about 3.84 t ha^{-1} having daily growth rates of 4.6% in August and 1.5 to 2.4% in September through November. Assuming four harvests per year, with each harvest removing half the standing crop, these beds would yield 5.8 to 6.9 t ha^{-1} $year^{-1}$.

In the Old World Tropics, vast areas have lost immense masses of soil to the sea as a result of mining, deforestation and poor management of farm soil. As a result, mud flats are rapidly extending on many of the shores of the dozen or so countries involved. Hence there are vast areas, for example off the west coasts of Taiwan and peninsular Malaysia, suitable for fishpond and mud-flat *Gracilaria* farming. In southern Chile, land sinking after earthquakes is thought (Santelices and Ugarte, 1987) to have increased the area of productive mud flats.

Disregarding the presence of soft sediment, the association of *Gracilaria* with estuarine areas probably can be explained as due to the micronutrient input brought by the associated fresh-water streams.

Lowered salinity is commonly associated with the occurrence and growth of wild *Gracilaria* often as monocrops. This is quite often seen as *Gracilaria* appears to tolerate low or variable salinity (Causey et al., 1946; Santelices and Fonck, 1979; Bird and McLachlan, 1986; Zablackis, 1986). Many species are euryhaline, often with tolerance ranges from 10–15‰ to 55–60‰ salt, the maximum growth rates being obtained between 15‰ and 40‰. It is interesting to note that in some species of *Gracilaria* there is an inverse correlation between salinity and number of branches (Zablackis, 1986), a growth pattern that might be important from the point of view of biomass production.

In some cases, competition appears to be a controlling factor among seaweeds, and the removal of the competing seaweeds can result in a large increase in the *Gracilaria* crops (Kim, 1970). In the deeper ends of Chilean beds, *Gracilaria* populations are replaced by populations of *Neoagardhiella gaudichaudii*. This seems to be an example of competitive displacement under low light intensities. In some Chilean areas (ca. 35°S), the brown alga *Desmarestia herbacea* grows intermixed with *Gracilaria* during the summer. This is deleterious not only because of its competitive interference but also because it is cast ashore together with the *Gracilaria* (Romo et al., 1979) and appears to induce decomposition of the drift within 24 h. In Manila Bay, *Acanthophora* is abundant from August through October, when the annual increase in the *Gracilaria* crop begins; thus, since the two algae occupy about the same habitat (Trono, 1981), the removal of *Acanthophora* might increase the *Gracilaria* crop.

2.3 Management of wild crops

Several practices have been used to harvest wild crops. Passive or active catching of drift materials with nets has been used in various places (Santelices and Fonck, 1979; Luxton, 1981). Raking in 1 to 12 m depths from boats has been used to make experimental quantitative harvests on mud flats. However, raking may alter the bottom and reduce productivity. The underground thallus system of *Gracilaria* must be preserved if future harvesting of the site is expected.

Management programs in Chile (Santelices et al., 1984; Poblete, 1986; Westermeier, 1986) have addressed the questions of how, when, and with what frequency to harvest, as well as what amounts of materials should be left in a *Gracilaria* sandy mud bed for regrowth (Fig. 4). Where winter production is low, winter is recommended to be a closed season. The low seasonal values are recommended as the minimum crop allowed to remain in a bed after harvesting. In central Chile, harvesting is restricted to spring and summer months, with either monthly or bimonthly frequency.

In practice, a harvesting strategy is adopted after an initial study of the bed. The strategy recommended is different for essentially each commercial bed in Chile (Poblete, 1986; Westermeier, 1986) and appropriate management measures have been enforced in several of them. Time-related restrictions on harvesting have changed the seasonal pattern of wild crop production in southern Chile to one that is still seasonal; but with harvesting allowed every other month, the yield is more regular (Santelices and Ugarte, 1987). In one bed where all the management recommendations have been enforced (Poblete, 1986), bed area and production are gradually increasing. In other beds, however, and es-

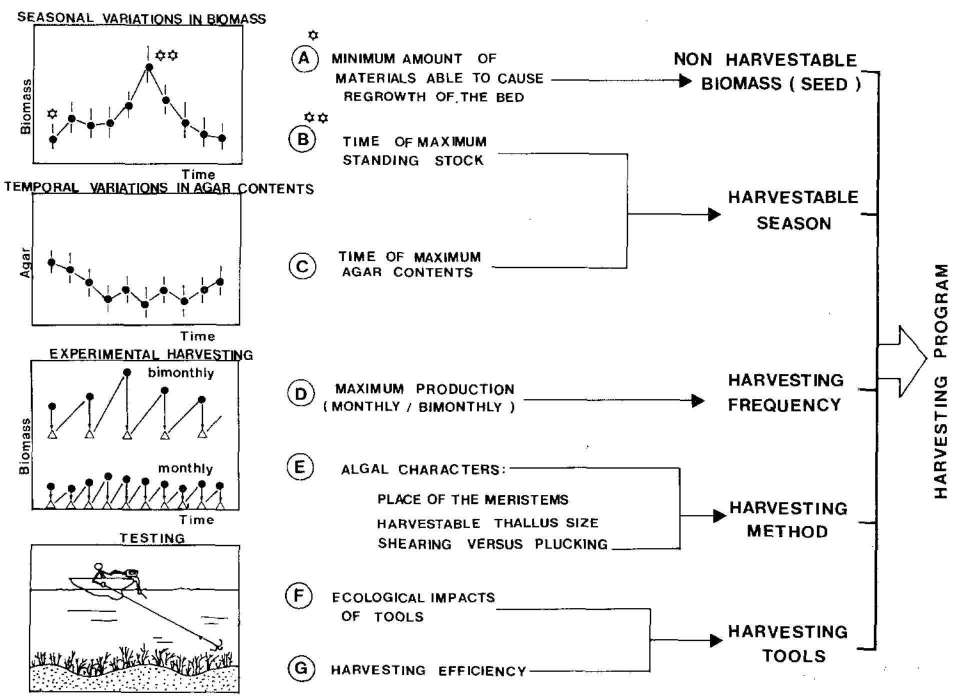

Fig. 4. General management diagram for harvesting the *Gracilaria* beds in Chile.

pecially in the most accessible beds of central Chile, the enforcement of regulations was undertaken too late and failed because of lack of personnel or because of socio-economic pressures. Under these circumstances, the *Gracilaria* beds have gradually lost their productivity where harvesting is opportunistic and occurs at all seasons. As productivity drops, fishermen start raking the bottom to increase their harvests. However, this practice removes the underground thallus system and ultimately results in the destruction of the entire bed. Much of the current management practices in these beds consists in encouraging the re-establishment of the underground thallus systems to support growth of the normal harvest.

