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Adaptation to High-Intensity, Low-Wavelength Light among Surface Blooms of the Cyanobacterium *Microcystis aeruginosa*

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Natural populations of the nuisance bloom cyanobacterium *Microcystis aeruginosa* obtained from the eutrophic Neuse River, N.C., revealed optimal chlorophyll *a*-normalized photosynthetic rates and resistance to photoinhibition at surface photosynthetically active radiation (PAR) intensities. At saturating PAR levels these populations exhibited higher photosynthetic rates in quartz than in Pyrex vessels. Eucaryotic algal populations obtained from the same river failed to counteract photoinhibition. At saturating PAR levels, such populations generally yielded lower photosynthetic rates in quartz containers than they did in Pyrex containers. Cultivation of natural *Microcystis* populations under laboratory conditions led to physiologically distinct populations which had photoinhibitory characteristics similar to those of other cultured cyanobacterial and eucaryotic algae. Our findings indicate that (i) photosynthetic production among natural surface populations is best characterized and quantified in quartz rather than Pyrex incubation vessels; (ii) extrapolation of natural photoinhibitory trends from laboratory populations is highly subjective to culture and PAR histories and may yield contradictory results; and (iii) buoyant surface-dwelling populations, rather than exhibiting senescence, are poised at optimizing PAR utilization, thereby maintaining numerical dominance in eutrophic waters when physicochemical conditions favor bloom formation.

During active growth periods, blooms of aquatic bluegreen algae (cyanobacteria) often accumulate and proliferate as surface scums (21, 22, 27). High epilimnetic primary production rates associated with such scums lead to nuisance conditions, as characterized by hypolimnetic oxygen depletion, associated fish and benthic invertebrate mortalities, and foul odors and tastes, as well as poor aesthetic values of affected waters (9). Scumming is a result of enhanced buoyancy, attributable to intracellular gas vacuolation in bloom-forming genera (27). Vacuolation has been shown to be a physiological response to suboptimal cellular photosynthetic rates (6, 13, 14, 19). In particular, deficiencies in either photosynthetically active radiation (PAR) (28) or inorganic carbon availabilities (19) tend to promote scum formation.

Recent studies collectively indicate that scum formation benefits cyanobacteria faced with PAR or inorganic carbon deficiencies or both, since orientation near the air-water interface alleviates growth limitation by these parameters (2, 16, 19). However, exposure to high PAR levels and, in particular, to abundant near-UV and UV radiation at the surface leads to potential stress in the form of photooxidation (1, 7). Thus far, most investigations of photooxidative stress and death have been conducted on laboratory isolates, whereas little is known of photosynthetic responses among natural populations persisting as surface scums. In a previous field study (18), we observed a lack of in situ photoinhibition among cyanobacterial surface blooms, whereas noncyanobacterial populations (largely diatoms, green algae, and flagellates) consistently revealed surface photoinhibition (on a year-round basis) in the eutrophic Neuse River, N.C. Surface inhibition of photosynthesis was linked to excessive PAR conditions, since incubation of surface samples at subsurface depths overrode such inhibition (18). We linked the ability of cyanobacteria (*Microcystis aeruginosa*) to counter photoinhibition to cellular carotenoid enhancement during bloom periods (18).

Since carotenoid pigments are effective in absorbing near-UV as well as UV radiation (12) and have also been implicated in transferring absorbed PAR to chlorophyll *a* (Chl *a*) for photoreductive energy production (5, 18), in situ testing of the potential effectiveness of carotenoids in counteracting photooxidation and their contribution to photosynthetic performance would prove relevant to our understanding of adaptation to and survival in surface waters. By dispensing natural and cultured cyanobacterial and noncyanobacterial species into Pyrex (Corning glass works, Corning, N.Y.) glass and fused quartz incubation vessels of equal wall thickness, we selectively observed the impacts and utilization of near-UV and UV radiation on photosynthetic production in situ. Results presented here reveal that adapted natural *Microcystis* populations are able to resist potential photoinhibition in the presence of near-UV and UV radiation and that interpretations of photosynthetic responses among natural as opposed to cultured populations can deviate dramatically, if not contradict themselves, among single species. Accordingly, extrapolation of potential photooxidative conditions from laboratory isolates or laboratory-adapted natural populations may be questionable.

