

Ecological differences among Chilean populations of commercial *Gracilaria**

B. Santelices & R. Ugarte

Departamento de Ecología, Facultad de Ciencias Biológicas, P. Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Received 1 September 1989; revised 5 December 1989; accepted 7 December 1989

Key words: agronomic traits, ecological differences, epiphytes, *Gracilaria* cultivation, sand abrasion, sand burial

Abstract

Field farming of *Gracilaria* is gradually replacing use of the wild crop in Chile. The most popular planting method consists of establishing underground thallus systems for patches of *Gracilaria* on wave-sheltered, soft-bottom habitats. Commercial cultivation often involves transplanting vegetative material to distant places along the coast. This study shows that native populations possess some ecological differences that might affect cultivation success. Seven environmental factors were tested for their effects on growth of four geographically separated populations belonging to two species of *Gracilaria*. No specific or population differences were found under various temperature or salinity regimes. Specific differences occurred in responses to irradiance, daylength, sand burial and sand abrasion. Responses to epiphytes differed among both population and species. Epiphyte recruitment was inhibited by some populations and stimulated by others. Given the farming methods presently used in Chile, these results have ecological and economical importance, as they suggest that transplanting randomly from one to other type of habitat does not assure cultivation success.

Introduction

Field farming is gradually replacing the gathering of *Gracilaria* in Chile. Between 1984 and 1988, the wild harvest decreased from 110 000 to 36 500 wet t y⁻¹ (SERNAP, 1988) while the farmed crop increased from 680 to 23 109 wet t y⁻¹. Thus, the importance of *Gracilaria* farmed has increased from 0.6 to 38.8% of the total crop in the last 5 years.

Several factors suggest that *Gracilaria* farming will increase further in the future. Present (1988) total production represents less than 55% of the

maximum annual crop harvested in Chile during the mid-1980's which, in turn, was insufficient to saturate the market (Santelices & Ugarte, 1987). In addition, the potentially productive area remaining unfarmed seems very large. By the end of 1987, the state had already licensed 2,700 ha for *Gracilaria* production (Ponce, 1987). Assuming an annual farm yield of 10–15 dry t ha⁻¹ (Pizarro & Barrales, 1986), the 1988 farmed crop values represent the net production of only 250–350 ha.

The most popular planting method in Chile consists of establishing underground thallus sys-

*Presented at the XIIIth International Seaweed Symposium, University of British Columbia, Vancouver, Canada, August 1989.

tems (*sensu* Santelices & Fonck, 1979) for patches of *Gracilaria* in wave-sheltered, soft-bottomed habitats. On intertidal flats bundles of *Gracilaria* fronds are inserted directly into the bottom. In subtidal habitats the bundles are anchored by soft polyethylene tubes filled with sand (see Santelices & Doty, 1989, for details).

To be successfully farmed by this planting method, the species of *Gracilaria* should exhibit several agronomically desirable traits, that include quick regeneration, tolerance of both sand abrasion and burial, and resistance to epiphytes. However, it was hitherto unknown whether the farmed taxa exhibit sufficient intra- or inter-specific variation in respect to any of these traits, as to permit selection and propagation of desirable native populations for future farming expansion.

Farming expansion frequently involves transplanting materials to distant places along the extensive Chilean coastline. So far, this has been done with little concern for significant differences in abiotic factors between sites (e.g. irradiance, photoperiod, salinity and temperature) or for the possibility of population differentiation associated with the original habitat. Physiological differentiation in relation to salinity gradients (Jordan & Vadas, 1972), nutrient concentrations (Espinoza & Chapman, 1983), temperature (Johnstone, 1978), photoperiod (Lüning, 1980) and irradiance (Durako & Dawes, 1980; Peckol & Ramus, 1985; Gerard, 1988) is known for several algal species. In a few cases, some of these physiologically different populations have been shown to correspond to physiological ecotypes.

Two major types of habitats are used at present for *Gracilaria* farming in Chile. One is represented by sheltered, sandy bays in northern and central Chile (17° S–38° S). The other is found in estuaries and mud flats in southern Chile (40–50° S). Transplants of *Gracilaria* from one to another type of habitat have not always been successful and species or population differences are suspected.

From the above information we hypothesized that agronomic and ecological differences occurred among four populations of commercial *Gracilaria* found in these two types of habitats. To

test this hypothesis, differences in interspecific and intraspecific sensitivities to sand abrasion, sand burial and epiphyte recruitment, as well as growth effects at various temperature, salinities, irradiances and photoperiods were examined.