3. FARMING *GRACILARIA*

As the *Gracilaria* market and the sophistication of use increase, the pressure for farming increases. Farming produces a crop that is more reliable in volume and quality, and the volume can be expanded as the market increases. Several methods of farming have been devised for *Gracilaria*. In some cases, farming consists merely in growing the species after branches have been pushed into an unconsolidated bottom. In more advanced farming the *Gracilaria* is grown, attached or unattached, on unconfined shallow bottoms or in ponds, raceways or tanks.

Undertaking the production of *Gracilaria* for its hydrocolloids means producing thousands of dry tonnes per year economically so as to be cost competitive in the raw materials world market. Hence, *Gracilaria* farming is particularly attractive in low-labor-cost areas where socio-economic benefits largely match or exceed the capital-returns benefits. In the descriptions of these methods, below, more detail is provided for those that are being used or are apt to be used most widely. For example "lines" seem sure to replace the more expensive and inconvenient "nets", or the *Laminaria* type of farm construction used by Ren et al. (1984) in relatively deep water.

3.1 Farming open waters

Basically, three approaches are used for planting *Gracilaria* crops: (a) on bottoms; (b) on nets or lines; and (c) on floating rafts. In each of these three approaches, either vegetative materials or spores can be used as planting material.

3.1.1 Bottom planting

Two completely different ways have been developed for planting bottom habitats with *Gracilaria*; one starts from vegetative thalli and the other from spores.

3.1.1.1 Bottom planting of vegetative material. The simplest form is to transfer rocks bearing the thalli to places where an increase in density is wanted. If the species is already growing on a site, this labor-intensive method is often successful. A more complex procedure is to remove thalli or major branches and put them in places where they are wanted. Two further common approaches are to tie the thalli to rocks, or to secure them to rocks by means of rubber bands. Another method used on non-consolidated bottoms is to push the proximal ends of whole thalli or major branches into the planting site bottom. This is feasible and is used in Chile with some promise (Fig. 5A). It is especially useful for intertidal mud flats where farmers can easily push bundles of thalli into the sand or mud during low tides.

These simple planting methods have three major problems. *Gracilaria* survival is usually poor when the source site is not identical to the planting site. Required conditions could involve water quality or sediment/mud ratios, and that may not be evident at the time of planting. Secondly, materials planted in substrate may tear loose during harvesting or during periods of much water movement. This latter problem has been common in the shallow intertidal flats of southern Chile. Thirdly, planting and harvesting are high labor-consuming activities which can be economic only in areas with low labor costs.

A more elaborate system has been designed (Fig. 5B) for subtidal beds on sandy bottoms. *Gracilaria* is anchored using soft polyethylene tubes 1 m long, 0.1 mm thick and about 4 cm in diameter, which are completely filled with dry sand (ca. 2.5 kg) and knotted at both ends. Keeping them wet and cool, apical

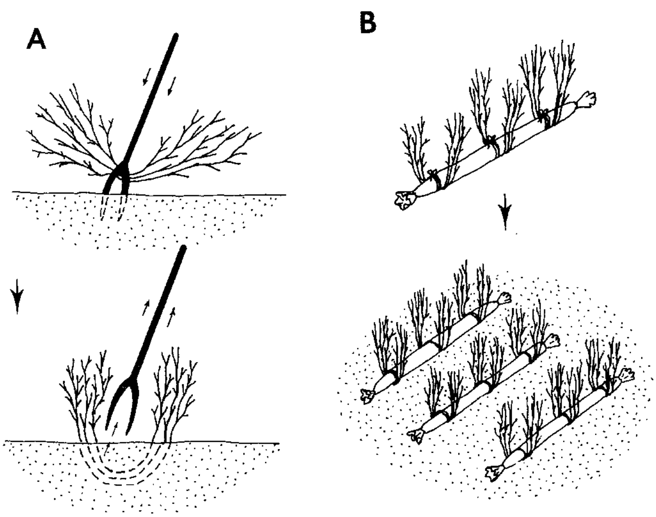

Fig. 5. Planting of *Gracilaria* in sediment bottoms with a forked planting tool (left) and with sand-filled polyethylene tubes (right). Polyethylene tubes are dropped to the bottom from a boat and arranged in rows.

and middle portions of thalli about 4.5 cm long, collected from natural beds, are secured to the sand-filled polyethylene tubes with rubber bands. Five to six strands of the *Gracilaria* (about 90 g) are tied along one side of each anchoring unit. These units are then placed on a boat, transported to the planting area, dropped from the boat and arranged underwater by divers. Normally they are set in parallel rows, about 1 m apart and positioned perpendicular to the coastline. When setting up the rows, precautions are taken to rest the centers of the bundles directly on the substratum, where they are held in place by the weight of the sand in the tubes.

The above method was developed in the late 1970s after two major biological findings. One was the description of the already-discussed underground thallus system. The other was the experimental demonstration of a significant correlation between higher growth and smaller inter-thallus distance (Santelices and Fonck, 1979). From the farming point of view, this means that patches of *Gracilaria* rather than isolated, individual thalli should be planted. The method has gained popularity among the *Gracilaria* farmers because it is economic, the planting units can be effectively handled under water, and as the polyethylene tubes disintegrate, they leave the *Gracilaria* thalli immersed in the sand, creating an underground thallus system. Furthermore, even though it is labor consuming, the method allows the mechanization of some stages.

Experimental evaluation of the polyethylene tube method has suggested (Pizarro and Barrales, 1986) potential yields of about 21 t (dry) per ha for a 6-month growing period which included late winter, spring and early summer. Several commercial companies in Chile are reputed to have sustained profitable production using the method over a recent 2-year period. According to official statistics (Lopehandía, 1986) as much as 10% of the *Gracilaria* currently produced in Chile comes from cultivation with this method.

3.1.1.2 Setting spores or small cuttings onto the bottom. The necessity for initiating crops by the use of spores or cuttings is becoming recognized for, in mass, *Gracilaria* is a small seaweed and thus planting of vegetative thalli manually on the bottom can be prohibitively expensive. Along with spore manipulation, genetic engineering promises to play a role.

The materials to which cuttings are attached are most frequently gravel crushed from reef rocks, or bivalve shells such as clams. If the reef rock and shells are from a local site, one is not putting foreign material into the sea, and they are often free to the farmer. The idea of bivalve shells was first suggested by Wood (1945) and successfully used by Doty and Fisher (1987).

Spore germination and growth of *Gracilaria* have been repeatedly described (Killian, 1914; Oza and Krishnamurthy, 1967; Rao and Thomas, 1974; Oza, 1975; Bird et al., 1977a) and no ecological difference has been found either in the pattern of growth or in the ecology of tetraspores or carpospores, except perhaps temporal differences in their seasonal formation and discharge. Compared to the adults, juvenile plants are more opportunistic in habitat selection, at least in *G. foliifera*, and are more broadly adapted to environmental extremes than mature thalli (Friedlander and Dawes, 1984).

