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Photosynthesis and Growth of the Filamentous Blue-green Alga *Lyngbya birgei* in Relation to its Environment[1]

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ABSTRACT

Lyngbya birgei G. M. Smith is a filamentous blue-green alga causing increasing weed problems in the Southern U.S. In the summer, standing stock biomass values of up to 12.0 and 1.8 kg/m² were measured for benthic growth and floating mats, respectively. The net photosynthetic rate of this alga had a high temperature optimum, low light requirement, and was O_2 insensitive up to 200% of air-equilibration O_2 levels. In addition, *Lyngbya* was an efficient HCO_3^--user, showing saturation of photosynthesis at 0.3 mM. In the laboratory, growth under lake-like conditions of light and temperature was saturated at 2 mM HCO_3^-, a concentration commonly found in lakes containing *Lyngbya*. The "opportunistic" photosynthetic traits, which may be the basis for *Lyngbya's* success, are discussed with respect to environmental conditions typically prevailing in dense *Lyngbya* mats.

Key words: pH, bicarbonate-utilization, temperature, light, biomass, competition.

INTRODUCTION

It has become apparent during the past few years that filamentous algae, including blue-greens (Cyanobacteria), increasingly contribute to aquatic weed problems in the southern U.S. This trend is substantiated by records of yearly increases in coverage by filamentous algae in several Florida lakes (12, 13, 14). In addition, aquatic plant managers have reported limited success in controlling these plants with herbicides labeled for aquatic use (e.g. P. Myers, pers. comm.).

Among the blue-green filamentous algae causing noxious growth in the midwest are the genera *Oscillatoria* and *Lyngbya* (7). Similarly, in a preliminary survey of four southern Georgia and Florida lakes containing large amounts of filamentous algae (July, 1985), we found *Lyngbya birgei* to be the predominant species. Two of the lakes had previously been successfully managed with herbicides to control angiosperms. *Lyngbya birgei* was also present in a fifth, *Hydrilla*-dominated, lake although in small amounts. Thus, it appears that the growth of this species is becoming a major nuisance in several bodies of water.

The literature contains little information on the ecophysiology of filamentous blue-green algae such as *Lyngbya*. It is of relevance, however, to note that several species of laboratory-cultured unicellular blue-greens possess an efficient system to actively take up exogenous dissolved inorganic carbon (DIC) in the form of HCO_3^- (5). This trait, if present also in the filamentous forms, would be advantageous in stagnant waters of high pH where DIC diffusion rates are low and HCO_3^- is the predominant DIC source. Indeed, it has been noted that *Lyngbya* thrives in water of high pH (16).

It is not clear whether algal species such as *Lyngbya* directly compete with, and displace, macrophytes such as *Hydrilla* or grow opportunistically in niches cleared of vascular species by successful management. In any event, once established, a filamentous algal mat could potentially by itself augment the high pH conditions favoring its growth, and thus impede the re-establishment of indigenous species.

The aim of this work was to investigate the photosynthetic and growth responses of *Lyngbya* under conditions prevailing in *Lyngbya*-infested lakes. Such data should provide initial indications as to the strategies of *Lyngbya* growth and infestations in lakes of the Southern U.S.

MATERIALS AND METHODS

Field studies. Biomass was determined for benthic growth and floating mats in five lakes or ponds (Lake Blackshear, Crisp County, Georgia; Horseshoe Lake, Polk County, Florida; Ewing Pond, Polk County, Florida; Hammock Pond, Alachua County, Florida; Newnins Lake, Alachua County, Florida). The plants were collected from inside 0.25 m² quadrats placed on the bottom as well as on the floating mat. Samples were thoroughly rinsed of debris before being drip dried and weighed (fresh weight, FW), and then oven dried (80°C) and weighed (dry weight, DW).

At the time of sampling, temperature, quantum irradiance, O_2 concentration and pH were measured both in the floating mat and open water. These measurements, as well as titrations and calculations of HCO_3^-, CO_3^{2-} and CO_2 concentrations, were also performed in Lake Blackshear on a diel basis.

