Ecophysiology of the Cyanobacterium *Dactylococcopsis salina*: Effect of Light Intensity, Sulphide and Temperature

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Dactylococcopsis salina is a planktonic gas-vacuolated cyanobacterium that forms a distinct bacterial plate at the metalimnion of Solar Lake, Sinai. Temperature, light intensity and sulphide concentration were examined as possible limiting factors determining the distribution of *D. salina* during the annual limnological cycle of Solar Lake. Both laboratory cultures and *in situ* samples were examined for their photosynthetic activity at a wide range of temperature, light intensity and sulphide concentrations. The cyanobacterium showed a considerable light adaptation and a capacity for photosynthetic activity at high light intensities. It also showed anoxygenic photosynthesis using H_2S as an alternative electron donor, but this activity was only 4% of oxygenic photosynthesis. Furthermore, H_2S was highly toxic to *D. salina* and no CO_2 photoassimilation could be detected at pH 7 and 1 mM-sulphide. Temperature is the primary environmental factor governing the distribution of *D. salina* in Solar Lake.

INTRODUCTION

Solar Lake is a hypersaline waterbody situated on the Sinai coast of the Gulf of Eilat. It is stratified for 10 months of the year and shows a mesothermal profile. Temperatures of up to 63.5 °C were recorded at the metalimnion, while surface temperatures were 25 °C during maximal stratification (Cohen *et al.*, 1977a). The distribution of the main photosynthetic organisms has been described by Cohen *et al.* (1977b). Gas-vacuolated organisms were not described due to inadequate sampling methods used during those investigations. Recently Walsby *et al.* (1983) described the occurrence of the gas-vacuolated cyanobacterium *Dactylococcopsis salina*; during summer holomixis of the lake this cyanobacterium can be found in small numbers throughout the whole watercolumn. With the onset of stratification of the lake a distinct layer of *D. salina* is formed just at the thermocline and this layer persists during the entire period of stratification. In 1981, maximal concentrations of 12900 cells ml^{-1} were found at the peak of stratification in February (Walsby *et al.*, 1983). In spring, during partial mixing of the watercolumn, *D. salina* can be found in a wider layer extending deeper into the watercolumn. Later, with total mixing, *D. salina* is dispersed throughout the whole waterbody of Solar Lake.

Light is a major factor influencing the distribution of this cyanobacterium in Solar Lake. At the depth of occurrence of *D. salina* light intensities of up to 1000 $\mu\text{E m}^{-2} \text{s}^{-1}$ have been measured, which is half of the ambient light intensity in this desert area. The occurrence of sulphide in the lower part of the region where *D. salina* was found to occur is another possible factor influencing the distribution of this cyanobacterium in Solar Lake. Growth of cyanobacteria in the presence of sulphide has been recorded by several investigators (Nakamura, 1937, 1938; Knobloch, 1966; Stewart & Pearson, 1970). Cohen *et al.* (1975) showed sulphide to act as an alternative electron donor in the process of anoxygenic photosynthesis of the cyanobacterium *Oscillatoria limnetica*. Garlick *et al.* (1977) examined 21 strains of

Abbreviation: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea.

cyanobacteria for anoxygenic photosynthesis and showed that this is a common phenomenon in a number of cyanobacteria. *Dactylococcopsis salina* was not found in Solar Lake under high sulphide concentrations, yet it was found to occur at sulphide concentrations of 10 μM during the night (Jørgensen *et al.*, 1979). Sulphide may thus be a limiting factor for the occurrence of *D. salina*. In this paper we report the rate of photosynthesis of *D. salina* under various sulphide concentrations and under different light intensities. The results obtained are compared with those obtained for other non-heterocystous cyanobacteria by Garlick *et al.* (1977).

METHODS

Growth. The growth medium had the following composition (l^{-1}): NaCl, 125 g; $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 10 g; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 3.5 g; KCl, 2.5 g; NaNO_3 , 0.75 g; $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 0.5 g; K_2HPO_4 , 15 mg; Na_2CO_3 , 20 mg; $\text{Na}_2\text{EDTA} \cdot 2\text{H}_2\text{O}$, 0.5 mg; ferric ammonium citrate, 3 mg; citric acid, 3 mg; and 0.1 ml of the trace metal mix A5 (Stanier *et al.*, 1971).