The spore method, in short, consists of spores from selected fertile adult thalli attaching themselves to materials which after a time are outplanted. This method requires the most apparatus but also provides farmers with better control in starting or enhancing *Gracilaria* productivity at a favorable site. Wood (1945) noted that the spores of *Gracilaria* settle and grow on suitable cultch (usually oyster shells), and he suggested this might be a way of expanding the natural beds. Lin et al. (1979) attempted to develop *Gracilaria* farming from spores grown on bamboo blocks in fishponds but without economic success.

The *Gracilaria* spore-setting method, as developed in Malaysia and Hawaii, requires a nursery unit (Fig. 6) for setting the spores and for germling growth. Also it requires preparation of the outplanting site previous to outplanting.

Features that might be combined in a seedling nursery unit are illustrated in Fig. 6; however, in practice much less sophistication is usually seen. The tank can be a discarded bathtub or other container large enough that the water does not vary widely in temperature during the period of its use. In it, perhaps one-third to one-half meter from the bottom, a net is suspended horizontally and the bottom of the unit is covered with the cultch or lines. Then the nursery unit is filled with seawater. The level of the seawater can be adjusted by changing the angle of a pipe placed at one end of the unit.

To obtain a source of spores, fertile *Gracilaria* is harvested from a wild crop. Fertile thalli are brought to the nursery in buckets or bags, with care given to preserve the vitality of the seaweed so that it does not lose the ability to shed viable spores. The care is generally keeping it cool, moist if not submerged in aerated seawater, clean and not crowded so as not to put a strain on the thalli. The seaweed is then spread on the horizontal net. The level of the seawater is kept deep enough to prevent the fertile *Gracilaria* on the horizontal net from ever being in the air. Usually spores are shed within the following 36 h. If 0.5 m of water is maintained between the spores and the substratum, the spores will spread, settle and attach within 24 h of their release.

At this important stage any maltreatment usually means failure, and failure to get viable spores can be frequent. In sophisticated circumstances, microscope slides may be included in the cultch and their examination used to detect success at this, otherwise invisible, stage in the farming. Maltreatments that may cause failure include such procedures as heating, drying, exposure to petroleum fumes, rough handling, and delay in transporting the fertile *Gracilaria* to the nursery in an abundant supply of clean aerated water.

While outplanting can be done immediately after attachment, it is perhaps wiser to let growth proceed for 1–3 days before outplanting. During growth in the nursery unit, the farm site should receive preparation. The whole operation should be appropriately timed if tidal control of water depth would otherwise

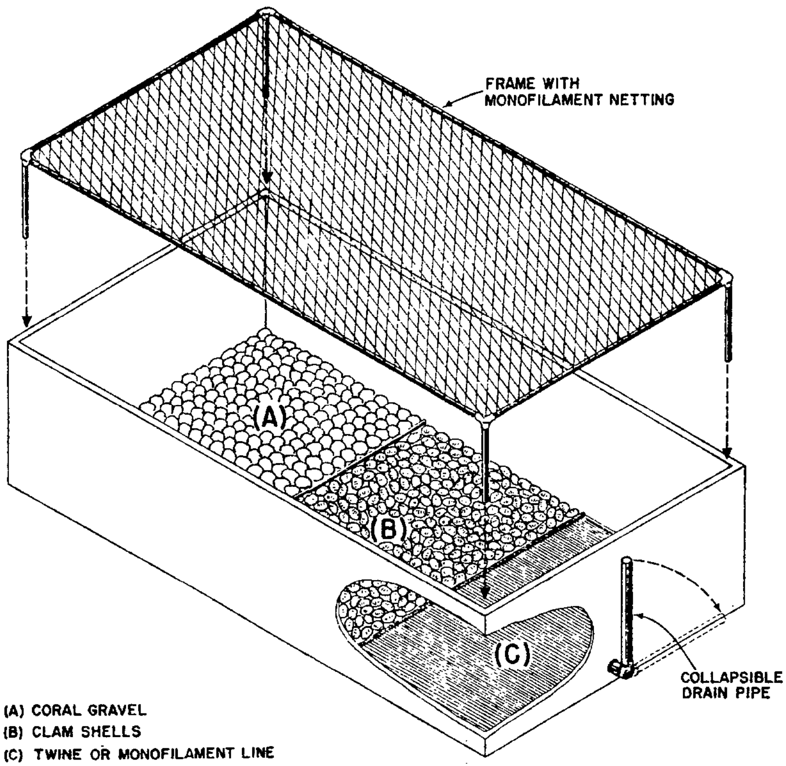

Fig. 6. Diagram of a nursery tank constructed for field use so that water can be exchanged during appropriate tides by manipulation of the drain pipe. Coral gravel, clam shells and plastic line wound on a frame as cultch are shown as alternatives A, B and C, respectively. The horizontal net to hold the fertile *Gracilaria* above the cultch during spore shedding, normally under water, is shown raised out of the tank.

be a problem. In Malaysia, some of the best growth of *Gracilaria* has been obtained (Doty, 1986) in water where the Secchi disc depth was about 2 inches (5 cm). If the bottom is of waist-deep, very soft mud, close approach by boat or raft may be desirable for carrying heavy buckets of sporeling-bearing gravel or anything else to the planting site.

Any weeds or pests should be removed before outplanting time. Actually, this and other problems are usually taken care of by the farmer in preparing his farm site. If *Gracilaria* does not grow naturally at a site, planting there may not result in success. It is advisable to conduct test planting before investing in planting a whole farm.

Shells and gravel can be handled roughly before and when the seeds are of outplanting size. Carried into the field in buckets or trays, they can be broadcast by hand, shovel or other means. Those that land upside down will most likely be unproductive, but they are so inexpensive that this is not an important cost factor. As mentioned, clam shells (valves) when cast on the water usually settle on the bottom of the nursery unit (e.g. Fig. 6) and, during the later final broadcasting, on the substratum at the farm site. Clam shells may have to be treated, e.g. with acid or abrasive, so that spores or cuttings attach and grow on them favorably.

Seed-bearing gravel (Fig. 7) or shells of *Anadara* with attached *Gracilaria* fragments should be broadcast so that one *Gracilaria* tuft will be produced on the average for each 100 cm^2. This is only a suggested initial spacing that should be further modified by experience for any particular site.

In general, once a farm is started and has stabilized in a relatively non-seasonal area, fertile *Gracilaria* thalli will appear. Should new clean shells or gravel devoid of any growth be added to the bottom, when the fertile thalli shed spores, the spores can be expected to attach to the new materials, and these may be used to improve or expand the bed. Getting spores to attach in a farm setting may replace the use of remote nursery units. However, since the spores of the macroalgae in the water at a farm are random mixes of the genera and species present in the area, natural seeding does not ensure that a new crop of *Gracilaria* will appear on the chosen substratum, whereas the planting involving a nursery unit and clean cultch does.

