Offprint Botanica Marina Vol. 44, 2001, pp. 371–374

The Effects of Light and Temperature on Different Phases of the Life Cycle in the Carrageenan Producing Alga *Chondracanthus chamissoi* (Rhodophyta, Gigartinales)

C. R. Bulboa and J. E. Macchiavello*

Departamento de Biología Marina, Facultad de Cs. del Mar, Universidad Católica del Norte, Casilla 117, Coquimbo, Chile

* Corresponding author

Growth of female gametophyte and sporophyte phases of *Chondracanthus chamissoi* was measured under controlled laboratory conditions, examining effects of different combinations of photon flux density and temperature. Apical segments of both (isomorphic) phases of this alga were cultivated in Von Stosch medium using 12 combinations of photon flux density (PFD; 20 to 120 μmol m^{-2} s^{-1}) and temperature (10 to 25 °C), comparing the wet weights of thalli produced after 15 days. A difference in the growth rate was noted between the isomorphic phases in which the female gametophyte grew more than the sporophyte at 15 °C and above. In both phases, there was a tendency towards increasing growth with increasing temperature, whereas changes in PFD did not produce significant changes in growth in all treatments. However, a significant growth effect due to interaction of the two variables was noted. Within the range of variables studied, temperature was the controlling factor in the growth of *Chondracanthus chamissoi* mediated by factors of light and life cycle phase. The differential growth of different life cycle phases in response to environmental variables may explain the dominance of one phase over another in natural stands of this alga.

Introduction

Chondracanthus chamissoi (C. Agardh) Kützing is a seaweed of economic importance among the several species which are commercially harvested off the coast of Chile (Santelices 1988). This species is used to produce carrageenan and in recent years it has been exported to Asian countries for direct consumption (Gonzalez *et al*. 1997, SERNAP 1999). This seaweed is normally found in the lower intertidal zone to a depth of about 15 m, most commonly in calm bays protected from wave action (Hoffman and Santelices 1997). Previous studies carried out at Puerto Aldea (30°15′ S) demonstrated that the biomass of both isomorphic phases of *C. chamissoi* increased seasonally through the summer months, with thalli of the gametophyte phase strongly outnumbering those of the sporophytic phase (González and Meneses 1996, González *et al*. 1997).

The present research quantitatively evaluates the effects of light and temperature, recognized as important environmental factors, on the growth regulation of seaweeds (Lapointe *et al*. 1984, Lüning 1990, Kim and Lee 1996), as well as their effects on differential growth in alternate life cycle phases (Norton *et al*. 1985). This research aims to supply basic data for the eventual management of this species in the future, as well as to see if the growth patterns could explain the higher frequency of gametophytes over sporophytes observed in the field.

Material and Methods

Adult thalli of *Chondracanthus chamissoi* were obtained by diving at Puerto Aldea, Tongoy Bay, Chile (30°15′ S). Two kilograms (drained weight) of the alga were harvested, taking care to obtain complete specimens. In our laboratory plants were separated by life cycle phase into female gametophytes (bearing cystocarps) and sporophytes (bearing tetrasporangial sori). Apical segments (ca. 3 cm) not bearing reproductive structures were then cut from the thalli, cleaned with a soft brush, and rinsed in seawater. These segments were maintained *in vitro* for subsequent growth under a photon PFD of 40 μmol m^{-2} s^{-1}, a temperature of 15 °C, a photoperiod of 12:12 L:D and continuous aeration. Seawater for maintenance of the algae was filtered to 0.45 μm, passed through an UV treatment unit, and finally enriched with Von Stosch solution (Edwards 1970) diluted to 50 %.

Growth of the algal segments was evaluated in an experimental matrix under temperatures of 10, 15, 20 and 25 °C and PDFs of 20, 70 and 120 μmol m^{-2} s^{-1}. Temperatures were obtained using an aluminium temperature gradient table (Edding *et al*. 1987), and light from fluorescent lighting fixtures arranged at suitable distances and measured using a Li-Cor Co. Model # 250 quantameter. Each experimental system consisted of a 250 mL Erlenmeyer flask containing 250 mL seawater culture medium (as above) and one

apical segment randomly selected whose wet weight was determined. Media were changed after seven days, at which time the algae were cleaned with a soft brush and rinsed with fresh seawater. Drained wet weight was measured after 15 days. Each treatment was replicated 3 times for each of the two life cycle phases. Growth rates were calculated according to Guillard (1973): $k = Log_2 (W_1/ W_0) / T$, where k = daily growth rate; W_1 = final weight (g); W_0 = initial weight (g) and T = time (d).