Materials and methods

Study site and species

Gracilaria populations occurring in four geographically separated localities were chosen. The sites were Isla Santa Maria in Antofagasta (23° 56' S; 70° 25' W), Changa beach in Coquimbo (29° 56' S; 71° 21' S), San Vicente Bay in Concepción (36° 46' S; 73° 08' W) and Maullín, near Puerto Montt (41° 37' S; 73° 36' W). The first three localities are sheltered sandy bays. The *Gracilaria* beds extend here between 2 and 9 m deep; temperatures range from 10 °C to 20 °C and salinity is relatively constant at 35‰ (Romo *et al.*, 1979; Santelices & Fonck, 1979; Pizarro, 1986). Seasonal or periodical storms modify the bottom relief, enhance sand abrasion, and often remove part of the crop. Maullín represents the estuarine and mudflat systems of southern Chile. The *Gracilaria* beds extend between depths of 1 to 3 m on wave-sheltered, horizontal or slightly inclined plane surfaces, of muddy sand. Salinity and temperatures vary between 18 to 32‰ and 9 to 16 °C respectively (Westermeier *et al.*, 1984).

Commercial *Gracilaria* in Chile is often infertile. Therefore, all experiments were performed without knowing the identity of the plants involved. It was known, however, that the Antofagasta population had been transplanted about 10 years ago from either Talcahuano or Coquimbo (Diaz, 1986). According to fishermen accounts and to statistical data in the Regional Fisheries Offices, the other three stocks existed in the respective places at least for the last 30 years. Morphological and cultural studies done after the experimental work revealed that the Antofagasta, Coquimbo and Talcahuano populations belong to *Gracilaria chilensis* Bird, McLachlan & Oliveira.

The individuals from Maullín correspond to an unidentified *Gracilaria* species, with verrucosa-type male conceptacles.

General experimental conditions

A broad sample (about 2 kg from each of 25 different *Gracilaria* patches) of each experimental population was collected by SCUBA diving and transported to the laboratory in temperature-controlled containers during the night.

In the laboratory, the 50 kg sample of each population was cleaned, weighed and inoculated at stocking densities of 5 kg m^{-2} into 1-m^3 plastic tanks with SWM-3 culture medium. These materials were maintained for the entire study period under constant conditions of temperature (15°C), irradiance ($75 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$), salinity (35‰) and photoperiod (12:12). The growth medium was changed every 6 days and the plants regularly cropped back to the original stocking density every 10 days. All the experiments used these population stocks but the acclimation time under standard growing conditions varied for different experiments. It was 30 days for the first experiment (sand abrasion) to 365 days for the last one (summer irradiance).

Six of the seven experiments were done in environmental cabinets (Forma Scientific, model 24). The experimental temperature was 15°C except when the effects of temperature (10 , 15 and 20°C) were studied. Incident illumination inside the growth chambers was provided by Cool-White, 40-W fluorescent tubes. The experimental irradiance was $75 \mu\text{mol m}^{-2} \text{ s}^{-1}$ except when the effects of irradiance (10 , 50 and $100 \mu\text{mol m}^{-2} \text{ sec}^{-1}$) were being tested. A light : dark cycle of 12:12 was used in all experiments, except when daylength effects (8:16; 12:12; 16:8) were tested. The SWM-3 culture medium was changed every 6 days. Salinity of the culture medium was 35‰, except when the effects of salinity (10 , 20 , 30%) were being tested. Aeration was provided continuously during the hours of light by means of oil-free compressors (Schultz) and pressure was adjusted to keep the water constantly moving.

Sand abrasion

Six 1000 ml beakers, each with 500 ml SWM-3 and 4 previously weighed, 10-cm-long *Gracilaria* thalli, were used for each experimental population. Sterilized, fine sand (70 g) was poured into three of six beakers, and the *Gracilaria* thalli inserted in the sand. Thalli in the other 3 beakers (controls) were attached to glass rods to keep them in a fixed position. All beakers were randomly distributed on shakers rotating at 150 rpm, and incubated for 50 days under the controlled conditions described above.

Sand burial

The basic experimental unit was a $30 \times 30 \times 30$ cm plastic tank with a 20 cm deep layer of fine sand, exposed to ambient light and temperature and receiving a water flow of 25 L min^{-1} . Three previously weighed, 10-cm-long thallus fragments of a given *Gracilaria* population (experimental) were incubated underneath the sand layer while the other three (controls) were placed on top of the sand layer. After 30, 60 and 120 days, 1 experimental and 1 control thallus was recovered from each tank, wet weighed and incubated in an individual deep Petri dish (Pyrex 3250) under the controlled conditions described above. The growth rates exhibited by the thalli during the 7 ensuing days were taken to indicate the recovery capacity of these populations after sand burial. Three replicate tanks were used per population. After 60 days, it was discovered that the *Antofagasta* thalli used as controls were dead, probably due to rough handling during the first weight measurement (after 30 days). This treatment was therefore eliminated from further analysis.

