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## Phytoplankton photosynthesis parameters in central Canadian lakes

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**Abstract.** Values for two biological parameters — (i)  $P_m^B$ , the light saturated rate of photosynthesis per unit of chlorophyll and (ii)  $\alpha$ , the slope of the light limited part of the photosynthesis versus light curve per unit of chlorophyll — must be known in order to be able to estimate rates of phytoplankton primary production from chlorophyll data. These parameters were measured for periods of up to 9 years in central Canadian lakes located in temperate, subarctic and arctic climatic zones. Regardless of their geographic locations, lakes where integral photosynthesis was nutrient limited had lower values of these parameters than did lakes where integral photosynthesis was light limited. Temperature set an upper limit to the variability of  $P_m^B$  but was not a good predictor of its actual value. Year-to-year variability of photosynthesis parameters in the most intensively studied group of lakes was large: annual means varied by a factor of three over a 9-year period. Until the sources and extent of this variability are known, accurate production estimates can be obtained from chlorophyll data only if  $P_m^B$  and  $\alpha$  are measured in each water body and in every year. Implications for estimating primary production from remotely-sensed chlorophyll data are discussed.

### Introduction

Numerical primary production models (e.g. Fee, 1984) convert chlorophyll concentrations into production estimates by simulating *in situ* photosynthesis versus light curves. In order to do this, values for two photosynthesis parameters must be known (Jassby and Platt, 1976). These parameters are: (i)  $P_m^B$ , the rate of photosynthesis per unit of chlorophyll at irradiances that are optimal for photosynthesis, and (ii)  $\alpha$ , the slope of the light limited part of the curve relating photosynthesis per unit of chlorophyll to light. Values of these parameters reported in the literature vary over more than two orders of magnitude (Platt and Subba Rao, 1975). However, it is unclear how much of this variation is real, since so many different methods have been used to measure both rates of primary production and chlorophyll concentrations.

Therefore, two questions must be answered before phytoplankton primary production can be routinely estimated from chlorophyll data alone: (i) Do different types of water bodies have consistently different values of  $P_m^B$  and  $\alpha$ ? (ii) How variable are these parameters within any given type of water body on a year-to-year basis? Over a 9-year period we made extensive measurements of epilimnetic values of  $P_m^B$  and  $\alpha$  in central Canadian lakes located in temperate, subarctic and arctic climates (Figure 1). All photosynthesis measurements were made with a single method in which field samples were incubated under controlled laboratory conditions. Our data are consequently well suited to addressing these important questions.

### Study areas

The greatest quantity of data (1976–1983) was obtained from temperate zone lakes in the Experimental Lakes Area (ELA), Northwestern Ontario (49°49'N, 93°54'W).

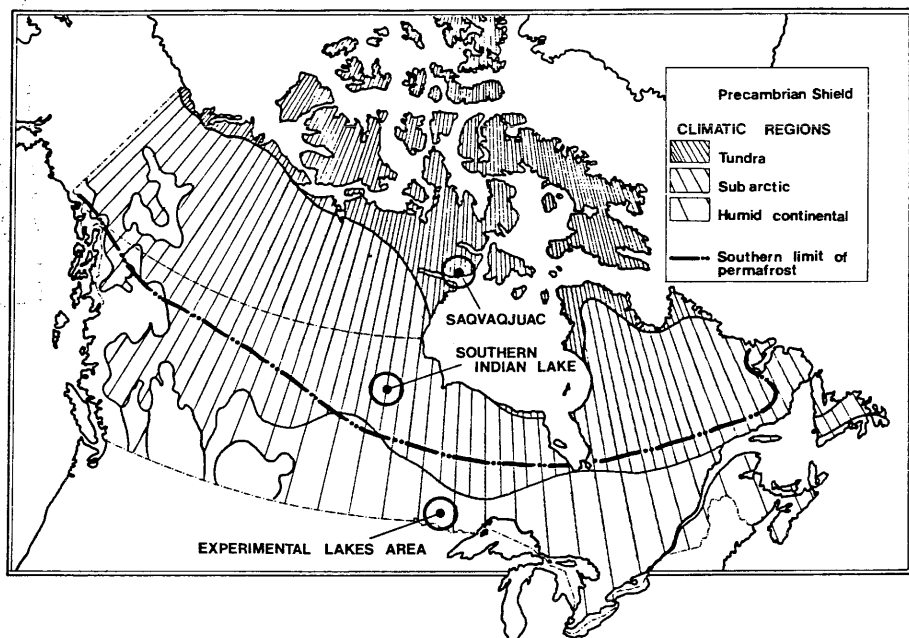


Fig. 1. Map of Canada showing the locations of the three lake areas that were studied.

