Environmental tolerances in culture and agar content of *Gracilaria verrucosa* (Hudson) Papenfuss (Rhodophyta, Gigartinales) from Saldanha Bay

H.R. Engledow and J.J. Bolton*

Department of Botany, University of Cape Town, Rondebosch, 7700 Republic of South Africa

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Culture studies have been carried out on a local population of the agar-producing red seaweed *Gracilaria verrucosa* to ascertain the optimum range of environmental factors for growth, with a view to potential mariculture. The plants grew well at 15 – 25°C, poorly at cooler temperatures, and did not survive 30°C. Despite little salinity variation in the natural habitat, the population was shown to be euryhaline, with reasonable growth from 9 to 45‰ salinity, although plants grew maximally around the salinity of full seawater. An irradiance of 80 μmol m^{-2} s^{-1} was sufficient for maximal growth, and growth was not severely reduced at 850 μmol m^{-2} s^{-1} (the highest experimental irradiance). Agar content was 32 – 34% of the dry weight, and this level was not significantly affected by 4 weeks' growth at various temperatures.

Kultuurstudies is uitgevoer op 'n inheemse populasie van die agar-produserende rooi seewier *Gracilaria verrucosa* om die optimale bereik te bepaal van omgewingsfaktore wat die groei beïnvloed, met die oog op moontlike marikultuur. Plante groei goed tussen 15 en 25°C, swak by laer temperature, en hulle oorleef nie 30°C nie. Ondanks min skommelinge in die soutgehalte van die natuurlike omgewing, blyk die populasie eurihalien te wees, met 'n redelike groei tussen 9 en 45‰ soutgehalte, alhoewel plante maksimaal gegroei het by 'n soutgehalte rondom dié van normale seewater. 'n Beligting van 80 μmol m^{-2} s^{-1} is voldoende om optimale groei te bewerkstellig, terwyl groei nie ernstig afgeneem het by 250 μmol m^{-2} s^{-1} (die hoogste eksperimenteel toegepaste beligting) nie. Die agargehalte bedra 32 – 34% van die droë gewig, en hierdie waarde is nie beduidend beïnvloed deur vier weke se groei by verskillende temperature nie.

*To whom correspondence should be addressed.

Introduction

The terete, filamentous red seaweed *Gracilaria verrucosa* (Hudson) Papenfuss [formerly *Gracilaria confervoides* (L.) Grev.] has been collected, dried and exported from populations in Saldanha Bay for the production of agar since soon after the Second World War (Anderson *et al.* 1989). The seaweed has not been harvested, but is gathered on the shore as wash-ups from subtidal beds. Peak exports were almost 2000 dry tons in 1967, although a large drop in the yield occurred in the mid 1970's 'ostensibly as a result of dredging and the construction of a large ore-loading jetty' (Anderson *et al., op. cit.*). This was followed by a steady increase to a peak of 372.5 dry tons in 1988 (Rotmann 1990), following which the yield crashed again to very low current levels. Herbivory by fish and invertebrates may be implicated in this reduction (Anderson *et al.* 1990). There is also a considerable industry based on *Gracilaria* in Lüderitzbucht in Namibia (Rotmann 1987; Molloy 1990).

In many parts of the world where *G. verrucosa* and other terete species of the genus are economically important, increases in the yield of the seaweed have been accomplished by a variety of methods, including supplementing natural stocks by various planting methods, and tank or fishpond cultivation (these are reviewed in Santelices & Doty 1989). When any attempt is made to farm natural stocks or begin mariculture of a seaweed, it is obviously a benefit to know the environmental tolerances of the organism to be used. A number of local companies are currently showing interest in the cultivation of *G. verrucosa* for agar, or as a possible feed for the more lucrative culture of abalone (*Haliotis* spp.), and pilot mariculture studies are being carried out both in Saldanha Bay and Lüderitz, Namibia (R.J. Anderson, C. Dawes, pers. commun.). Although care must be exercised in extrapolating laboratory results to field tolerances, this investigation presents the first published data on environmental tolerances in culture of local *G. verrucosa*, and comparisons are made with literature on populations of the species from other parts of the world.