Epiphyte recruitment

The experimental epiphytes used were *Enteromorpha compressa*, *Ulva rigida* and an *Ectocarpus* sp. Four (5 cm long, 1.5 cm diam) fragments of *Gracilaria* were placed inside a deep Petri dish with 250 ml of culture medium. A spore solution of either *Ulva*, *Enteromorpha* or *Ectocarpus* was added to each dish. Three replicate dishes were used per *Gracilaria* population epiphyte. Four

5-cm-long glass rods in a deep petri dish were used as controls. Three replicate control dishes per epiphyte were inoculated and incubated. After 15 days, the number of germlings of epiphytes found along a 2-cm-long transect laid on each experimental thallus, or on the glass controls, were counted under the microscope. Totals per dish were averaged.

Other abiotic factors

Experimental plants from the four populations were grown for 30 days under various treatments to determine the effects of salinity (10, 20 and 30‰), and temperature (10, 15, 20 °C), and the interacting effects of three photoperiods (8:16, 12:12 and 16:8) and three irradiance levels (10, 50, 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Outdoor tank cultivation

The irradiance levels inside the growth chambers are low compared to full sunlight. Effects of irradiance and temperature were tested further using outdoor, 1-m³ fibreglas tanks. Water was supplied by a 3 HP pump and exchanged every 15 days. Aeration was supplied for 30 min during

each hour of sunlight, with one turnover min^{-1} of the 6 kg m^{-2} of *Gracilaria* used as stocking density. The culture medium was seawater enriched with $(\text{NH}_4)_2\text{SO}_4$ and $\text{NaH}_2\text{PO}_4 \times \text{H}_2\text{O}$. The amount of nutrient added was calculated under the assumptions that N was about 5% the dry weight of *Gracilaria*, that the expected growth rate was about 3% daily and that the N:P ratio was 10:1. Variations in the pH (7.0–8.5) of the culture medium were used to determine frequency and duration of CO_2 additions. The biomass produced was cropped every 5 days back to its original weight and each experiment lasted 30 days. The 4 populations were grown simultaneously, using 4 replicate tanks per population, during a summer and a winter month. Average water temperature in the tanks during the summer month (January) was 18 ± 0.6 °C and radiant energy was 480 ± 30 $\text{cal m}^{-2} \text{d}^{-1}$. In winter (August) water temperature decreased to 12 ± 0.4 °C and radiant energy to 175 ± 25 $\text{cal m}^{-2} \text{d}^{-1}$.

In all experiments, growth rate was defined as increments in wet weight per unit of time and was calculated using a compound interest program.

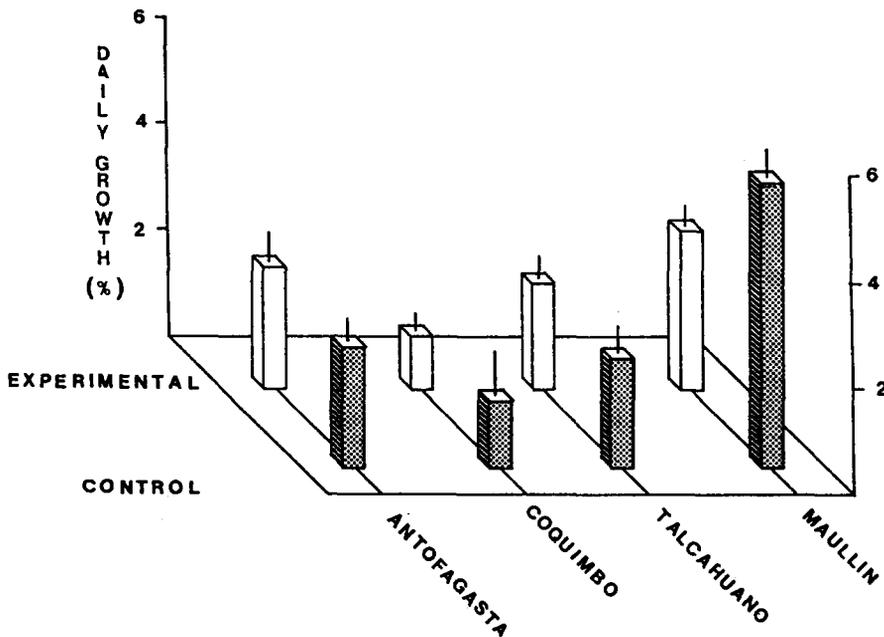


Fig. 1. Growth differences among four populations of *Gracilaria* subjected to sand abrasion under laboratory conditions.

Results are subjected to factorial analysis of variance after arcsine transformation of growth rate values. *A posteriori* tests (Tuckey's w-procedure; Sokal & Rohlf, 1981) are used whenever necessary.