The ELA lakes which were studied are small (5–50 ha) and relatively deep (< 30 m). Epilimnion temperatures in these lakes reach 22–24°C during midsummer and those lakes deeper than 5 m stratify for periods of 4–5 months. The epilimnia of ELA lakes are transparent (euphotic zone depths 2–3 × the depth of the mixed layer in midsummer) and epilimnetic primary production is not light-limited, even in the least transparent lakes (Fee, 1979).

ELA lakes occupy depressions on the surface of a massive batholith of pink granodiorite, a rock which contains few algal nutrients and weathers very slowly. Further, glacial overburden and postglacial lacustrine deposits are unusually sparse in the ELA region (Brunskill and Schindler, 1971). These geological factors lead to very low nutrient loading rates. Consequently, epilimnetic phytoplankton are invariably deficient (usually severely deficient) in phosphorus and to a lesser extent nitrogen (Healey and Hendzel, 1980). Many of the ELA lakes that were studied were fertilized with phosphorus, nitrogen, and/or carbon or were acidified with sulfuric or nitric acid (Schindler, 1985). Others were completely or partially burned or logged (Beatty, 1981). However, none of these manipulations changed the basic conditions for phytoplankton growth in these lakes — epilimnetic phytoplankton remained nutrient and not light limited (Healey and Hendzel, 1980).

Saqvaqjuac (SAQ) is located in the arctic region of the Northwest Territories on the northwest coast of Hudson Bay (63°38'N, 90°40'W). Lakes in this region were studied from 1977–1981 (Welch, 1985). SAQ lakes are similar in size, depth and geological setting to ELA lakes. Because they are close to the sea, SAQ lakes have higher concentrations of sodium, chloride and sulfate than ELA lakes. Nutrient inputs, however, are

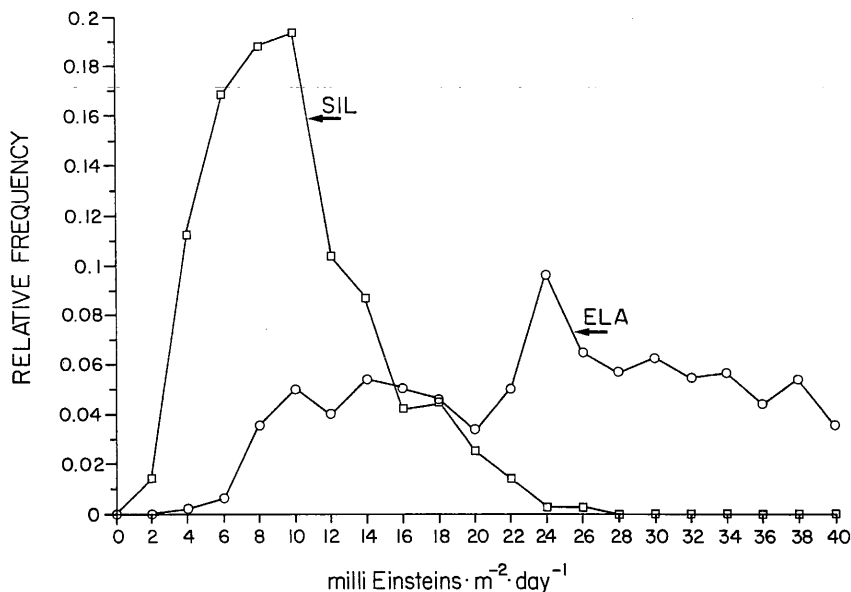


Fig. 2. Frequency distributions of mean water column irradiances at ELA and SIL. The distributions have been normalized by dividing them by the total number of data points (ELA = 475, SIL = 356).

similar to ELA lakes. Probably the most important differences from ELA lakes are related to temperature: SAQ lakes have shorter ice-free seasons (3–4 months, compared to 6–7 at ELA), lower water temperatures during the summer (12–15°C maxima), and they stratify infrequently, if at all. Like ELA lakes, nutrient loading rates to SAQ lakes are low and transparencies are high.

Although no nutrient deficiency measurements have been made at SAQ, it is probable that because of their high transparencies, low mean depths (3–4 m) and low nutrient inputs, that algae in these lakes are also nutrient and not light limited. As at ELA, much of the SAQ data are from lakes that were experimentally manipulated by additions of phosphorus and nitrogen (Welch, 1985).