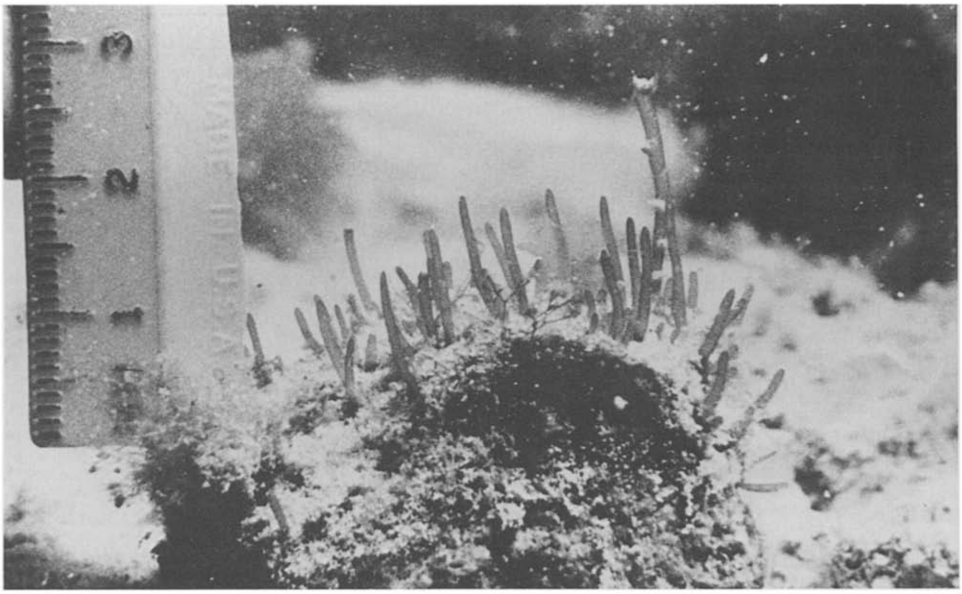

Fig. 7. *Gracilaria* juveniles on gravel outplanted on a sediment bottom for grow-out in the field. The ruler indicates this lot was mostly over 1 cm tall at the time. (Photo 32280.16 taken by Earl Zablackis in Kaneohe Bay, Hawaii.)

Finally, altering the bottom itself has been done experimentally to enhance wild crop production. However, there is little control of what, besides *Gracilaria*, may grow due to such bottom changes. Sometimes areas with little growth of *Gracilaria* are merely devoid of the stones or shell materials to which the spores might attach naturally. Such sites often have small bottom depressions filled with mud or sand; this can easily be improved by adding bottom material with stones or mollusk-shell particles. Indeed, Trono (1981) found that adding suitable substratum in an otherwise desirable habitat did lead to higher standing crops.

3.1.2 Line farming

As with the case of bottom planting, two different kinds of line farming have been developed: one from vegetative thalli and the other from spores settled on lines and ropes. (See also under 3.1.1.1.)

3.1.2.1 Securing vegetative materials to lines or nets. Large cuttings, or even whole thalli, may be planted by inserting them in ropes or by tying them to ropes, monofilament or other lines. Such materials are suspended stretched between stakes driven into the bottom.

This approach has been used in such widely diverse places as Burma (Dr. U. Min Thein, pers. commun., 1985), India (Raju and Thomas, 1971; Thomas and Krishnamurthy, 1976), West Indies (Smith et al., 1984; Smith, 1986) and Brazil (Camara-Netto, 1987). It was first used on the Atlantic coast of the United States (Kim and Humm, 1965). Vegetative cuttings are inserted between the strands of coir or 5- to 8-mm polypropylene rope or nets suspended between stakes in sites such as mud bottoms along shores lined by mangroves. The materials used are often posts and coir rope of local origin plus foreign imports of the man-made lines used by the local fishermen. Nylon line (stranded and twisted) or polyethylene rafia (an irregularly folded membrane) largely have been used (Smith et al., 1984; Camara-Netto, 1987) to tie *Gracilaria* to the farm lines or nets. Both Smith and Camara-Netto inserted vegetative portions of *Gracilaria* between the strands of rope. In time, the use of nets is always abandoned in favor of lines. In the farming of other seaweeds (unpublished) monofilament "150-lb test" nylon lines have been found to last more than 10 years in seawater if kept submerged. Stakes of *Avicennia nitida*, the black mangrove tree, last more than 1 year in the Caribbean (Smith et al., 1984) but those from *Laguncularia racemosa*, the white mangrove (Smith, 1986), are also suitable.

Preliminary *Gracilaria* rope farming trials in Ceylon indicated that fresh weights of 3.5 kg m^{-1} could be obtained per crop. In two other cases, nets planted with 0.35 g of seed-stock per m^2 yielded 4.4 g fresh weight in 80 days. This 12.57 -fold net increase is equivalent to growth at 3.21% per day. The wet-to-dry weight ratio was 6.15. In India, percent yield of agar in similar experimental trials ranged between 30 to 40% while gel strength increased from the first to the third month after planting (Thomas and Krishnamurthy, 1976). Commercial production in Saint Lucia (West Indies) has included both the coarse *Gracilaria debilis* and the long, finely branched *G. dominguensis* (Smith et al., 1984). For the production of *Gracilaria* as a table vegetable or as a food supplement, with prices well over US$ 6.00 kg^{-1} (Smith et al., 1984), the method seems adequate. However, the large amount of hand labor needed for planting may prevent its extensive use in the production of commercial agar.

Problems encountered in this type of farming include grazing by parrot fish and surgeon fish (Smith et al., 1984), and sediment accumulation on *Gracilaria debilis* thalli. This sediment had to be washed off by hand for reasons of thallus health during growth or to assure marketability after harvesting. However, by interspacing the thalli with *G. dominguensis*, a species with long branches, it was found that the movements of this second species induced by water motion on the farm swept the sediment off the *G. debilis*. In addition, it was found that the delicate *G. dominguensis* tends to break where inserted in braided polypropylene ropes, which are rather stiff and harsh, though unusually enduring and inexpensive. Coir rope is softer and less damaging, but it is weak and endures only in calm water. Harvesting by cutting the thalli off a few centimeters above their bases led to regeneration from the cut ends and the potential of as many as ten harvests per year.

3.1.2.2 Setting spores on lines or nets. The rationale and generalities for this variation of *Gracilaria* farming have been outlined above, in 3.1.1.2. As in the case of spores settling on cultch, setting spores on lines or nets also requires nursery units appropriate to the particular substratum to be used, preparation of the outplanting site and transferring of the seed-bearing line to the planting area. Therefore the following discussion concerns specific aspects of farming of *Gracilaria* on lines or nets starting from spores.