Results

Sand abrasion

The four *Gracilaria* populations survived sand abrasion (Fig. 1) but exhibited significant ($F = 5.82$; $P < 0.05$) interpopulation growth differences. The control and the experimental thalli from Coquimbo grew significantly more slowly while both types of thalli from Maullín grew significantly faster ($P < 0.05$, Tuckey) than any of the other populations. Maullín experimental plants were the only one exhibiting significantly ($P < 0.05$, Tuckey) less growth than controls. Although these plants from Maullín exhibited the fastest growth rates, they also were the most sensitive to sand abrasion.

Sand burial

Thalli of the four *Gracilaria* populations survived sand burial for up to 120 days and exhibited recovery growth that varied according to burial time and population (Fig. 2). Thirty days of burial resulted in significant growth differences between populations (factorial ANOVA, $F = 6.18$, $P < 0.01$), treatments ($F = 8.66$, $P < 0.01$) and interactions between populations and treatments ($F = 8.06$, $P < 0.01$). Compared to their respective controls, the Maullín population exhibited significantly slower recovery growth ($P < 0.05$, Tuckey) than other populations. Comparisons among controls indicate that thalli from Maullín grew significantly faster ($P < 0.05$, Tuckey) than all others. These results, therefore, reproduce those already found with sand abrasion.

Recovery growth after 60 and 120 days indicates significant differences between populations (ANOVA, $F = 18.13$; $P < 0.01$ for 60 days and $F = 4.27$; $P < 0.05$ for 120 days) and treatments ($F = 38.3$; $P < 0.01$ for 60 days and $F = 7.07$; $P < 0.05$ for 120 days) but not for interactions (population \times treatments). Control thalli from

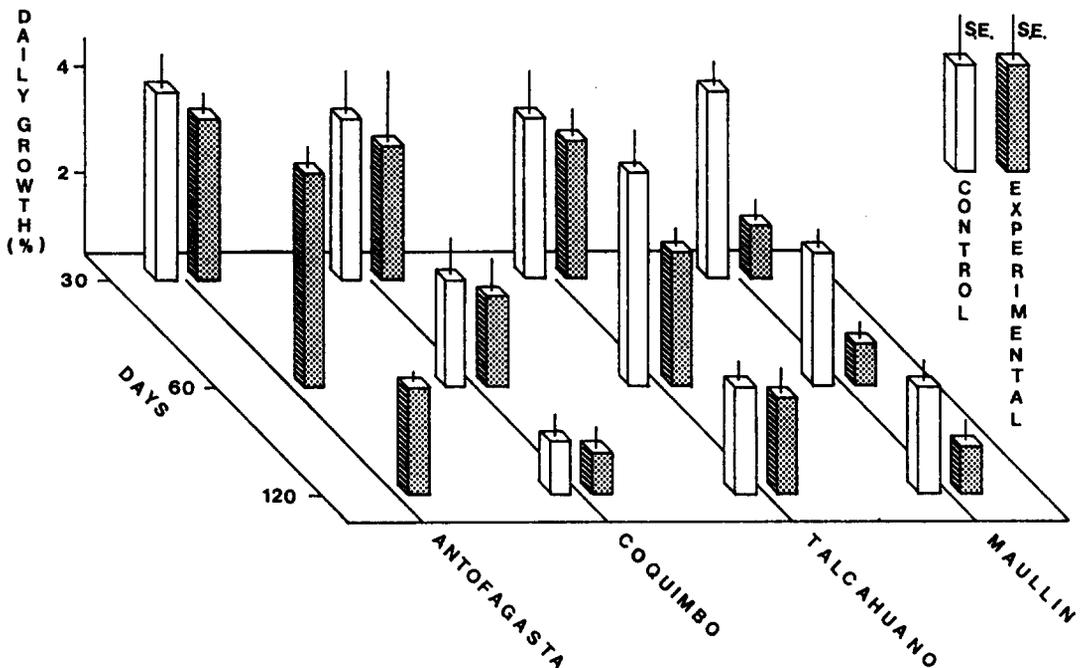


Fig. 2. Recovery growth of thalli from 4 commercial *Gracilaria* populations after being maintained buried in sand for 30, 60 and 120 days.

Maullín grew significantly faster ($P < 0.05$, Tuckey) than thalli buried for 60 and 120 days, a difference not shown by the Coquimbo and Talcahuano populations. Thalli from Coquimbo grew significantly slower ($P < 0.05$, Tuckey) than those from Talcahuano, Antofagasta and than the unburied thalli from Maullín. Buried thalli from Antofagasta grew as fast as the Talcahuano population or control thalli from Maullín and showed no adverse effect due to burial.

