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Interactions between light and temperature on the physiological ecology of *Gracilaria tikvahiae* (Gigartinales: Rhodophyta)

I. Growth, photosynthesis and respiration

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Abstract

Main effects and interactions of light and temperature on rates of growth (μ), net photosynthesis (P_s), and dark respiration (R) of the red seaweed *Gracilaria tikvahiae* were investigated in outdoor, nutrient-replete continuous-flow seawater culture chambers. Below 15 °C, *G. tikvahiae* did not grow and between 15° and 30 °C, both main effects and interactions of light and temperature on μ and P_s were significant, which explains the occurrence of this alga as a summer annual in its northern range. Temperature interacted with light (I) through its influence on the μ vs I and P_s vs I curves. The initial slope of the μ vs I curve, α , the light saturation intensity, I_s , and maximum growth rate, μ_{max} , were all significantly lower at 15 °C compared to 20°, 25°, or 30 °C. Maximum values of μ_{max} , the P_s :R ratio and the net photosynthesis:gross photosynthesis ratio (P_s : P_g) all occurred at 25 °C, suggesting that this is the best temperature for growth of *G. tikvahiae*. Values for P_{max} increased up to 30 °C, indicating that the temperature for maximum growth and net photosynthesis are not the same for *G. tikvahiae*. Significant photoinhibition of growth and photosynthesis at full incident sunlight (I_0) occurred at 15 °C but not at 20°, 25°, or 30 °C. Steele's equation fit the 15 °C μ vs I data best, whereas the hyperbolic tangent function fit the 20°, 25°, and 30 °C data best. Main effects and interaction of light intensity and temperature on rates of R were also significant ($P < 0.001$). R was highly inter-correlated with μ and P_s ($0.86 \leq r \leq 0.94$), indicating that R in *G. tikvahiae* is primarily regulated by growth rate and not temperature *per se*. Environmental factors that regulate growth, such as light intensity, exert a great influence on R in *G. tikvahiae*.

Introduction

Algal growth rates may be regulated by light and temperature (Kanwisher, 1966; Hellebust, 1970; Gessner, 1970; Soeder and Stengel, 1974; Rhee and Gotham, 1981). These environmental factors must be particularly important in regulating seasonal growth patterns of *Gracilaria tikvahiae* (= *G. foliifera* v. *angustissima* [Harvey] Taylor), a tropical alga in the Americas (Taylor, 1972) whose range during summer extends as far north as Prince Edward Island, Nova Scotia (Taylor, 1957). Although seasonal growth rates of *G. tikvahiae* in outdoor cultures in Florida are correlated with both light and temperature (Lapointe and Ryther, 1978), the quantitative importance of these factors on growth of *G. tikvahiae* is not known. Generally, algal growth (μ , doublings of biomass d^{-1}) is a hyperbolic function of light intensity (I) (see Goldman, 1979, for review) and several mathematical formulations have been proposed to represent this relationship (Steele, 1962; Jassby and Platt, 1976). Three parameters common to algal μ vs I curves are usually determined to describe mathematically the μ vs I curve: (1) the initial slope, α ; (2) the asymptote and maximum growth rate, μ_{max} ; and (3) a relative measure of the light saturation intensity, I_k . Temperature interacts with light in determining the shape of the μ vs I curve by controlling the values of μ_{max} (Eppley, 1972) and I_k (Talling, 1957). Thus, to represent mathematically the interaction between light and temperature in predictive growth models of *G. tikvahiae*, one must quantify the relationship between the parameters of the μ vs I curve and temperature.

The relationship between steady-state rates of photosynthesis, dark respiration and growth at different levels of light and temperature is fundamental to the understanding of the energetics underlying growth of *Gracilaria tikvahiae*. Seaweed ecologists often equate growth with net photosynthesis, but this may not be valid with respect to temperature. The maximal temperature (T_{max}) for phytoplankton growth is lower than that for photosynthesis, presum-

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ably because of accelerating losses due to dark respiration and excretion at high temperatures (Rabinowitch, 1956; Li, 1980). Reports of low Q_{10} values for dark respiration of algae within their physiological temperature range (Newell and Pye, 1968; Jones, 1977; Durako and Dawes, 1980) suggest that rates of dark respiration may often be temperature-independent in nature. This may occur because of a primary dependence of dark respiration on algal growth rates *per se* (Raven and Glidwell, 1975; Laws and Caperton, 1976).

The present study sought to determine the degree of interaction between natural levels of light intensity and temperature on growth, net photosynthesis and dark respiration of *Gracilaria tikvahiae*. The major objectives were to (1) determine reasonably accurate models of the growth of *G. tikvahiae* as a function of light intensity, temperature, and their interaction and (2) elucidate the energetic basis for growth of this alga. Such studies should reveal the scope for seasonal growth of this alga along the eastern coast of North America.

Material and methods

Experimental design and operation

The clone of *Gracilaria tikvahiae* (McLachlan, 1979) used in this study was obtained in April, 1978 from a drift population growing in shallow (ca 1 m) water in the Indian River, near Vero Beach, Florida, USA. A stock culture of this clone (ORCA) was maintained at the Skidaway Institute of Oceanography in outdoor, flowing-seawater tanks. The culture temperature was regulated during winter to maintain tank temperatures at $> 15^{\circ}\text{C}$ as this clone of *G. tikvahiae* could not be grown below 15°C (Lapointe, unpublished data).

The growth experiments were conducted in outdoor continuous-flow seaweed culture chambers (see Lapointe and Tenore, 1981, for details). Each chamber received 5- μ filtered, temperature-regulated seawater at a turnover rate of 24 volumes d^{-1} and oil-free compressed air to provide water motion. All chambers received uniform nutrient enrichment of nitrogen and phosphorous (as NaNO_3 and NaH_2PO_4 at an atomic N:P ratio of 10:1) metered by single-channel peristaltic pumps. Residual concentrations ranged from 25.0 to 30.0 μM for NO_3^- and 2.0 to 3.0 μM for PO_4 . Daily incident light was measured with an Eppley pyranometer as total energy flux in langley d^{-1} (ly d^{-1}) and limited to photosynthetically active radiation (PAR) by multiplying by 0.5 (Goldman, 1979). Various light levels were obtained with different layers of neutral density fiberglass screening. Changes in wet weight (damp-dried) of *Gracilaria tikvahiae* over time were used to calculate growth rates (μ , doublings $\cdot \text{d}^{-1}$ of biomass) as:

$$\mu = \log_{10} (B/B_0) 3.32/t,$$

where B_0 is the initial biomass (100 g wet weight per chamber) and B is the final biomass with time (t, 2 to 3 d).

Density of *G. tikvahiae* during these experiments was between 0.4 and 0.8 kg wet weight m^{-2} to minimize self-shading and to maximize growth rates (Lapointe and Ryther, 1978).