If lines are to be used, rectilinear frames will be needed, sunk on the bottom of the nursery unit, so that the lines can be wound around them. Such frames may be made of wood, non-metal pipe, bamboo or reasonably straight tree limbs. While the spores are attaching and growing on the lines in the nursery units, stakes to hold the lines should be driven into place (Fig. 8) on the outplanting site. During planting, lines with seeds growing on them are taken from the nursery unit into the field for planting, still wrapped around the frames. To prevent drying, each frame is placed while very wet in a large plastic bag so that neither interrupted respiration nor exposure to air will damage the seed stock. When the farmer removes a planting frame from its bag to put the line in place, he ties the free end of the line around an end post on the farm at a suitable height so as to keep the lines off the bottom. The farmer then walks, unrolling the line from the line frame as he goes (Fig. 8) to the other end post, opposite the first, and ties the other end (the "bitter" end) of the line to it at

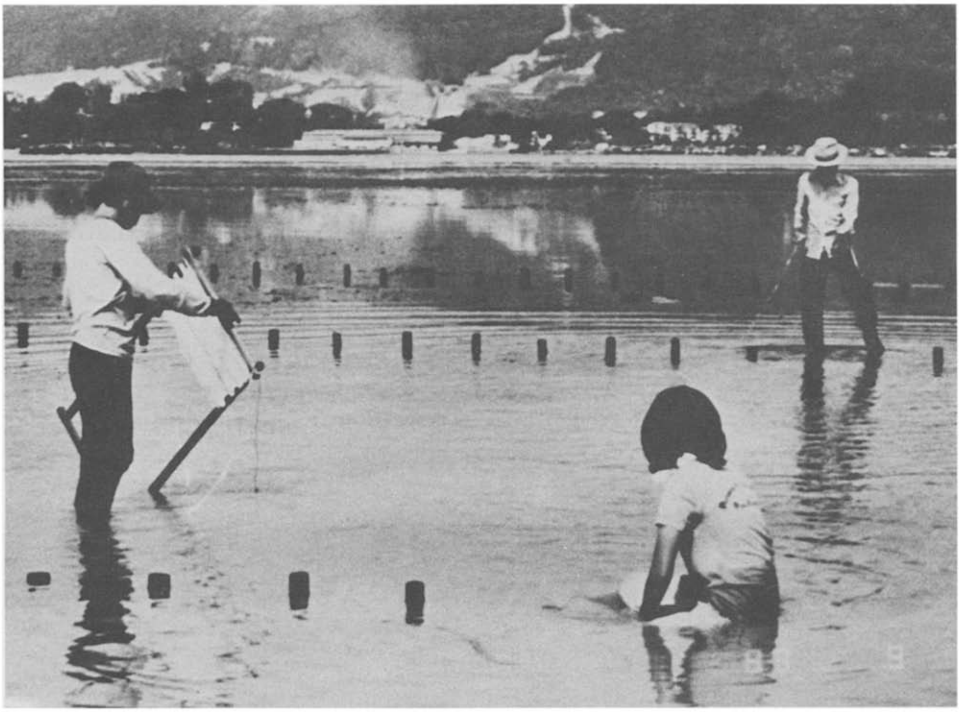

Fig. 8. Outplanting of *Gracilaria* juveniles grown on plastic line wound on a frame in a nursery. Note the rows of pegs to which the ends of the lines are attached such that they are parallel to one another. (Photo 32816.2 taken by Jack R. Fisher on Middle Bank, Penang, Malaysia.)

the same chosen elevation. The line must be tied tight enough to keep it taut, to prevent its rubbing on the bottom or becoming buried in the bottom sediments, or becoming burdened with loose objects drifting along the bottom.

The lines should run parallel to the principal tidal currents (Fig. 9). This is thought to provide freer and more uniform access to water exchange, to impose less strain on the lines, to reduce the hang-up of flotsam and to reduce lateral entanglement of the lines.

As in the case of spores settling on shells and gravel, it is recommended that after the *Gracilaria* crop has become stabilized, new lines devoid of sporelings should be tied parallel to, and between, the old crop-bearing lines. When the old crop sheds spores, the spores can be expected to attach to the new lines (as well as the old ones) and provide planting material to expand the farm or replace old, damaged, or lost lines.

Spore attachment on new lines placed in dense wild crops was successful (Smith et al., 1984) and seemed practical in the West Indies. In Malaysia (unpublished) the *Gracilaria* species originally obtained from spores on lines under nursery control was replaced (Doty, 1986) on the lines by another *Gra-*

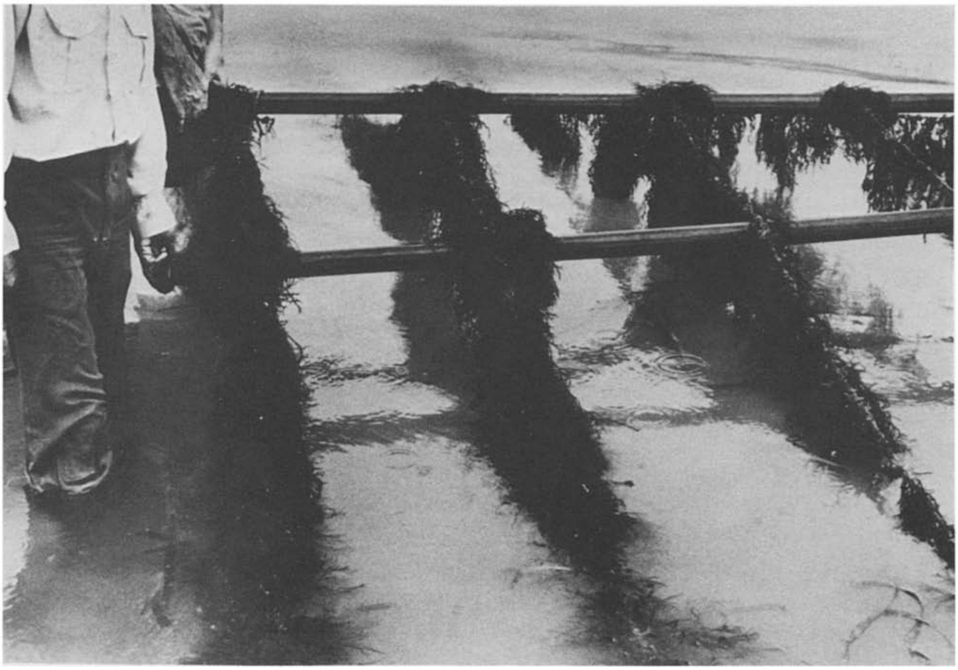

Fig. 9. The same outplanting as in Fig. 8, showing the resulting *Gracilaria* growth in 8–9 months. A half-harvest would seem feasible at bimonthly intervals. (Photo 32816.11A taken by Jack R. Fisher on Middle Bank, Penang, Malaysia.)

cilaria species in the field in about 6 months. At the pilot farm the two *Gracilaria* species were the only ones to be found between the farm's tide levels. In any case, the crop on such lines reached 1 wet kg m^{-1} of line (Doty, 1986) and it seemed that four or five lines could cross each square meter of farm, with several harvests per year.