Cultures were grown at 37 °C under continuous illumination provided by white fluorescent light (2300 K, 20 W). Light intensity was adjusted to 35 $\mu\text{E m}^{-2} \text{s}^{-1}$ or 130 $\mu\text{E m}^{-2} \text{s}^{-1}$ (see Results).

CO_2 photoassimilation. Laboratory cultures of *D. salina* were harvested in the exponential phase of growth; in other experiments the cyanobacterium was collected by means of a peristaltic pump from the layer of maximum cell concentration in Solar Lake. Cells were washed twice in growth medium or in filtered Solar Lake water and the experiments were carried out in 3 ml cell suspensions introduced to 5 ml Vacutainers (Becton-Dickinson, Rutherford, N.J., U.S.A.). The cell suspension was preincubated for 1 h at 37 °C under a light intensity of 35 $\mu\text{E m}^{-2} \text{s}^{-1}$. Experiments were carried out in a temperature-controlled Perspex cell with continuous mixing. Light was provided by a 150 W slide projector (Braun, Germany). Various light intensities were obtained by changing the distance between the reaction vessel and the light source. After 5 min preincubation in the described system, 10 μl $\text{NaH}^{14}\text{CO}_3$ [Amersham, U.K.; 500 μCi (18.5 MBq) ml^{-1} , 60 mCi (2.2 GBq) mmol^{-1} , made up in 0.1 M-Tris buffer, pH 9.2] was added. Experiments were carried out for 5 min and then the cell suspension was filtered immediately through a GF/c filter (Whatman, U.K.). Filters were exposed overnight to fuming HCl in a desiccator. Then 5 ml Insta Gel (Packard) was added and the radioactivity was measured using a Tri-Carb liquid scintillation counter (Packard, model 3255).

In experiments to measure the anoxygenic CO_2 photoassimilation, the cells were buffered with Tricine (1 mM, pH 8), and DCMU (5 μM) was added. Sulphide in the form of Na_2S was added to each sample after flushing the medium with N_2 . In these experiments the samples were preincubated in the light for at least 2 h to ensure an adequate induction period for anoxygenic photosynthesis (Oren *et al.*, 1977).

Temperature tolerance. Cells were grown in Solar Lake water. The cultures were preincubated for 10 min at a given temperature and then $\text{NaH}^{14}\text{CO}_3$ with a final concentration of 0.5 μCi (18.5 kBq) ml^{-1} [260 μCi (9.6 MBq) mmol^{-1}] was added. After 30 min incubation, cells were filtered through GF/c (Whatman, U.K.) filters and the filters were counted for radioactivity after being exposed overnight to HCl fumes. The following temperatures were used: 27 °C, 35 °C, 40 °C, 45 °C, 50 °C, 55 °C and 60 °C.

Assays. Chlorophyll *a* and carotenoids were measured according to Strickland & Parsons (1968). Sulphide was determined by the methylene blue method (Cline, 1969). Light intensity was measured with a Lamda photometer (QRP 361).

RESULTS

Light adaptation experiments

Two photosynthetic parameters were determined in order to define the photosynthetic activity of *D. salina* under different environmental conditions: P_m , the maximal rate of photosynthesis at light saturation, and I_k , the light intensity at which a photosynthetic rate numerically equal to P_m would be reached in the absence of light saturation (Talling, 1957).

A batch culture of *D. salina* grown under low light conditions (35 $\mu\text{E m}^{-2} \text{s}^{-1}$) was examined for CO_2 photoassimilation. The light saturation curve of this culture of *D. salina*, with a carotenoid:chlorophyll *a* ratio of 0.4, showed a P_m of $2.96 \times 10^5 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$ and an I_k of 280 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 1). Another batch culture of *D. salina* was grown in the laboratory under a constant illumination of 130 $\mu\text{E m}^{-2} \text{s}^{-1}$. The light saturation curve indicated a considerable increase in I_k up to 540 $\mu\text{E m}^{-2} \text{s}^{-1}$, with a lower P_m value of only $1.05 \times 10^4 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$, using a culture with a carotenoid:chlorophyll *a* ratio of 1.1 (Fig. 1). The light saturation curve of *D. salina* collected from Solar Lake on the day of