Resistance to epiphytes

Experimental results indicate significant differences between populations (ANOVA, $F = 237.9$; $P < 0.001$), between epiphytes ($F = 588.8$; $P < 0.001$) and between interactions (populations \times epiphytes; $F = 24.16$; $P < 0.001$) in regard to epiphyte recruitment (Fig. 3).

The density of *Ectocarpus* sp. on thalli from Antofagasta and Talcahuano is statistically similar to the density on the glass rods used as control, suggesting neither inhibition nor stimulation of this epiphyte recruitment by either of these two *Gracilaria* populations. On the Coquimbo and Maullín thalli, *Ectocarpus* was significantly more abundant ($P < 0.05$, Tuckey) than on the control glass rods, suggesting stimulation of epi-

phytic recruitment. The density of *Ectocarpus* on Coquimbo thalli was significantly higher ($P < 0.05$, Tuckey) than on the thalli from Maullín.

Maullín and Coquimbo populations exhibited significantly ($P < 0.05$, Tuckey) more recruitment of *Enteromorpha* than control glass rods, while the opposite was true for the Talcahuano and Antofagasta populations, suggesting some inhibition effect. No significant differences occurred between the Maullín and Coquimbo populations or between Talcahuano and Antofagasta thalli.

Ulva rigida recruited significantly more intensively ($P < 0.05$, Tuckey) on control glass rods than on thalli of any of the four *Gracilaria* populations, suggesting that all of them have some resistance to *Ulva* epiphytism. No significant differences in *Ulva* recruitment ($P < 0.05$, Tuckey) were found between Coquimbo and Maullín or Antofagasta and Talcahuano thalli. However, the first two populations exhibited significantly higher densities of epiphytic *Ulva* than the last two.

Other abiotic factors

Thalli from the four *Gracilaria* populations grew equally well under all the experimental tempera-

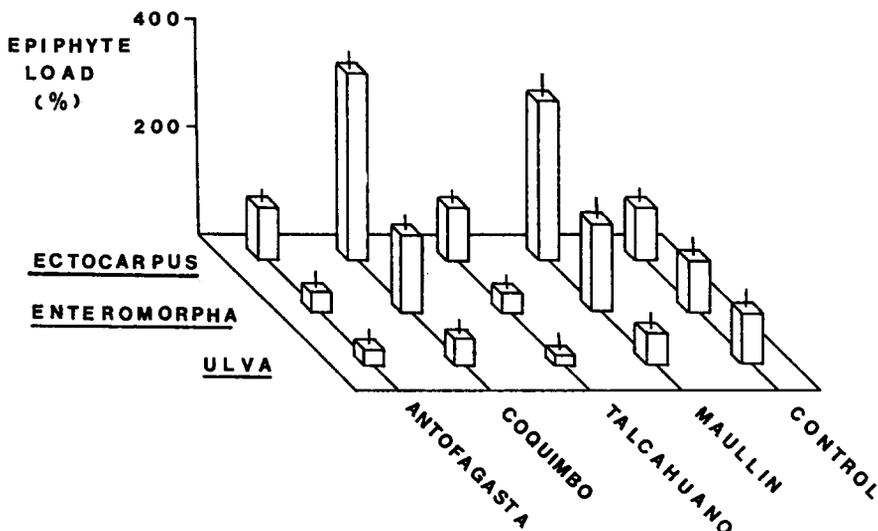


Fig. 3. Recruitment of three species of epiphytes on thalli from 4 commercial *Gracilaria* populations.

tures (Table 1). Results indicate no significant differences either among populations or treatments.

Thalli of the four *Gracilaria* populations could grow in culture media with salinities ranging from 10 to 30‰ (Table 1). Results indicate significant differences among populations ($F = 13.05$, $P < 0.01$) but not among treatments. At all treatments, the Coquimbo population grew significantly more slowly ($P < 0.05$, Tuckey) than the other three populations.

The thalli of the four *Gracilaria* populations grew under the several irradiance-photoperiod combinations (Table 1). However, growth differences were significant only for photoperiods (ANOVA; $F = 16.79$; $P < 0.01$) and for the interactions photoperiod-irradiance ($F = 6.22$; $P < 0.01$) and photoperiod-populations ($F = 4.74$; $P < 0.025$). Growth of thalli from

Antofagasta, Coquimbo and Talcahuano was significantly less ($P < 0.05$, Tuckey) under 8 than 12 h of daily light. Growth under 16 h of light was slightly less but not significantly different than under 12 h. By contrast, the thalli from Maullín grew significantly more under long days ($P < 0.05$, Tuckey) than under 12 or 8 h of light, without exhibiting any significant difference in growth under these last two conditions.

