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Adaptation of the Cyanobacterium *Microcystis aeruginosa* to Light Intensity[1]

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ABSTRACT

Light intensity adaptation (20 to 565 microeinsteins per square meter per second) of *Microcystis aeruginosa* (UV-027) was examined in turbidostat culture. Chlorophyll *a* and phycocyanin concentrations decreased with increasing light intensity while carotenoid, cellular carbon, and nitrogen contents did not vary. Variation in the number but not the size of photosynthetic units per cell, based on chlorophyll a/P_{700} ratios, occurred on light intensity adaptation. Changes in the numbers of photosynthetic units partially dampened the effects of changes in light intensity on growth rates.

Many O_2-evolving photosynthetic organisms physiologically adapt to variations in light intensity (2, 7, 16, 23–26, 33). Light intensity adaptation is usually characterized by alterations in the photosynthetic apparatus, especially the light-harvesting components (7, 9, 12, 19, 22, 27). Cyanobacteria resemble eucaryotic algae and higher plants in that they contain Chl *a*, two photosynthetic reaction centers, carotenoids, and similar electron transport constituents, all associated with membranes. However, the light-harvesting Chl *a/b* protein, found in chlorophytes and higher plants, is absent in procaryotes. The light-harvesting function is filled instead by phycobiliproteins, organized into phycobilisomes, which transfer excitation energy predominantly to PSII reaction centers (4, 11, 20).

Microcystis aeruginosa is a ubiquitous freshwater cyanobacterium that has received much attention because of water management problems associated with its blooms (5). The blooms are occasionally toxic to domestic and wild animals (3), and are potentially harmful to man (1). In nature, the organism grows primarily at high light intensities (10). It is found throughout the summer and fall in the United Kingdom (28) and in North America (3), throughout the austral summer in South Africa (5), and Australia (10), and year-round at lower latitudes.

Successful cultivation of *M. aeruginosa* in laboratory batch culture has been reported only at low light intensities (17, 18, 29). We report here on the growth dynamics of *M. aeruginosa* in turbidostat culture at high light intensities approaching those found under natural conditions. The effects of variations in light intensity on steady-state photosynthesis characteristics, chemical composition, and growth rate of *M. aeruginosa* maintained in turbidostat culture are presented. Our objective was to determine the physiological strategies used by this cyanobacterium for light intensity adaptation.

MATERIALS AND METHODS

Organism and Culture. A cloned isolate of *M. aeruginosa* (UV-027) was kindly provided by Prof. J. N. Eloff, University of the Orange Free State, Bloemfontein, South Africa. It was collected from a fish pond near Beit Shean, Israel. The isolate was grown in a modified BG-11 medium (6).

Steady-state cell densities of *M. aeruginosa* were grown by turbidostat culture. A cylindrical glass turbidostat vessel, 10 cm in diameter and 55 cm long, was maintained at 29°C. The culture was continually mixed by magnetic stirring and bubbling with sterile air at 0.7 l/min. The pH remained between 7.4 and 7.6. Cell densities were monitored photometrically at 671 nm with a light-emitting diode and photodiode, and kept between 3 and 9 $\times 10^5$ cells/ml by addition of culture media with a pump. The photodiode with amplifier and pump were interfaced with a Hewlett Packard 85 computer to control and record culture media addition. The total light absorbed by the cells was <5% of the incident PAR. Growth rates were estimated using the equation, $\kappa = \log_2 (Vr + \Delta V/Vr) \times 24$; where κ represents divisions/day and Vr = 3200 ml and ΔV = culture media added (in ml/h). Continuous illumination was provided from opposite sides of the culture vessel by two banks HO fluorescent lamps. Light intensity was varied by changing the number of the lamps or their distance from the vessel. The light intensity (PAR) in the turbidostat was measured with a calibrated 4π quantum sensor (Biospherical Instruments, model QS-100). Cells were illuminated for at least 48 h, following a change in light intensity, to attain a new steady-state photosynthetic condition prior to sampling.

