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Experimental evidence of light and nutrient limitation of algal growth in a turbid midwest reservoir[1]

Matthew F. Knowlton and John R. Jones[2]

School of Natural Resources, University of Missouri

With 5 figures and 1 table in the text

Abstract: A series of 28 in situ algal growth experiments was conducted in a midwest reservoir during a 27 month period marked by extreme variation in nutrient concentrations and non-algal turbidity. Incubations in most experiments were conducted at several depths and yielded estimates of optimal (light saturating) and critical (compensatory) irradiances. During the study phytoplankton were usually light-limited but light and nutrient-limitation seemed to overlap along a gradient of mixed layer irradiance. Irradiance in situ was often less than saturating intensity and growth in light-saturated controls (no added nutrients) was correlated with the proportional increase in light exposure during incubation. But nutrients were probably co-limiting with light at irradiances of 1–6 E m^{-2} d^{-1} and became the primary limiting factor above ≈6 E m^{-2} d^{-1}. Phytoplankton biomass sometimes exhibited significant growth without nutrient addition even though ambient light exceeded saturating intensity. This result suggests that biomass was sometimes limited by losses rather than growth.

Introduction

Many lakes intercept flood waters carrying high concentrations of plant nutrients and suspended sediment. This is particularly true of artificial lakes many of which are built to control floods and store runoff (BAXTER 1977, THORNTON 1990). Phytoplankton in the turbid, nutrient-rich waters brought in by floods seem more likely limited by light than nutrients (JONES & NOVAK 1981, KIMMEL et al. 1990). But phytoplankton are widely adaptable to light conditions and requirements for light and nutrients vary widely among algal taxa (KIRK

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[2] **Authors' address:** School of Natural Resources, 112 Stephens Hall, University of Missouri, Columbia, MO 65211.

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1983, HECKY & KILHAM 1988). Also, a mixed algal community and even a single algal population can be simultaneously limited by both light and nutrients (HEALEY 1985). Thus it can be difficult to predict the occurrence and relative severity of light and nutrient limitation in a given lake or to estimate the overall effects of such conditions on total biomass and other community properties.

Algal growth is light-limited if the mean irradiance experienced by the algal community is less than is required to saturate photosynthesis. If mean irradiance falls to the point where algal growth balances losses then both growth and community biomass are light-limited in the sense that both will vary directly with irradiance (TALLING 1971, WOFSY 1983).

One approach to detecting light limitation is to measure the irradiance required to saturate the growth process (saturating irradiance) or the irradiance needed for growth to balance losses (compensatory irradiance) and to compare these values to measurements of mean irradiance in situ (HECKY & GUILDFORD 1984). Light limitation of community biomass can also be inferred from simple culture experiments analogous to those often used to detect nutrient limitation (ELSER et al. 1990). An increase in biomass resulting from incubation at greater than ambient irradiance implies light limitation just as a similar response to added nutrients suggests nutrient limitation.

We recently applied these techniques to investigate light limitation in large midwestern reservoir. During 1989–1991 we performed a series of algal growth experiments in Mark Twain Lake, Missouri, as part of a limnological study of this usually turbid waterbody (KNOWLTON & JONES 1995). Our experiments initially focused on nutrient limitation but after heavy flooding drastically reduced light penetration we adapted our experimental design to assess effects of irradiance. We measured algal growth in a light gradient with and without added nutrients in order to estimate saturating and compensatory irradiances and the response of growth to greater than ambient irradiance. Our principal interest in this endeavor was to determine conditions under which light would replace nutrients as a dominant factor controlling algal biomass. We hypothesized that across a wide range of in situ light conditions that light and nutrient limitation would intergrade and perhaps be co-limiting in some intermediate range of light (HEALEY 1985).

Study area

Mark Twain Lake (39° 30′ N, 91° 50′ W) is a U.S. Army Corps of Engineers flood control reservoir on the Salt River in northeastern Missouri. It has a mean surface area of 7550 ha and mean and maximum depths of 8.9 m and 26 m, respectively. Physical fea-

tures, hydrology, and spatial variability of turbidity, nutrients and algal biomass are described by KNOWLTON & JONES (1995).

Materials and methods

Between September 1989 and November 1991 we completed 28 in situ algal growth experiments in which unfiltered lake water collected near the surface was incubated 3–8 days in polyethylene cubitainers with or without added nutrients. Treatment groups consisted of controls (no additions), P (potassium phosphate equivalent to ≈100 % ambient TP), N (ammonium nitrate equivalent to ≈50 % of ambient TN) and N+P (both potassium phosphate and ammonium nitrate). In one experiment (November 1990) we used two forms of nitrogen separately (ammonium chloride and potassium nitrate). Nutrient spikes were made up from reagent grade chemicals. The N+P treatment was not included after June 1990.