A stress symptom called ice-ice appears under such conditions as low light, low water motion or low inorganic micronutrients. It is not a disease. The thallus segments, usually deep within the thallus, become discolored, and then as the tissues die they become white, soft, and finally dissolve away. The portions of a thallus isolated by ice-ice can be expected to fall off and become lost; thus they might as well be harvested and either replanted or dried for sale.

Ice-ice indicating stress may appear seasonally at a particular site, e.g., if water motion becomes intolerably low in relation to micronutrient content. If this seems likely, when the ice-ice appears, it may be advisable to alter the farm or to move the planting to an area of greater water motion. Depending on tidal or wind-driven currents, changing the direction of the lines may effectively change the water motion and provide relief from the problem. Adding fertilizer has also proven helpful.

Detecting the presence of adverse seasonality at a site is one of the reasons for pilot farming, and it should be done for at least a year preliminary to any major investment. Where ice-ice is bad, it may be best to discontinue farming at the site until favorable conditions return. Having to restart farms every year or provide fertilizer may not be economical.

3.1.3 Raft farming

In Qingdao, People's Republic of China, methods are being developed to cultivate *Gracilaria* in low fixed rafts. Ropes, each about 70 cm long, with 15 g of *Gracilaria* fragments on them are hung horizontally on these low fixed rafts, or vertically, on long-tethered floating rafts (Ren et al., 1984; Ren and Wang, 1987). In April–May, the amount of sunlight reaching the thalli suspended from the floating raft was higher than on the fixed raft. However, as temperature increased, the transparency in the area became greater and the growth of *Gracilaria* in both systems became similar, with a maximum of 7 to 7.5% daily. During June–July, the strong sunlight and high temperature produced detrimental effects on the algae, but the maximum growth rates in these experiments, were then up to 10 to 12% daily. When temperature was below 15°C, epiphytes, mainly *Ectocarpus, Ulva* and *Polysiphonia,* were a serious problem with this method. Yet production is (J.S. Liu, pers. commun., 1986) about 2 dry t ha^{-1} of *Gracilaria* with good agar quality. Epiphytes such as diatoms are removed using low concentrations of formaldehyde (1 part per 50 000), while larger marcroalgal pests are removed by hand.

3.2 Pond farming

Pond farming is characterized by the absence of enough water motion to significantly move the thalli, though wind-driven currents in a pond do move the materials downwind. The cultivation of *Gracilaria* in ponds is successful because *Gracilaria* is perhaps the largest red alga and one of the largest of the seaweeds that grow well both in low salinity and low water-motion pond environments. However, it seems to grow well only when other water qualities are favorable. The pH should be near the 8.1 of seawater.

Indeed, ponds do not usually have natural populations of *Gracilaria* in them; it usually has to be planted there. However, what appeared to be naturally occurring sterile populations of *G. arcuata* have been observed in Philippine salt ponds in both Cavite and Navotas. Normally *Gracilaria* does not become fertile under pond circumstances. Thus, when environmental extremes eliminate the macroscopic vegetative crop, *Gracilaria* must be reintroduced to be maintained as a pond crop.

In Hainan, Taiwan and Hawaii where commercial farming follows this method, the process is extremely simple. Farmers with a pond to plant obtain their planting materials from the wild or from nearby planted ponds. The material is often chopped into hand-length pieces, put on a raft and then scattered so as to sink onto the bottom where wanted (Shang, 1976; Chiang, 1981; Yang et al., 1981; Chueh and Chen, 1982; Wang et al., 1984).

Gracilaria ponds are basically marine to brackish-water ponds located in places where no strong wind prevails and where both seawater and freshwater can be obtained easily. Small ponds are preferable to larger ones because the thalli in large ponds tend to aggregate at the pond corners due to wind action (Chiang, 1981). Water in such ponds in Taiwan is usually kept about 50 to 80 cm deep, and water exchange is controlled by the use of one or two inlet–outlets. The bottom is flat and formed of clay loam or sand-and-silt loam mixtures. In the central portion of a pond larger than 1 ha, there are one or two rows of windbreaks made of bamboo pieces installed perpendicular to the direction of the wind to protect the seaweed from being moved to the downwind shore.

Young ponds usually do not support *Gracilaria* growth: the pH of the water must be near 8, the salinity should be relatively stable and the temperature between 20 and 30°C. In tropical mangrove areas where ponds are often built, the organic content of the mud used or exposed in the construction is initially high, and the pH is low. In time, the pH rises and the water quality may stabilize; only then does *Gracilaria* thrive.

The depth of the pond water is usually kept at 30 to 40 cm. From June to August, however, air temperature in southern Taiwan very often reaches 32°C or more. Therefore, during summer, the pond water depth is usually increased to 50 to 60 cm, to prevent damage from increased water temperature. On the other hand, when the air temperature is below 10°C, the depth of the pond is reduced to 20 to 30 cm.

One water exchange every 2 to 3 days is the usual practice to maintain a proper range of salinity and provide mineral nutrients for algal growth. Sometimes additional fertilization of the pond is needed, and usually this can be done by adding 3 kg ha^{-1} of urea or 120 to 180 kg ha^{-1} of fermented manure from pigs or chickens.

About 5 to 6 t ha^{-1} of fresh thalli are seeded initially. Harvesting is then carried out every 30 to 35 days in summer and every 45 days in winter. Generally about one-third to one-half of the seaweed is harvested by gathering it with scoop nets or raking it into nets. After harvesting, the thalli remaining in the pond are torn into pieces and are rebroadcast. The harvested thalli are brought ashore, spread out and dried.