A number of articles have been written on the use of local *Gracilaria* as an agarophyte, and on aspects of the industry (reviewed by Anderson *et al.* 1989, p.286). Despite the fact that *G. verrucosa* is one of our most important economic seaweeds, these authors state that 'there are still no data on commercial agar yields from good quality raw material'. Laboratory estimations of agar content in plants from the Saldanha Bay population are, thus, also presented.

Materials and Methods

Specimens of *Gracilaria verrucosa* were collected from Saldanha Bay (33°01'S, 17°59'E) between April and July 1989. Each experiment consisted of two replicate 200-ml crystallizing dishes, each containing ten 15-mm apical segments of *Gracilaria verrucosa*, obtained randomly from 8 – 10 individual plants, under each of the various treatments. The culture medium used was Provasoli Enriched Seawater medium (Provasoli 1968). The basis of the medium was prefiltered seawater with a salinity of 31‰ (diluted with distilled water for salinity experiments). A small amount of GeO_2 (2.5 μg l^{-1} of culture solution) was added to inhibit growth of diatoms (see Markham & Hagmeier 1982). The culture medium in all experiments was changed every 7 days. The small amount of material per

culture dish prevented problems with pH changes. At the end of each 14-day experiment, the specific growth rate (SGR) was determined using the following formula (as used by Rueness & Tananger 1984):

$$\text{SGR (\% day}^{-1}) = \frac{100 \ln N_t / N_0}{t}$$

where t is the time (days), N_0 is the initial length (mm) and N_t is the length at time t (mm).

In the temperature experiments, the segments were grown at 5, 10, 15, 20, 25 and 30°C (all ± 0.5°C) in water baths in controlled temperature rooms. The following irradiances were tested in the light experiment: 0, 4, 10, 50, 80, 160, 360, 500 and 850 μmol m^{-2} s^{-1}, measured using a YSI quantum irradiance meter. These were maintained using a cool white fluorescent light source (banks of Crompton 65-W tubes) supplemented with a 500-W Ushio Halogen lamp.

In the salinity experiments, the segments were grown at 0, 9, 16.5, 31, 45, 59 and 75‰. Temperature in the light and salinity experiments was 21 ± 0.5°C. Irradiance in the temperature and salinity experiments was 35 ± 5 μmol m^{-2} s^{-1}.

In the studies of agar content, four replicate cultures of approximately 100 g wet weight of alga were grown at 10, 15 and 20°C for 28 days at 50 ± 5 μmol m^{-2} s^{-1} in square glass boxes containing 1750 ml of medium. The harvested material was then dried at 60°C to constant weight, and 5 – 8 g of dry seaweed was boiled in 400 ml distilled water for 1 h. The evaporated water was then replaced and the suspension strained through a coarse (1 mm^2) strainer. The resulting suspension was centrifuged at 2000 r/min (Beckmann model J2-21 centrifuge) for 25 min at 4°C, the supernatant poured off and retained, and the remaining residue re-extracted as above. The supernatant from both extractions was put into a freezer for 1 – 2 h to gel. The gel was then filtered out using two layers of pre-weighed nappy liner, for approximately 12 h. The agar-containing filters were then dried at 60°C to constant weight. The agar content was calculated as a percentage of the dry weight (Carter & Anderson 1986).

Results

Gracilaria verrucosa showed maximum growth (Figure 1) at 25°C, with growth rates greater than 50% of maximum in the range 15 – 25°C. The segments at 30°C showed a growth rate comparable to those at the optimum temperature for the first 7 days, but they began to discolour after 10 days, and were dead at 14 days. The alga survived the experimental period in the range 5 – 25°C, although growth was negligible at 5°C and poor at 10°C.

Growth was maximal in the medium prepared using full seawater (Figure 2), and was significantly reduced in higher and lower salinities: roughly 50% of maximum in $^1/_2$-strength seawater medium and 40% of maximum in $1^1/_2$-strength seawater medium. The survival range of the experimental material over the 14-day period was from 0.3 to 1.5 times the salt concentration of full seawater. The segments in distilled water ES medium discoloured after 4 days, showed no increase in length, and were dead by the 12th day. The segments at 9‰ exhibited bleaching of the tips, and those at 59‰ and above were dead after 4 days.