Experiments were conducted near the dam and, until June 1990, at a shallower site ≈30 km "uplake" [throughout this paper we use the terms "uplake" and "downlake" in place of their lotic counterparts, "upstream" and "downstream"]. Prior to September 1990 4 L or 10 L cubitainers were usually incubated at 0.5 and 2 times the Secchi disk depth with three replicate containers per treatment. In March and June 1990 we employed several additional incubation depths for control and N+P treatments to characterize the effects of the light gradient. In September 1990 we standardized the light-gradient procedure using duplicate 1 liter cubitainers incubated at depths approximating 100, 30, 5, and 1 percent incident irradiance (I_0). In five experiments in 1991 we also incubated controls at 1–3 additional depths (<0.01 %–0.4 % I_0).

Containers were incubated in situ attached to weighted lines suspended from anchored floats. Incubated containers were returned to the laboratory in the dark at ambient lake temperature and subsampled (250 mL/subsample) for chlorophyll (CHL) within 4 hours of collection. CHL was determined in duplicate for each container.

Lake water used to fill experimental containers was analyzed for total CHL (ethanol-fluorometric method – SARTORY & GROBBELAAR 1984, KNOWLTON 1984), total and filtrate phosphorus (PREPAS & RIGLER 1982), total and filtrate nitrogen (CRUMPTON et al. 1992), ammonium-N (STAINTON et al. 1977), nitrate-nitrite-N (A.P.H.A. 1980), volatile and non-volatile suspended solids (Whatman AH-934 filters, A.P.H.A. 1980), total and filtrate turbidity (NTU), and absorbance (total and filtrate) at 440 nm. Filtrates for determination of nutrients, turbidity and absorbance were prepared with the glass fiber filters (Gelman A–E) used in CHL determinations. Nutrients and suspended solids were determined on duplicate subsamples. CHL determinations were performed on 2–3 subsamples in 1989 and on four subsamples in 1990–1991. Filtrates sometimes contained large quantities of fine suspended material not retained by glass fiber filters (nominal retention ≈1 µm). Thus the "filtrate" fraction of TP and TN (fTP and fTN) was not necessarily equivalent to "dissolved" TP and TN (KNOWLTON & JONES, 1995).

Secchi transparency (20 cm disk) and profiles of temperature and dissolved oxygen (YSI Model 51B meter) were taken before each experiment. Vertical extinction of PAR

(k_{par}, m^{-1}) was measured on several occasions (n = 12 experiments) using Li-Cor LI-1000 data logger fitted with a submersible spherical quantum sensor and deck mounted reference sensor. For the remaining experiments k_{par} was estimated from Secchi depth using a regression model based on 230 light profiles from Mark Twain Lake in 1989–1991 ($\log_{10} k_{par} = 0.863 \cdot \log_{10}$ Secchi depth + 0.200; $r^2 = 0.95$). We estimated the proportion of k_{par} due to phytoplankton (k_{chl}) as 0.02 · CHL and light attenuation by non-algal seston (k_S) as $k_S = k_{par} - (k_{chl} + 0.3)$ following KNOWLTON & JONES (1995).

Incident irradiance (I_0) was estimated indirectly from United States National Weather Service "minutes of sunshine" data as described by KNOWLTON & JONES (1995). Temperature and dissolved oxygen profiles were used to estimate mixing depth (Z_m). These values were then corrected for local basin morphometry based on lake surface elevation using hypsographic data developed from planimetry using pre-impoundment topographic maps. Average irradiance in the mixed layer during the incubations ($I_{mix\text{-}i}$) was calculated according to Riley (1957) as:

$$I_{mix\text{-}i} = I_0 \cdot (1\text{-}e^{-k_{par} \cdot Z_m})/(k_{par} \cdot Z_m).$$

We also estimated mean irradiance for the week ending at the start of each experiment ($I_{mix\text{-}7}$) as an index of prior exposure. We made no correction for reflected and back-scattered light which may have amounted to ≈10 % of I_0 during periods of high turbidity (STEFAN et al. 1983).

Algal growth was measured as the ratio of initial to final CHL (CHL_i and CHL_f, respectively). Growth (positive or negative) for a given treatment and depth combination was considered significant if two-tailed t-tests (SAS 1991) showed CHL_f/CHL_i to differ from 1.0 at $p < 0.05$ for all replicate containers in that group.

Treatment averages of CHL_f/CHL_i from experiments conducted at four or more depths were used to estimate irradiance required to saturate growth (I_{max}) and irradiance at the onset of light saturation (I_k). We also estimated compensatory irradiance (I_{comp}) – the irradiance at which net growth was zero ($CHL_f/CHL_i = 1$). I_{max} was the irradiance producing maximum growth and I_k was estimated from the maximum growth rate and the initial slope of the growth-irradiance curve (Fig. 1). I_{comp} was estimated by interpolation. We also made provisional estimates of I_{comp} for experiments conducted at only two depths if $CHL_f/CHL_i \leq 1$ at the greater depth. Values of I_{max}, I_k, and I_{comp} were estimated from incubation depth, k_{par} and average I_0 during the incubation. These values were corrected downward by 7 % which was the average light attenuation by container walls as measured in six trials during the study (range 5–9 %).