Outdoor tank cultivation

Experimental results indicate significant differences among populations (ANOVA; $F = 19.79$; $P < 0.01$), seasons ($F = 42.3$; $P < 0.01$) and interactions between populations and seasons ($F = 23.4$; $P < 0.01$). During winter the Maullín

Table 1. Effect of various abiotic factors on the daily growth (%) of four populations of commercial *Gracilaria* from Chile.

	<i>Gracilaria chilensis</i>			<i>Gracilaria</i> sp.
	Antofagasta $X \pm S.E.$	Coquimbo $X \pm S.E.$	Talcahuano $X \pm S.E.$	Maullín $X \pm S.E.$
<i>Temperature</i>				
10 °C	1.6 ± 0.10	1.5 ± 0.07	2.0 ± 0.15	1.4 ± 0.10
15 °C	1.5 ± 0.08	1.6 ± 0.10	1.9 ± 0.08	1.7 ± 0.04
20 °C	1.6 ± 0.09	1.4 ± 0.10	2.1 ± 0.10	1.5 ± 0.07
<i>Salinity</i>				
10‰	2.9 ± 0.10	1.3 ± 0.10	2.8 ± 0.15	3.3 ± 0.10
20‰	3.0 ± 0.05	2.3 ± 0.20	3.5 ± 0.20	3.3 ± 0.20
30‰	3.4 ± 0.10	2.0 ± 0.10	3.5 ± 0.15	3.2 ± 0.20
<i>Photoperiod/irradiance</i> ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$)				
8:16/				
10	0.9 ± 0.08	1.1 ± 0.04	0.9 ± 0.05	1.1 ± 0.08
50	1.1 ± 0.10	1.1 ± 0.10	1.1 ± 0.08	1.4 ± 0.09
100	1.3 ± 0.05	1.0 ± 0.18	1.1 ± 0.07	1.2 ± 0.10
12:12/				
10	1.0 ± 0.03	1.2 ± 0.10	1.2 ± 0.10	1.3 ± 0.05
50	1.3 ± 0.05	1.2 ± 0.05	1.3 ± 0.04	1.3 ± 0.05
100	1.3 ± 0.10	1.2 ± 0.08	1.3 ± 0.03	1.4 ± 0.03
16:8/				
10	1.1 ± 0.02	1.0 ± 0.03	1.0 ± 0.10	1.5 ± 0.10
50	1.1 ± 0.05	0.9 ± 0.10	1.2 ± 0.05	1.5 ± 0.04
100	1.2 ± 0.10	1.0 ± 0.04	1.1 ± 0.08	1.3 ± 0.05

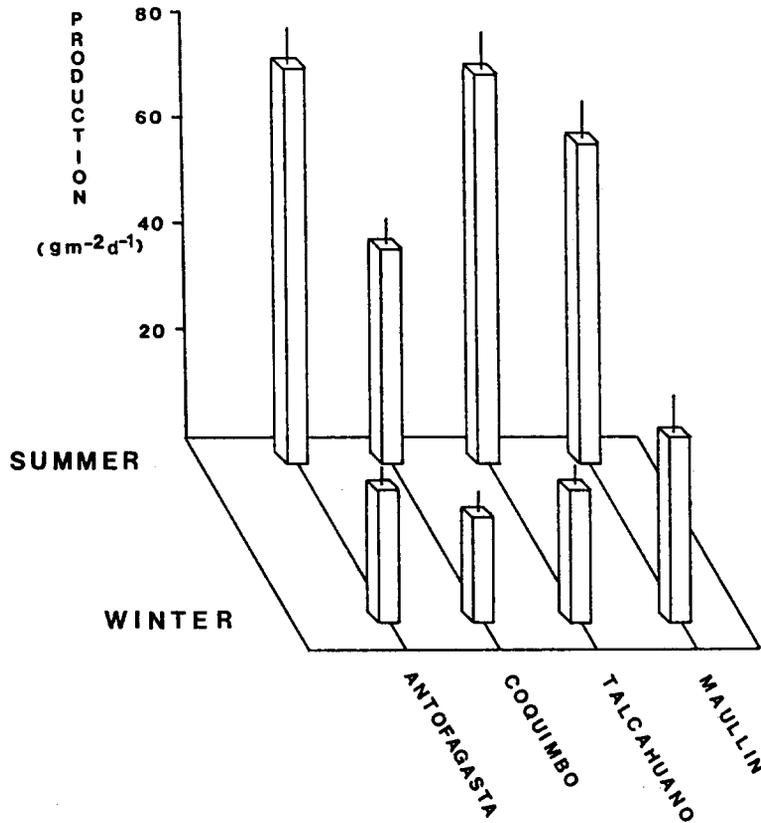


Fig. 4. Production of 4 commercial populations of *Gracilaria* in outdoor tanks under summer and winter conditions.

population produced significantly more biomass ($P < 0.05$, Tuckey) than the other three populations (Fig. 4). During summer however, Talcahuano and Antofagasta populations produced significantly more ($P < 0.05$, Tuckey) than the Maullín population and, in turn, this later produced more ($P < 0.05$, Tuckey) than the Coquimbo population. Since the temperature experiment (Table 1) showed but small interpopulation differences within the range of 10–20 °C, these seasonal differences are most likely to be produced by seasonal irradiance changes.