MATERIALS AND METHODS

Both freshly sampled natural and cultured populations were used in this study. Natural populations of *M. aeruginosa*, a dominant (92 to 95% of total phytoplankton biomass) colonial cyanobacterium, and noncyanobacterial populations were obtained from the lower Neuse River, a highly eutrophic, slow-flowing, freshwater river located in eastern North Carolina (16). Samples were collected during spring (March through June) and summer (June through September) of 1982 and 1983, when noncyanobacterial and cyanobacterial (*M. aeruginosa*) species were respectively dominant. Vertical-profile samples were collected with a 3-liter polyvinyl chloride Van Dorn sampler, mounted horizontally to

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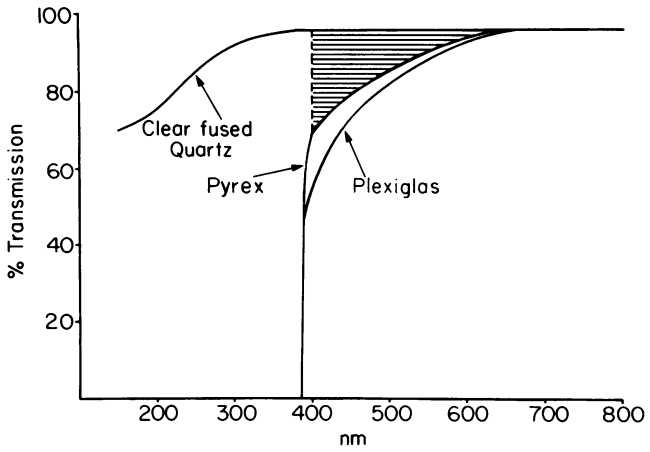

FIG. 1. Optical transmission properties of clear fused quartz and Pyrex glass vessels used for photosynthetic incubations. Transmittance was determined by scanning spectrophotometry.

obtain close-interval, near-surface samples. Additional vertical profiles were sampled in the Newport River estuary, a mesotrophic oligohaline (0 to 5 ppt) system, and Bogue Sound, the adjoining marine (31 to 35 ppt) system separated from the Atlantic Ocean by Beaufort Inlet. Field samples were subsampled for in situ ^{14}C primary productivity measurements and laboratory O_2 evolution per ^{14}C assays of photosynthesis.

Nonaxenic laboratory cultures of algal isolates from nature were also examined. These included: (i) *M. aeruginosa*, isolated from the Neuse River and grown in either static or slowly gyrating (20 to 50 rpm) 2-liter Fernbach flasks with ASM-J (20) medium; (ii) *Anabaena oscillarioides*, isolated by K. Lam from a bloom in the Waikato River, New Zealand, and grown in 9-liter magnetically stirred Pyrex culture flasks with Chu-10 (4) nitrogen-free (N_2-fixing conditions) medium; (iii) *Chlorella vulgaris* from Carolina Biological Supply, Co., Burlington, N.C., grown in 2-liter magnetically stirred Fernbach flasks with ASM-J medium; (iv) *Scenedesmus quadricauda*, isolated from the Neuse River and also grown in 2-liter magnetically stirred Fernbach flasks with ASM-J medium; and (v) *Cyclotella meninghiana*, also isolated from the Neuse River, and grown in 1-liter magnetically stirred Erlenmeyer flasks with ASM-J medium. All cultures were maintained between 20 and 28°C under 350 microeinsteins $\cdot m^{-2} \cdot s^{-1}$ PAR; illumination was provided by a combination of cool-white and Gro-Lux fluorescent lamps. We periodically checked for inorganic carbon limitation of photosynthesis in all cultures by comparing O_2 evolution rates under prescribed as well as HCO_3^--amended culture conditions. Using experimental biomass densities and short-term (less than 1-h) incubations, we found ASM medium to be carbon sufficient over the entire range of illumination. However, Chu-10 medium did occasionally lead to carbon-limited growth at high PAR intensities; accordingly, HCO_3^- supplementation was routinely used to avoid potential inorganic carbon limitation.

Primary productivity incubations were conducted in situ, either off a buoy suspended in the Neuse River or in outdoor ponds housed at the laboratory. Triplicate samples from each depth were dispensed into 30-ml, 15-cm-long, 2-cm-wide Pyrex and fused quartz (Quartz Scientific Inc.) tubes, both having a 1.3-mm-thick wall. Light transmittance characteristics of these materials as well as Plexiglas (Rohm & Haas Co., Philadelphia, Pa.) are given in Fig. 1. The ends of the tubes were sealed with 20-mm-diameter natural rubber serum stoppers. A 2.5-μCi (0.3-ml) sample of [^{14}C]$NaHCO_3$ (58 mCi $\cdot$ mmol^{-1}) was added to each tube. The tubes were then placed on horizontal racks made of Plexiglas and incubated at respective sampling depths. Single dark controls were run in parallel with all clear tubes. Dark ^{14}C assimilation was routinely subtracted from light values; dark values never accounted for more than 1.5% of light values. Surface and subsurface samples were also incubated over a range of depths to examine the photoadaptation and photoinhibition characteristics of the populations under investigation. Laboratory isolates were incubated under natural and artificial light sources in identical fashion.