Results

Ambient conditions

This study began in summer 1989 near the end of a prolonged drought that reduced sediment input and produced relatively high water clarity ($k < 0.7$/m, $k_S < 0.5$/m, Fig. 2 a) and low nutrient concentrations (fTP <15 µg/L, dissolved inorganic N <20 µg/L). Floods in early 1990 sharply increased turbidity and nutrients. Near the dam, k_S peaked in July 1990 at >4.0/m (Fig. 2 a) correspond-

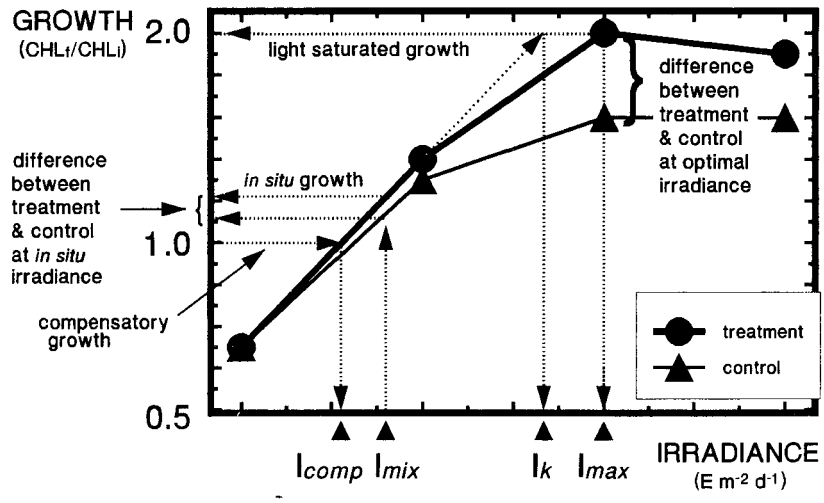

Fig. 1. Hypothetical growth-irradiance plot illustrating graphical estimation of I_{max}, I_k, I_{comp} and growth of controls and nutrient treatments at in situ and optimal irradiances. Terms are defined in the text.

ing to about 60 mg/L total suspended solids (KNOWLTON & JONES 1995). At the uplake site k_S and TSS peaked in March at ≈18/m and 200 mg/L, respectively. Filtrate TP and DIN both increased several fold after the floods (Fig. 2 b–c). Additional flooding during 1991 occurred largely after the onset of thermal stratification (KNOWLTON & JONES 1995) and had little effect on surface waters near the dam. Except for small increases during fall destratification, k_S and phosphorus downlake generally declined after summer 1990. DIN also declined after the 1990 floods but exhibited a large peak in spring 1991. Chlorophyll was also highly variable ranging from <2 µg/L during winter overturn to >20 µg/L during summer blooms in 1990 and 1991 (Fig. 2 d).

Mean mixed layer irradiance varied widely in response to incident light, stratification (KNOWLTON & JONES 1995) and non-algal turbidity (Fig. 2 a). Weekly mean $I_{mix\text{-}7}$ near the dam ranged from 0.9 to >17 E m^{-2} d^{-1} and remained less than 5 E m^{-2} d^{-1} from October 1989 until May 1991 except for brief periods when $I_{mix\text{-}7}$ reached 6–11 E m^{-2} d^{-1} as a result of shallow stratification during warm, calm weather in summer 1990 (Fig. 2 d).

Growth – irradiance

Algal growth, measured from the yield of CHL in experimental containers varied consistently with irradiance, showing an initial linear increase followed by an asymptotic or inhibitory response at higher light intensities. Fig. 3 shows results of a typical experiment (June 1991).