Discussion

Results suggest specific as well as population differentiation between the four commercial *Gracilaria* beds studied in Chile. Growth effects of sand burial, sand abrasion and photoperiod are

similar among the three populations of *G. chilensis* and different from the Maullín population of *Gracilaria* sp. It is known that some species of Rhodophyta (e.g. *Gymnogongrus*, Markham & Newroth, 1973; Santelices *et al.*, 1989) and the crustose phase of some Rhodophyta and Phaeophyta (e.g. *Scytosiphon*, Littler & Littler, 1983) can survive sand scouring and burial. It is also known that thallus fragments of *Gracilaria* can survive sand burial (Santelices *et al.*, 1984). However, experimental testing of this character according to species had not been undertaken. The different responses are also related to habitat differences. The bottom of sandy bays along northern and central Chile is much less stable than in sheltered estuaries and mud flats of southern Chile. Given the farming methods presently in use in Chile, the different specific responses to sand abrasion and burial are of significant economic importance.

Growth responses to irradiance varied according to species and population. Under winter irradiances, *Gracilaria* sp. from Maullín grew faster than any of the three *G. chilensis* populations. Under the intense summer sun, the Antofagasta and Talcahuano populations of *G. chilensis* were more productive than the Maullín population. These differences also are related to differences in light regimes between southern and central Chile and also could be understood as specific adaptations to original habitats. However, the low growth rates exhibited by the Coquimbo population under all experimental conditions is not well understood. Differences in agar production are not included in this study and perhaps the Coquimbo population produces higher yields or better quality agars, as often these gel characteristics are inversely related to growth.

Sensitivity to epiphytes was variable among the four populations. Thalli from Talcahuano and Antofagasta inhibited recruitment of some epiphytes, while those from Coquimbo and Maullín showed a reduced capacity to do so. That some seaweed species exert allelopathic effects on the recruitment of its epibiota has been known since the pioneer studies by Conover & Sieburth (1966). However, such effects as well as the important population variations found in this study have not been reported previously for species of *Gracilaria*. Epiphytes are a common problem to several types of *Gracilaria* farms (see Santelices & Doty, 1989 for review). Finding strains that inhibit epiphyte recruitment constitutes another approach to the yet unsolved problem of epiphyte control.

Since no work was performed with the offspring of the three populations of *Gracilaria chilensis*, it is unknown if the above experimental results are indicative of ecotypic (genetic) differentiation (Chapman, 1986). However, these differences persisted after extended acclimation and through vegetative propagation, the most widely used farming technique at present in Chile. Furthermore, there is a remarkable similarity in ecological responses between the Antofagasta and Talcahuano populations. As mentioned, the Antofagasta population was planted about

10 years ago, and the similarities of responses found suggest Talcahuano rather than Coquimbo as its possible origin. If this is so, ecological responses might have persisted unchanged in transplanted materials for about 10 years.

The combination of results reported above suggest that different population stocks should be used for farming *Gracilaria* on different types of soft-bottom habitats along Chile. The fast growth rates exhibited under low light intensities and long photoperiods suggests *Gracilaria* sp. from Maullín as the most suited for future farm expansion onto mud flats and into estuaries in southern Chile. Even though this species grows rapidly in winter, its higher sensitivity to summer irradiances, sand abrasion and burial makes it less suited than the Talcahuano or the Antofagasta populations for more northern sites where farming is in sandy bays, where water movement is more intense, where the bottom relief changes more significantly throughout the year and irradiances are higher.

Acknowledgements

We are grateful to I.A. Abbott and M.S. Doty for reading and commenting on the manuscript. This research was supported by CORFO-Chile; our gratitude to A. Kalergis and A. Sanhueza for many contributions towards the completion of this study. The paper was written while the senior author was a Guggenheim Fellow and a Visiting Professor at the Department of Botany of the University of Hawaii. The International Foundation for Sciences and Fundación Andes contributed additional funds and Pontificia Universidad Católica de Chile granted sabbatical and study leave. He is grateful to all these Institutions for their support.

References

- Chapman ARO (1986) Population and community ecology of seaweeds. In: Blaxter JHS, Southward AJ (eds), *Advances in Marine Biology*, Vol. 23. Academic Press, London, 1-161.

