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Correlation between *Gracilaria parvispora* (Rhodophyta) biomass production and water quality factors on a tropical reef in Hawaii

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Abstract

The factors controlling the growth of the edible, red seaweed, *Gracilaria parvispora* Abbott (long ogo), on the south reef of Molokai, HI, were investigated to determine where productive new plantings could be located. Experiments were conducted in October, 1997, and March and June, 1998, in which *G. parvispora* biomass production was correlated with water quality factors measured at six sites over each 21-day experiment. Water motion, temperature, salinity, nitrate and phosphate varied among sites and experiments, but were not significantly ($P > 0.05$) correlated with growth. A strong correlation, however, was found between biomass production and ammonia concentration ($r = 0.91$, $P < 0.001$). Ammonia levels ranged from 0.2–4.0 mmol m^{-3} over sites and experiments but were skewed towards low values, as was biomass production. The transient nature of ammonia distribution on this reef explains the patchy distribution of locations at which *G. parvispora* is productive, noticed in previous experiments. Large-scale *Gracilaria* culture on such a reef would require adding an external source of fertilizer, which may disrupt the reef ecology. An alternative is to develop a dispersed form of cultivation at sites that receive ammonia enrichment from the land, in which case the crop can help absorb excess nutrients entering the reef. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: *Gracilaria*; Coral reef ecology; Nutrient limitation; Ammonia; Growth

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1. Introduction

Gracilaria species are widely exploited as fresh seafoods and sources of agar. Land-based aquaculture methods using tanks or ponds have been developed (Hanisak, 1987), but most of the commercial crop comes from the harvest of wild or planted beds in natural water bodies (Santelices and Doty, 1989). Although much is known about the growth requirements of *Gracilaria* in artificial cultures (e.g., Friedlander and Dawes, 1985; Hanisak, 1987; Dawes and Koch, 1990; Friedlander, 1991), relatively little is known of the factors controlling productivity in natural settings (Santelices and Doty, 1989). *Gracilaria* often grows well only at specific sites within a harvest region and, in these cases, attempts to extend the growing areas may be unsuccessful (Doty et al., 1986; Glenn et al., 1998). The factors controlling the growth of fleshy seaweeds on tropical reefs in general are in dispute, and may be species-specific or habitat-specific (e.g., Larned, 1998).

We previously developed a culture system for *G. parvispora* at Molokai, HI, in which spore-coated rocks are produced in a hatchery operated by a central cooperative (Glenn et al., 1996). The rocks are distributed to local growers who establish patches of *G. parvispora* on Molokai's extensive south reef (Glenn et al., 1998). The growers periodically harvest seaweed from their patches for sale back to the cooperative, which multiplies the harvest in floating cages in a pond and markets the product.

One of the roadblocks to expanding production and community participation has been our inability to predict where on the reef productive patches can be established (Glenn et al., 1998). The south reef of Molokai presents nearly 100 km of apparently similar nearshore conditions along the coast (Glenn and Pfund, 1992), yet only about 10–15% of the sites that have been inoculated with spore-coated rocks have developed harvestable crops. To better understand the factors controlling productivity, we established test sites along a short stretch of coastline and correlated *G. parvispora* biomass production with physical and chemical water quality factors measured at different times of year.

2. Materials and methods

2.1. Source of plant material and selection of test sites

Smooth, flat river rocks (5–10 cm diameter) were inoculated with *G. parvispora* spores in 1995–1996 and placed in Puko'o Pond for growout (Glenn et al., 1996). Three growth experiments were conducted: in October, 1997, March, 1998 and June, 1998. For each experiment, *Gracilaria*-bearing rocks were selected from the pond, trimmed so that the thalli were 2.5 cm in length, and placed at 6 locations on the reef for regrowth. Twenty rocks per site were used in Experiment 1 and 10 rocks per site were used in Experiments 2 and 3. Rocks were placed near each other on the reef bottom and the locations were marked so the rocks could be relocated. The sites were approximately

0.5 km apart along a relatively short stretch of coastline, 21–25 km east of Kaunakakai, from which commercial quantities of *G. parvispora* have been harvested since 1996 (Glenn et al., 1998). The land adjacent to the reef is used for rural and residential purposes. All sites were within 50 m of shore and in water less than 50 cm deep at low tide. The reef bottom was silty at all sites due to runoff from the land. The 6 sites were not chosen randomly, but were locations from which local growers had harvested *G. parvispora* in the past.