Laboratory studies. Plants were grown in 1 l Erlenmeyer flasks at 30/22 °C (day/night), a 14-h photoperiod and a quantum irradiance of 200 μmol/m²•s (400-700 nm). Each flask contained 0.1-0.2 g FW initially. The growth medium was a 5% (v/v) Hoagland solution (6) containing 5 mM NaCl to which, in some cases, 1, 2 or 10 mM $NaHCO_3$ was added. These growth solutions were changed every other day. Plants were blotted dry and weighed every third day over a three week period, and growth was expressed as the relative growth rate.

The responses of net photosynthetic rate to light, temperature, O_2 concentration, pH and DIC concentration were measured in a Hansatech O_2 electrode system. The

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standard conditions used were 30°C, 200 μmol/m^2•s quantum irradiance, and 1.0 mM HCO_3^- at pH 8.05. Routinely, 20-50 mg of *Lyngbya* filaments were incubated in 2.5 ml of the Hoagland solution in the O_2 electrode system. In experiments starting with more than 1 mM HCO_3^-, O_2 levels in the experimental solution were reduced to about 80 μM by N_2 sparging before closing the system and starting measurements. In some cases, N_2, O_2 or air was bubbled through the system in order to provide low, high, or air-equilibriated (246 μM at 30°C) O_2 levels prior to measurements. Because of the alkaline pH, the total DIC concentration was lowered by less than 5% during such spargings. Photosynthetic rates were calculated from the slopes of the O_2 evolution graphs.

Levels of DIC were varied in two ways. In the first, 5% Hoagland solutions were prepared with the addition of 0.05, 0.10, 0.25 and 2.0 mM $NaHCO_3$. These solutions were sparged, at 30°C, with air containing 340 μl CO_2/l for at least 15 h. When a final stable pH was attained, the solutions had reached equilibrium between HCO_3^-, dissolved CO_2 and air-CO_2. The final pH values were within 0.1 pH unit of the calculated values, the latter being 6.75, 7.05, 7.45 and 8.35, respectively. By this method, different HCO_3^- concentrations were prepared while maintaining the dissolved free CO_2 concentration at air-equilibrium levels (11.2 μM at 30 C). This method has been described in more detail previously (2). To retard pH changes which would alter the balance between HCO_3^- and CO_2, during photosynthesis, 20 μl aliquots of HEPES (N-2-hydroxyethylpiperazine-N'-2-ethanesulfonic acid) for pH values below 7.5 and TRIZMA BASE (tris(hydroxymethyl)aminomethane) above 7.5, at the appropriate pH, were injected into the O_2 system immediately after closing it to give a final concentration of 10 mM.

In the second technique, the HCO_3^- concentration was varied by injecting various amounts of $Ba(OH)_2$ into the experimental solution, during steady state photosynthesis, while monitoring pH as well as O_2 evolution. The initial 5% Hoagland solution was prepared with 1 mM $NaHCO_3$ (pH 8.05 at 30°C). Using this system, it was possible to determine photosynthesis solely as a function of the HCO_3^- concentration, because the free CO_2 concentrations were negligible. This method also has been described earlier (2). A computer program ("CARBON") was used to calculate concentrations of the various DIC forms as a function of pH, temperature, total DIC (or CO_2 concentrations of the air phase) and ionic strength for both the first (open) and second (closed) equilibrated system. This program is available upon request.

Chlorophyll a was extracted in N,N-dimethyl formamide. The concentrations were measured spectrophotometrically and calculated according to Moran (9).

RESULTS

The *Lyngbya* biomass usually occurred both attached to the hydrosoil and as floating mats. The *in situ* measured biomass varied from 0.7 to a high of 13.8 kg/m^2. In all cases, much more biomass occurred on the bottom than in the floating mats. *Lyngbya* thus showed variable amounts of plant material in all lakes studied (Table 1). Microscopic examination revealed that at least 95% of the plant material in the mats was *Lyngbya birgei.* The data shown from Lake Blackshear would suggest that substantially greater biomass occurred during the summer months. The mean DW/FW ratio of *Lyngbya* was 0.14. With only one exception, the daytime pH was alkaline, even in open water.

TABLE 1: STANDING STOCK BIOMASS OF *LYNGBYA BIRGEI* IN FIVE LAKES AND PONDS. t, TOP (FLOATING MAT); b, BOTTOM; m, MAT; o, OPEN WATER; MEANS OF FIVE MEASUREMENTS (FOR BIOMASS ± S.D.).