Incubations were generally conducted between 1000 and 1400 h on clear days; incubation intervals ranged from 30 min (in the outdoor ponds) to 3 h (in the Neuse River). After incubation, samples were transported in a light-tight container to the laboratory. Samples for experiments conducted at the Institute of Marine Sciences outdoor ponds were filtered within 15 min of collection, and samples for experiments conducted in the Neuse River were filtered within 1.5 h of collection. All samples were filtered under gentle vacuum (200 torr [ca. 26 kPa]) on 25-mm-diameter Whatman GFF glass fiber (0.2-μm-pore-size) filters, followed by air drying and fuming under an HCl atmosphere for 20 min to remove abiotically precipitated ^{14}C. Non-acid-labile ^{14}C in filtrates proved to be less than 8% of the ^{14}C fixed in particulate matter. Because these values were consistently low, an extensive survey of extracellular ^{14}C release was not pursued during this study. Filters were placed in 10 ml of Fisher Scintilene, a xylene-based cocktail, and analyzed for radioactivity in a Beckman LS-7000 liquid scintillation counter. Samples were corrected for quenching with a [^{14}C]hexadecane (New England Nuclear Corp., Boston, Mass.) internal standard. Counting efficiencies ranged from 92 to 97%.

Photosynthetic rates, using O_2 evolution measurements, were also determined in the laboratory on natural and cultured populations. A range of PAR intensities was provided by a projector having a quartz-iodide lamp. The projector lens was covered with various layers of neutral-density screening. Samples were dispensed in a 40-ml Plexiglas chamber having a 3-mm-thick wall. The chamber was equipped with a small magnetic stirrer, a YSI 5750 dissolved-O_2 probe, a Fisher polymer-body combination pH probe, and a circulating water jacket to maintain constant temperatures during measurements. The YSI and Fisher probes were connected to YSI 54 ARC dissolved-oxygen and Fisher Accumet 310 pH meters, respectively. The meter outputs were graphically recorded on a Houston Instruments model 5000 dual-pen recorder. Using this system, O_2 evolution rates could be determined within 5 min of the initiation of incubation.

All samples were routinely analyzed for Chl *a* (corrected for phaeopigments) by the trichromatic procedures of Strickland and Parsons (24) as modified by Burnison (3). Samples were filtered on 25-mm-diameter GFF filters (at 200-torr vacuum), rinsed with 2 to 5 ml of a saturated $MgCO_3$ solution to neutralize algal material, sonicated in $MgCO_3$-buffered 90% acetone, and extracted for 4 h. Extracts were then centrifuged for 10 min at 2,600 rpm; the supernatant was analyzed for absorbance at 630, 647, 663, and 750 nm with a Bausch & Lomb Spectronic 2000 spectrophotometer. The Chl *a* content of experimental incubations ranged from 200 to 700 μg of Chl *a* $\cdot$ liter^{-1}, whereas among natural populations, the range was from 21 to 126 μg of Chl *a* $\cdot$ liter^{-1}.

All PAR measurements were made with a Li-Cor LI-185 photometer-radiometer having an LI-192S underwater, planar (nonspherical) quantum sensor.

RESULTS

Spectral transmission characteristics of 1.3-mm-thick Pyrex and fused quartz walls and 3-mm-thick Plexiglas walls were determined through spectrophotometric scans (Fig. 1). In the PAR region (400 to 700 nm), fused quartz revealed greater transmittance than Pyrex and Plexiglas. Transmittance differences ranged from 27.5% at 400 nm to less than 1% at 630 nm, as indicated by the shaded region in Fig. 1.

Distinct differences in photosynthetic performances were observed between (i) natural cyanobacterial and noncyanobacterial populations, (ii) cultured versus natural cyanobacteria, and (iii) cultured cyanobacterial and noncyanobacterial species incubated in Pyrex versus quartz vessels. In situ primary productivity profiles, normalized for Chl *a* content and PAR, revealed consistent inhibition of photosynthesis at the surface when spring noncyanobacterial populations were encountered (Fig. 2). Inhibition occurred in both Pyrex and quartz vessels; however, phytoplankton incubated in quartz vessels were most severely inhibited (Fig. 3). The inhibition was related to light intensity, since placement of surface samples at 0.5 m alleviated the inhibition. Nutrient levels (as NO_3^-, NH_4^+, and PO_4^{3-}) were not significantly different between the surface and 0.5 m at the time of sampling. Hence, it appeared unlikely that contrasting nutrient regimes were responsible for the observed inhibition.

In contrast to the above scenario, cyanobacterial populations showed no significant surface photoinhibition (Fig. 2, 3, and 4). Throughout the summer sampling period, *M. aeruginosa* accounted for 92 to 95% of the total phytoplankton community biomass; the remainder was composed of diatoms, chlorophyceans, and other subdominant cyanobacteria, including *Oscillatoria* spp., *Anabaena spiroides*, and *Anabaena circinalis*. Accordingly, we considered community photosynthetic responses to reflect largely the responses of the dominant *M. aeruginosa* population. Microautoradiographic examinations of species-specific primary productivity confirmed this assumption (16). While exhibiting a biomass dominance of from 92 to 95%, the share of primary productivity attributable to *M. aeruginosa* ranged from 83 to 94% during our examinations. On several occasions there were noticeable and significant ($P < 0.01$) differences in photosynthetic performance between Pyrex- and quartz-incubated *M. aeruginosa* populations. However, contrary to our findings among noncyanobacterial populations, *M. aeruginosa*-dominated populations often exhibited higher photosynthetic rates in quartz than in Pyrex vessels (Fig. 3). When photosynthetic rates were examined among *M. aeruginosa* populations freshly sampled from surface scums (*M. aeruginosa* accounted for 97% of the phytoplankton biomass), quartz-incubated populations consistently and significantly ($P < 0.01$) surpassed Pyrex-incubated populations (Fig. 3) at surface PAR levels (1,260 microeinsteins · m^{-2} · s^{-1}). At approximately half this level (650 microeinsteins · m^{-2} · s^{-1}), photosynthetic performance of quartz-incubated populations still surpassed that of Pyrex-incubated populations, although differences were not statistically significant (Fig. 3). PAR light intensities lower than 650 microeinsteins · m^{-2} · s^{-1} elicited virtually identical photosynthetic responses in quartz or Pyrex vessels (Fig. 3).