Fig. 1. Rate of oxygenic CO_2 photoassimilation per mg chlorophyll *a* of *D. salina* as a function of irradiation. Cells were collected in the exponential phase of growth in the laboratory or from the depth of maximum occurrence in Solar Lake. $\text{NaH}^{14}\text{CO}_3$ incorporation was carried out for 5 min at a specific light intensity. O, Cells grown in the laboratory under $35 \mu\text{E m}^{-2} \text{s}^{-1}$; ● (right-hand scale), cells grown in the laboratory under $130 \mu\text{E m}^{-2} \text{s}^{-1}$; Δ, cells collected from Solar Lake. The P_m and I_k of each experiment are shown on the ordinate and abscissa, respectively, by the extrapolated dashed lines.

Fig. 2. Rate of anoxygenic CO_2 photoassimilation per mg chlorophyll *a* of *D. salina* as a function of Na_2S concentration. Cells were preincubated for 2 h under Na_2S and $5 \mu\text{M}$ -DCMU in the light before $\text{NaH}^{14}\text{CO}_3$ incorporation was carried out (for 5 min). The broken line indicates the level of residual CO_2 photoassimilation of cells which were incubated with $5 \mu\text{M}$ -DCMU in the absence of sulphide.

experimentation showed a linear increase in CO_2 photoassimilation up to $860 \mu\text{E m}^{-2} \text{s}^{-1}$, and the P_m was $8.33 \times 10^4 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$ (Fig. 1). The interpolated I_k value was $920 \mu\text{E m}^{-2} \text{s}^{-1}$ and the carotenoid:chlorophyll *a* ratio was 1.2.

Anoxygenic CO_2 photoassimilation

Figure 2 shows the CO_2 photoassimilation of *D. salina* under different sulphide concentrations. An increase in CO_2 photoassimilation was observed from $0.1 \text{ mM-Na}_2\text{S}$ to $1 \text{ mM-Na}_2\text{S}$. Yet even at the latter sulphide concentration the CO_2 photoassimilation rate was only $7.67 \times 10^3 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$. In the sulphide range $1.1\text{--}3 \text{ mM-Na}_2\text{S}$ the rate was constant at $7.08 \times 10^3 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$. Increasing the Na_2S concentration to 4 and 5 mM resulted in a considerable drop of CO_2 photoassimilation to a minimum rate of $3.58 \times 10^3 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$. The residual CO_2 photoassimilation of *D. salina* under oxic conditions with the addition of DCMU was 38% of the maximum CO_2 photoassimilation.

The light saturation curve of *D. salina* under $0.4 \text{ mM-Na}_2\text{S}$ showed a linear increase in CO_2 photoassimilation up to $250 \mu\text{E m}^{-2} \text{s}^{-1}$ (Fig. 3); the P_m was $5.67 \times 10^3 \text{ nmol CO}_2 (\text{mg chl. } a)^{-1} \text{ h}^{-1}$.

Fig. 3. Rate of anoxygenic CO_2 photoassimilation per mg chlorophyll *a* of *D. salina* as a function of irradiation. Cells were collected in the exponential phase of growth in the laboratory or from the depth of maximum occurrence in Solar Lake. Cells were preincubated under sulphide and DCMU for 2 h before addition of $\text{NaH}^{14}\text{CO}_3$. ○, Anoxygenic CO_2 photoassimilation under 0.4 mM- Na_2S ; ●, anoxygenic CO_2 photoassimilation under 1.0 mM- Na_2S ; △, anoxygenic CO_2 photoassimilation under 1.2 mM- Na_2S . The P_m and I_k of each experimental condition are shown by the extrapolated dashed lines.

Fig. 4. Oxygenic (○) and anoxygenic (●) CO_2 photoassimilation per mg chlorophyll *a* of *D. salina* as a function of pH. Up to pH 7.5 cells were buffered with 1 mM-HEPES, and from pH 7.5 and higher cells were buffered with 1 mM-Tricine.

chl. *a*) $^{-1}$ h $^{-1}$, the I_k was 400 $\mu\text{E m}^{-2} \text{s}^{-1}$, and the carotenoid:chlorophyll *a* ratio was 0.6. Under 1.0 mM- Na_2S (Fig. 3) a linear increase in CO_2 photoassimilation up to 150 $\mu\text{E m}^{-2} \text{s}^{-1}$ was observed; the P_m was 4.58×10^3 nmol CO_2 (mg chl. *a*) $^{-1}$ h $^{-1}$, the I_k was 240 $\mu\text{E m}^{-2} \text{s}^{-1}$, and the carotenoid:chlorophyll *a* ratio was 0.5.