		Biomass		Temp	pH	
		FW (kg/m^2)	DW	(C)	m	o
Lake Blackshear						
July 15, '85	t	1.8±0.20	0.14±0.03	31	9.2	8.5
	b	12.0±2.2	1.3±0.27	27	—	—
Oct. 14, '85	t	1.6±0.17	0.21±0.04	see Figure 1		
	b	2.4±0.15	0.35±0.03	—	—	—
Feb. 18, '86	t	none		18	—	7.0
Horseshoe Lake						
Sept. 9, '85	t	none		31	—	8.5
	b	2.8±1.0	0.34±0.12	—	—	—
Feb. 4, '86	t	none		20	—	8.5
	b	0.76±0.16	0.12±0.01	—	—	—
Ewing Pond						
Sept. 9, '85	t+b	5.5±1.9	0.61±0.28	31	9.5	9.0
Feb. 4, '86	t	none		21	—	8.3
	b	1.2±0.44	0.25±0.01	—	—	—
Hammock Pond						
Jan. 6, '86	t	1.8±0.58	0.27±0.06	19	10.8	8.0
	b	1.1±0.80	0.17±0.03	14	—	—
Newnins Lake						
Jan. 21, '86	t	none		17	—	6.6
	b	1.0±0.16	0.16±0.10	—		—

Diel fluctuations in various environmental parameters of a *Lyngbya* mat in Lake Blackshear during late summer are shown in Figure 1. Both temperature and O_2 concentrations in the mat increased drastically during the day, but then declined during the late afternoon and evening (Fig. 1A). The O_2 concentrations were well above air equilibrium levels between 8:30 and sunset, reaching a high at noon of over 200% air equilibration. A continuous increase in pH throughout the day was paralleled by decreasing HCO_3^- concentrations as CO_3^{2-} was being formed; free CO_2 was rapidly reduced to below measurable levels (<1 μM) following the first few hours of daylight (Fig. 1B). Typical quantum irradiances found below floating *Lyngbya* mats were 25-50 μmol/m^2•s on sunny days when the surface irradiance approached 2000 μmol/m^2•s.

Table 2 shows the relative growth rates as a function of DIC concentration for plants grown in a controlled environment chamber under temperature and photoperiod conditions similar to those encountered during the summer in Florida lakes. In one experimental series, pH was allowed to drift as in lake situations within a *Lyngbya* mat. In the other series, pH was maintained with buffers. No significant difference in growth rates were detected between buffered and non-buffered solutions. Growth occurred even in solutions lacking added HCO_3^-, probably as a result of dissolved air CO_2. However, a four-fold increase in growth was found upon addition of 2 mM HCO_3^-. A higher level of HCO_3^- did not further enhance growth rates.

The photosynthetic response of *Lyngbya* to light, at saturating DIC levels, revealed low compensation and saturation quantum irradiances of 20 and 150 μmol/m^2•s, respectively (Fig. 2A). Dark respiration rates were about 25% of the maximum photosynthetic rates. In a similar experi-