The growth experiment was a 4×4 incomplete block design factorial, with four levels (I_0 , full incident light; $0.57 I_0$, $0.33 I_0$, $0.33 I_0$; and $0.07 I_0$) of natural light, four temperatures (15° , 20° , 25° and 30°C ; all $\pm 2^{\circ}\text{C}$) and two replicate chambers per treatment. For the photosynthesis and respiration measurements, three light levels (I_0 , $0.57 I_0$, $0.07 I_0$) were used (i.e. 3×4 factorial). As only one controlled temperature could be maintained at a given time, the experiments were conducted between April and August, 1981, which resulted in the incomplete block design. Only the growth data obtained during clear, sunny growth periods at each temperature were used (= "high light" growth periods). Thus, I_0 ($265 \pm 20 \text{ ly d}^{-1}$) in this design represents an average of maximum levels of daily incident natural light measured during the experiments. Because of shading by the culture chamber itself, *in-situ* light levels at the average depth of the chamber are 70% of I_0 values. Each temperature experiment lasted for ca four weeks to insure an adequate acclimation period before assay of growth, photosynthesis and respiration. During this period, growth of *Gracilaria tikvahiae* was monitored and normalized to incident light (as doublings ly^{-1}) to detect possible lag growth periods because of temperature shifts (Li, 1980). Also, because photoperiod varied by ca 1.25 h between April and August, a control culture, maintained at I_0 , $20^{\circ}\text{C} \pm 2^{\circ}\text{C}$, was used to test for confounding effects of photoperiod on growth of *G. tikvahiae* (as doublings ly^{-1}). Salinity during these experiments ranged between 26 and 29‰ S.

To examine the influence of light intensity on growth rate and respiration, *Gracilaria tikvahiae* was grown at 20°C , I_0 for 10 d. Subsequently, these plants were transferred to $0.07 I_0$ to reduce growth rates. Growth and respiration were monitored to follow their change over time.

Analysis of μ vs I curves

Four mathematical models used to describe phytoplankton P_s vs I curves were statistically tested for their goodness of fit to the growth data. All models were two parameter models:

$$\mu = \mu_{\max} I / (\mu_{\max} + I); \text{ Baly (1935);} \quad (1)$$

$$\mu = \mu_{\max} (I/I_k + I); \text{ Michaelis and Menten (1913);} \quad (2)$$

$$\mu = \mu_{\max} I/I_s \exp (I - I/I_s); \text{ Steele (1962);} \quad (3)$$

$$\mu = \mu_{\max} I/I_s \tan (I/\mu_{\max}); \text{ Jassby and Platt (1976).} \quad (4)$$

For each temperature tested, μ_{\max} values represent the maximum observed growth rate; α values were estimated

by least-squares linear regression of the light-limited growth data (i.e. $0.07 I_0$, and $0.33 I_0$); I_k values were estimated as:

$$I_k = \mu_{\max} / \alpha$$

and I_s values were determined by differentiation of Steele's (1962) equation, giving the relationship:

$$I_s = 2.72 I_k.$$

These parameters were estimated independently of the equations and their values can be used in all equations (Lederman and Tett, 1981). To compare the ability of the models to describe the growth data statistically, a FORTRAN IV program was written to compute a residual sums of squares between the actual growth data and that predicted from the models (Silvert, 1979). The resulting sums of squares (i.e. SSE's) of each model was tested using a two-tailed F-test.

Measurement of photosynthesis and respiration

Rates of net photosynthesis (P_s) and dark respiration (R), expressed as $\text{mg O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$, were determined using "light and dark" bottle O_2 techniques (Strickland and Parsons, 1972). All measurements were made between 11.00 and 14.00 hrs on clear, sunny days. Light intensities incident (I_0) to the chambers during photosynthesis measurements were measured with a Li Cor LI-188 integrating meter and averaged 0.60 ly min^{-1} (PAR); corresponding values incident to the bottles within the chambers were 70% of the reported ($0.07 I_0$, $0.57 I_0$ and I_0) values. Whole plants (1 to 2 g wet wt for P_s ; 2 to 4 g wet wt for R) and seawater were obtained from the growth chambers under study, placed in 500-ml B.O.D. bottles, and incubated in their respective growth chambers for periods up to 1 h for photosynthesis and 1 to 3 h for respiration. Time-course experiments, using measurements at 5-min intervals, indicated that apparent rates of photosynthesis and respiration were linear over the course of these incubation periods. For photosynthesis measurements, the seawater was initially bubbled with N_2 to reduce O_2 levels to ca $3 \text{ mg O}_2 \text{ l}^{-1}$ to avoid bubble formation that occurs at O_2 levels near saturation. Seawater in all B.O.D. bottles was mixed using stir-bars and air-driven, submersible magnetic stirrers. Four replicates for both light and dark bottles, as well as two light and dark blanks, were used. O_2 levels were determined with a BECKMAN FIELDLAB O_2 analyzer using an O_2 -free solution to "zero" the meter and air-saturated seawater of known temperature and salinity for calibration. Measured rates of P_s and R were also used to calculate $P_s:R$ and $P_s:P_g$ ratios for *Gracilaria tikvahiae*. The $P_s:R$ ratio is net photosynthesis/dark respiration and the $P_s:P_g$ ratio is net photosynthesis/gross photosynthesis.

Statistical analyses

Two-way analysis of variance was used to assess the main effects and interaction of light intensity and temperature

on growth rate, photosynthesis, respiration, the $P_s:R$ and $P_s:P_g$ ratios. The Statistical Package for Social Sciences (Nie *et al.*, 1975) was used to determine Pearson correlation coefficients (r values) between growth rate, P_s , R , and the $P_s:R$ and $P_s:P_g$ ratios; a two tailed F-test was applied to the coefficients to determine levels of significance. Duncan's New Multiple Range Test was used for *a-priori* comparisons of treatment means. Estimates for standard deviations of means for samples of small size ($n=2$) were corrected for bias according to the methods of Snedecor and Cochran (1967). Significance reported in the results below implies the probability of the null hypothesis is < 0.05 .

Results

Growth rate of the control cultures of *Gracilaria tikvahiae* during these experiments, normalized to incident light, did not vary significantly between April and August (Fig. 1). Thus, photoperiod effects and seasonal physiological variation of *G. tikvahiae* are not confounded within the experimental design of this study.

Following transfer of *Gracilaria tikvahiae* from field seawater temperature (25° to 30°C) to the 20° , 25° and 30°C treatments, no lag period in growth rate was observed. However, a lag period of between 5 and 9 d was observed before steady-state growth was attained after transfer from field temperature (22°C) to the 15°C treatment (Fig. 2). During this period, growth of *G. tikvahiae* was depressed to levels below that of the steady-state growth rates characteristic for this temperature (Fig. 2).