The anoxygenic CO_2 photoassimilation of a natural population of *D. salina* was examined under 1.2 mM- Na_2S (Fig. 3). CO_2 photoassimilation increased linearly up to 110 $\mu\text{E m}^{-2} \text{s}^{-1}$. The P_m was 3.33×10^2 nmol CO_2 (mg chl. *a*) $^{-1}$ h $^{-1}$, the I_k was 120 $\mu\text{E m}^{-2} \text{s}^{-1}$, and the carotenoid:chlorophyll *a* ratio was 1.2.

Effect of pH on aerobic and anaerobic CO₂ photoassimilation

The CO_2 photoassimilation of *D. salina* was examined at different pH values under oxic and anoxic conditions (Fig. 4). Under oxic conditions the CO_2 photoassimilation rate was constant over the pH range 6.5–9.2. The average CO_2 photoassimilation was 2.33×10^4 nmol CO_2 (mg chl. *a*) $^{-1}$ h $^{-1}$. In a similar experiment under anoxic conditions (1.2 mM- Na_2S), no CO_2 photoassimilation could be detected below pH 7. A steady increase in CO_2 photoassimilation was measured at higher pH values, with a maximum rate of 2.25×10^4 nmol CO_2 (mg chl. *a*) $^{-1}$ h $^{-1}$ at pH 9.2 (Fig. 4). Both experiments were carried out with the same culture of *D. salina* at a light intensity of 75 $\mu\text{E m}^{-2} \text{s}^{-1}$.

Fig. 5. Relative CO₂ photoassimilation rate of a culture of *D. salina* at different temperatures. Cells were preincubated at the indicated temperature for 10 min prior to incubation with NaH¹⁴CO₃ (for 30 min).

Effect of temperature on photosynthetic activity

The photosynthetic activity of *D. salina* at different temperatures revealed a sharp optimum curve, with maximal CO₂ photoassimilation activity at 40–45 °C (Fig. 5). The temperature sensitivity was observed in short incubation periods of 30 min.

DISCUSSION

Dactylococcopsis salina responded to different light intensities by increasing its I_k considerably with increasing light intensity. Growth under high light intensity also resulted in a decrease in the chlorophyll *a* content and a consequent increase in the carotenoid:chlorophyll *a* ratio. The adaptation to high light intensities was demonstrated by electron microscopy, which showed a marked decrease in the photosynthetic lamellae and cytoplasmic space (Fig. 6). Though the organism grows *in situ* under high light intensities, the P_m of organisms grown under low light was considerably higher than that of organisms grown in the laboratory under high light intensities and that of organisms collected directly from Solar Lake.

Walsby *et al.* (1983) have shown that *D. salina* is found throughout the hypolimnion at the onset of stratification. With the buildup of mesothermy in Solar Lake (Cohen *et al.*, 1977a), the distribution of *D. salina* is limited to the metalimnion. The light intensity at the peak of distribution is suboptimal yet the organism is well adapted to growth under those conditions. The adaptability of *D. salina* to growth at different light intensities is much more pronounced than that reported for other cyanobacteria and green algae (Table 1).

Dactylococcopsis salina appeared blue-green in colour when grown under low light intensities, becoming a deep orange colour when grown under high light intensities. This colour change is due to a drastic increase in the carotenoid:chlorophyll *a* ratio, which suggests a protective role for carotenoids in the adaptation of the organism to high light intensity (Krinsky, 1966).

Since *D. salina* showed a considerable degree of adaptation to high light intensities, light cannot be the major limiting factor controlling its distribution.