All data were analysed using SYSTAT 8.0 Software (SPSS INC., Chicago, U. S. A.). Data were log-transformed and submitted to a three factor multifactorial analysis (ANDEVA). Homogeneity of the variances was reviewed for all results. A Tukey test was used when treatments showed significant differences (Sokal and Rohlf 1982).

Results

Both gametophytic and sporophytic phases grew in all combinations of light and temperature to which they were exposed. At 10 °C both phases had the slowest growth at all three light levels, with 10 °C at 120 µmol m^{-2} s^{-1} giving the slowest growth in the entire experiment (Fig. 1). At 10 °C at all light levels, there was no significant ($p > 0.05$) difference in growth rates between the two life cycle phases (Table II). The effect of temperature on growth was highly significant ($fc = 124.382$; $p < 0.01$; Table I), however, the Tukey test demonstrated no significant difference ($p > 0.05$) between the growth rates of gametophytes and sporophytes at temperatures of 15, 20 and 25 °C, although there was a tendency towards increased growth with an increase in temperature (Fig. 1). In combinations of the three PFD with temperatures of 15, 20 and 25 °C, growth was always significantly larger ($p < 0.01$) in gametophytes than in sporophytes. These differences were increasingly evident with each increment in temperature. Maximum growth values were recorded in the combination of 25 °C with 70 µmol m^{-2} s^{-1} for gametophytes and 120 µmol m^{-2} s^{-1} for the sporophytes (Fig. 1).

The multifactorial ANOVA did not show significant differences ($p > 0.05$) in growth with increasing PFD, however, there was an interaction of the first order between PFD and temperature, as well as between temperature and reproductive phase of the alga (Table I).

Discussion

The present results suggest that temperature was the major factor influencing the growth of *Chondracanthus chamissoi* within the range of variables examined, interacting with PFD as well as with the life cycle phase of the alga. These temperature and light effects have been well documented for red algae (Hannach and Santelices 1985, Lapointe *et al.* 1984, Luxoro and Santelices 1989). Macchiavello *et al.* (1998) proposed a similar set of circumstances for five species of *Gracilaria*. Paula and Oliveira (1980) and Breeman (1988) proposed that the interaction of these parameters had an important role in tropical and subtropical

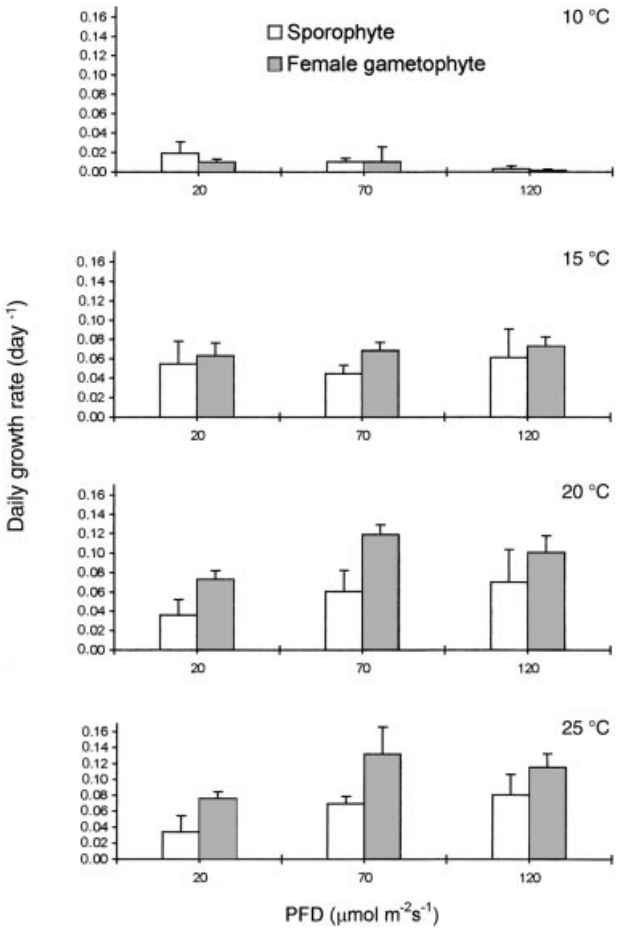

Fig. 1. Mean growth rates of female gametophytes and sporophytes of *C. chamissoi* in relation to temperature and photon flux density (PFD). Error bar = 1 standard error of mean.