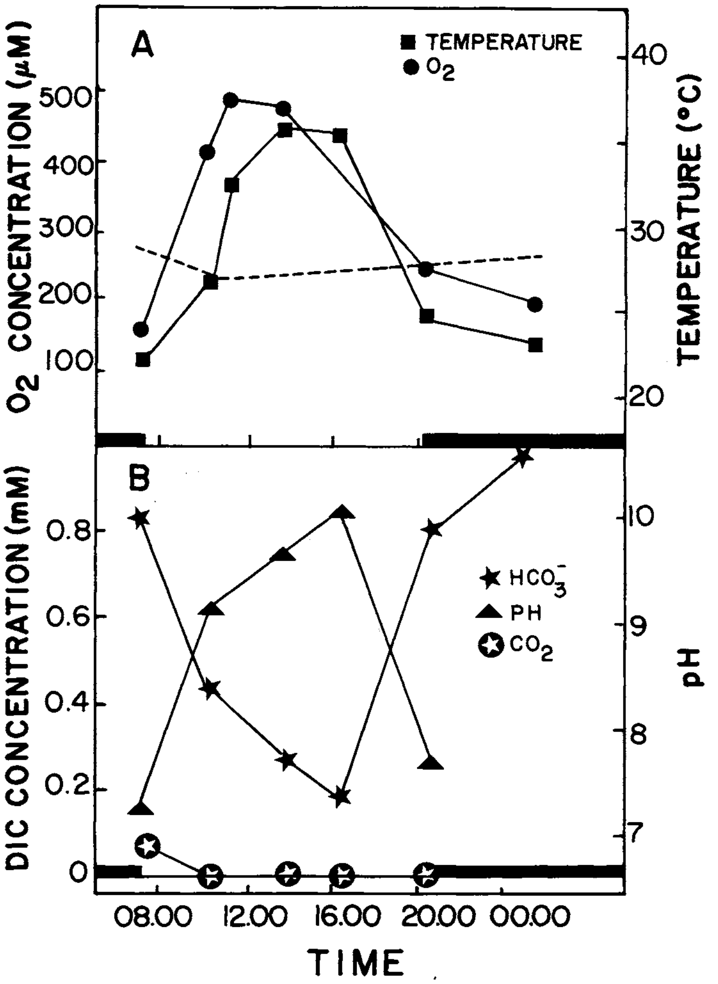

Figure 1. Diel fluctuations in A) temperature and O_2 levels and B) pH and dissolved inorganic carbon (DIC), in Lake Blackshear, Oct. 13-14, 1985, as measured in a floating *Lyngbya birgei* mat. Dashed line represents air equilibration O_2 concentrations at the respective temperatures.

ment, at saturating light and DIC, net photosynthesis showed a linear response to increasing temperature between 10 and 40°C (Fig. 2B). Both of these effects were studied on a field-grown material soon after collection.

The photosynthetic response of field-grown *Lyngbya* to DIC is depicted in Figure 3. Saturation was reached at 0.25-0.30 mM; the slightly lower value was obtained when 11.2 µM CO_2 was present (the first technique described in Materials and Methods) while the higher value represents the response to HCO_3^- only (the second technique described in Materials and Methods). The photosynthetic rate at an air-equilibrated CO_2 concentration (11.2 µM at 30°C) from extrapolation to zero HCO_3^- is about 40% of the maximal rates obtained at HCO_3^- saturation. The HCO_3^- response curve of net photosynthesis passing almost through the origin indicates a very low DIC compensation point for *Lyngbya*. A similarly low free CO_2 compensation point of less than 10 µl CO_2/l has been measured with an infra-red CO_2 gas analysis system (Spencer, Beer and Bowes, 1985, unpublished data).

TABLE 2: RELATIVE GROWTH RATES (RGR) OF LABORATORY-GROWN *LYNGBYA BIRGEI* AT A QUANTUM IRRADIANCE OF 200 µMOL/M²•S, 30/22°C DAY/NIGHT TEMPERATURE AND A 14-H PHOTOPERIOD. PLANTS WERE GROWN IN 5% HOAGLAND GROWTH MEDIUM WITH OR WITHOUT THE ADDITION OF HCO_3^- AND WITH (+) OR WITHOUT (–) THE ADDITION OF 10 MM BUFFER. DATA ARE MEANS OF SEVEN MEASUREMENTS ± S.D.

HCO_3^- conc. (mM)	Buffer	RGR (% week^{-1})	Initial pH
0.0	–	10.2± 3.0	6.0
0.0	+	11.4± 3.1	8.2
2.0	–	41.2± 7.0	8.3
2.0	+	45.4±10.4	8.2
10.0	–	38.5±10.0	8.8
10.0	+	29.4± 8.8	8.2

TABLE 3: O_2 EFFECTS ON LABORATORY-GROWN *LYNGBYA BIRGEI* NET PHOTOSYNTHETIC RATES (PS) AT TWO DIFFERENT DIC CONCENTRATIONS. DATA ARE MEANS OF FOUR MEASUREMENTS ± S.D. CHL A CONTENT AVERAGED 1.81 ± 0.31 MG/G FW.