Another possible environmental factor limiting the distribution of *D. salina* in Solar Lake is sulphide. Sulphide concentrations in the hypolimnion of Solar Lake build up to 3 mM (Cohen *et al.*, 1977b), yet *D. salina* was never found at sulphide concentrations higher than 10 µM. It was found to carry out anoxygenic photosynthesis under a broad range of sulphide concentrations (0.2–4.5 mM-Na₂S). The maximal rate of anoxygenic photosynthesis was comparable to the rates found by Garlick *et al.* (1977) for a variety of cyanobacteria. As expected, the toxicity of sulphide was pH dependent (Fig. 4), as was found by Hawsley & Pearson (1979). The oxygenic photosynthesis, on the other hand, was unaffected by changes in pH from 6.5 to 9.2. No anoxygenic photosynthesis could be recorded at pH values below 7. A steady increase of this activity was demonstrated with increasing pH values and the anoxygenic photosynthetic rate at pH 9.2 was similar to the oxygenic photosynthetic rate. This finding points to a H₂S sensitivity

Fig. 6. Transmission electron micrograph of *D. salina* grown under a light intensity of $35 \mu\text{E m}^{-2} \text{s}^{-1}$ (a), and $130 \mu\text{E m}^{-2} \text{s}^{-1}$ (b). CW, cell wall; TH, thylakoids; PB, polyphosphate bodies; PP, polyphosphate granules. The bar markers represent $1 \mu\text{m}$ (magnification $\times 13750$).

Table 1. I_k values obtained with cyanobacteria and green algae grown at different light intensities

The I_k values were interpolated by the present authors. Where possible, the light intensities were converted into $\mu\text{E m}^{-2} \text{ s}^{-1}$. The following conversion factors were used: $1 \text{ W cm}^{-2} = 1/40952 \mu\text{E m}^{-2} \text{ s}^{-1}$; $1 \text{ quantum cm}^{-2} \text{ s}^{-1} = 1.47 \times 10^{15} \mu\text{E m}^{-2} \text{ s}^{-1}$; $1 \text{ foot-candle} = 0.1807 \mu\text{E m}^{-2} \text{ s}^{-1}$.

Organism	Light intensity during growth ($\mu\text{E m}^{-2} \text{ s}^{-1}$)	Temperature during growth ($^{\circ}\text{C}$)	I_k ($\mu\text{E m}^{-2} \text{ s}^{-1}$)	Author(s)
Cyanobacteria				
<i>Anacystis nidulans</i>	10	30	200	Vierling & Alberte
	100	30	300	(1980)
<i>Anacystis nidulans</i>	80 W	39	72	Myers & Kratz
	960 W	39	260	(1955)
<i>Synechococcus elongatus</i>	50	NG	80	Jørgensen (1969)
	500	NG	160	
<i>Dactylococcopsis salina</i>	35	40	260	This paper
	130	40	540	
	1000	37–42	920	
Green algae				
<i>Chlorella vulgaris</i>	11	20	22	Steemann Nielsen
	110	20	51	(1962)
<i>Scenedesmus obliquus</i>	20	30	122	Senger & Fleishhacker
	115	30	400	(1978)

NG, Not given.

of *D. salina*. Since the *in situ* pH values at the depths of sulphide occurrence are around 7.5 (Cohen *et al.*, 1977a), anoxygenic photosynthesis of *D. salina* cannot be significant. Furthermore, under these conditions even at low sulphide concentrations H_2S is toxic for *D. salina*.

Dactylococcopsis salina shows optimal photosynthetic activity at 40–45 $^{\circ}\text{C}$, with a sharp drop in activity at higher and lower temperatures (Fig. 5). *In situ* measurements of photosynthetic activity were carried out on a natural population of *D. salina* collected from the peak distribution layer and later placed in light and shaded dialysis bags and incubated at various depths (Walsby *et al.*, 1983). CO_2 photoassimilation was inhibited in dialysis bags incubated both in the epilimnion – above peak distribution, at 25 $^{\circ}\text{C}$ – and at the hypolimnion – below peak distribution, at 52 $^{\circ}\text{C}$. Inhibition of CO_2 photoassimilation was observed in both the shaded and light dialysis bags, possibly ruling out photoinhibition as a major controlling environmental factor. Inhibition of CO_2 photoassimilation at the epilimnion under low temperatures and at the hypolimnion under high temperatures coincided well with the temperature sensitivity of cultures of *D. salina*. Thus we conclude that vertical migration of the planktonic gas-vacuolated *D. salina* during the annual limnological cycle of Solar Lake is governed primarily by water temperature.

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