Pond farming of *Gracilaria* in Taiwan started (Chiang, 1981) as an offshoot of rope cultures in ditches associated with fishponds; this ditch habitat seems to have been its origin in Shantou (Swatow) on mainland China (Wang et al., 1984) and in Hawaii (unpublished). Positive culture became significant in associated fishponds in about 1966 in Taiwan (Chiang, 1981; Chueh and Chen, 1982). The Taiwanese government planned that in 1967, Taiwan would produce 1000 t of *Gracilaria* by polyculture in fishponds to meet the local shortage of agar. A nearly seven-fold increase was obtained up to 1977, when 6804 t was produced. In 1979 approximately 12 000 t (fresh weight) was produced from some 300 ha of farm ponds (Chiang, 1981). Shang (1976) reported that the average productivity of dry *Gracilaria* in Taiwan ponds was 7 to 12 t ha^{-1} $year^{-1}$. A few years later Chiang (1981, p. 573) felt 16 to 43 t ha^{-1} $year^{-1}$ could be expected. In reporting raw-material shortages in the Shantou area at ca. 23°N, Wang et al. (1984) give no overall production figures for the area or for mainland China. They do note that there are thousands of hectares of suitable fish-ponds available, and *Gracilaria* potential growth of 2 to 3% per day. Thus, it would seem feasible to produce enough *Gracilaria* in that area to keep the current seasonally operating agar-extraction factories open all the year around.

The recent discovery of terrestrial sources of salt in mainland China has led (Tseng Fen, pers. commun., 1985) to the farming of *Gracilaria* in several of the otherwise abandoned salt pond systems on Hainan Island. The cultivation method was later extended to Guandong where 1500 ha of ponds are said (S.J. Liu, pers. commun., 1986) to be producing about 2000 t $year^{-1}$ of dry *Gracilaria* for agar purposes. Ponds here are 0.7 to 1.0 ha in size, 60 to 70 cm deep, with sandy or muddy bottoms; the temperature range is 15 to 30°C and salinity range is 10 to 20‰. The species under cultivation is *Gracilaria tenuistipitata* forma *liui* which, although able to withstand infrequent water exchange, requires a pH between 7.0 and 8.0 to grow. These ponds are dried in winter to kill spores and propagules of epiphytes, then some 50 kg of CaO_2 per 0.15 ha of pond are added to the bottom to stabilize the pH. Water is exchanged every 6 to 15 days and about 1 g/l of urea or ammonium sulfate is added as fertilizer after each water exchange. Planting starts by introducing cuttings at densities of 0.4 kg m^{-2}. Harvesting is done every 30 days, and epiphytes and pests are removed by hand at irregular intervals. Agar yield and strength are low; therefore dry algal prices are also low (US$ 0.25–0.35 kg^{-1}). For this reason, the ponds are now preferentially being used to cultivate shrimp.

In Hawaii, the pond and tank grown *Gracilaria* is sold only to the fresh vegetable market. It was originally grown to purify the effluent from the growth of oysters, but the oyster effort has been abandoned. Currently, *Gracilaria* is being grown on the effluent from shrimp and tilapia production, resulting in the sale of about 1 t wet weight of the seaweed per week.

The water from nearby animal aquaculture systems flows through a variety of channels into a 1-ha pond and from there percolates into the brackish groundwater system. The *Gracilaria* appears to be maintained in a steady massive bloom stage in these waterways. The present harvesting rate seems to make little impression on the standing stock. In association with this is the report (Tookwinas et al., 1986) that in southernmost Thailand a farmer has obtained a production rate of 6442 kg ha^{-1} $year^{-1}$ from a 12×17 m pond 1 m deep.

Problems with this rather undisciplined pond production method for the table food market at present include the fact that the thalli are relatively highly branched, the branches are too small, and the thalli are too dark in color to provide a product of attractive appearance. Also there is often a wealth of small green algae and diatoms, largely *Cocconeis*, attached to the surface of the *Gracilaria*. Most of the diatoms can be removed by post-harvest washing.

Several different problems have been identified in the more advanced farming of *Gracilaria* in Taiwan (Shang, 1976; Chiang, 1981; Yang et al., 1981). Epiphytes characteristically develop on the thalli under these conditions of reduced water movement. They may be species of diatoms, but often they are macrophyte species: *Chaetomorpha, Enteromorpha* or *Ectocarpus*, and they develop to such densities that they become serious pests. Control with tilapia and *Chanos chanos* (milkfish) seems very satisfactory but the sizes and densities of these fish must be kept under control because they both begin to consume *Gracilaria* as the epiphyte population is reduced and/or the fish grow larger. Thus, to maintain the desired balance, the larger fish must be removed and smaller fish reintroduced. In Hawaii another fish, a small *Poecilia* species which, like tilapia, breeds in the ponds but remains small (perhaps less than 7 cm long), has not become a pest.

Tilapia (*Oreochromis mossambicus*) often gets into tropical *Gracilaria* ponds during the water exchange. The fish grow rapidly, damaging the *Gracilaria* thalli and the ponds. Unless removed, they will consume *Gracilaria* as well as clear nest holes of various sizes through it to the pond bottom.

Perhaps the most important limitation of this cultivation system is that only food-grade agar is produced with gel strength values of 150 to 400 g cm^{-2} and little sugar reactivity. Several explanations have been adduced for this reduced gel quality. Since gel strengths of alkali-modified agars showed a strong inverse relationship with growth at increasing temperatures (Craigie and Wen, 1984), the increased summer temperature of these ponds might be responsible for the low gel strengths. Since the price of the algae so produced is about US$ 275 per dry ton in Taiwan (Shang, 1976), polyculture of *Gracilaria* with the grass shrimp (*Penaeus monodon*) and a crab (*Scylla serrata*) has been developed to provide additional income. At present (Chang, pers. commun., 1987) *Gracilaria* is more prized as food for the abalone, *Haliotis*, than for its agar.

3.3 Tank farming

Growing *Gracilaria* in tanks permits control over the whole production process. Also the method has the promise of achieving more sophisticated ends, e.g., the processing of polluted water to obtain some specific material (e.g. agarose) in addition to clean water. This method is particularly attractive in high-labor-cost areas, where capital returns are the principal benefits.

The methods used, principal achievements and perspectives of this type of cultivation have been recently summarized by Hanisak and Ryther (1986).

Gracilaria tikvahiae was considered a prime candidate for this type of mariculture due to its fast growth and widespread distribution along the eastern coast of the United States (Bird et al., 1977b). The final goal of this type of farming (Ryther et al., 1979; Hanisak, 1981a,b) was the simultaneous production of agar, biogass conversion, fertilizer production and sewage treatment. Mean production rates in the system of Hanisak and Ryther et al. (1981) have been 34.8 g dry weight m^{-2} day^{-1} (equivalent to 127 t ha^{-1} $year^{-1}$) with maximum growth of 46 g m^{-2} day^{-1} and minimal of 12 g m^{-2} day^{-1}. Maximal yields occurred at relatively low nutrient enrichments (10 to 100 μM nitrogen and 1 to 10 μM phosphorus) and at a stocking density of 2 to 3 kg (wet) m^{-2}, when plants were harvested back to that density at approximately weekly intervals.