Natural noncyanobacterial populations obtained from surface waters of Bogue Sound consistently showed photoinhibition at PAR levels ranging from 650 to 1,300 microeinsteins · m^{-2} · s^{-1}, (Fig. 4). This inhibition was enhanced in quartz vessels at surface irradiations; however, at subsurface light intensities below 650 microeinsteins · m^{-2} · s^{-1}, no noticeable differences in photoinhibition were observed between Pyrex and quartz containers (Fig. 4). Surface photoinhibition significantly ($P < 0.01$) reduced

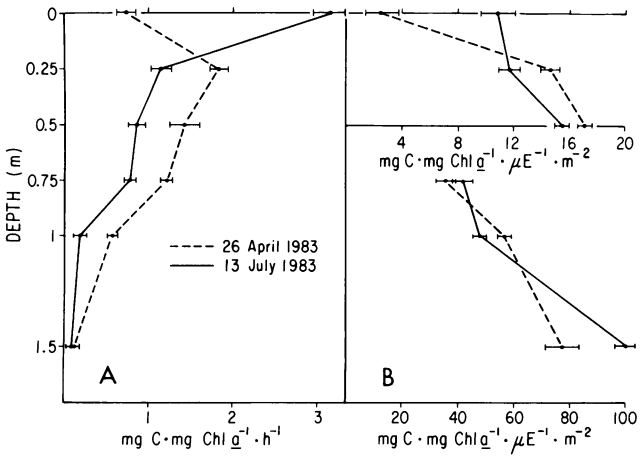

FIG. 2. (A) Vertical profile of in situ photosynthesis measurements in the Neuse River, using the ^{14}C method. Incubations were conducted in Pyrex containers. CO_2 fixation rates were normalized for Chl *a* content. The variability among triplicate samples is shown with error bars. On 26 April 1983 the phytoplankton community was dominated by green algae, diatoms, and microflagellates with cyanobacteria making up only 3% of the biomass. On 13 July 1983 approximately 94% of the phytoplankton biomass was dominated by the cyanobacterium *M. aeruginosa*. (B) Chl *a*-specific photosynthetic rates normalized for PAR flux at respective incubation depths, including the surface. The upper portion has an expanded scale to differentiate photosynthetic efficiencies in surface waters. μE, Microeinsteins.

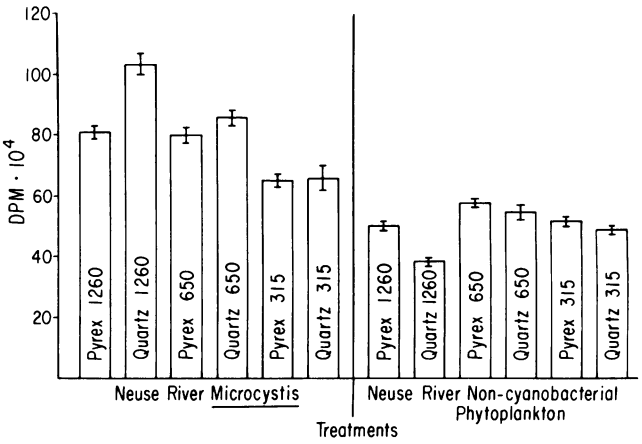

FIG. 3. Photosynthetic $^{14}CO_2$ fixation, as disintegrations per minute (dpm) per sample, in quartz versus Pyrex vessels incubated over a range of PAR intensities. PAR is given as microeinsteins · $meter^{-2}$ · $second^{-1}$. Neuse River water dominated by *M. aeruginosa* (96% of the phytoplankton biomass) was compared with river water dominated by a noncyanobacterial phytoplankton community.