DIC conc. (mM)	O_2 conc. (µM)	O_2 in air (%)	Net PS rates (µmol O_2/gFW•h)
0.2	140-170	12-16	248.3±26.8
	230-270	20-23	254.4±53.2
	310-350	26-30	240.0±45.0
1.0	80-120	7-10	284.8±52.0
	230-270	20-23	257.8±24.2
	350-460	30-39	267.8±25.2

Table 3 shows the photosynthetic response of *Lyngbya* to various O_2 concentrations in the experimental medium. No significant differences in net photosynthetic rate were found between low, ambient and high O_2 levels, at either DIC concentration utilized. The somewhat lower photosynthetic rates at 0.2 mM DIC are probably due to this DIC concentration being below the saturation requirement (cf. Fig. 3).

DISCUSSION

The naturally occurring standing crops of *Lyngbya* we have measured in infested lakes show, for submersed aquatic macrophytes, very high biomass values. At peak season, they are about 10-20 times higher than those reported for *Limnophila* and *Hygrophila* (15), and *Elodea* (10). With a standing crop of up to 12 kg/m², *Lyngbya* even surpasses *Hydrilla* for which maximal biomass values of 5-8 kg/m² have been reported (3, 8). Apparently *Lyngbya*, like *Hydrilla*, has the capacity to produce dense mats of vegetation at the water surface, and therefore has the potential to be a serious weed problem.

Where found in large quantities, *Lyngbya* appears in two growth states: attached to the bottom, and as floating, unattached mats. *Lyngbya* can under both these conditions be considered a monoculture since the presence of other, mostly filamentous, algae was less than 5%. Infestations of this weed appear with lush growth on sandy and silty hydrosoils. When the bottom layer has acquired sufficient biomass, masses of filaments become buoyant due to entrapped O_2 bubbles, and float up to the surface. These floating mats can be of considerable thickness (up to 0.5 m), and may well be an important means of dispersal of the plant to different areas of the lake. Filaments on the upper side of the mat often have a bleached appearance, while those in the middle and bottom parts are of "healthy", blue-green, color. The floating mat is photosynthetically active as indicated by the high pH and O_2 concentration in the surface water. The data acquired indicate that seasonal changes in biomass take place with a peak occurring in the summer months.