Although growth rates were measured continuously throughout the experimental periods at each temperature (Fig. 3), mean growth rates and best-fit μ vs I models represent growth during two "high-light" growth periods at each temperature (Fig. 4). Temperature strongly influences the μ vs I curve of *Gracilaria tikvahiae* between 15° and 30°C (Fig. 4) as evidenced by the temperature-dependency of the μ vs I parameters (Table 1). Values of α

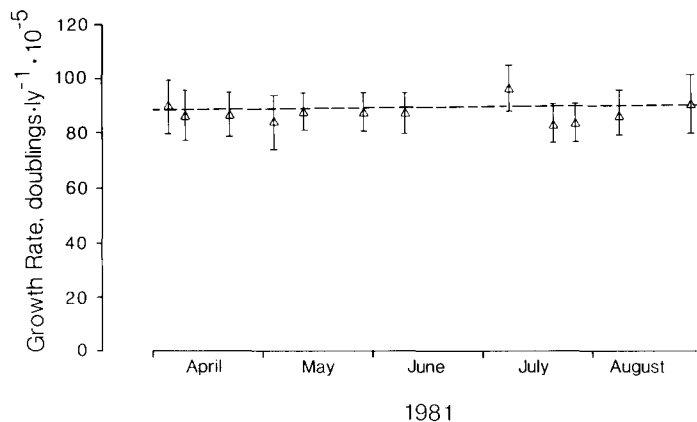


Fig. 1. *Gracilaria tikvahiae*. Growth rate (normalized to incident light) of control cultures (I_0 , $20^\circ \text{C} \pm 2^\circ \text{C}$) between April and August, 1981, i.e. during the experimental period. Values represent means ± 1 SD ($n=2$)

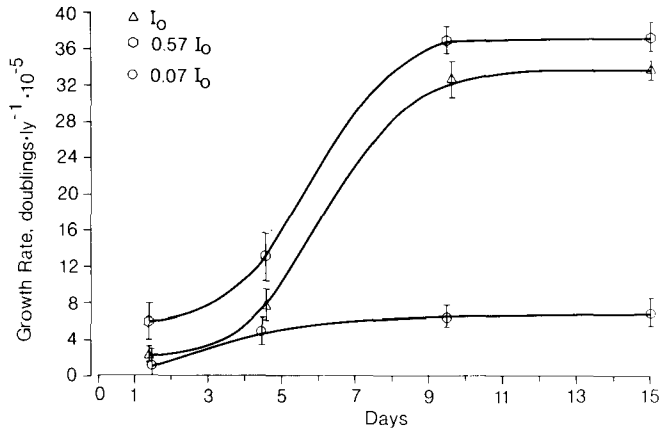


Fig. 2. *Gracilaria tikvahiae*. Time course of growth (normalized to incident light) during exposure to three light intensities (I_0 , $0.57 I_0$, $0.07 I_0$) at $15^\circ\text{C} \pm 2^\circ\text{C}$. Previously, *G. tikvahiae* was growing at I_0 , 22°C . Values represent means ± 1 SD ($n=2$); data are plotted at the midpoint of the growth intervals

and μ_{\max} generally increased with temperature and were relatively similar between 20° and 30°C compared to lower values at 15°C . Values of I_k and I_s increased from 15° to 25°C but decreased significantly from 25° to 30°C (Table 1).

Two μ vs I models gave the best fit to the growth data at the different temperatures (Table 2). Between 20° and 30°C , the hyperbolic tangent function gave the lowest residual sums of squares; at 20° and 30°C , this model fitted best of the three models considered. At 15°C , Steele's equation fitted best ($P < 0.05$). Significant photo-inhibition of both growth and photosynthesis occurred at I_0 at 15°C but not at the higher temperatures.

Main effects and interaction of light intensity and temperature on growth, photosynthesis, and respiration were all significant (Table 3). Light intensity accounted for most of the variation in growth, photosynthesis and respiration – 62, 52 and 45%, respectively, compared to 26, 33 and

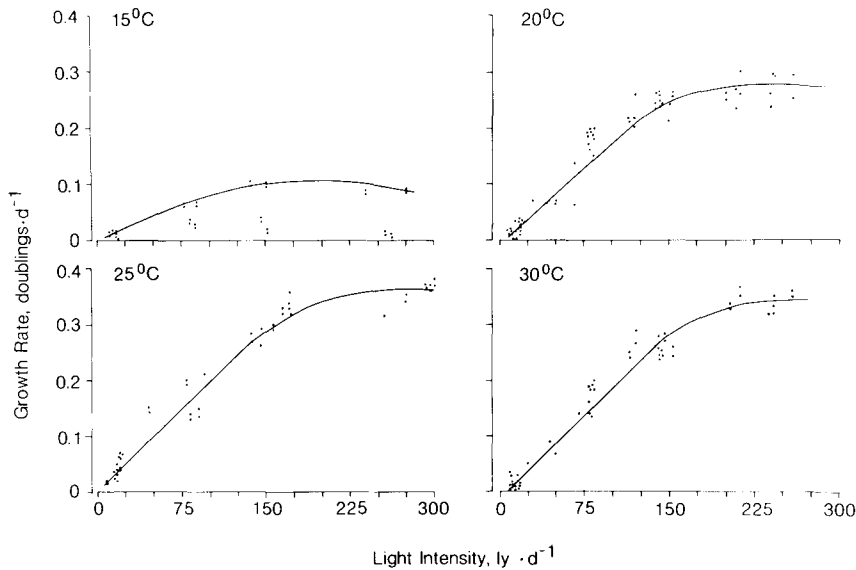


Fig. 3. *Gracilaria tikvahiae*. Growth data for *G. tikvahiae* grown at four temperatures (15° , 20° , 25° and 30°C , $\pm 2^\circ\text{C}$) and four light intensities (I_0 , $0.57 I_0$, $0.33 I_0$, $0.07 I_0$). The μ vs I curves were fitted by eye. Note data points at 15°C that occurred during the lag-period following initial exposure to 15°C : this curve is fitted to acclimated growth data only

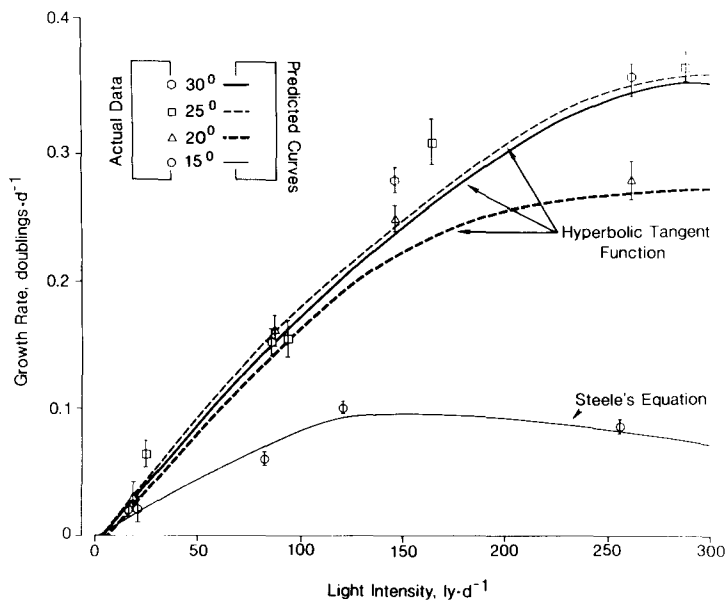


Fig. 4. *Gracilaria tikvahiae*. Actual growth data and μ vs I curves predicted from the hyperbolic tangent function (20° , 25° , and 30°C) and Steele's equation (15°C) for *G. tikvahiae* grown at four light intensities (I_0 , $0.57 I_0$, $0.33 I_0$, $0.07 I_0$). Actual data represent means ± 1 SD ($n=4$)