Southern Indian Lake (SIL) is a very large (239 100 ha), shallow (10–20 m), multibasin lake in the subarctic region of northern Manitoba (57°20'N, 98°20'W) that was studied from 1974–1978 (Hecky and Guildford, 1984). Unlike SAQ and ELA, the SIL basin contains large amounts of glacial clays and postglacial lacustrine deposits (Newbury *et al.*, 1984). It also receives runoff from non-Shield areas to the west. SIL waters are consequently much more turbid than at ELA or SAQ (Hecky, 1984). Another factor that reduces the mean light levels in the mixed layer of SIL is that it mixes to the bottom (mean depth 9 m) throughout the ice-free season while ELA and SAQ lakes mix only to depths of 3–5 m for periods of up to 5 months. The light climate experienced by phytoplankton in SIL is contrasted with ELA in Figure 2.

Nutrients are never as limiting to SIL algal populations as at ELA (Healey and Hendzel, 1980; Planas and Hecky, 1984). Rather, as a consequence of the high turbidity levels and greater mixed layer depths, primary production in most parts of SIL is light limited (Hecky and Guildford, 1984). Summer surface water temperatures at SIL

(15–18°C) are intermediate between SAQ and ELA, and SIL never developed a prominent thermocline during the period of our measurements (Hecky, 1984).

While under study SIL was impounded and raised in level by 3 m (Newbury *et al.*, 1984). Impoundment increased the depth of the mixed layer and caused extensive shoreline erosion which increased turbidity and added nutrient materials. These processes acted together to make SIL phytoplankton populations more severely light limited and less nutrient limited than they had been before impoundment (Hecky and Guildford, 1984; Planas and Hecky, 1984).

## Materials and Methods

Samples were taken from the epilimnia of the lakes with opaque non-metallic integrating water bottles (Fee, 1976) and were returned to shore-based laboratory facilities for processing. In order to avoid problems associated with diurnal variability of photosynthesis (Fee, 1975), samples were taken in the morning, normally between the hours of 08:00 and 11:00 local time. Subsamples were taken from the integrated sample for dissolved inorganic carbon and chlorophyll analyses (Stainton *et al.*, 1977). The remainder of the sample was siphoned into Pyrex bottles for  $^{14}\text{C}$  productivity measurements (Shearer *et al.*, 1985, give methodological details).

Primary production samples were incubated in duplicate at four irradiances in artificial light incubators maintained at *in situ* temperatures. Incubator light levels on any day were fixed; they were changed seasonally in accordance with seasonal changes of available light. Before 1979, incubator light levels were measured with quantum cells (Lambda Instruments Co.) fitted with cosine corrected flat plate collectors. In 1979 measurements at ELA showed that these flat plate collectors failed to measure a significant part of the available light in our incubators (as measured with spherical collectors, see DeClercq and Shearer, 1980, for details). The same correction factors were later measured in the incubator at SIL. We assume that these factors also apply to the SAQ data because the incubator used there was of the same type that was used at ELA and SIL. All light measurements made with flat plate collectors have been corrected with these factors to make them comparable to measurements made with spherical collectors.

The parameters  $P_m^B$  and  $\alpha$  were calculated from the incubator data in the following way: the replicates at each of the four irradiance levels were averaged and  $P_m^B$  was taken as the maximum of these mean rates divided by the chlorophyll concentration. After obtaining  $P_m^B$ , the equation below was iteratively fit to the unaveraged production versus light data to obtain the best (least squares) estimate of  $\alpha$ . The photosynthesis equation is:

$$\begin{aligned} P^B &= 0 && \text{for } I \leq I_k/20 \\ &= \alpha I' [1 - \alpha I' / (4P_m^B)] && \text{for } I_k/20 \leq I < 2I_k \\ &= P_m^B && \text{for } 2I_k \leq I \end{aligned}$$