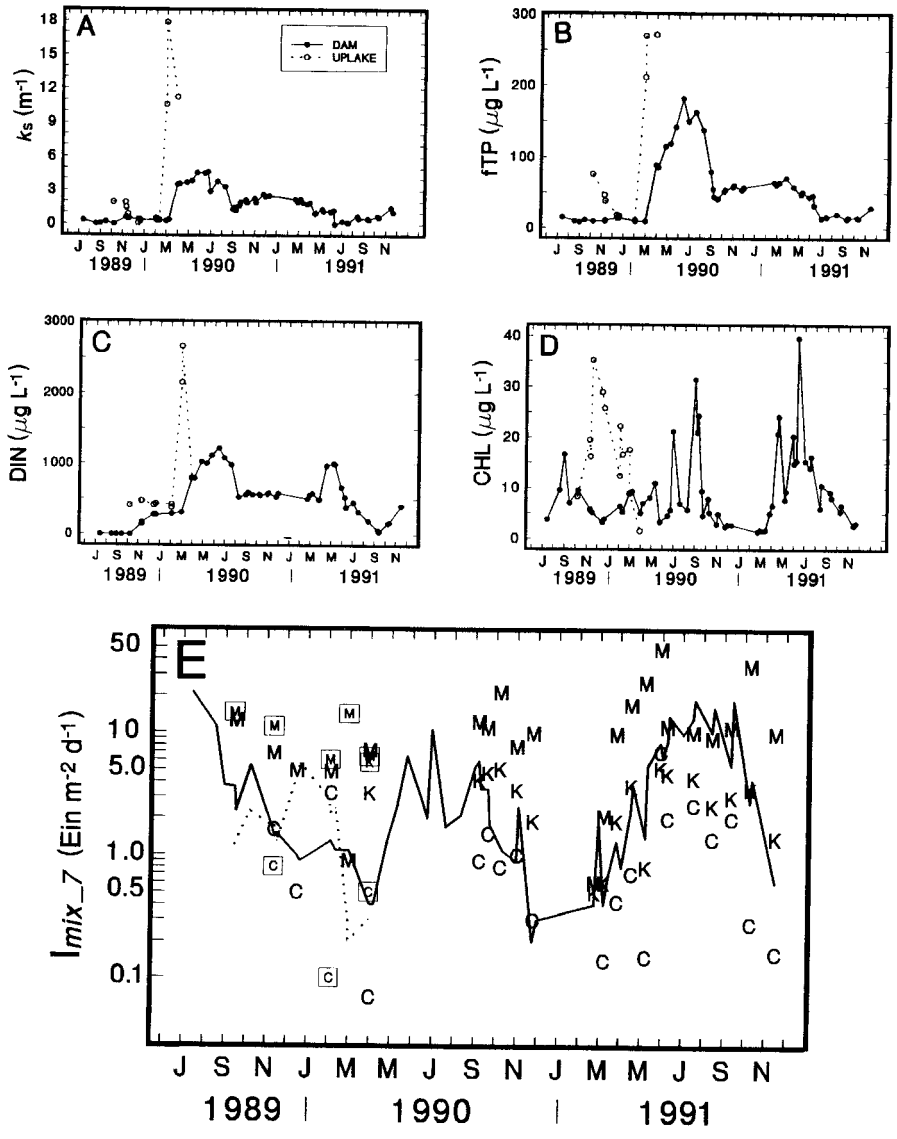

Fig. 2. Time series plots of A) light attenuation by non-algal seston (k_S), B) filtrate total P (fTP), C) dissolved inorganic N (DIN), D) chlorophyll (CHL), and E) mean mixed layer irradiance ($I_{mix\text{-}7}$). Open circles joined by a dashed line represent the uplake site used in the first 9 months of the study. In panel E, point estimates of I_{max}, I_k, and I_{comp} are superimposed on the $I_{mix\text{-}7}$ series and are respectively indicated by letters "M", "K", and "C". Estimates from the uplake site are boxed.

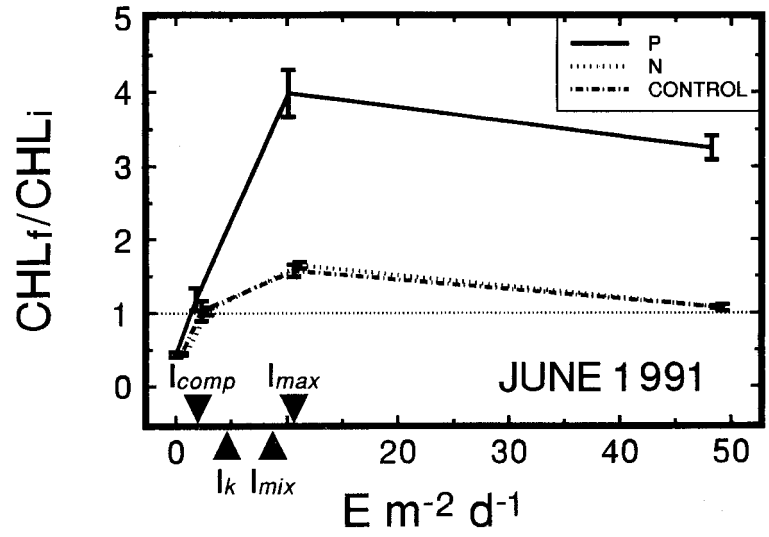

Fig. 3. Growth-irradiance data from 7 June 1991. Vertical bars indicate variation (standard error) among replicate containers. Plotted data have been adjusted horizontally to reduce overlap. Irradiances corresponding to I_{max}, I_k, I_{comp} and I_{mix} are indicated by solid triangles.