2.2. Biomass and water quality measurements

The thalli were allowed to regrow on the rocks for 21 days, then they were trimmed back to 2.5 cm and the wet weight of the new growth was determined (moisture content is approximately 82%). The growth period represents the approximate interval at which rocks can be trimmed for partial harvest when growth is rapid. Samples for water quality determination were taken at 7 day intervals on the same day at each site during the experiment (3 sample dates per experiment). Duplicate water samples for inorganic nutrient analyses were collected in acid-washed, plastic bottles after first rinsing the bottles with site water. Samples were kept frozen until they were analyzed at the Analytical Services Laboratory, University of Hawaii, Honolulu, within 30 days of collection. Temperature was measured with a hand-held thermometer and salinity was measured by refractometer. Water motion was measured by the weight loss from duplicate plaster standards (clod cards) placed at each site for 24 h; weight loss was converted to water velocity (cm s^{-1}) based on calibration equations derived by placing clod cards on a rotating arm in a tank of seawater in a greenhouse (Thompson and Glenn, 1994).

2.3. Analytical methods

Inorganic nutrients were analyzed on a 4-channel, Technicon AA-II continuous flow autoanalyzer system at the University of Hawaii SOEST Analytical Services Laboratory (Honolulu, HI) which specializes in seawater analyses. The analytical techniques followed standard Technicon methods for inorganic nutrients (Technicon, 1977). Soluble reactive phosphorous was determined by the ascorbic acid reduction method. Nitrate (and nitrite, which is included but is minimal) was analyzed by the copperized cadmium reduction and azo dye method. Ammonium (also referred to as ammonia) was determined by the hypochlorite-nitroprusside procedure. Distilled and deionized (Barnstead ultrapure mixed bed column) water was used for the sampler wash, baseline 0, and all reagent and nutrient standard dilutions. Detection limits were lower than 0.02 mmol m^{-3} for phosphate and 0.03 mmol m^{-3} for nitrate and ammonium. Quality control samples for each analysis included low-nutrient, open-ocean water (nutrients below detection limits); standards made up in open-ocean seawater with the addition of 1, 5 and 5 mmol m^{-3} of phosphate, nitrate and ammonia, respectively; and a composite standard containing all three constituents to check for interference.

2.4. Statistical analyses

We conducted a correlation analysis, in which mean biomass production at each site was correlated with the mean value of each water quality factor measured at each site over each experiment ($n = 18$)(Glenn and Doty, 1990, 1992). We also determined correlation coefficients among the water quality factors across experiments and sites and conducted a multiple correlation analysis to determine the best set of water quality factors to predict biomass production (Glenn et al., 1990). Statistical analyses were conducted with Systat statistical software.

3. Results

3.1. Growth and water quality among sites and experiments

Biomass production varied widely among sites and experiments (Table 1). The highest production was 26 g per rock at Site 1, during Experiment 1; these thalli reached a length of approximately 30 cm by the end of the experiment. This is the length at which plants are normally cut back for harvest. Site 1 is one of the main harvest sites for seaweed on the reef. Although this site had the highest productivity overall, there was considerable variability over the three sampling periods. Sites 2 and 3 had moderate, but more consistent, overall productivity. On the other hand, there was no net growth of test thalli at Site 6 during any of the experiments, even though growers also occasionally bring in *G. parvispora* from this location. Overgrowth of *G. parvispora* by epiphytes or other fouling organisms was not a problem at any of the sites in this study, perhaps due to the relatively short duration of the experiments.

Water quality factors also differed among sites and experiments (Table 1). Water temperature ranged narrowly from 24–28°, with the highest temperatures recorded in the June experiment (mean = 26.5°C) and the lowest (mean = 24.6°C) in the October experiment. Temperature variability among sites was low, as these locations are all washed by water from the open reef. Water motion was moderate, ranging from 7–12 cm s^{-1} among sites, while salinity ranged from 25–32 ppt. Open ocean water is 32 ppt but these near-shore sites were diluted by land runoff and artesian springs. Both ammonia and nitrate concentrations tended to be low, with nitrate (mean = 0.81 mmol m^{-3}, s.d. = 0.50) lower than ammonia (mean = 1.04 mmol m^{-3}, s.d. = 0.91) across sites and sample dates. The mean phosphate concentration was 0.45 mmol m^{-3} (s.d. = 0.18), for a mean N:P ratio of 5.8:1.