Analyses. Approximately 150 ml of the turbidostat culture was sonicated for 1 min at 90 w/cm^2 to disrupt cell aggregates prior to analyses and cells were counted with a hemocytometer. A 30- to 50-ml aliquot was filtered on a Whatman GF/F glass fiber filter and ground in 90% acetone in a glass tissue homogenizer with a Teflon pestle. The homogenate was clarified by filtration, and Chl *a* and carotenoid concentrations in the 90% acetone extracts were determined spectrophotometrically using extinction coefficients of 75.05 mM^{-1} cm^{-1} at 665 nm and 2500 mM^{-1} cm^{-1} at 480 nm, respectively (8, 15, 21). An average mol wt of 537 was used for carotenoid calculation (21). Carotenoids were separated by two-dimensional TLC (14). Particulate organic C and N were analyzed with a Perkin-Elmer model 240B elemental analyzer following filtration of 10- and 20-ml samples on precombusted 13-mm glass-fiber filters.

O_2 Evolution. Steady-state photosynthetic O_2 evolution was measured at twelve or more light intensities with a Clark-type O_2 electrode (Yellow Springs Instruments) as previously described (8). The sonicated culture sample was bubbled with N_2 to approximately 80% O_2 saturation, and 4 ml was placed in a flat-faced

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Table I. *Pigment and Chemical Composition of M. aeruginosa at Several Light Intensities*

I Growth	No. of Observations	Chl *a*/Cell[a]	Carotenoid/Cell[a]	Phycocyanin/Cell[a]	Phycocyanin/Chl	Carbon/Cell[a]	Carbon/Nitrogen
$\mu E\ m^{-2}\ s^{-1}$			$mol \times 10^{-16}$		*mol/mol*	*pg*	*wt/wt*
20	4	1.13 ± 0.12	1.13 ± 0.25	0.73 ± 0.18	0.64	7.22 ± 1.19	3.2
40	3	1.30 ± 0.35	1.57 ± 0.37	ND[b]		ND	ND
72	3	0.98 ± 0.01	1.09 ± 0.03	0.87 ± 0.03	0.89	7.73 ± 1.82	3.7
160	4	0.87 ± 0.12	1.32 ± 0.04	0.70 ± 0.07	0.80	9.22 ± 1.79	4.1
240	5	0.59 0.06	1.27 ± 0.51	0.46 ± 0.09	0.78	8.83 ± 2.25	3.6
565	4	0.35 ± 0.08	1.27 ± 0.27	0.43 ± 0.02	1.23	8.76 ± 1.36	3.8

[a] Mean ± SD.
[b] Not determined.

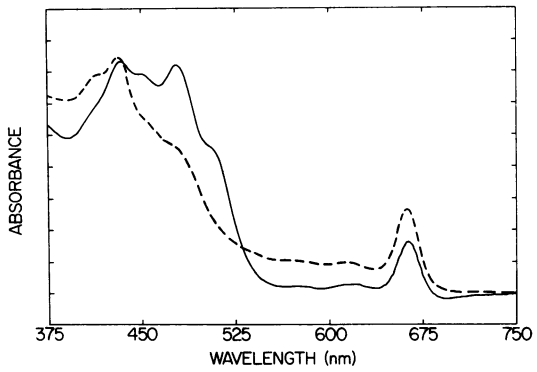

FIG. 1. Absorbance spectra of 90% acetone extracts from *M. aeruginosa* grown at 72 μE m^{-2} s^{-1} (- - -) and 565 μE m^{-2} s^{-1} (——). Note the increase of carotenoids relative to Chl *a* in the high-light-adapted cells as indicated by the peak at 480 nm and a shoulder at 510 nm.

Lucite chamber held at 29°C and magnetically stirred. Illumination was provided by a 500-w tungsten-halogen lamp attenuated with neutral density filters. Irradiance was measured with a Lambda LI-185 2π quantum sensor (Licor, Inc.). O_2 consumption and evolution were recorded for at least 10 min at each light intensity. Dark respiration was taken as the steady-state rate of O_2 consumption prior to light exposure in the O_2 electrode chamber. The culture was not changed between each light intensity. Replicate measurements were made on successive days.