Growth increased rapidly with increasing irradiance to a maximum at 80 μmol m^{-2} s^{-1} (Figure 3). At higher irradiances, growth was reduced to approximately 50% of maximum in the range 160 – 850 μmol m^{-2} s^{-1}. There was no further significant drop in growth at the higher end of this range.

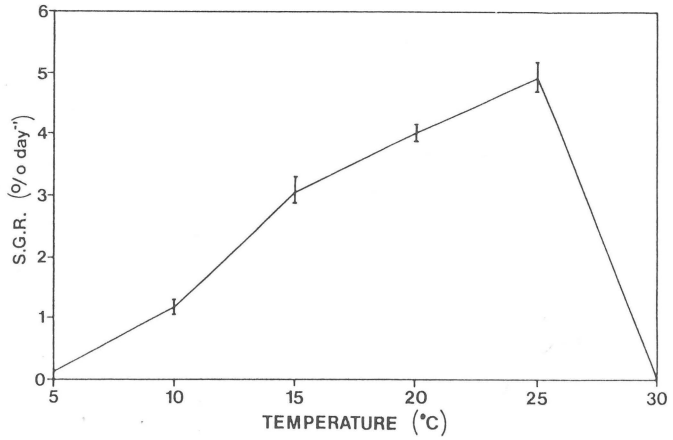

Figure 1 The effect of temperature on the specific growth rate of apical tips of *Gracilaria verrucosa*. (Vertical lines represent ± one Standard Error, $p = 0.05$.)

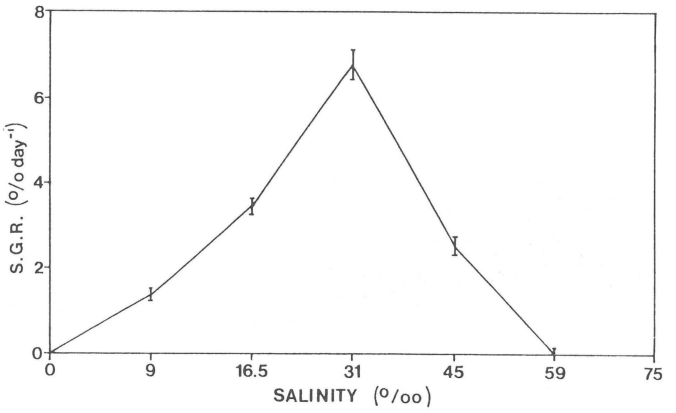

Figure 2 The effect of salinity on the specific growth rate of apical tips of *Gracilaria verrucosa*. (Vertical lines represent ± one Standard Error, $p = 0.05$.)

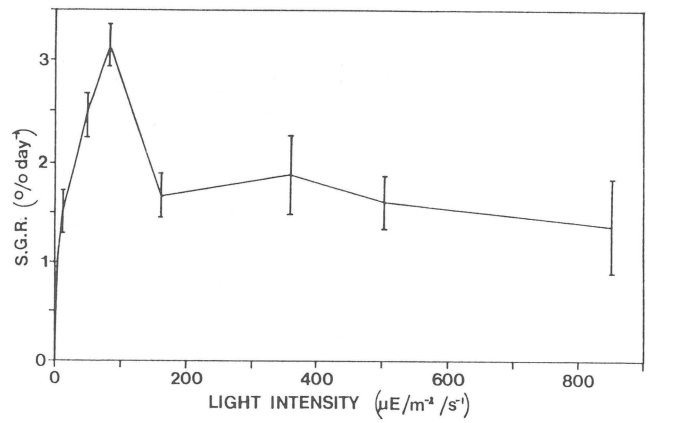

Figure 3 The effect of irradiance on the specific growth rate of apical tips of *Gracilaria verrucosa*. (Vertical lines represent ± one Standard Error, $p = 0.05$.)

The mean percentage agar contents was in the range 32 – 34%, with no significant difference according to culture temperature (Table 1).