3.2. Correlation analyses

Biomass production was strongly correlated with ammonia ($r = 0.91$, $P < 0.001$) but was not significantly ($P > 0.05$) correlated with any other water quality factor (Table 2). In general, the individual sites and water quality factors appeared to vary independently of each other; the highest correlation ($r = 0.66$, $P < 0.01$) being between nitrate and ammonia. When all water quality factors were combined in a multiple correlation

Table 1
Means (top number) and standard errors (bottom number) of *Gracilaria parvispora* biomass production and water quality factors measured at 6 sites over 3 experiments conducted in October, 1997 and March and June, 1998, on the south reef of Molokai, HI

	Biomass (g)	Salinity (ppt)	Water Motion (cm s^{-1})	Temperature (°C)	NO$_3^{-2}$ mmol m^3	NH$_4^+$ mmol m^3	PO$_4^{-2}$ mmol m^3
October							
Site 1	25.87	31.8	10.1	24.5	1.42	4.04	0.40
	7.86	0.2	2.1	0.8	0.66	2.15	0.09
Site 2	8.44	32.0	11.6	24.8	1.31	1.96	0.26
	1.78	0.6	1.1	1.2	0.44	0.58	0.02
Site 3	3.10	30.8	10.2	24.9	1.05	1.40	0.51
	1.27	0.6	1.5	1.1	0.26	0.34	0.17
Site 4	2.88	31.8	11.4	24.3	0.97	1.22	0.21
	0.97	0.8	1.7	1.1	0.38	0.32	0.02
Site 5	1.38	31.3	12.1	24.4	1.31	1.35	0.37
	0.35	0.5	2.6	1.0	1.02	0.92	0.09
Site 6	0.01	28.8	9.8	24.7	1.20	0.52	0.34
	0.01	0.5	1.3	1.2	0.54	0.18	0.09
March							
Site 1	0.68	31.3	9.0	25.0	0.04	0.22	0.41
	0.40	0.5	1.0	1.7	0.01	0.02	0.03
Site 2	6.60	31.0	9.8	26.0	0.56	0.83	0.43
	4.24	0.4	1.2	2.0	0.28	0.32	0.05
Site 3	0.50	29.8	7.5	25.0	0.19	0.40	0.33
	0.18	0.3	1.0	1.7	0.05	0.08	0.05
Site 4	9.09	30.3	9.7	27.1	1.56	1.76	0.72
	4.88	0.3	1.0	1.7	0.05	0.58	0.05
Site 5	1.60	29.5	12.2	24.8	0.52	0.20	0.38
	0.61	0.5	1.9	1.8	0.07	0.02	0.02
Site 6	0.00	28.0	7.2	25.8	1.29	0.85	0.76
	0.00	0.7	1.8	1.3	0.26	0.12	0.04
June							
Site 1	0.00	30.8	7.7	28.3	0.25	0.90	0.59
	0.00	0.5	2.6	1.5	0.05	0.23	0.08
Site 2	3.91	28.8	9.9	25.3	0.32	0.52	0.38
	1.37	0.5	0.9	0.5	0.06	0.18	0.21
Site 3	1.08	27.0	6.6	26.0	0.42	0.56	0.43
	0.99	0.7	1.1	0.7	0.09	0.14	0.06
Site 4	0.84	29.8	9.5	26.0	0.51	0.62	0.42
	0.45	0.3	0.5	0.7	0.24	0.14	0.22
Site 5	0.42	29.5	12.4	26.8	0.43	0.29	0.31
	0.32	1.0	1.0	0.5	0.06	0.11	0.05
Site 6	0.00	25.0	8.7	26.8	1.34	1.06	0.88
	0.00	1.7	0.6	0.3	0.66	0.18	0.08

analysis to predict biomass production, ammonia was the only factor whose partial correlation coefficient was significantly ($P < 0.05$) correlated with biomass.