Light response parameters, I_{max}, I_k and I_{comp} usually varied only slightly among treatments in a given experiment (e.g. Fig. 3), even when maximum growth rates responded strongly to nutrient addition. Thus, we herein assume that growth-irradiance parameters were independent of nutrient treatment.

Light limitation

Our estimates of irradiance required to saturate growth suggest that phytoplankton were light-limited during most of the study. I_{max} averaged >10 times the ambient irradiance in the mixed layer (Table 1, Fig. 2 e). The biggest differences between saturating and ambient irradiances occurred after the initial flooding in spring 1990 and after fall overturn in 1990 and 1991 (Fig. 2 d) during periods when mixed layer irradiance was consistently declining. In contrast, growth seems to have been light-saturated during part of summer 1991 when I_{max} and I_k dropped below $I_{mix\text{-}i}$ (Fig. 2 d). Light-saturation may also have occurred during the clear water period at the start of the study (before we began using light-gradient incubations) and also during brief periods of shallow stratification and high irradiance in summer 1990. Unfortunately, the two experiments conducted during the latter time period were lost to accidents.

Ambient irradiance during the study was often substantially greater than compensatory irradiance (I_{comp} – Fig. 2 d), thus indicating that phytoplankton

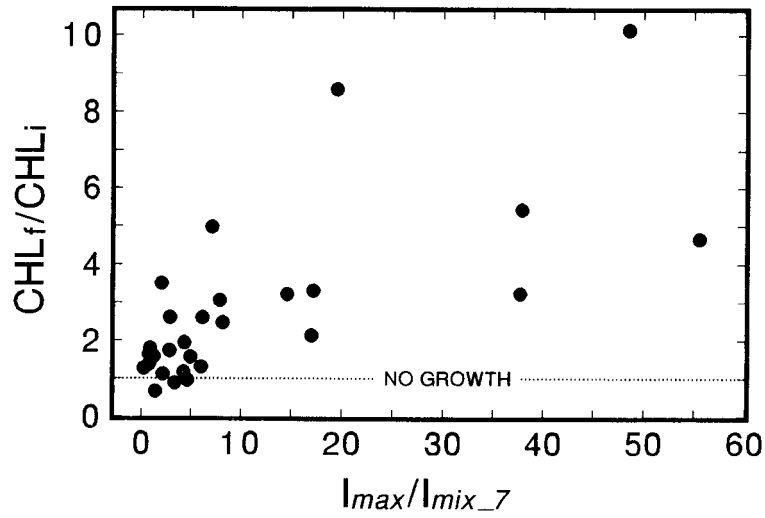

Fig. 4. Growth (CHL_f/CHL_i) in light-saturated controls as a function of the ratio of irradiance during incubation (I_{max}) to mean mixed layer irradiance in the week preceding incubation ($I_{mix\text{-}7}$).

had sufficient light to achieve net positive growth. I_{comp} was less than $I_{mix\text{-}i}$ in only 6 of 26 experiments with appropriate data (Table 1). Thus phytoplankton may often have occupied a middle position in the light limitation continuum with light sufficient to produce net gains but insufficient for optimal growth.

Biomass response

Another indication of the prevalence of light limitation in Mark Twain Lake is given by the growth of biomass in controls. In control containers incubated at saturating irradiance, CHL increased significantly in 24 of 28 experiments (Table 1) including 15 experiments in which CHL more than doubled. At the uplake site in March 1990, mean CHL_f for controls was >1000 % of CHL_i (Table 1). In the majority of these experiments growth seemed to be a response to increased light insofar as the irradiances yielding maximum growth were greater than in situ irradiance prior to the experiment. Growth as a proportion of initial biomass was highly correlated (r=0.7) to the proportional increase in light ($I_{max}/I_{mix\text{-}7}$) experienced by the controls as a result of incubation (Fig. 4).

Nutrient limitation

Saturating irradiance

Analysis of variance showed significant effects of N, P, or N+P at growth-saturating irradiances in 24 of the 28 experiments (Table 1). Variation among rep-

Table 1. Partial results of algal growth experiments. I_{mix-i}, I_{comp}, I_k, and I_{max} are given in $E\,m^{-2}\cdot d^{-1}$. The I_{comp}, I_k, and I_{max} values shown are based on the maximum CHL_f in each experiment irrespective of nutrient addition. Values of I_{comp} in parenthesis are rough estimates based on only two depths. Mean maximum CHL_f for each treatment is given as a proportion of CHL_i. An asterisk marks values of mean CHL_f which did not differ significantly from CHL_i ($p>0.05$). In the 11–22–90 experiment maximum treatment means for ammonium addition (NH) and nitrate addition (NO) are listed in the +N and +NP columns, respectively. Dates marked by an asterisk indicate experiments at the uplake site. Analysis of variance (ANOVA) results show significant differences ($p<0.05$) among treatment means at the same irradiance as determined by Duncan's multiple range test (SAS, 1991). Where treatment maximums occurred at different irradiances CHL_f and ANOVA results for both irradiances are shown.