Table 1 Agar content of *Gracilaria verrucosa* after four weeks at various temperatures

Temperature (°C)	Agar content[a] (percentage of dry weight)
10	31.9 (± 2.7)
15	34.1 (± 2.2)
20	32.7 (± 2.3)

[a] ± Standard Error, $p = 0.05$.

Discussion

The taxonomy of terete species of *Gracilaria* is complex (McLachlan & Bird 1984; Abbott *et al.* 1985; Rice & Bird 1990). Populations of terete *Gracilaria* in many world regions, from which agar is commercially extracted, are known in the literature as *G. verrucosa*, sometimes erroneously. The type of this species is from England, but the existence of *G. verrucosa* in the western Atlantic and probably the Pacific has recently been established (Rice & Bird 1990). Problems in identification arise mainly because these species are morphologically plastic, and populations in nature often reproduce entirely asexually. For example, the last report of fertile material from a South African population of *G. verrucosa* was by Isaac (1956). No fertile material was observed in field or cultured material in the present study. These problems may only be solved by new molecular or biochemical systematic techniques, which are being carried out in a number of laboratories (*e.g.* Goff & Coleman 1988; Bird & Rice 1990). A further difficulty has arisen with the discovery that plants from a number of regions which were originally described as *Gracilaria* belong in fact to a different genus, *Gracilariopsis* (Fredericq & Hommersand 1989; Bird & Rice 1990). A key characteristic of *Gracilariopsis* is the possession of tubular nutritive cells connecting the inner gonimoblast cells with cells of the pericarp or the floor of the cystocarp in the female fertile structures. Isaac (1956) commonly observed these 'filamentous cells' in material from Langebaan Lagoon. Thus it is likely that material from Langebaan Lagoon is *Gracilaria* rather than *Gracilariopsis*. Nevertheless, comparisons of environmental tolerances and agar contents between the local entity and other populations must be regarded as preliminary until these taxonomic questions are fully answered.

The genus *Gracilaria* is primarily tropical, with species numbers increasing as latitude decreases (McLachlan & Bird 1984; Hommersand 1986), and has a thermal survival range of <0 to 34°C (McLachlan & Bird 1984). Local *G. verrucosa* did not survive 30°C for 14 days. McLachlan and Bird (1984) found that species of *Gracilaria* that were able to tolerate 30°C or higher were from warm-water areas; *e.g.*, apical segments of *G. verrucosa* from the Philippines grow well at 30°C (Hurtado-Ponce & Umezaki 1987). The optimum temperature for growth that we observed, 25°C, is much higher than occurs in the local habitat. Mean monthly temperatures in Saldanha Bay and Langebaan Lagoon range from around 13°C to 18°C (Bolton 1986; Grindley 1976), with a highest documented temperature of 23.9°C in Langebaan Lagoon (Day 1959). The thermal optimum is also higher than for most temperate species of *Gracilaria* tested, which tend to grow fastest in the 15 – 20°C range (McLachlan & Bird 1984). A relatively high optimum temperature would, of course, be useful in prospective local commercial mariculture, as cooling is expensive. In studies on upper tolerance limits of temperate seaweeds, species in certain taxonomic groups tend to survive much higher temperatures than the ambient regime in the collecting sites (Lüning 1984; Lüning & Freshwater 1988). This has led these authors to consider upper temperature survival limits to be a conservative taxonomic trait.

The salinity tolerance range of local *G. verrucosa* corresponds with the findings of numerous authors (*e.g.* Rueness & Tananger 1984; Trono & Azanza-Corrales 1981; Bird & McLachlan 1986) who view *G. verrucosa* as a relatively euryhaline species. Most populations studied have an optimum at the salinity of full seawater, although Chiang (1981) reports on a Taiwanese isolate with an optimum salinity for growth of 15‰. Detailed taxonomic investigations are necessary to ascertain whether this Taiwanese population really is *G. verrucosa*. Salinity would appear to have little effect on the ecology of the species in Saldanha Bay, where there is little freshwater inflow, and maximum salt content at the head of the lagoon (41.5‰, Grindley 1976) is within the tolerance range of the population.