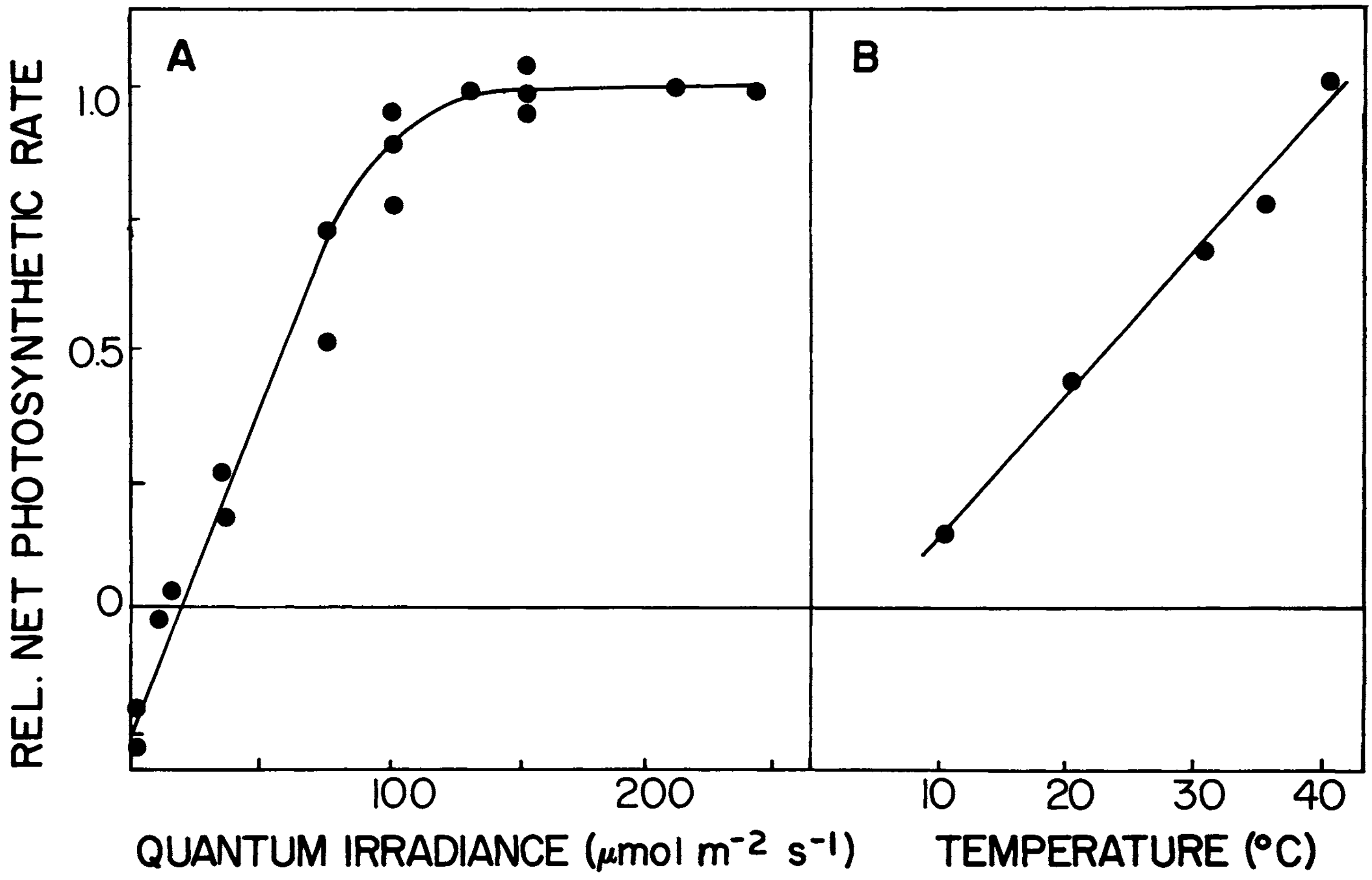

Figure 2. Net photosynthetic rates of field-grown (from Lake Blackshear) *Lyngbya birgei* in response to A) quantum irradiance and B) temperature. Each data point represents one measurement (A) or the mean of three measurements with S.D. being <15% of the means (B). The light- and DIC-saturated rate at 30°C was 380 ± 40.5 μmol O_2/gFW•h. Chlorophyll a content average 2.11 ± 0.21 mg/gFW.

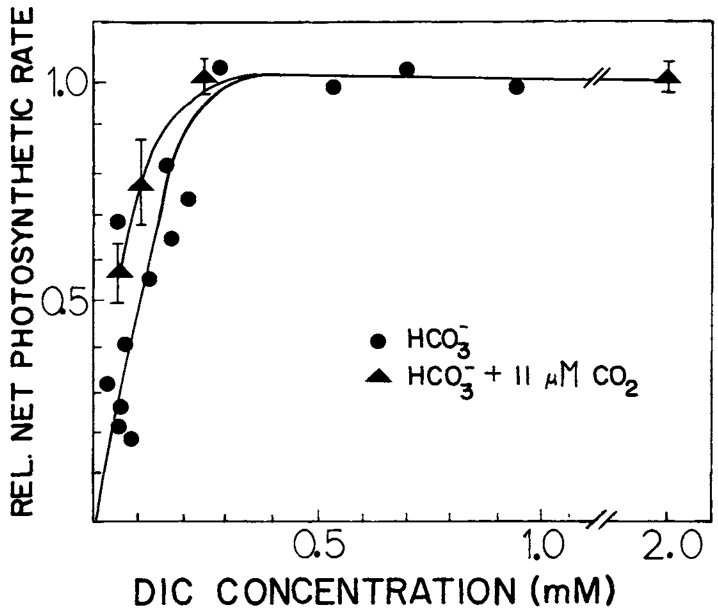

Figure 3. Net photosynthetic rates of field-grown *Lyngbya birgei* as a function of dissolved inorganic carbon (DIC). Circles, each data point represents one measurement; triangles, each data point represents the mean of four measurements ± S.D. The maximum photosynthetic rate was 328 ± 47.3 μmol O_2/gFW•h. Chlorophyll a content as in Figure 2.