For several reasons not completely understood, tank yields have been found to be directly proportional to seawater exchange rates of between 1 and 30 culture volumes/day. De Busk and Ryther (1984) have demonstrated that carbon dioxide addition and pH adjustments can substitute for up to ten water exchanges per day. The highest growth rates of *G. tikvahiae* were obtained (Lapointe and Ryther, 1978) by growing it in small tanks (55 l) supplied with vigorous aeration and rapid (20 to 30 times a day) exchange of enriched seawater. The cultivation system of Ryther et al. (1979) was successfully scaled up to larger tanks (i.e., 2.4 to 29 m^2 in surface area and 2400 to 24 000 l in volume). Over the last 5 years, the mean productivity of *Gracilaria* in such tanks was 22 to 25 g dry weight m^{-2} day^{-1} (80 to 91 dry t ha^{-1} $year^{-1}$) and involved particular clones of *G. tikvahiae* able to propagate themselves vegetatively.

Through a number of experiments, the effects of several variables in the system have become better understood. Under low water flow, *Gracilaria* growth may be limited not only by mineral nutrient availability (Parker, 1982) but also by CO_2 limitations (Lapointe and Ryther, 1979; De Busk and Ryther, 1984). Accepting this, high production of *Gracilaria* in a land-based pond or raceway culture system would be carbon limited; the solution would be to add large volumes of water or large amounts of CO_2 gas to the culture. In addition, there must be sufficient aeration to maintain the seaweed in suspension and to rotate it. Periodic aeration (15 min per hour, for a total of 6 h a day) proved to be as efficient as continuous aeration. Guerin and Bird (1987) found increases in duration of aeration up to 24 h per day were accompanied by increases in productivity but at such cost that little economic gain occurred after about 12 h; 11 h daily appeared to be the most economical. Hanisak and Ryther (1986) have suggested that aeration requirements could perhaps be fulfilled through other methods of providing circulation in such seaweed culture tanks.

Contrary to common expectations, continuous mineral nutrient additions to the tanks resulted in a reduction in the growth of *Gracilaria* due to enhanced growth of epiphytes. However, two biological findings suggested an optimum nutrient management program for *Gracilaria*. First, Harlin et al. (1979) found that epiphytes such as *Enteromorpha* take up nitrogen mainly in response to light, while *Gracilaria* takes up nitrogen at night as well as by day (Hanisak and Ryther, 1984). Secondly, seaweeds have the capacity (Chapman and Craigie, 1977; Hanisak, 1979) to store mineral nutrients when external supplies are available and then draw upon these reserves when external concentrations are low. Therefore, if fertilizing is done only at night, and at 3- to 6-day intervals, such green algae as *Enteromorpha* may not become a pest. Nutrient supply to cultures has been successfully provided by pulse feeding of various concentrations at suitable frequencies (Lapointe, 1985).

An inverse correlation between *Gracilaria* nitrogen and carbon content (or between protein and polysaccharide fractions; Bird et al., 1982) is also found in nutritional studies. A wide range of C:N ratios is common because different factors determine the uptake of the two elements (Lapointe et al., 1984; Lapointe and Duke, 1984). For *G. tikvahiae* a C:N ratio greater than 10 has been suggested (Lapointe and Ryther, 1979; Lapointe, 1981) to represent nitrogen deficiency, hence reduced growth. Extremely low C:N ratios probably reflect carbon limitations and also may result in limited growth. These findings might be applied to other farming techniques as well as seasonal variations in the protein/carbohydrate ratio. In wild populations of *G. verrucosa* such variations have been suggested (Bird, 1984) to be indicative of the nutritional status of the population.

Experiments leading to methane production from the biomass of *G. tikvahiae* (Hanisak and Ryther, 1986) showed about 47% conversion efficiencies (i.e., the proportion of energy recovered as methane in relation to the total energy content of the *Gracilaria* loaded in the digester). However, the agar from these thalli was broken down into more-fermentable carbohydrates (Bird et al., 1981) and so was lost as agar. When attempts were made to obtain both methane and agar from the same batch of *Gracilaria*, only one of these products could be obtained at a time, as agar appeared to be the principal substrate for methane production. The residues in the digester, after the fermentation process is complete, could be used as fertilizer. They could be recycled within the farm to produce additional seaweed biomass. Experiments performed using such residues, both liquids and solids (Hanisak, 1981b; Habig et al., 1984a,b), indicated that *Gracilaria* could grow on the residues as well as on inorganic fertilizers.

Although the sustained yield of *Gracilaria tikvahiae* in tanks was among the highest for any seaweed tested, Hanisak and Ryther (1986) feel the production system for biomass will not be economic on a commercial level, at least in the near future. The method of cultivation employed is very energy intensive because it requires large amounts of flowing seawater and aeration. In addition, in the U.S.A., the requirement of large acreages of coastal land for land-based tank or raceway systems seems to be economically prohibitive. Still, the idea has not been abandoned, but current research tends toward evaluating (Hanisak and Ryther, 1986) in situ cultivation in the ocean, or cultivation in desert saline waters on low-cost desert land.

4. CONCLUSIONS

Farming activities with *Gracilaria*, more than with any other seaweed, have encouraged the development of a diversity of approaches and farming methods. As populations and markets continue their growth, these methods probably will be in large-scale use in the future to supply consumer needs. It is likely that bottom planting and line farming techniques for *Gracilaria*, either from spores or from vegetative fragments, may provide the raw material for agar and agarose; the species so cultured yield relatively large amounts of good quality seaweed by labor-intensive means but at low cost in the less-developed countries. It is difficult to predict the future of the fishpond and tank culture of *Gracilaria*, as alternative fishpond uses include shrimp cultivation with much higher economic returns to the fishermen. Perhaps farmers will continue to cultivate *Gracilaria* as a component in a polyculture system or as feed for economically more important organisms such as larval shrimp or adult sea urchins or abalone. Tank cultivation or mixed systems of pond cultivation, with or without air pumping or CO_2 additions, probably will become restricted to supplying *Gracilaria* for the most competitive and highly demanding fresh vegetable market in geographic areas where high prices are accepted. Such markets normally require products likely to be obtained only under conditions of cultivation where the farmer can control the quality, as in tank farming.

A variety of production ecology studies has been important in the development of these various farming methods. Field population studies provide the basis for management of wild crops and bottom planting of vegetative thalli; ecophysiological studies, and especially research on *Gracilaria* nutrient metabolism, are crucial for tank cultivation systems. Studies of environmental effects on gel production are beginning to provide understanding of the qualitative and quantitative differences in growth and gel obtained under different cultivation practices and in natural beds at different times and latitudes. Increased requirements for farmed *Gracilaria* in the near future are likely to require support for further research and, as well, stimulate new approaches. Farming involving the outplanting of spores indicates a need for applied *Gracilaria* spore biology and an opportunity to benefit from the application of gene manipulation, while biomass demands and water quality maintenance will probably stimulate new efforts in strain selection and *Gracilaria* biomass farming methods.

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