- Conover JT, Sieburth JMcN (1966) The effects of tannins excreted from Phaeophyta on planktonic animals surviving in tide pools. *Proc. Int. Seaweed Symp.* 5: 99–100.
- Díaz M (1986) Cultivo y explotación de *Gracilaria* en la II Región, Chile. Un análisis crítico. En K. Alveal (ed.), *Memorias Seminario Taller Manejo y Cultivo de Gracilaria en Chile*. pp. 71–101 (no indication of publisher).
- Durako MJ, Dawes CJ (1980) A comparative seasonal study of two populations of *Hypnea musciformis* from the east and west coast of Florida, U.S.A. I. Growth and Chemistry. *Mar. Biol.* 59: 151–156.
- Espinoza J, Chapman ARO (1983) Ecotypic differentiation of *Laminaria longicuris* in relation of seawater nitrate concentration. *Mar. Biol.* 74: 213–218.
- Gerard VA (1988) Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Mar. Biol.* 97: 25–36.
- Johnstone IM (1978) Phenotypic plasticity in *Draparnaldia* (Chaetophoraceae). II. Physical environment and conclusions. *Am. J. Bot.* 65: 608–614.
- Jordan AJ, Vadas RL (1972) Influence of environmental parameters on intraspecific variation in *Fucus vesiculosus*. *Mar. Biol.* 14: 248–252.
- Littler MM, Littler DL (1983) Heteromorphic life history strategies in the brown algae *Scytosiphon lomentaria* (Lyngb.) Link. *J. Phycol.* 19: 425–431.
- Lünning K (1980) Control of algal life-history by day-length and temperature. *Syst. Assoc. spec.* vol. 17(6): 915–945.
- Markham JW, Newroth PR (1973) Observations on the ecology of *Gymnogongrus linearis* and related species. *Proc. Int. Seaweed Symp.* 7: 127–130.
- Peckol P, Ramus J (1985) Physiological differentiation of North Carolina nearshore and offshore populations of *Sargassum filipendula* C. Ag. *Bot. Mar.* 28: 319–325.
- Pizarro A (1986) Conocimiento actual y avances recientes sobre el manejo y cultivo de *Gracilaria* en Chile. *Monografías Biológicas* 4: 63–96.
- Pizarro A, Barrales H (1986) Field assessment of two methods for planting the agar-containing seaweed, *Gracilaria*, in northern Chile. *Aquaculture* 59: 31–43.
- Ponce F (1987) Evaluación del desarrollo de las actividades pesqueras para cultivo de *Gracilaria*. En Libro de Programas y Resúmenes, I Congreso Latinoamericano de Ficología Marina y III Symposium sobre algas marinas chilenas. Universidad de Concepción, Chile, pp. 74.
- Romo H, Alveal K, Delarrosa V (1979) Biología de *Gracilaria verrucosa* (Hudson) Papenfuss en Chile central. In: Santelices B (ed.), *Actas del Primer Symposium sobre Algas Marinas Chilenas*. Subsecretaría de Pesca, Ministerio de Economía, Fomento y Reconstrucción, Santiago, Chile, pp. 155–163.
- Santelices B, Camus P, Hoffmann AJ (1989) Ecological studies for harvesting and culturing *Gymnogongrus furcellatus* (Rhodophyta, Gigartinales) in central Chile. *J. appl. Phycol.* 1: 171–181.
- Santelices B, Doty MS (1989) A review of *Gracilaria* farming. *Aquaculture* 78: 95–133.
- Santelices B, Fonck E (1979) Ecología y cultivo de *Gracilaria lemaneiformis* en Chile central. In: Santelices B (ed.), *Actas del Primer Symposium sobre Algas Marinas Chilenas*. Subsecretaría de Pesca, Ministerio de Economía, Fomento y Reconstrucción, Santiago, Chile, pp. 165–200.
- Santelices B, Ugarte R (1987) Production of Chilean *Gracilaria*: problems and perspectives. *Hydrobiologia* 151/152: 295–299.
- Santelices B, Vasquez J, Ohme U, Fonck E (1984) Managing wild crops of *Gracilaria* in central Chile. *Hydrobiologia* 116/117: 77–89.
- SERNAP (1988) Anuario estadístico de pesca. Ministerio de Economía, Fomento y Reconstrucción. Servicio Nacional de Pesca, Santiago, Chile.
- Sokal RR, Rohlf J (1981) *Biometry*. Freeman Press, San Francisco, 776 pp.
- Westermeier R, Steubing L, Rivera PJ, Wenzel H (1984) *Gracilaria verrucosa* (Hudson) Papenfuss en X Región (Maullín y Quenuir. Prov. de Llanquihue). Chile. *Mem. Asoc. Latinoam. Acuicult.* 5: 419–430.