where

$I$  = irradiance

$P^B$  = the rate of photosynthesis per unit of chlorophyll,

$I_k = P_m^B / \alpha$ ,

$I' = (I - I_k/20)$

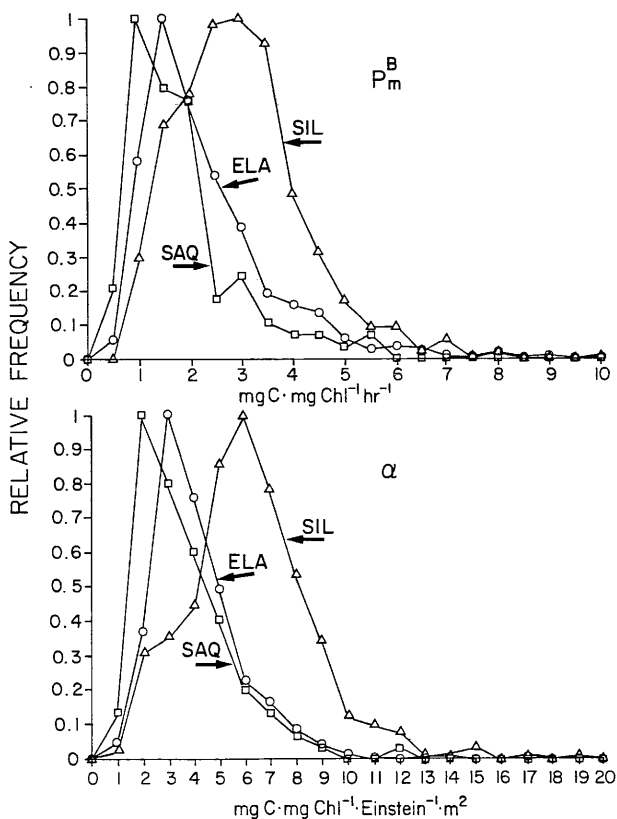


Fig. 3. Frequency distributions of photosynthesis parameters at the three study sites. The distributions have been normalized by dividing them by the modal frequency. The total number of data points are: ELA = 723, SIL = 443, SAQ = 102.

This equation was adapted from one given in Jassby and Platt (1976); it was used instead of their recommended hyperbolic tangent function because it differs insignificantly from that function and requires only one-fifth of the computer time to calculate. As formulated, photosynthesis is zero at an irradiance of  $I_k/20$ ; this constant was determined empirically and corresponds to the constant  $R^B$  defined by Jassby and Platt. The units for  $P_m^B$  are  $\text{mg C mg}^{-1}\text{chl h}^{-1}$  and for  $\alpha$  are  $\text{mg C mg}^{-1}\text{chl E}^{-1} \text{m}^2$ .

## Results and Discussion

Figure 3 shows the frequency distributions of epilimnion parameter values at the three study sites. The shapes of these curves are similar at ELA and SAQ, while at SIL the curves are broader and have modes at distinctly higher values.

It is tempting to ascribe the small differences between the SAQ and ELA frequency distributions to the temperature differences between the temperate and arctic sites. This argument is convincing for  $P_m^B$  since temperature has been shown to be the primary variable controlling this parameter in single species experiments (Talling, 1957; Eppley, 1972). However,  $\alpha$  is not influenced by temperature (Talling, 1957; Rabinowitch

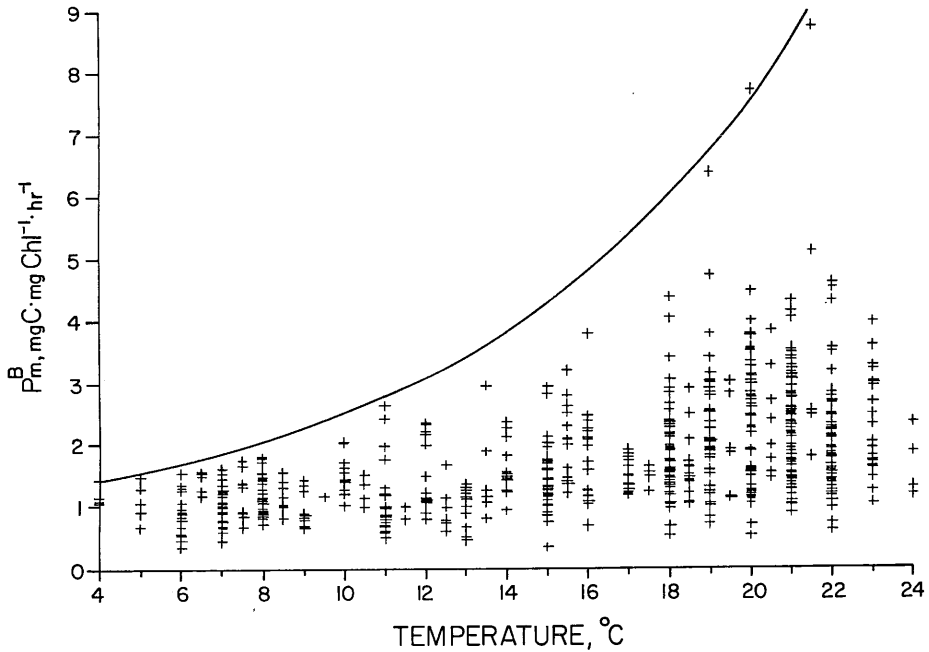


Fig. 4. The relation between temperature and  $P_m^B$  at ELA.