Table 1. *Gracilaria tikvahiae*. Physiological parameters used to model growth as a function of light and temperature. Values represent means \pm 1 SD ($n=4$)

Temp. (°C)	α (doublings ly^{-1}) $\times 10^{-2}$	I_s^* (ly d^{-1})	I_k^* (ly d^{-1})	μ_{max} (doublings d^{-1})
15	0.032 \pm 0.004	373 \pm 43	138 \pm 16	0.09 \pm 0.002
20	0.098 \pm 0.005	462 \pm 30	171 \pm 11	0.28 \pm 0.02
25	0.085 \pm 0.003	591 \pm 38	219 \pm 14	0.37 \pm 0.01
30	0.10 \pm 0.01	497 \pm 51	184 \pm 19	0.36 \pm 0.01

* Photosynthetically Active Radiation

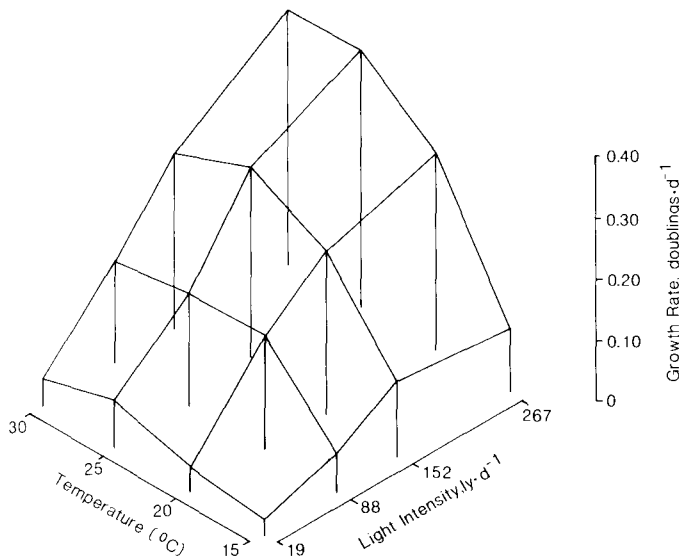


Fig. 5. *Gracilaria tikvahiae*. Steady-state growth rates at four light intensities (I_0 , $0.57 I_0$, $0.33 I_0$, $0.07 I_0$) and four temperatures. Values represent means; coefficients of variation \leq 0.06 ($n=4$)

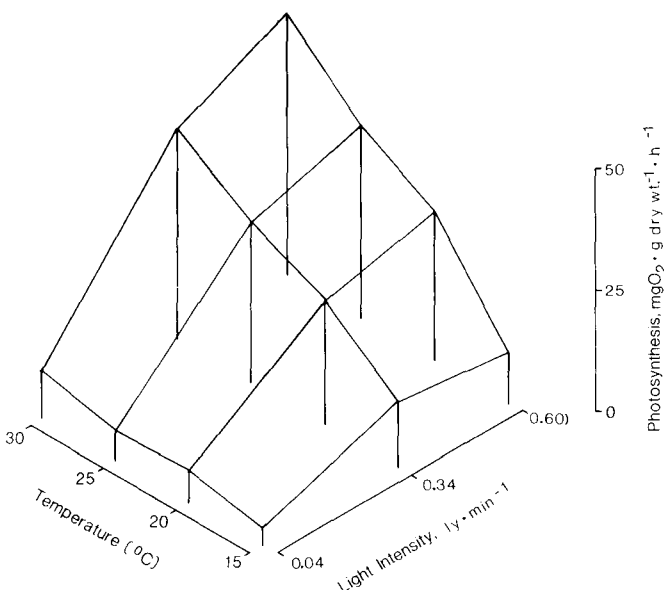


Fig. 6. *Gracilaria tikvahiae*. Steady-state rates of photosynthesis measured at midday at three light intensities (I_0 , $0.57 I_0$, $0.07 I_0$) and four temperatures. Values represent means; coefficients of variation \leq 0.07 ($n=4$)

25% for temperature. The response surface curves of growth rate, photosynthesis and respiration illustrate the interaction between light and temperature (see Figs. 5, 6, and 7) and the similarity of these response surfaces reflects the high intercorrelation ($0.86 \leq r \leq 0.94$) between these three physiological processes. The effects of light intensity on growth, photosynthesis and respiration were most significant at the higher temperatures (20° to 30°C) and the effects of temperature were most significant at the higher light intensities (I_0 , $0.57 I_0$). However, while photosynthesis at I_0 and $0.57 I_0$ increased significantly from 25° to 30°C (Fig. 6), growth rate did not (Fig. 5). This suggests that T_{max} for growth is less than T_{max} for photosynthesis in *Gracilaria tikvahiae*.

Main effects and interaction of light intensity and temperature on the $P_g:P_g$ (Fig. 8) and the $P_g:R$ ratio (Fig. 9) of *Gracilaria tikvahiae* were also significant (Table 3).

Table 2. *Gracilaria tikvahiae*. Residual sums of squares (SSE) and ranking of four μ vs I models fitted to growth data for *G. tikvahiae* as a function of temperature ($n=16$)

Temperature		Hyperbolic tangent function	Michaelis Menten	Baly equation	Steele's equation
15 °C	SSE	628.82	1 022.90	2 846.94	84.25*
	Rank	2	3	4	1
20 °C	SSE	439.50*	2 177.14	4 607.88	979.29
	Rank	1	3	4	2
25 °C	SSE	250.00*	835.39	1 709.10	548.16
	Rank	1	3	4	2
30 °C	SSE	243.87*	1 829.63	2 282.53	2 775.83
	Rank	1	2	3	4

* Best fit at given temperature ($P < 0.05$)

Table 3. Summary of two-way analysis of variance of measured variables as a function of light intensity (I), temperature (T) and the light \times temperature interaction ($I \times T$)

Variables	Source of variation	% of total variation explained	F
Growth (μ)	I	62	376.01**
	T	26	158.07**
	I \times T	12	24.02**
Net photosynthesis	I	52	393.66**
	T	33	167.86**
	I \times T	13	32.03**
Respiration	I	45	459.40**
	T	25	166.50**
	I \times T	30	99.2**
Net photosynthesis: respiration	I	30	14.05**
	T	45	245.6**
	I \times T	18	32.1**
Net photosynthesis: gross photosynthesis	I	28	139.13**
	T	46	148.50**
	I \times T	22	36.13**