Table I. Analysis of variance summary of growth of female gametophyte and sporophyte phases of *Chondracanthus chamissoi* in relation to temperature and photon flux density.

Source	df	MS	*F*	*p*
T	3	1.924	124.382	< **0.01**
PFD	2	0.040	2.591	> 0.05
P	1	0.274	17.705	< **0.01**
T × PAR	6	0.092	5.961	< **0.01**
T × P	3	0.106	6.874	< **0.01**
PAR × P	2	0.006	0.418	> 0.05
T × PAR × P	6	0.006	0.357	> 0.05
Residual	48	0.015		

Multifactorial ANOVA with factors: temperature (T), photon flux density (PFD) and phases (P). (PAR) = photosynthetically active radiation. Significant *p*-values are shown in bold.

Table II. Results of Tukey test on the *Chondracanthus chamissoi* female gametophyte and sporophyte growth rates at different temperatures.

	10 °C	15 °C	20 °C	25 °C
Female gametophyte	0.200	0.890	1.023	1.057
Esporophyte	0.288	0.783	0.788	0.817
p	> 0.05	< **0.01**	< **0.01**	< **0.01**

Tukey test (α 0.05). Significant *p*-values are shown in bold.

regions where extremes in variation of temperature and light were not strongly limiting for algal growth.

The optimal temperature for the growth of the *Chondracanthus chamissoi* under the experimental conditions (25 °C) was higher than the average sea surface temperature in our region (19 °C, Moraga and Olivares 1993). A similar situation was also reported by Edding *et al*. (1987) for *Gracilaria chilensis* Bird, McLachlan *et* Oliveira from Herradura Bay (29°58″ S). Growth of *Chondracanthus chamissoi* under the full range of temperatures tested may be a reflection of its adaptation to its extensive latitudinal distribution from southern Peru (5 °S) to the Island of Chiloé (42 °S) (Acleto 1986, Hoffman and Santelices 1997). The results suggest that the physiologically optimal temperature for this alga *in vitro* may be outside that found in the environment, as discussed by Yokoya and Oliveira (1992) for several other algae of economic importance.

Our data, obtained *in vitro*, support the field data of Gonzalez *et al*. (1997), who found a higher biomass of gametophytes during the summer months.

Although growth in the two life cycle phases of *Chondracanthus chamissoi* was similar under our experimental conditions, the responses differed in magnitude, with the gametophyte showing higher growth rates. These results agree with the proposal made by Norton *et al*. (1985) that environmental variables control and regulate alternative phases in algal life cycles, although in the present case the parameters observed were not strong enough to exert exclusive selection between the isomorphic phases as has been suggested for *Chondrus crispus* Stackhouse (Mathieson and Burns 1975).

Higher growth rates of the gametophytic phase were also described for *Iridaea laminaroides* Bory and *I. ciliata* Kützing by Hannach and Santelices (1985). These authors suggested that an intrinsically higher growth rate of the gametophytic phase could explain its dominance in the field which in the family Gigartinales, cannot be the result of a higher level of ploidy.

The higher growth rate of *Chondracanthus chamissoi* gametophytes found in the present study, in addition to its differential recruitment which favors settlement of tetraspores (Gonzalez and Meneses 1996), may be interpreted as a selective advantage for the gametophytic phase which helps explain its dominance in natural beds.

Acknowledgements

We gratefully appreciate the efforts of the Fisherman Association of Puerto Aldea. We also thank Dr E. Oliveira for discussion of and comments on the manuscript. This study was supported by the International Foundation for Sciences, Research Grant Application N1 AA / 9877.

Accepted 15 March 2001.

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