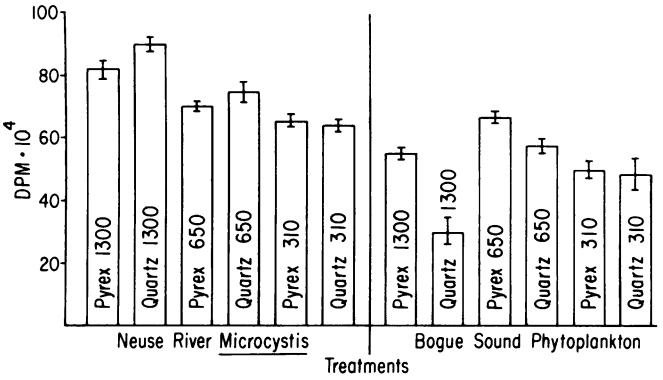

FIG. 4. Photosynthetic $^{14}CO_2$ fixation, as disintegrations per minute (dpm) per sample, in quartz versus Pyrex vessels incubated over a range of PAR intensities. *M. aeruginosa*-dominated (93% of the phytoplankton biomass) Neuse River water was compared with Bogue Sound water, which contained a marine phytoplankton community dominated by diatoms and microflagellates.

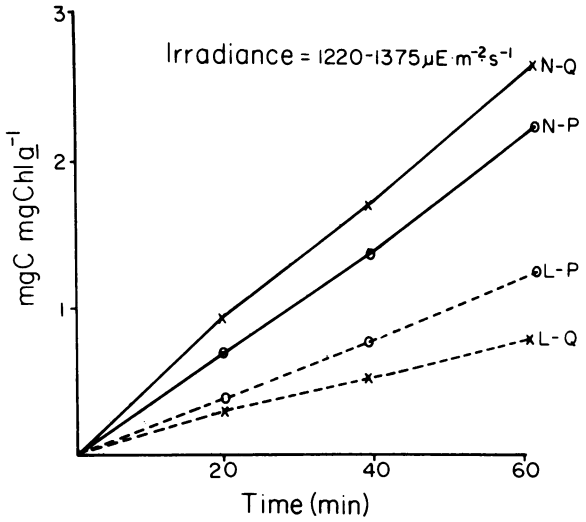

FIG. 5. Comparison of Chl *a*-specific surface photosynthesis between naturally occurring, freshly sampled *M. aeruginosa* populations (N) and laboratory-grown *M. aeruginosa* (L). The range of natural PAR intensities encountered during a 1-h midday exposure period is given. Samples were withdrawn every 20 min. Photosynthetic performances in quartz (Q) versus Pyrex (P) vessels are illustrated. μE, Microeinsteins.

photosynthetic rates by 15 to 35% in noncyanobacterial species incubated in Pyrex flasks, whereas photoinhibition of these species incubated in quartz significantly ($P < 0.001$) reduced photosynthesis by as much as 65% at the surface.

Since both cyanobacterial and noncyanobacterial populations tested for degrees of photoinhibition were subsampled from the same surface sample, photosynthetic performances directly reflected $^{14}CO_2$ fixation results (Chl *a* concentrations were identical among the various treatments). Similarly, laboratory isolates were subsampled from a single batch, thereby normalizing photosynthetic performance for constant amounts of Chl *a*. Some detectable photobleaching (and presumably degradation) of Chl *a* did occur among noncyanobacterial populations and laboratory isolates during incubations lasting longer than 1 h. Furthermore, inorganic carbon limitation of photosynthesis was occasionally detected among incubations exceeding 1 h. Therefore, all incubations discussed here were kept to less than 1 h.

Laboratory isolates incubated in both Pyrex and quartz vessels consistently showed photoinhibition under either surface (PAR = 1,200 to 1,300 microeinsteins · m^{-2} · s^{-1}) or subsurface (PAR = 650 to 500 microeinsteins · m^{-2} · s^{-1}) natural irradiation. Photoinhibition was most profound in quartz vessels, both among noncyanobacterial species (*Chlorella vulgaris*, *Cyclotella meninghiana*) and cyanobacterial species (*M. aeruginosa* and *A. oscillarioides*) (Table 1). When compared with freshly sampled surface scum populations, cultured *M. aeruginosa* revealed distinct photoinhibition under high PAR conditions (in quartz vessels) (Fig. 5). Natural *M. aeruginosa* populations exhibited slight enhancement of $^{14}CO_2$ fixation in quartz containers incubated at either 0 or 0.25 m depth (respective PAR levels of 1,220 and 540 microeinsteins · m^{-2} · s^{-1}), but no such enhancement could be observed among any laboratory isolates.