Table 2
Correlation matrix of *Gracilaria parvispora* biomass production and water quality factors measured at 6 sites over 3 experiments on the south reef of Molokai, HI

	Biomass	Salinity	Water motion	Temperature	NO_3^{-2}	NH_4^+	PO_4^{-2}	Site
Biomass	1.00	0.43ns	−0.23ns	0.12ns	0.43ns	0.91***	−0.10ns	−0.46ns
Salinity		1.00	0.47*	−0.35ns	−0.00ns	0.39ns	−0.61*	−0.55*
Water Motion			1.00	−0.39ns	0.24ns	0.15ns	−0.46*	0.16ns
Temperature				1.00	−0.18ns	−0.20ns	0.63**	−0.10ns
NO_3^{-2}					1.00	0.66**	0.17ns	0.35ns
NH_4^+						1.00	−0.30ns	−0.31ns
PO_4^{-2}							1.00	0.28ns
Site								1.00

Significance level is indicated as $P < 0.001$ (***), $P < 0.01$ (**), $P < 0.05$ (*) or not significant (ns).

3.3. Quantitative relationship between biomass production and ammonia

A scatter-plot of biomass production versus ammonia shows that most of the data points were concentrated near the low ends of the graph axes (Fig. 1), as both biomass production and ammonia were low over most sites throughout the study. Note that the y-intercept was negative, indicating that a threshold level of ammonia (above 0.44 mmol m^{-3}) is needed to produce a positive biomass response. The strength of the relationship between biomass production and levels of ammonia in the surrounding water is striking.

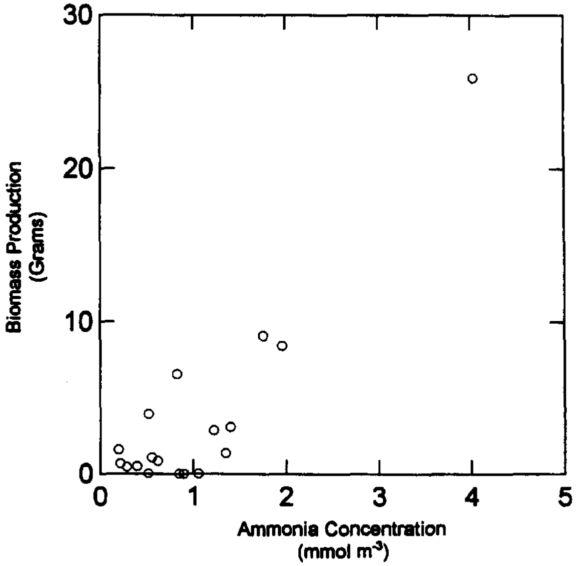

Fig. 1. Scatter-plot of *Gracilaria parvispora* biomass production versus ammonia concentration measured at 6 sites over 3 experiments on the south reef of Molokai, Hawaii. The equation of best fit was: $y = 6.22x - 2.77$ ($r^2 = 0.83$, $P < 0.001$), where y is grams of biomass over 21 days and x is mmol m^{-3} of ammonia.

However, it should be noted that the high mean productivity found at the highest ammonia level (Table 1, data for Site 1 in the March experiment) has a large leverage in the correlation analysis. When this outlying data point is excluded from the correlation analysis, the relationship between biomass production and ammonia is still significant ($r = 0.67$, $P < 0.01$).

4. Discussion

The temperature, water motion and salinity conditions on Molokai's south reef are similar to those measured on other shallow reefs exposed to the trade winds in Hawaii (Doty et al., 1986; Glenn and Doty, 1990, 1992; Glenn et al., 1990). The salinity at most sites was diluted by approximately 10% and N and P levels were higher than open-ocean values, presumably due to runoff from the land. However, in general, this reef could be described as oligotrophic. The main finding was that biomass production by *G. parvispora* was strongly correlated with ammonia in the range of 0.2–4.0 mmol m^{-3} on this reef.

Thalli of *Gracilaria* have been shown to be capable of rapidly exploiting ammonium in the environment by diffusive and active uptake (D'Elia and DeBoer, 1978). Uptake is followed by storage of the nitrogen to facilitate growth later, under nutrient-poor conditions (Ryther et al., 1981). Thalli of *Gracilaria* that are exposed to elevated ammonium levels of 10 mmol m^{-3} respond with an immediate increase in photosynthesis (Nelson, 1985). The remarkable ability of *Gracilaria* to scavenge and store nitrogen allows them to be pulse-fertilized in culture (e.g., Hanisak, 1987), thereby reducing the growth of epiphytes. Ammonia is present on tropical reefs mainly as a transient species that is quickly taken up by algae or oxidized to nitrite and nitrate by bacteria.