P_{700} Unit Size. The Chl *a*/P_{700} ratio was used to estimate the average P_{700} unit size (2, 9, 32, 33). A 400-ml culture sample was centrifuged for 10 min at 10,000*g*. The sedimented cells were suspended in 1 to 2 ml of 50 mM Tris-HCl (pH 7.8) and centrifuged for 2 min at 12,000*g*. The washed cells were suspended in 2 ml of 50 mM Tris-HCl (pH 7.8) containing 0.02% Triton X-100 (v/v) and sonicated for 90 s at 0°C with a Kontes microsonicator. The sample was centrifuged for 1 min at 12,000*g*. The supernatant was kept in darkness at 4°C prior to P_{700} analysis.

The reversible, light-induced oxidation of P_{700} was measured as previously described (8). Chl *a* concentration was determined spectrophotometrically using an extinction coefficient of 60 mM^{-1} cm^{-1} at A_{674} (29). The concentration of P_{700} was determined using an absorption difference coefficient of 64 mM^{-1} cm^{-1} at A_{697} relative to the isosbestic point at 720 nm (30). The ratio of 674/620 nm absorbancies of the 50 mM Tris-HCl (pH 7.8), 0.02% Triton X-100 (v/v) extract was used to provide an estimate of the phycocyanin content of the cells (24). The phycocyanin per cell was estimated by setting up a proportionality such that, if A_{674} nm is made proportional to the amount of Chl *a* per cell, the A_{620} nm should be proportional to the amount of phycocyanin per cell. The Chl *a* absorbance at 620 nm was corrected in the estimation of phycocyanin by using the equations of Myers *et al.* (24).

RESULTS AND DISCUSSION

Photosynthetic Pigment Content. The photosynthetic pigment changes associated with growth of *M. aeruginosa* in turbidostat culture at white light intensities between 20 and 565 μE m^{-2} s^{-1} were examined. Cellular Chl *a* content decreased 3-fold as cells adapted from low to high light intensities (Table I). Above 40 μE m^{-2} s^{-1}, the decrease is a logarithmic function of light intensity: Chl *a*/cell (mol $\times$ 10^{-16}) = -0.32 ln I (μE m^{-2} s^{-1}) + 2.40 (r^2 = 0.97, n = 16) (Table I). Below 40 μE m^{-2} s^{-1}, the cells tended to become slightly bleached. Similar changes in Chl *a* content per cell with growth irradiance have been observed in other cyanobacteria (23, 33) and eucaryotic algae (7, 8).

The ratio of phycocyanin to Chl *a* was essentially constant from 20 to 240 μE m^{-2} s^{-1}, but increased at 565 μE m^{-2} s^{-1} (Table I). Phycocyanins reached a minimum level per cell prior to Chl *a* with increasing light intensity. These results are similar to those reported by Myers and Kratz (23) for *Anacystis nidulans*. In contrast, Oquist (25) and Vierling and Alberte (33) found that increasing light intensities resulted in a decreased phycocyanin/Chl *a* ratio in *A. nidulans*.

M. aeruginosa was yellow-green at high light intensities and characteristically blue-green at low light intensities. These color changes were primarily associated with changes in Chl *a* and phycocyanin per cell. Quantitatively, the total carotenoid content per cell remained relatively constant with changes in light intensity (Table I). Qualitative changes in the major carotenoid components were observed. Three major carotenoids, readily separated by TLC, were found in cells grown at low light intensities: β-carotene, echinenone, and zeaxanthin. Cells grown at high light intensities also contained myxoxanthophyll, detected by TLC and as a shoulder at 510 nm in absorbance spectra of 90% acetone extracts (Fig. 1) (13). The qualitative changes in carotenoids may be related to their protective role against Chl photooxidation. These data suggest that the average light intensity incident on a population of *M. aeruginosa* could be estimated by measuring Chl *a*/carotenoid ratios as well as carotenoid composition.