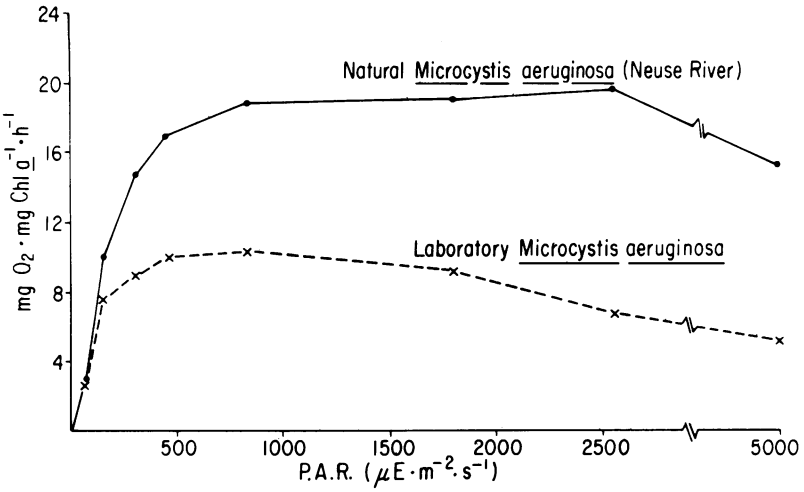

FIG. 6. Photosynthetic responses of natural versus laboratory-grown *M. aeruginosa* populations over a range of PAR intensities. Eight independent O_2 evolution determinations were conducted for each population. All O_2 evolution rates were normalized for Chl *a* content of samples. μE, Microeinsteins.

TABLE 1. Photosynthetic rates[a] for a variety of phytoplankton

Organism[b]	mg of C · mg of Chl a^{-1} · h^{-1}[c]					
	1,275 μE · m^{-2} · s^{-1}		620 μE · m^{-2} · s^{-1}		350 μE · m^{-2} · s^{-1}	
	Pyrex	Quartz	Pyrex	Quartz	Pyrex	Quartz
Chlorella vulgaris	2.05 ± 0.11	1.86 ± 0.09	2.26 ± 0.13	2.13 ± 0.06	2.41 ± 0.08	2.45 ± 0.09
Cyclotella meninghiana	1.96 ± 0.06	1.72 ± 0.08	2.05 ± 0.07	1.88 ± 0.08	2.31 ± 0.14	2.19 ± 0.12
Microcystis aeruginosa	2.18 ± 0.11	1.88 ± 0.06	2.39 ± 0.12	1.95 ± 0.13	2.49 ± 0.13	2.45 ± 0.06
Anabaena oscillarioides	2.39 ± 0.13	2.05 ± 0.10	2.51 ± 0.17	2.31 ± 0.16	2.55 ± 0.16	2.41 ± 0.13

[a] Measured by the ^{14}C method.
[b] Isolated from the Neuse River and subsequently maintained in the laboratory.
[c] Results of triplicate determinations, incubated at three PAR intensities in either Pyrex or quartz vessels, are given. Standard errors among replicates are given. μE, Microeinsteins.

Photoinhibitory trends were also observed when O_2 evolution was monitored in response to various PAR levels, including those levels causing inhibition in nature. When comparing photosynthetic rates normalized to Chl *a* between natural and cultured *M. aeruginosa* populations, we observed that photosynthetic rates were generally higher among natural populations and that PAR levels in excess of approximately 1,000 microeinsteins · m^{-2} · s^{-1} led to photoinhibition among cultured populations, whereas natural populations showed no significant photoinhibition until PAR levels were in excess of 2,500 microeinsteins · m^{-2} · s^{-1} (Fig. 6). Such PAR levels are far in excess of the levels surface scums would experience. Maximum recorded PAR, as measured with the Li-Cor LI-192S flat sensor, ranged from 1,800 to 1,900 microeinsteins · m^{-2} · s^{-1} in North Carolina, whereas PAR fluxes of 2,000 to 2,200 microeinsteins · m^{-2} · s^{-1} have been measured in tropical regions (R. Alberte, personal communication). Among noncyanobacterial cultured species, photoinhibition was commonly observed when PAR levels were in excess of 750 microeinsteins · m^{-2} · s^{-1}, while the cultured cyanobacterium *A. oscillarioides* exhibited photoinhibition at PAR levels exceeding 1,000 microeinsteins · m^{-2} · s^{-1} (Fig. 7).

O_2 evolution assays revealed additional contrasting photosynthetic characteristics in a comparison of natural versus cultured *M. aeruginosa* populations. Per amount of Chl *a*, photosynthetic O_2 evolution was consistently higher in natural as opposed to cultured populations; at times this difference was as great as 60 to 75% (Table 2). It was possible that such differential photosynthetic responses were due to variations in cellular Chl *a*-to-dry weight ratios. Cultured *M. aeruginosa* revealed slightly higher ratios, never exceeding natural population values by 10% during both ^{14}C uptake and O_2 evolution determinations discussed. It is therefore concluded that a majority of the differential photosynthetic responses was attributable to factors other than intrinsic differences in cellular Chl *a*-to-dry weight ratios among laboratory and natural populations. It therefore would appear that natural *M. aeruginosa* populations exhibit more efficient PAR use per milligram of Chl *a* than cultured populations. Combined with the fact that photoinhibition is more effectively blocked in natural populations, the data presented here point to very significant differences in overall photosynthetic performance between populations originally obtained from similar habitats but having different physicochemical and photosynthetic histories.