							CHL_f/CHL_i				
Start date	days	I_{mix-i}	I_{comp}	I_k	I_{max}	CHL_i	CON	+P	+N	+NP	ANOVA
9–15–89	5	6.9	–	–	11.6	5.3	0.96*	1.01*	2.71	4.05	NP>N>P=C
9–15–89*	5	2.5	–	–	13.6	9.7	3.21	3.20	8.12	10.58	NP>N>C=P
11–09–89	5	1.5	(1.5)	–	6.4	5.5	1.94	2.80	1.92	2.23	P>NP=C=N
11–09–89*	5	1.7	(0.7)	–	10.4	16.2	2.60	3.44	2.71	4.37	NP>P>N=C
12–13–89	8	0.8	(0.5)	–	4.5	3.2	1.17	1.12*	1.16	1.16	C=N=NP=P
1–31–90*	8	2.0	(0.1)	–	5.6	12.4	0.99*	2.07	1.04*	2.22	NP>P>N=C
							1.28	–	–	1.69	NP>C
2–01–90	7	0.9	(2.9)	–	4.5	6.3	0.88	0.93	0.91	1.05	NP>P=N P>C N=C
2–27–90*	8	0.4	–	–	13.3	17.5	3.23	3.33	3.46	3.46	NP=N=P N>C P=C
2–28–90	7	1.6	–	–	0.9	9.0	1.37	–	–	1.64	NP>C
							0.91	1.39	0.88	1.41	NP=P>C=N
3–29–90*	7	0.2	0.5	5.7	5.9	1.5	10.14	9.09	10.48	10.16	N=NP=C=P
3–30–90	6	0.4	0.1	3.2	6.7	5.0	–	–	–	6.77	no test[1]
							4.67	4.89	4.92	4.99	NP=N=P=C
9–04–90	3	6.0	0.9[2]	4.1	11.5	21.0	3.51	4.70	3.35	–	P>C=N
9–17–90	3	1.3	1.5	4.7	10.4	9.4	1.74	4.12	1.74	–	P>C=N
10–05–90	3	1.0	0.9	5.1	20.2	7.9	8.59	8.86	10.04	–	N>P=C
10–29–90	3	0.9	<0.1[2]	3.4	7.3	2.9	2.47	2.41	2.93	–	N>C=P
11–22–90	6	0.2	0.3	1.9	9.4	2.5	5.43	5.39	8.24	6.32	NH>NO>C=P
2–20–91	6	0.5	–[2]	<0.5	0.5	1.4	1.26	1.25	1.31	–	C=N>P
							1.31	1.23	1.28	–	N=C=P
3–06–91	7	0.6	0.1	0.6	2.0	1.6	1.57	1.60	1.72	–	N>P=C
3–25–91	6	1.5	0.4	1.9	9.2	5.0	4.97	5.14	6.49	–	N>P=C
4–15–91	3	4.9	0.7	3.7	16.0	20.8	3.06	3.29	3.63	–	N>P=C
5–06–91	3	1.1	0.2	0.8	24.2	7.7	3.31	3.52	4.40	–	N>P=C
5–28–91	3	11.5	7.1	5.2	45.3	20.3	0.39	2.41	0.54	–	P>N=C
							0.66	1.34*	0.66	–	P=N=C
6–07–91	3	8.8	2.0	4.6	10.6	15.4	1.58	3.99	1.65	–	P>N=C
7–15–91	3	15.8	2.6	4.3	9.6	14.0	1.64	2.78	1.62	–	P>C=N
8–12–91	3	11.8	1.4	2.5	8.6	6.0	1.80	2.29	1.80	–	P>C=N
9–09–91	3	6.2	2.0	3.0	10.4	9.2	1.12*	1.11*	1.28	–	N=C=P
10–07–91	3	2.9	0.3[2]	3.5	33.3	5.4	2.18	4.66	2.14	–	P>C=N
							2.60	3.76	2.90	–	P>N>C
11–13–91	6	0.3	0.2	1.4	9.3	2.6	2.13	2.36	2.42	–	N=P=C

[1] Control containers at I_{max} were lost so no treatment comparison was made.

[2] Net growth was positive in deepest containers, so I_{comp} (also I_k for 2–20–91) was extrapolated from the two greatest depths.

licate containers was low (mean CV <7 %), so even small differences were usually statistically significant ($p<0.05$). Effects of N and P added singly were usually mutually exclusive. Only one experiment (3-6-91) showed both N and P to significantly increase growth rates at the same irradiance. But in that case P had no significant effect at the irradiance at which experiment-wide growth rate and response to N were maximal (Table 1). Early experiments included an N+P treatment and this combination usually yielded significantly greater growth than either nutrient separately. In effect, the combination of nutrients enhanced the response to individual treatments. Either N or P alone produced significant effects in all the experiments in which N+P was significant.