The number of PSI reaction centers per cell was proportional to the Chl *a* per cell over the entire light intensity range examined (Tables I and II). The Chl *a*/P_{700} ratio was constant between 20 and 240 μE m^{-2} s^{-1}, averaging ~300 Chl *a* molecules per PSI reaction center (Table II). The P_{700} unit size at 565 μE m^{-2} s^{-1}

Table II. *Photosynthetic Activity, PSI Unit Size and Number, and Growth of M. aeruginosa at Several Light Intensities*

I Growth	No. of Observations	P_{700} Unit Size[a]	PSI/Cell	Cell Basis		Chl *a* Basis		I_k	τ[f]	κ
				α[b]	P_{max}[c]	α[d]	P_{max}[e]			
$\mu E\ m^{-2}\ s^{-1}$		*Chl a*/P_{700}	$\times 10^4$					$\mu E\ m^{-2}\ s^{-1}$	*ms*	*divisions/d*
20	4	300 ± 22	22.7	0.045	4.7	0.043	4.8	100	12.1	0.35
40	3	328 ± 45	ND[g]	ND	ND	ND	ND	ND	ND	0.96
72	3	316 ± 70	18.7	0.034	5.2	0.035	5.2	150	8.9	1.30
160	4	328 ± 54	16.0	0.027	5.3	0.030	5.7	200	7.5	1.45
240	5	263 ± 34	13.5	0.020	5.8	0.034	8.4	250	5.8	1.58
565	4	245 ± 10	8.6	0.008	11.3	0.023	32.3	1400	1.9	1.93

[a] Mean ± SD.

[b] $\frac{\mu mol\ O_2\ cell^{-1}\ min^{-1}}{\mu E\ m^{-2}\ s^{-1}} \times 10^{10}$.

[c] $\mu mol\ O_2\ cell^{-1}\ min^{-1} \times 10^{10}$.

[d] $\frac{\mu mol\ O_2\ \mu mol\ Chl\ a^{-1}\ min^{-1}}{\mu E\ m^{-2}\ s^{-1}}$.

[e] $\mu mol\ O_2\ \mu mol\ Chl\ a^{-1}\ min^{-1}$.

[f] Turnover time of PSI reaction centers (e/PSI).

[g] Not determined.

averaged 245. The smaller P_{700} unit size at the high light intensity corresponded to a 40% increase in the proportion of phycocyanin to Chl *a*. Essentially, the P_{700} unit size remained relatively constant while the number of PSI reaction centers per cell decreased with increasing light intensity (Table II). Similar results have been reported for other cyanobacteria (16, 25, 33).

The Chl/P_{700} ratios reported here are about 30% larger than those reported for *Anacystis nidulans* (23, 33) or *Anabaena variabilis* (16). This difference could reflect interspecific variations in the ratios of PSI/PSII reaction centers (9, 23), where the Chl associated with PSII is included in the measurement of Chl/P_{700} ratios but is not functionally involved in light harvesting for the PSI reaction center. Alternatively, the stoichiometry of the 'core' Chl *a* associated with the PSI reaction center could be species specific, as for phycobilisome structure and composition (31).

Carbon and Nitrogen Content. Changes in growth irradiance levels were not accompanied by significant variations in cellular C or N contents. At light intensities between 20 and 565 $\mu E\ m^{-2}\ s^{-1}$, cellular carbon content averaged 8.35 pg C/cell. Similarly, C/N (w/w) ratios averaged 3.7 over the range of light intensities examined (Table I).

Photosynthetic Characteristic. Photosynthesis *versus* irradiance measurements were made to determine the light utilization efficiency (α), the saturating light intensity for photosynthesis (I_k), and the maximum rate of photosynthesis at light saturation (P_{max}), for cells grown at each light intensity. Normalized on a per cell basis, α (equivalent to the initial slope of each *P versus I* curve) systematically decreased as the cells became high light adapted (Table II). The changes in α were related to Chl *a* per cell and no significant differences were observed when α was normalized to Chl *a*. These results are similar to those reported by Myers and Kratz (23) for *A. nidulans*. As the increase in Chl *a* per cell was accompanied by an increase in phycocyanin concentration, there was an overall increase in light-harvesting ability at low light intensities (Table I). The increase in phycocyanin was indirectly correlated with an increased number of P_{700} units per cell, suggesting that there was potentially more PSI activity at low light intensities (Table II).