DISCUSSION

Findings presented here point to basic physiological differences in photosynthetic PAR utilization and photoinhibitory trends between natural cyanobacterial and noncyanobacterial populations. In addition, examinations of the cyanobacterium *M. aeruginosa* are likely to yield contrast-

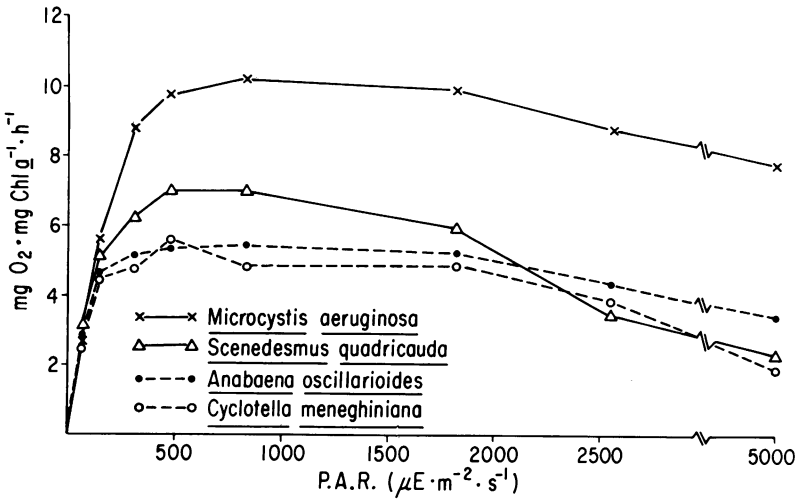

FIG. 7. Photosynthetic response curves for a variety of laboratory-grown phytoplankton isolates, all of which were originally obtained from the Neuse River. All O_2 evolution rates were normalized for Chl *a* content of samples. μE, Microeinsteins.

TABLE 2. Comparison of photosynthetic O_2 evolution rates between natural and laboratory populations of *M. aeruginosa*[a]

Population	mg of O_2 · mg of Chl a^{-1} · h^{-1}	
	Pyrex	Quartz
Natural	14.32 ± 0.19	14.49 ± 0.17
Laboratory	8.67 ± 0.06	7.59 ± 0.10

[a] Incubated under 1,260 microeinsteins · m^{-2} · s^{-1} PAR in either Pyrex or quartz vessels.

ing, if not contradicting, results when comparing natural and laboratory populations. Natural populations, particularly those present in surface scums, reveal a high degree of resistance to photoinhibition and subsequent photooxidation and the ability to more efficiently photosynthesize in quartz as opposed to Pyrex vessels. Since the PAR transparency of both vessel types is identical between 630 and 800 nm, differences in photosynthetic performance among natural populations are likely to reflect differential transparencies in the 400- to 600-nm region (Fig. 1). Furthermore, since quartz vessels are virtually transparent to near-UV and UV irradiation in the 200- to 400-nm region, natural cyanobacterial populations present in surface scums exhibit a high degree of insensitivity to, and compatibility with, this component of surface irradiation. Non-surface-dwelling taxa, including a diatom and green algal species, as well as cyanobacteria grown under artificial (UV-free) irradiation are either less effective in utilizing low-wavelength PAR in the 400- to 600-nm region or more susceptible to damaging impacts of near-UV and UV irradiation transmitted by quartz vessels. Natural cyanobacterial populations are also capable of more efficient overall use of PAR at surface irradiation levels encountered during this study (1,000 to 1,700 microeinsteins · m^{-2} · s^{-1}) than cultured counterparts or natural noncyanobacterial populations.

These results yield implications with respect to (i) interpretations of in situ primary productivity assays conducted on near-surface or surface phytoplankton populations; (ii) evaluations of photosynthetic performance, photoinhibition, and photooxidation of specific taxa based on either the testing of naturally occurring or cultured populations; and (iii) understanding of the relationships between physiological states and phytoplankton community dominance among surface-dwelling cyanobacteria.

The results shed doubts on the quantitative accuracies of previous studies (including our own) which have solely used near-UV- and UV-opaque vessels. It is likely that among surface blooms, primary productivity will be underestimated among cyanobacteria, and noncyanobacterial populations may be more severely inhibited by ambient light levels than previously assumed. High-light inhibition of photosynthesis is not a new observation, and our results support those of Goldman et al. (11), Abeliovich and Shilo (1), and Eloff et al. (7) in this regard. However, our results additionally demonstrate that specific taxa not only fail to exhibit photoinhibition under surface PAR intensities but actually make efficient use of low-wavelength irradiation to the extent that significant enhancement of photosynthetic production can be observed in quartz as opposed to Pyrex vessels. It would therefore seem likely that proper interpretations of in situ primary productivity would be most troublesome in the event of cyanobacterial surface blooms. In aquatic ecosystems dominated by more homogeneously dispersed phytoplankton populations, the overall impacts of differential PAR utilization and inhibition of photosynthesis at near-surface depths are less likely to alter proper quantification of primary productivity. Nevertheless, inhibition of photosynthesis can be observed in significant portions of the euphotic zones of marine (8) and freshwater (10, 23, 26) habitats. A prime example is oligotrophic Lake Tahoe, Calif., where photosynthetic production per unit of Chl *a* or per unit of dry weight is markedly lower in the upper 10 to 20 m of the water column than at 20- to 50-nm depth intervals (10). Such inhibition is most directly attributed to excessive ambient PAR levels; placement of 20- to 50-m depth samples near the surface also elicited inhibitory responses, whereas ambient nutrient levels were not significantly different from those of the upper 10 to 20 m of the water column (25).