Nutrient effects at in situ irradiance

Irradiance in the mixed layer was usually far below the saturating intensities at which we observed large differences among nutrient treatments (Fig. 3, Table 1). To estimate the effect of nutrient addition at irradiances similar to those in the lake, we used growth-irradiance curves to interpolate differences among treatments at ambient mixed layer irradiance (Fig. 1).

Not surprisingly, differences among treatments at in situ irradiance varied with in situ irradiance. Nutrient effects were negligible when ambient irradiance was less than $1\,E\,m^{-2}\,d^{-1}$ (Fig. 5 a). In this range of irradiance, final CHL (CHL_f) for nutrient treatments minus CHL_f in controls was never more than 20 % greater than initial CHL (CHL_i). Between 1 and $6\,E\,m^{-2}\,d^{-1}$, N and N+P had more substantial effects (up to 65 % of CHL_i) while the effect of P was inconsistent. But the largest positive effects of nutrients on growth (up to 175 % of CHL_i) and the largest effects of phosphorus added singly occurred at I_{mix} above $\approx 6\,E\,m^{-2}\,d^{-1}$.

The pattern illustrated by data in Fig. 5 a is our best estimate of the effect of adding nutrients without altering the irradiance experienced by phytoplankton in the lake. Fig. 5 b, which portrays percent growth in controls, shows the analogous effect of increasing light without altering nutrients. Ignoring the vertical scale, the two plots are mirror images. Response to light was least where response to nutrients was greatest and vice versa. But there was a broad middle ground where both light and nutrients seemed to be important.

Discussion

Our principal interest in conducting these experiments was to determine the conditions under which light would replace nutrients as a dominant factor controlling algal biomass. We hypothesized that the two types of limitation would intergrade along a gradient of in situ irradiance and results in Fig. 5 support

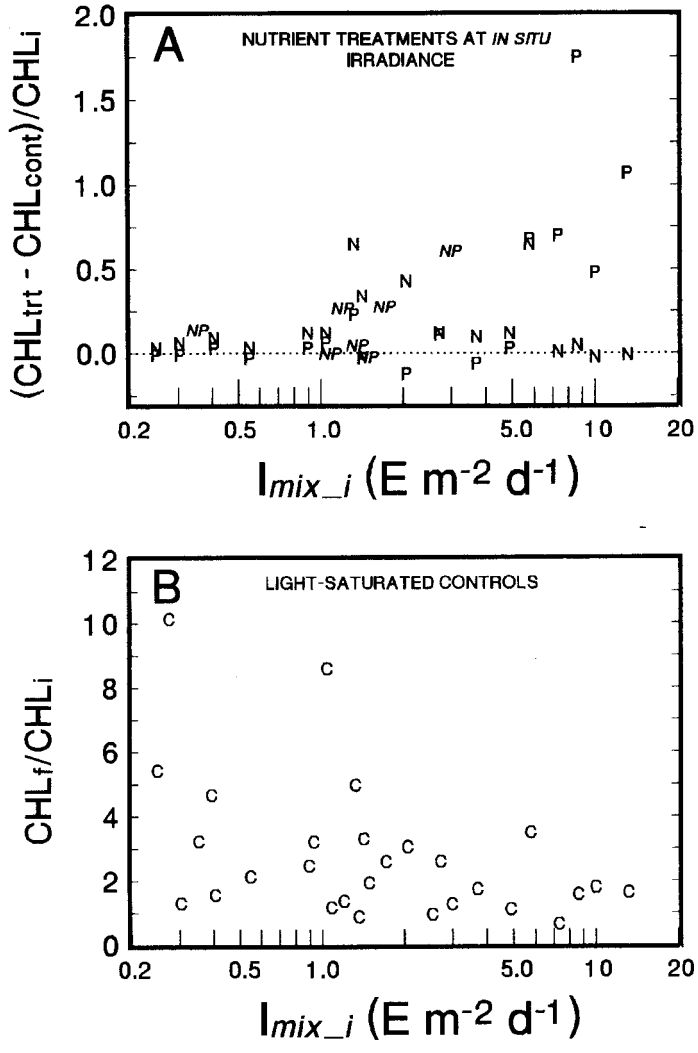

Fig. 5. Effect of mixed layer irradiance ($I_{mix\text{-}i}$) on A) growth response to nutrient addition at in situ irradiance and B) growth in light-saturated controls. In A, growth-irradiance plots were used to interpolate final CHL at in situ irradiance for nutrient treatments (CHL_{trt}) and controls (CHL_{cont}) and the response to nutrient addition expressed as the difference between the two divided by CHL_i.

this supposition. These data suggest that light limitation of algal community biomass was supplanted by nutrient limitation at mixed layer irradiances above $\approx 6\,E\,m^{-2}\,d^{-1}$, similar to the value of $\approx 7\,E\,m^{-2}\,d^{-1}$ recently put forth by CARIGNAN & PLANAS (1994). Our results, however, show small, but unantici-

pated, effects of added N at considerably lower irradiances where light also limited growth.