Irradiance levels for saturation of growth in seaweeds range from around 300 μmol m^{-2} s^{-1} (upper eulittoral species) to 10 μmol m^{-2} s^{-1} or less (sublittoral species) (see Table 6.5 in Lüning 1990). A saturation irradiance for growth of *G. verrucosa* at 80 μmol m^{-2} s^{-1} thus correlates with the species' vertical distribution, that is in the lower eulittoral and shallow sublittoral zones. The pattern of increase in growth with irradiance, with a very rapid increase in the range 0 – 80 μmol m^{-2} s^{-1}, followed by a considerable decrease at 160 μmol m^{-2} s^{-1}, then levelling off to a fairly constant growth up to the highest experimental irradiance (850 μmol m^{-2} s^{-1}) is very similar to that obtained using apical tips of five species of large brown algae (intertidal Fucales) by Strömgren (1977). This pattern differs from the usual simple saturation curve. Additional, more detailed physiological studies need to be carried out on irradiance requirements for growth of these seaweeds, particularly under natural light conditions. From a mariculture standpoint it is clear that relatively low irradiances are sufficient for maximum growth, and that fairly high irradiances (up to at least 850 μmol m^{-2} s^{-1}) are not severely detrimental. Photoinhibition occurs in deeper subtidal seaweeds above 200 μmol m^{-2} s^{-1} (Drew 1983). A further advantage for mariculture of *G. verrucosa* is that a considerable specific growth rate of 1% per day (over 30% of mean maximum) was achieved at a very low irradiance (4 μmol m^{-2} s^{-1}). In Saldanha Bay, healthy material of the local population occurs buried in the sediment, with the only possible light source being *via* prawn holes (R.J. Anderson, Sea Fisheries Research Institute, pers. commun.). The plants appear to be able to survive for a considerable period under the sediment.

It is apparent that there are somewhat different maximum

growth rates in the different experiments presented here. It is possible that different plants have some variation in growth rates. For example, it has proved possible to select for many attributes, including growth rate, in populations of a number of seaweeds (see van der Meer 1986; Levy *et al.* 1990). This could also have been affected by the combination of suboptimal conditions of temperature and irradiance used in the experiments.

The only published report of agar concentration in southern African *G. verrucosa* is a figure of 15% of the dry weight for low grade waste material unsuitable for export, which is collected and commercially extracted in Lüderitz, Namibia (Rotmann 1927). Apart from the effect of excessive impurities and other defects on this percentage, it must be borne in mind that the yield in this case was estimated using commercial alkali extraction methods, which yield only about 50% of the total agar content (Levy *et al.* 1990).

Our mean agar content of 32 – 34% of dry weight is in line with data for agar content of other populations of *G. verrucosa* extracted in the laboratory (Table 2). Many factors have been found to have significant effects on agar yield in *Gracilaria* including temperature, nitrogen, light, salinity and developmental stage (Bird 1988; Lignell & Pedersen 1989). Christiaen *et al.* (1987) found the greatest yields of French *G. verrucosa* at 5°C, with agar content reduced by more than half at 18°C. Conversely, Bird (1988) reported greater gel strength and yield with increasing temperature. Although culturing of field-collected thalli over a range of temperatures had no effect on agar yield over 28 days, longer-term trials are necessary to study the effects of environmental factors on yield, particularly if mariculture is planned. Some species have a seasonal pattern of agar yield under field conditions, including the other main South African commercial agarophyte *Gelidium pristoides* (Carter & Anderson 1986).

In comparison with most other seaweeds, *Gracilaria verrucosa* is an easy seaweed to grow in culture, not least because of its wide tolerance ranges for all parameters tested. This, together with the almost total reliance on vegetative means for reproduction and the presence of a high content of good quality agar, makes this species ideal for mariculture.

Table 2 Agar yield of *Gracilaria verrucosa* from various localities

Location	Percentage agar yield		Reference
	Minimum	Maximum	
P.R. China	23.2	31.1	Shi *et al.* 1984
Taiwan	22	52	Liu *et al.* 1980
New Zealand	21.3	24.9	Lignell & Pedersen 1989
Canada (Pacific)	24.8	39	Whyte *et al.* 1984
France	23.6	31.9	Christiaen *et al.* 1987
South Africa	31.9	34.1	This study

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