It has been our experience that natural populations, even if maintained in culture for only a few days, will reveal photosynthetic responses quite distinct from those of the original stocks. Often laboratory populations exhibit irreversible photoinhibition, whereas natural populations consistently fail to reveal such characteristics. These conclusions support the previous findings of Falkowski (8) and Mur and Beijdorff (15), among others, illustrating contrasting ecophysiological traits among natural versus laboratory populations. Numerous rationales can be offered to explain such differential responses, including altered PAR, nutrient, mixing (turbulence), and biotic interactions induced under laboratory conditions, leading to cultured variants of the same initial population. It is not within the scope or objectives of this paper to discuss the suite of intricate physiological conditions leading to variant formation. Of more direct concern are the potentially contrasting interpretations one can expect when using natural versus cultured populations as test organisms in an examination of the physiological impacts of light stress and photoinhibitory conditions. It is obvious that contradictory results can readily be obtained depending on the choice of experimental populations and incubation vessels employed. Natural *M. aeruginosa* populations were shown to effectively protect themselves, and at times benefit, from simultaneous in situ exposure to high-PAR and low-wavelength radiation, whereas cultured populations of the same species exhibited photoinhibition, and ultimately death, during similar exposures. Such differential responses may be linked to the fact that natural populations normally contain abundant cellular carotenoid concentrations, whereas these pigments are either less abundant or absent in cultured variants from the same populations (17).

In previous field studies we (18) showed that a strong ($r^2 = 0.89$; $P < 0.01$) direct relationship existed between cellular carotenoid content and in situ Chl *a*-specific photosynthetic rates among summer surface populations in the lower Neuse River. This relationship provides support for laboratory-derived findings from a variety of procaryotic and eucaryotic algae (5, 12) showing that carotenoids can serve as: (i) accessory pigments, able to transfer captured PAR energy in the 400- to 500-nm region to Chl *a*, and (ii) photoprotective pigments, able to absorb potentially photooxidative UV light, subsequently transferring such reactive light energy to a harmless ground state as heat, without the formation of Chl *a* singlet states leading to potential photooxidation of the latter pigment. Laboratory isolates deficient in carotenoids can to some extent be conditioned to increase cellular carotenoid concentrations in response to near-UV irradiation (17), an adaptive feature which may play a role in maintaining abundant cellular carotenoids in natural populations thriving in UV-rich surface waters. However, under normal laboratory culturing conditions, UV irradiation is absent. It is likely that natural populations harbor additional

photoadaptive features that have yet to be studied in the laboratory or the field.

Unfortunately, virtually all previous studies have employed silica glass, Pyrex, or polycarbonate incubation vessels, all of which effectively absorb UV radiation. The deployment of quartz incubation vessels would help to clarify whether photoinhibition is detectable and common among high-light species and whether photoinhibition is linked to excessive (supersaturated) PAR levels, incident UV light, or both in nature.

Evidence thus far obtained demonstrates that the surface-dwelling cyanobacterium *M. aeruginosa* exhibits photoprotective characteristics, allowing this nuisance organism ample access to abundant PAR, while simultaneously shading underlying nonbuoyant phytoplankton. In addition to harboring photoprotective capabilities, *M. aeruginosa* also makes effective use of low-wavelength PAR of from 400 to 500 nm; PAR captured in this region enhances photosynthesis, measured both as $^{14}CO_2$ fixation and O_2 evolution, whereas a similar photosynthetic enhancement could not be documented for cultured populations of *Microcystis* spp., *Anabaena* spp., and several eucaryotic algae.

We therefore conclude that the formation of cyanobacterial surface scums is not only on ominous sign of eutrophication but also represents an ecological strategy poised at assuring optimal growth and dominance when climatic conditions favor bloom formation. Buoyancy alteration allows for rapid transport from PAR- or CO_2-deficient waters or both to regions in the water column where such growth-restricting parameters can be alleviated. Due to their ability to effectively exploit surface regions of the water column, scums often persist for weeks to months in the lower Neuse River, as well as in other eutrophic freshwater habitats. The senescence and death of such scums is often attributable to unpredictable climatic events rather than to photoinhibition-photooxidation. In three successive years of field observations, major cyanobacterial die-offs have occurred largely in response to wind-driven accumulations of buoyant populations on shorelines, washout into high-salinity estuarine habitats, and rapid changes and oscillations in surface water temperatures. Surface entrainment on very warm days has at times lead to senescence in *Microcystis* spp. However, without the compounding effect of temperature extremes, photooxidation remains an uncommon feature of this cyanobacterium.

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