At irradiances between ≈1–6 E m^{-2} d^{-1} we often observed responses to added N (Table 1) even when results were adjusted to in situ irradiance (Fig. 5 a) and corrected for the usually substantial (>2 fold) growth in controls (Fig. 5 b). The puzzling aspect of this result is that most of these experiments occurred after the 1990 floods when DIN was >500 µg/L (Fig. 2 c), largely in the form of nitrate-nitrite (>95 %). Under such conditions, N limitation would not be anticipated (HECKY & KILHAM 1988).

The response to N in these experiments probably resulted from our use of ammonium and nitrate, rather than nitrate alone, in our additions. In November 1990 we added ammonium and nitrate separately in one experiment and observed a significantly greater response to ammonium (Table 1) despite evidence of severe light limitation in situ (I_{mix} = 0.2 E m^{-2} d^{-1}, I_{max}/I_{mix} = 47, maximum CHL_f/CHL_i for controls = 543 %). Thus, it may be appropriate to characterize the algal community of Mark Twain Lake as being co-limited by light and ammonium, rather than nitrogen per se, in the intermediate range of irradiances in which response to light and nutrients heavily overlapped (Fig. 5).

Another striking feature of our results is that increasing light stimulated considerably more growth of CHL (Fig. 5 b) than increasing nutrients (Fig. 5 a). Growth response to added nutrients, corrected for growth in controls never exceeded a factor of two, while controls grew by as much as 10 fold in response to light. This difference reflects relative nutrient availability. Our incubation periods (3–8 d) were sufficiently long, and algal growth rates (except in some winter experiments) were sufficiently rapid, that phytoplankton in our containers were probably at or near the limit of available nutrients by the end of the experiments. Thus the maximum growth observed in each treatment provides a crude index of nutrient availability at the start of the experiments.

At the upper end of the irradiance spectrum, where added P yielded the greatest response, nutrient availability was controlled by our P additions. We approximately doubled ambient TP and thus restricted maximum growth to about a factor of 2. More liberal additions of P might have produced larger responses as were observed at the lower end of the irradiance spectrum. But obtaining these large responses would likely also have required adding N because our data suggest a tendency toward co-limitation by the two nutrients during the period of high in situ irradiance in summer 1991 (Fig. 2 e). DIN declined consistently during that period (Fig. 2 c) as did the growth response to P (Table 1) and by early September neither P nor N treatments differed significantly from controls (Table 1). It is likely that both elements were in short supply at that time.

Another unanticipated feature of our results was that during periods of optimal light conditions we did not usually observe severe nutrient limitation.

Nutrients were usually sufficient to yield significant growth in controls. One experiment during the post-drought period in September 1989 did show evidence of severe N limitation (Table 1). In another experiment in September 1990 maximum CHL_f in the N treatment significantly exceeded CHL_i (t-test), while CHL_f for control and the P treatment did not. The inter-treatment differences, however, were too small to be distinguished by analysis of variance (Table 1). But in other experiments run during summer 1991 controls usually exhibited substantial growth (up to 180 % of CHL_i) suggesting the presence of excess nutrient despite the fact that irradiance in situ was near or above growth saturating intensity (Fig. 2 e). These results indicate that phytoplankton were not severely limited by either light or nutrients during that period. Comparable results were obtained by HECKY & GUILDFORD (1984) in a turbid Canadian lake in which phytoplankton showed no sign of nutrient limitation despite light intensities above saturation. Under such circumstances, some third phenomenon, perhaps related to loss factors, is probably involved in keeping biomass below the ultimate ceiling imposed by ambient nutrients (HARRIS 1986).

Simple experiments measuring the response of phytoplankton to added nutrients have been performed in many lakes using a variety of specific techniques (ELSER et al. 1990). But few workers have attempted to quantify effects of irradiance on algal response to nutrients (STERNER 1994, CARIGNAN & PLANAS 1994) or noted when substantial growth in controls indicated that biomass was not nutrient limited at the time of the experiment (DÀVALOS et al. 1989). Short term bioassays like those described here can yield useful indications about the nutrient status of the existing phytoplankton community (ELSER et al. 1988). But our results suggest that light exposure during incubation can substantially affect the outcome of such experiments. It would be informative to conduct incubations at two or more irradiances in turbid systems in which I_{mix} can vary greatly in response to mixed depth or cloud cover (CARIGNAN & PLANAS 1994). Quantifying effects of irradiance will aid in comparison and interpretation of experimental results and may eventually help clarify the roles of nutrient and light limitation in turbid lakes.

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