** $P < 0.01$

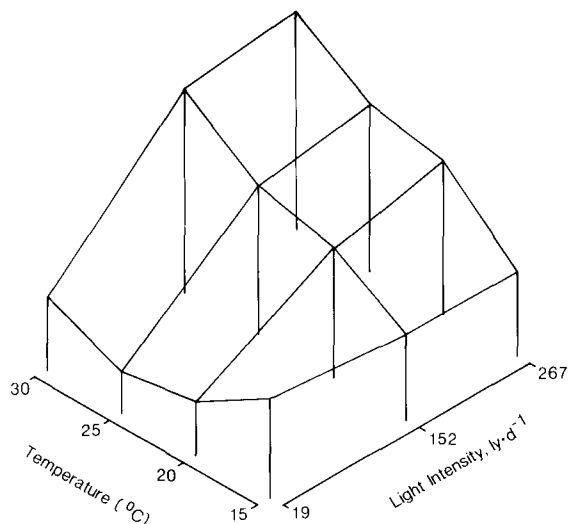


Fig. 7. *Gracilaria tikvahiae*. Steady-state rates of dark respiration measured at midday at three light intensities (I_0 , $0.57 I_0$, $0.07 I_0$) and four temperatures. Values represent means; coefficients of variation ≤ 0.09 ($n=4$)

Temperature accounted for most of the variation in the $P_s:R$ and $P_s:P_g$ ratios – 45 and 46%, respectively, compared to 30 and 28% for light intensity. This finding reflects the low respiration rates of the slowly growing algae in the $0.07 I_0$ treatments (Fig. 7) that resulted in disproportionately high values for the $P_s:R$ and $P_s:P_g$ ratios in those treatments (see Figs. 8 and 9 and compare with Fig. 5). Consequently, the $P_s:R$ ratio was significantly correlated with growth rate at I_0 and $0.57 I_0$ ($r=0.96$) but not at $0.07 I_0$ ($r=0.60$). Both the $P_s:R$ and $P_s:P_g$ ratios had maximal values at 25°C .

The interaction between light intensity and temperature on photosynthesis, respiration, and growth rate was reflected in the temperature coefficients (Q_{10}) for these processes (Table 4). Between 15° and 25°C , growth rate and photosynthesis at I_0 had Q_{10} values of ca 4.0; lower Q_{10} values occurred at $0.07 I_0$. Similarly, Q_{10} values for respiration at I_0 were ca twice the values at $0.07 I_0$. Between 20° and 30°C , lower Q_{10} values (i.e. <2.0 for μ and P_s) occurred (Table 4).

The high correlation between respiration and growth rate was particularly apparent during the time course of their changes with changes in light intensity. Initially, *Gracilaria tikvahiae* growing at steady-state at I_0 , 20°C , had a growth rate of 0.25 ± 0.02 doublings d^{-1} and respiration rate of 1.88 ± 0.15 mg O_2 $\text{g dry wt}^{-1} \text{h}^{-1}$ (Fig. 10). Upon transfer to $0.07 I_0$, growth rate dropped to <0.02 doublings d^{-1} while respiration dropped to <0.5 mg O_2 $\text{g dry wt}^{-1} \text{h}^{-1}$ (Fig. 10).

Discussion

The time course of stabilization to changes in temperature is necessary to understand the effects of temperature on algal growth. Lag-periods for growth, similar to those observed in *Gracilaria tikvahiae* at 15°C , occur in *Phaeodac-*

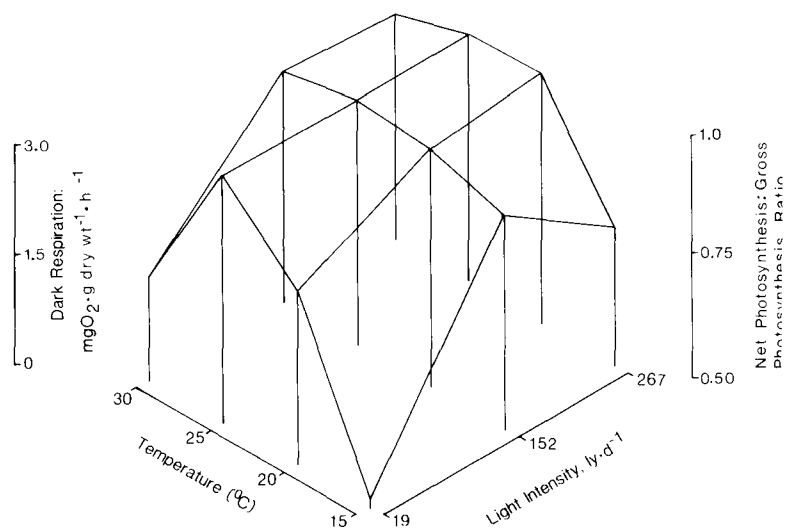


Fig. 8. *Gracilaria tikvahiae*. Net photosynthesis: gross photosynthesis ratio of *G. tikvahiae* grown at three light intensities (I_0 , $0.57 I_0$, $0.07 I_0$) and four temperatures. Values represent means; coefficients of variation ≤ 0.10 ($n=4$)

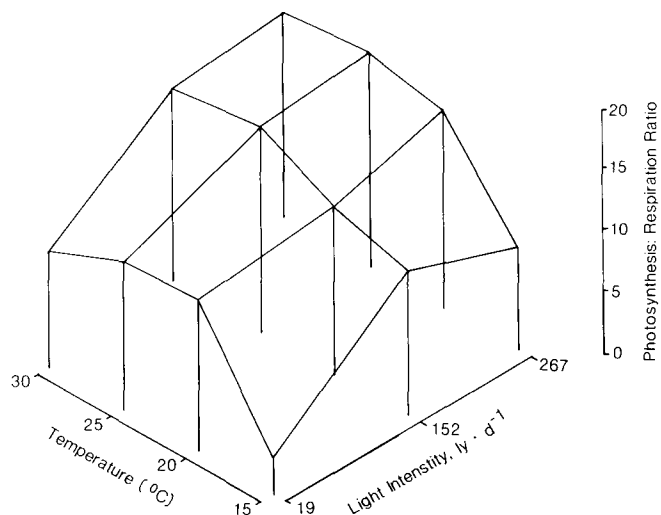


Fig. 9. *Gracilaria tikvahiae*. Photosynthesis: respiration ratio of *G. tikvahiae* grown at three light intensities (I_0 , $0.57 I_0$, $0.07 I_0$) and four temperatures. Values represent means; coefficients of variation ≤ 0.11 ($n=4$)