Between 20 and 240 $\mu E\ m^{-2}\ s^{-1}$, the light-saturated photosynthetic rate, P_{max}, normalized on a per cell basis, does not change significantly with light treatments, averaging $5.52 \pm 0.45 \times 10^{-16}$ mol O_2 $cell^{-1}$ min^{-1} (Table II). P_{max}, normalized to Chl *a*, increased from 4.8 to 8.4 $\mu mol\ O_2\ \mu mol^{-1}$ Chl *a* min^{-1} between 20 and 240 $\mu E\ m^{-2}\ s^{-1}$. At 565 $\mu E\ m^{-2}\ s^{-1}$, P_{max} increased to 11.3×10^{-16} $\mu mol\ O_2\ cell^{-1}\ min^{-1}$, which corresponded to 32.3 $\mu mol\ O_2\ \mu mol^{-1}$ Chl *a* min^{-1} (Table II). Apparently, *M. aeruginosa* adapts to high light intensities by increasing P_{max}. The increase implies a faster throughput of photosynthetically derived electrons. The minimum turnover times for PSI reaction centers was calculated from P_{max} and the numbers of PSI reaction centers/cell (Table II). The calculation assumes that at light saturation the evolution of each O_2 molecule is accompanied by four light-driven one-electron oxidation steps, each with a quantum yield of unity (9). Turnover times, calculated in this way, decreased from 12.1 ms/e at 20 $\mu E\ m^{-2}\ s^{-1}$ to 1.9 ms/e at 565 $\mu E\ m^{-2}\ s^{-1}$. Thus, as cellular Chl decreased, so did the potential turnover time of electrons in the photosynthetic electron transport chain. Additionally, the phycocyanin per cell decreased at 565 $\mu E\ m^{-2}\ s^{-1}$, and the phycocyanin/Chl *a* ratio increased. This resulted in a highly efficient light-harvesting assembly requiring fewer Chl *a* molecules as manifested by an increase in P_{max} per Chl *a* at 565 $\mu E\ m^{-2}\ s^{-1}$.

The I_k values which reflect the amount of light required to saturate photosynthesis at each growth irradiance increased with increasing growth irradiance. This was consistent with the observation that the number of photosynthetic units decreased (Table II). Examination of the I_k data calculated from short-term photosynthesis measurements indicated that even those cells grown at 565 $\mu E\ m^{-2}\ s^{-1}$ were not light saturated (Table II).

Growth Rate. The growth rate of *M. aeruginosa* increased with increasing growth irradiance levels over the range of light intensities examined. The growth (κ) and irradiance data (Table II) can be fit to a log function of the form:

$$\kappa\ (\text{divisions/d}) = 0.43 \ln I\ (\mu E\ m^{-2}\ s^{-1}) - 0.75\ (r^2 = 0.94).$$

Accordingly, the estimated compensation light intensity for growth is ~6 $\mu E\ m^{-2}\ s^{-1}$. There appears to be a high light transition state between cells grown at 240 and 565 $\mu E\ m^{-2}\ s^{-1}$. At the highest light intensity, the phycocyanin/Chl ratio and P_{max} increased,

while overall pigment content and α decreased. This response appeared to prevent the growth of *M. aeruginosa* from becoming light saturated; in effect the cyanobacteria continuously adapted to increased light intensities. Obviously, at some light intensity the growth of this organism must become light saturated, however, saturated growth irradiance levels appear to exceed 565 μE m^{-2} s^{-1}.

In conclusion, *M. aeruginosa* responds to changes in growth irradiance levels by altering the number of photosynthetic units. At low growth irradiance levels the photosynthetic response was associated with increased light utilization efficiencies. At higher growth irradiance levels, photosynthetic output increased via reduction in electron throughput times. Changes in growth rates are not accompanied by changes in cellular carbon or nitrogen quotas, and growth rates decrease markedly only at low growth irradiance (*e.g.* below 40 μE m^{-2} s^{-1}). The strategy of altering numbers of photosynthetic units with light intensity evidently evolved for an organism growing at relatively high light intensities, where electron flow rather than light harvesting limits photosynthesis (8).

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