The photosynthetic light response curve for *Lyngbya* shows lower saturation values than found in other mat forming aquatic macrophytes, including *Hydrilla* (17). On the other hand, the light compensation point is in the same range as for other indigeous species, but higher than that for *Hydrilla* (17). The low quantum irradiance requirements of *Lyngbya* may explain its lush growth at the bottom, as well as its bleached appearance at the upper part of the floating mats where light levels are high.

An apparent advantage of *Lyngbya* photosynthesis is its high temperature optimum of at least 40°C. This likely reflects the growth response, and stands in contrast to the 25-30°C optima found for other aquatic plants including *Hydrilla* (1, 15). The favorable response at high temperatures correlates with the high temperatures measured in dense floating *Lyngbya* mats during the summer and fall months.

Lyngbya can utilize HCO_3^- as an external DIC source very efficiently, as shown by the low DIC levels required to saturate photosynthesis and growth. By comparison, the HCO_3^- level required to saturate photosynthesis in aquatic angiosperms such as *Hydrilla* and *Myriophyllum* is about tenfold higher (4,17). This conforms with a typical algal mat situation where HCO_3^- is virtually the only DIC source available, although its level does decrease during the day, and CO_2 levels are close to zero. The efficient HCO_3^- utilization (or concentrating) system may, as in the unicellular blue-greens (5), give rise to high internal DIC levels which can suppress photorespiration.

Evidence for an apparent lack of photorespiration in *Lyngbya* can be seen in the lack of inhibition of photosynthesis in response to O_2 levels up to twice those of air-equilibrium values. This O_2-insensitivity is more pronounced than that found in other aquatic macrophytes (15). In *Hydrilla,* insensitivity of photosynthesis to 21% O_2 has been reported, but only in plants pre-adapted to summer (i.e. "stress") conditions (11). In contrast, this phenomenon was expressed by *Lyngbya* in field-grown plants even during the winter. The low DIC and CO_2 compensation points also are indicative of little, if any, photorespiratory CO_2 release in this organism.

There seems to be a positive relationship between many eco-physiological responses of *Lyngbya* and conditions prevalent in *Lyngbya* mats. The temperature in the mat, which from midday may exceed 30°C, would enhance *Lyngbya* photosynthesis. Also, the O_2 levels which may reach 200% oversaturation as compared with air equilibration levels at the ambient temperature, would not adversely affect net photosynthetic rates, as they would for plants that photorespire. Free CO_2 levels are drastically reduced in the mat during the first few hours of light as a result of both photosynthetic activity and, consequently, increases in pH. Under such conditions, it must be an advantage for the plant to utilize exogenous HCO_3^-. Also HCO_3^- concentrations of the mat decrease throughout the day as pH rises. However, when comparing HCO_3^- levels of the mat (Fig. 1) with the photosynthetic response to HCO_3^- (Fig. 3), it appears that *Lyngbya* would be exposed to saturating concentrations (>0.3 mM) until around midday. Later, HCO_3^- levels should become limiting for photosynthesis, but even the lowest values measured (0.15 mM) would provide for some 60% of the maximum photosynthetic rate. Of course, conditions in the mat vary from day to day depending on abiotic as well as biotic conditions such as mat density. It must also be pointed out that photosynthetic rates were measured under stirred conditions in the laboratory. Therefore, the photosynthetic responses to HCO_3^- may be overestimated as compared to *in situ* photosynthesis in the mat where stagnant conditions occur. It is clear, however, that under stagnant conditions 2 mM HCO_3^- added to the growth medium provides for maximum growth rates in the laboratory. Such a high HCO_3^- concentration has been found in several *Lyngbya* mats. Thus, the physiological responses of *Lyngbya* seem to be well adapted to those conditions prevailing in *Lyngbya* mats.

It is our working hypothesis that the "opportunistic" traits of *Lyngbya* described in this paper enable it to successfully compete with both indigenous and exotic higher aquatic plants, when the external conditions are favorable for its growth. Such conditions of high pH and HCO_3^- levels also favor the growth of *Hydrilla* (15). However, if *Hydrilla* were successfully managed by herbicide treatments, a new niche may open up for the reputedly more herbicide-tolerant *Lyngbya.* Once established, the dense growth of *Lyngbya* may prevent the original species becoming re-established. The validity of this working hypothesis has yet to be tested in controlled competition studies.

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