Table 4. *Gracilaria tikvahiae*. Temperature coefficients (Q_{10} 's) for growth rate (μ), net photosynthesis (P_s), and dark respiration (R) as a function of light intensity

Temperature range	Light intensity	μ	P_s	R
$15^\circ\text{--}25^\circ\text{C}$	I_0	4.1	3.6	1.8
	$0.57 I_0$	3.1	2.4	1.6
	$0.07 I_0$	3.5	2.2	1.0
$20^\circ\text{--}30^\circ\text{C}$	I_0	1.3	1.9	1.6
	$0.57 I_0$	1.1	1.7	1.5
	$0.07 I_0$	1.0	1.6	1.7

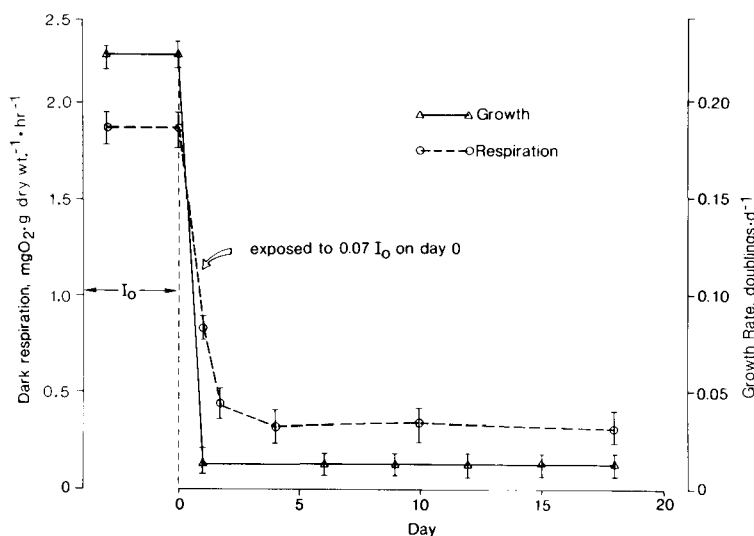


Fig. 10. *Gracilaria tikvahiae*. The correlation between growth rate and dark respiration. Previous to Day 0, *G. tikvahiae* was growing at steady-state, I_0 , $20^\circ\text{C} \pm 2^\circ\text{C}$; on Day 0, light intensity was reduced to $0.07 I_0$ and both growth rate and dark respiration decreased within 1 d. Values represent means ± 1 SD ($n=2$ for growth; $n=4$ for respiration); growth data are plotted at midpoints of the growth intervals

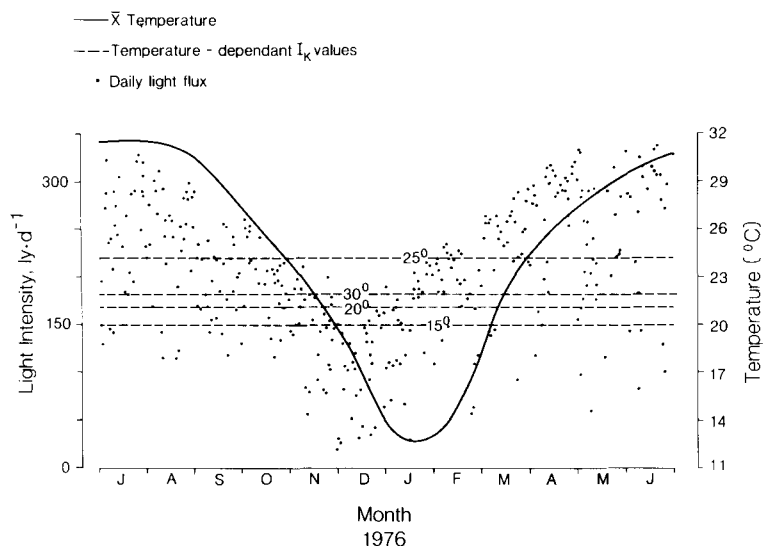


Fig. 11. *Gracilaria tikvahiae*. Seasonal variation of water temperature and incident light intensity during 1976 in the Indian River near Ft. Pierce, Florida, USA (data from Lapointe and Ryther, 1978). Also given are temperature-dependent I_k values for growth as determined in this study

tylum triconutum (Spencer, 1954; Morris and Farrel, 1971), *Dunaliella tertiolecta* (Morris and Farrel, 1971) and *Synechococcus lividus* (Meeks and Castenholz, 1971). Following an abrupt shift to a temperature within the "biokinetic" temperature range of the alga (i.e. range of no temperature stress, see Li, 1980), algal growth rates quickly become characteristic of a new temperature (i.e. μ_{\max} if temperature is limiting growth). However, abrupt shifts to temperatures outside the biokinetic range can result in lag-periods for growth. Physiological stabilization of algae to new temperatures has been called temperature adaptation (Stemann-Nielsen and Jorgensen, 1968; Jorgensen, 1968; Morris and Glover, 1974). As stabilization to temperature by *G. tikvahiae* in this study occurred on a time scale of days to weeks (i.e. 9 d, Fig. 7) and within a single generation, the phenomenon is better referred to as temperature acclimation (*sensu* Hochachka and Somero, 1973). Because 15°C is the lower temperature limit for growth of *G. tikvahiae*, this appears to be a resistance-type acclimation

(Precht, 1958). Such lag-periods for growth and resistance acclimations may be ecologically important in the seasonal growth of *G. tikvahiae* at low temperatures in its northern range or during rapid decreases in temperature that occur in winter in subtropical estuaries.

The pronounced effects of temperature on I_k , I_s , α , and μ_{\max} illustrate the importance of temperature on the photosynthetic mechanism and resultant growth of *Gracilaria tikvahiae*. The temperature-dependence of μ_{\max} supports observations of phytoplankton (Eppley, 1972) as well as concepts that enzyme-controlled dark reactions regulate μ_{\max} in algae (Goldman, 1979). However, our observed temperature-dependence of α does not concur with ideas of photosynthesis that consider α to be temperature-independent because of its strict control by photochemical events (Rabinowitch, 1956; Bannister, 1974; Harris, 1978). Increases in α (for growth) with temperature beyond that where μ_{\max} of *G. tikvahiae* plateaued (25°C) resulted in a decrease in I_k and I_s values between 25 and 30°C (Table 1,

Fig. 11). Three-fold changes in α due to temperature effects in *G. tikvahiae* in the present study and the diatom *Skeletonema costatum* (Yoder, 1979), both within physiological temperature ranges, suggest that temperature strongly influences light-limited algal growth. This disparity may be due to different temperature responses for growth and photosynthesis, although this was not resolved in the present study.