We have not been able to develop an artificial culture system for *G. parvispora* so we cannot compare the field results with ammonia enrichment experiments for this species. However, enrichment experiments have been conducted with *G. foliifera* (DeBoer et al., 1978), which responded positively to ammonia enrichment up to 5 mmol m^{-3}, overlapping the range of ammonia concentration to which *G. parvispora* responded on the reef. Similarly, *G. salicornia* responded positively to the addition of 6 mmol m^{-3} ammonia to unenriched seawater in Kaneohe Bay, HI (Larned, 1998). Experiments comparing the effectiveness of nitrate versus ammonia enrichment have produced variable results, depending on culture conditions. In most cases, however, *Gracilaria* spp. respond more strongly to ammonia than nitrate (DeBoer et al., 1978; Hanisak, 1983, 1987), consistent with our finding that ammonia rather than nitrate was correlated with growth on the reef.

Unpolluted reef water in Hawaii generally contains less than 0.5 mmol m^{-3} dissolved inorganic nitrogen (Larned, 1998) but anthropogenic sources can increase the base level. Land use practices on Molokai that may add substantial amounts of ammonia to the reef include: shoreline sewage treatment facilities (e.g., from an apartment complex at Site 1); cattle pasturage adjacent to the shoreline (at Site 2); silt runoff (at all six sites); and discharge from shrimp farms (sites not included in this study). Other, non-point-sources, include input from runoff from roads, houses and farms along the coast. Such ammonia sources are likely to be localized in nature, and this may explain, at least in part, the patchy distribution of sites at which *Gracilaria* grows well on this reef. Developing large-scale *Gracilaria* production across such a reef would require fertilizing the crop with an external source of ammonia, which may not be compatible with preserving the oligotropic nature of the reef ecosystem. On the other hand, concentrating *Gracilaria* production near points where ammonia already enters the reef may help to improve the local water quality as well as provide an income to local residents. Hence, we are developing a dispersed form of *Gracilaria* production utilizing hot-spots of ammonia concentration on Molokai's south shore. Such sites can develop dense stands of *Gracilaria* that are relatively uncomtaminated by epiphytes and can be repeatedly harvested (Glenn et al., 1998).

These results contribute to our understanding of the factors controlling algal productivity in tropical coastal regions, which have seen shifts from coral to algal domination due to nutrient enrichment from human activities (Richmond, 1993). Similar to our findings, most other studies have concluded that nitrogen is generally the limiting nutrient for algae growth in the marine environment (e.g., Birch et al., 1981; Fong et al., 1993). However, phosphorous has also been proposed to be limiting for the growth of fleshy seaweeds on oligotrophic tropical reefs (Littler et al., 1991; Lapointe et al., 1993). A direct test of nitrogen versus phosphorous limitation was conducted on *Gracilaria* and eight other fleshy seaweeds at Kaneohe Bay, HI, using enrichment experiments and measurements of nutrients in sediments and the water column on the reef (Larned, 1998). Eight of the nine species (including *Gracilaria*) were stimulated by ammonia, whereas phosphorous only stimulated one alga (*Codium edule*).

Rather than concluding that a single nutrient is limiting for algal growth, the site fertility hypothesis emphasizes that productivity is determined by the biological potential of a species and abiotic factors (light, water motion and nutrients) influencing growth in interacting and compensatory ways (Doty et al., 1986). For example, a species adapted to a low water motion habitat on the inshore portion of the reef might derive most of its nutrients from the sediments; while a species adapted to a wave-exposed habitat such as the reef edge might absorb most of its nutrients from the water column by generating high nutrient-advection rates driven by water motion (Larned, 1998). Our findings support this hypothesis, in that *G. parvispora*, a species of the inner reef, responded to ammonia but not water motion in this and a previous study (Glenn et al., 1998); whereas we found that Eucheumatoid red seaweeds, which grow on the reef edge, responded to water motion but not nutrients in Kaneohe Bay (Glenn et al., 1990, Glenn and Doty, 1992). On the other hand, algal productivity on a Waikiki, HI reef dominated by the brown seaweed, *Sargassum*, was controlled by temperature rather than nutrients or water motion (Glenn et al., 1990). Thus, the factors limiting algal growth are species and habitat specific for seaweeds on tropical reefs (Larned, 1998).

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