Because temperature strongly influences the shape of μ vs I curves in *Gracilaria tikvahiae*, equations that best describe this relationship are temperature specific. Steele's equation (1962), which includes a photoinhibition parameter, fits the 15 °C data best because of the photoinhibition that occurred at I_0 . Between 20° and 30 °C, Steele's equation (1962) overestimated the initial ascent (α) compared to the hyperbolic tangent function (Jassby and Platt, 1975), which fits best in this temperature range. The transition from light-limited to light-saturated photosynthesis is usually more gradual in optically dense material, such as parenchymatous thalli of *G. tikvahiae*, compared to optically thin material (Rabinowitch, 1956). Thus, the hyperbolic tangent function, which gradually ascends from light-limited to light-saturated growth, best describes the μ vs I curve of *G. tikvahiae* at temperatures near those for maximum growth. Two other models considered (Baly, 1935; Michaelis and Menten, 1913) are variations of rectangular hyperbolas and fit the growth data poorly at all temperatures as they consistently underestimated the asymptote, μ_{\max} .

That T_{\max} for growth is lower than T_{\max} for photosynthesis in *Gracilaria tikvahiae* suggests that growth at high temperatures becomes "costly" in terms of respiration and excretion. Temperature affects algal growth by controlling rates of reactions that enhance (i.e. P_s) as well as depress (i.e. R , excretion) the overall growth process (Johnson *et al.*, 1974). Accordingly, the $P_s:R$ and $P_s:P_g$ ratios, both representing the magnitude of these opposing reactions, should represent growth. Maximal values for growth rate and the $P_s:R$ and $P_s:P_g$ ratios occurred at 25 °C for all light levels, suggesting this is the T_{\max} for growth of *G. tikvahiae*. However, P_s increased to 30 °C, resulting in a lack of correlation between growth rate and net photosynthesis. Similarly, the T_{\max} for growth of phytoplankton is less than that for photosynthesis (Li, 1980). This lack of correlation between growth and net photosynthesis probably occurred in *G. tikvahiae* because of high rates of photorespiration and excretion at 30 °C that resulted in lower levels of carbon allocated to growth. This "hidden" loss of carbon to growth illustrates why instantaneous measurements of net photosynthesis alone cannot always be equated to growth.

The overall correlation between growth rate and respiration in *Gracilaria tikvahiae* and *Monochrysis lutheri* (Laws and Caperon, 1976) suggests that the dual function of respiration to provide energy for growth and maintenance in higher plants (Beevers, 1970) also occurs in marine algae. The low Q_{10} values for respiration (ca 1.0) in *G. tikvahiae* at 0.07 I_0 imply that a factor other than tem-

perature, i.e. light, is the major growth limiting factor and lessens the temperature-dependence of respiration (Soeder and Stengel, 1974). Reports of low Q_{10} values for respiration in field studies with seaweeds and phytoplankton (Newell and Pye, 1968; Jones, 1977; Durako and Dawes, 1980) may reflect this dominance of growth-limiting factors other than temperature, possibly light. Our findings of a high interaction term between light and temperature on respiration of *G. tikvahiae* (Table 3) is a good example of interactions between environmental factors, which may be more ecologically important than the main effects (of single factors) themselves.

Although light was the more important factor affecting growth and photosynthesis of *Gracilaria tikvahiae* in this study, temperature modifies the μ vs I curve of *G. tikvahiae* to maximize its seasonal growth. The high correlation between seasonal variation in light intensity and temperature in Florida (Fig. 11) produces this effect. Increasing temperatures during spring months increase I_k and α values for growth, allowing *G. tikvahiae* to utilize the increasing daily light flux more fully during this time. This suggests that temperature may be a "trigger mechanism" controlling seasonal acclimation of seaweeds whose photosynthetic responses in summer are greater than in winter (Zavodnick, 1973; Mathieson and Norall, 1975; Brinkhuis, 1977; Durako and Dawes, 1980). In regard to seasonality of growth limiting factors, the relatively small effect of temperature on μ_{\max} between 20° and 30 °C implies that light will be the more important factor between March and November in Florida. Because whole plants of *G. tikvahiae* can utilize nearly full intensity sunlight in this temperature range (see μ vs I curves, Fig. 4), plants which do not grow in clear, shallow waters will be light-limited. In contrast, temperature is responsible for most of the seasonal variation in growth of *Codium fragile* (Hanisak, 1979), probably because this alga has a low I_k value for photosynthesis and growth (Ramus, 1978).

When temperatures drop to <20 °C, i.e. between November and March in Florida, temperature will become growth-limiting to *Gracilaria tikvahiae* because of depression of μ_{\max} . Extreme temperature limitation would occur during January–February when temperatures drop to <15 °C. The 15 °C lower temperature limit for growth of the Floridian *G. tikvahiae* reported here has also been observed for Canadian *G. tikvahiae* (van der Meer, personal communication). This suggests that the lower temperature limit for growth of this species is genetically fixed and unaffected by the phenotypic plasticity that affects growth rate – temperature relationships in clones of phytoplankton (Sorokin, 1959; Hulbert and Guillard, 1968). Similarly, optimal growth and survival temperatures of four species of *Laminaria* from widely different temperature regimes is brought about by phenotypic plasticity and not genetic selection of races or ecotypes (Bolton and Lüning, 1982). Therefore, growth of *G. tikvahiae* in eastern North America may be restricted to water temperatures ≥ 15 °C, explaining the occurrence of this tropical alga as a summer annual in north temperate waters (Sears, 1971).

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Literature cited

- Baly, E. C. C.: The kinetics of photosynthesis. *Proc. R. Soc. Lond. Ser. B*, *117*, 218–239 (1935)
- Bannister, T. T.: Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. *Limnol. Oceanogr.* *19*, 1–12 (1974)
- Beevers, H.: Respiration in plants and its regulation. *In: Prediction and measurement of photosynthetic productivity*, pp 209–214. Pudoc: Wageningen 1970
- Bolton, J. J. and K. Lüning: Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Mar. Biol.* *66*, 89–94 (1982)
- Brinkhuis, B. H.: Seasonal variations in salt-marsh macroalgae photosynthesis II. *Fucus vesiculosus* and *Ulva lactuca*. *Mar. Biol.* *44*, 177–186 (1977)
- Durako, M. J. and C. J. Dawes: A comparative seasonal study of two populations of *Hypnea musciformis* from the east and west coasts of Florida, USA II. Photosynthetic and respiratory rates. *Mar. Biol.* *59*, 157–162 (1980)
- Eppley, R. W.: Temperature and phytoplankton growth in the sea. *Fish. Bull., U.S.* *70*, 1063–1085 (1972)
- Gessner, F.: Temperature: plants. *In: Marine ecology*, Vol. 2 (1). Ed. by O. Kinne. New York: Wiley-Interscience 1970
- Goldman, J. C.: Outdoor algal mass cultures II. Photosynthetic yield limitations. *Water Res.* *13*, 119–136 (1979)
- Hanisak, M. D.: Growth patterns of *Codium fragile* spp. *tomentosoides* in response of temperature, irradiance, salinity and nitrogen source. *Mar. Biol.* *50*, 319–332 (1979)
- Harris, G. P.: Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. *Ergeb. Limnol.* *10*, 1–171 (1978)
- Hellebust, J. A.: Light: plants. *In: Marine ecology*, Vol. 1 (1). Ed. by O. Kinne. New York: Wiley-Interscience 1970
- Hochachka, P. W. and G. N. Somero: Strategies of biochemical adaptation, 358 pp. Philadelphia: W. B. Saunders 1973
- Hulburt, E. M. and R. R. L. Guillard: The relationship of the distribution of the diatom *Skeletonema tropicum* to temperature. *Ecology* *49*, 337–339 (1968)
- Jassby, A. D. and T. Platt: Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.* *21*, 540–547 (1976)
- Johnson, F. H., H. Eyring and F. J. Stover: The theory of rates and processes in biology and medicine. New York: Wiley 1974
- Jones, R. I.: The importance of temperature conditioning to the respiration of natural phytoplankton communities. *Br. phycol. J.* *12*, 277–285 (1977)
- Jørgensen, E. G.: The adaptation of plankton algae. II. Aspects of the temperature adaptation of *Skeletonema costatum*. *Physiol. Plant.* *21*, 423–427 (1968)
- Kanwisher, J. W.: Photosynthesis and respiration in some seaweeds. *In: Some contemporary studies in marine science*, pp 407–420. Ed. by H. Barnes. London: Allen and Unwin 1966
- Lapointe, B. E. and J. H. Ryther: Some aspects of the growth and yield of *Gracilaria tikvahiae* in culture. *Aquaculture* *15*, 185–193 (1978)
- Lapointe, B. E. and K. R. Tenore: Experimental outdoor studies with *Ulva fasciata* Delile. I. Interaction of light and nitrogen on nutrient uptake, growth, and biochemical composition. *J. exp. mar. Biol. Ecol.* *53*, 135–152 (1981)
- Laws, E. and J. Caperon: Carbon and nitrogen metabolism by *Monochrysis lutheri*: measurement of growth rate dependent respiration rates. *Mar. Biol.* *36*, 85–97 (1976)
- Lederman, T. C. and P. Tett: Problems in modelling the photosynthesis–light relationship for phytoplankton. *Bot. Mar.* *24*, 125–134 (1981)
- Li, W. K. W.: Temperature adaptation in phytoplankton: cellular and photosynthetic characteristics. *In: Primary productivity in the sea*, pp 259–279. Ed. by P. Falkowski. New York: Plenum Press 1980
- Mathieson, A. C. and T. L. Norall: Physiological studies of subtidal red algae. *J. exp. mar. Biol. Ecol.* *20*, 237–247 (1975)
- McLachlan, J.: *Gracilaria tikvahiae* sp. nov. (Rhodophyta, Gigartinales, Gracilariaceae), from the northwestern Atlantic. *Phycologia* *18*, 19–23 (1979)
- Meeks, J. C. and R. W. Castenholz: Growth and photosynthesis in an extreme thermophile, *Synechococcus lividus* (Cyanophyta). *Arch. Mikrobiol.* *78*, 25–41 (1971)
- Michaelis, L. and M. L. Menten: Der Kinetic der invert Inwirkung. *Biochem. Z.* *49*, 333–369 (1913)
- Morris, I. and K. Farrel: Photosynthetic rates, gross patterns of carbon dioxide assimilation and activities of ribulose diphosphate carboxylase in marine algae grown in different temperatures. *Physiol. Plant.* *25*, 372–377 (1971)
- Morris, I. and H. E. Glover: Questions on the mechanism of temperature adaptation in marine phytoplankton. *Mar. Biol.* *24*, 147–154 (1974)
- Newell, R. C. and V. I. Pye: Seasonal variations in the effect of temperature on the respiration of certain intertidal algae. *J. mar. biol. Ass. U.K.* *48*, 341–348 (1968)
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent: Statistical package for the social sciences, 675 pp. New York: McGraw-Hill 1975
- Precht, H.: *In: Physiological adaptation*, Ed. by C. L. Prosser. Washington: American Physiological Society 1958
- Rabinowitch, E. I.: Photosynthesis and related processes, Vol. II, part 2. New York: Interscience 1956
- Ramus, J.: Seaweed anatomy and photosynthetic performance: the ecological significance of light guides, heterogeneous absorption, and multiple scatter. *J. Phycol.* *14*, 352–362 (1978)
- Raven, J. A. and S. M. Glidwell: Photosynthesis, respiration and growth in the shade alga *Hydrodictyon africanum*. *Photosynthetica* *9*, 361–371 (1975)
- Rhee, G. Y. and I. J. Gotham: The effect of environmental factors on phytoplankton growth: temperature and the interactions of temperature with nutrient limitation. *Limnol. Oceanogr.* *26*, 635–648 (1981)
- Sears, J.: Morphology, systematics and descriptive ecology of the sublittoral benthic marine algae of southern Cape Cod and adjacent islands. Ph. D. dissertation, University of Massachusetts 1971
- Silvert, W.: Practical curve fitting. *Limnol. Oceanogr.* *24*, 767–773 (1979)
- Snedecor, G. W. and W. G. Cochran: Statistical methods, 593 pp. Ames: Iowa State University Press 1967
- Soeder, C. J. and E. Stengel: Physico-chemical factors affecting metabolism and growth rate. *In: Algal physiology and biochemistry*, Ed. by W. D. P. Stewart. Oxford: Blackwell 1974
- Sorokin, C.: Tabular comparative data for the low and high temperature strains of *Chlorella*. *Nature, Lond.* *184*, 613–614 (1959)

- Spencer, C. P.: Studies on the culture of a marine diatom. *J. mar. biol. Ass. U.K.* **33**, 265–290 (1954)
- Steele, J. H.: Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.* **7**, 137–150 (1962)
- Steemann-Nielsen, E. and E. G. Jorgensen: The adaptation of plankton algae. I. General Part. *Physiol. Plant* **21**, 401–422 (1968)
- Strickland, J. D. H. and T. R. Parsons: A practical handbook of seawater analysis, 2nd edition, 310 pp. Ottawa: Res. Bd Can. 1972
- Talling, J. F.: Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New Phytol.* **56**, 29–50 (1957)
- Taylor, W. R.: Marine algae of the northeastern coast of North America, 509 pp. Ann Arbor: University of Michigan Press 1957
- Taylor, W. R.: Marine algae of the eastern tropical and subtropical coasts of the Americas, 870 pp. Ann Arbor: University of Michigan Press 1972
- Yoder, J.: Effect of temperature on light-limited growth and chemical composition of *Skeletonema costatum* (bacillariophyceae). *J. Phycol.* **15**, 362–370 (1979)
- Zavodnik, N.: Seasonal variations in rate of photosynthetic activity and chemical composition of the littoral seaweeds common to the North Adriatic. Part I. *Fucus virsoides* (Don). *J. Ag. Bot. Mar.* **16**, 155–165 (1973)