and Govindjee, 1969) and the differences between ELA and SAQ in this parameter were similar to the differences in  $P_m^B$ . Moreover, the fact that SIL had higher parameter values than either ELA or SAQ indicates that temperature was not the most important variable since temperatures at SIL were intermediate between SAQ and ELA. Our ELA data (Figure 4) support Eppley's (1972) conclusion that temperature only sets an upper limit on  $P_m^B$ ; other factors (nutrients, light) normally prevent phytoplankton from achieving this physiological limit.

The broader distribution of parameter values at SIL (Figure 3) reflects the greater diversity of environments in this spatially and temporally complex lake. Before impoundment, some parts of SIL had high transparencies (Hecky, 1984). Phytoplankton samples from these more transparent areas were deficient in phosphorus (Hecky and Guildford, 1984) and values of  $P_m^B$  and  $\alpha$  in these areas were lower than those from the more turbid parts of SIL. These low  $P_m^B$  and  $\alpha$  values were similar to values regularly observed at ELA and SAQ and are responsible for the distinct 'shoulders' on the left sides of the SIL pre-impoundment curves (Figure 5). After impoundment, turbidity increased throughout SIL (Hecky, 1984) and virtually all of the phytoplankton became light- instead of phosphorus limited (Hecky and Guildford, 1984; Planas and Hecky, 1984). The post-impoundment frequency distributions (Figure 5) reflected this change: values were much more strongly grouped around the upper modes and the 'shoulders' that had occurred at low parameter values on the pre-impoundment frequency distributions disappeared. We believe that there is a causal link between the increase in turbidity, the decrease in nutrient limitation and the disappearance of lower parameter values. Note that there were limits to the degree to which phytoplankton

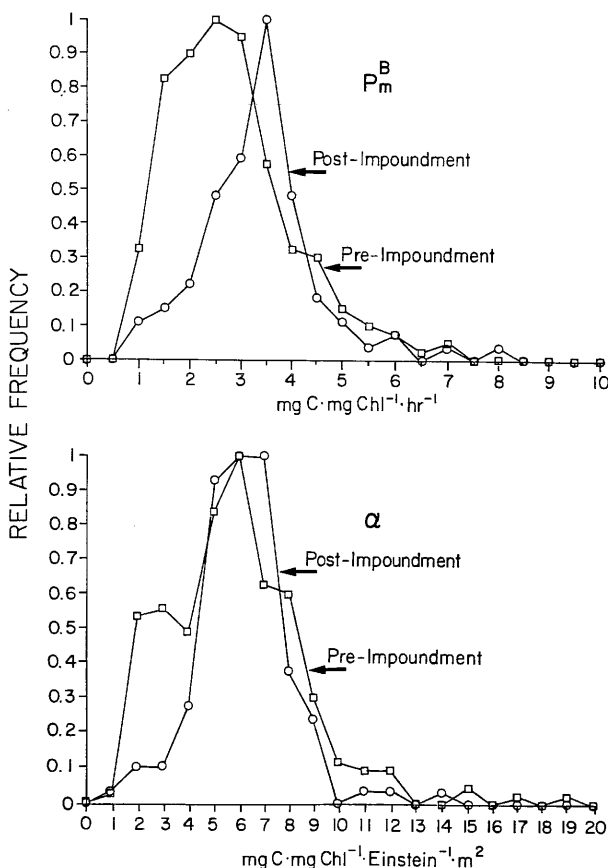


Fig. 5. Frequency distributions of photosynthesis parameters at SIL before and after impoundment. The distributions have been normalized by dividing them by the modal frequency. The total number of data points are: pre-impoundment = 224, post-impoundment = 95.

in SIL could compensate for decreased light availability by increasing their photosynthetic efficiencies: the upper modes of the pre-impoundment curves did not move further to the right after impoundment.

The answer to the first of the two questions posed at the start of this paper is now clear: phytoplankton in lakes where epilimnetic photosynthesis was primarily nutrient limited had lower values of both  $P_m^B$  and  $\alpha$  than did phytoplankton in lakes where light was the primary factor limiting epilimnetic photosynthesis. Unfortunately, our data are not as well suited to answering the second question — What is the long-term variability of a  $\alpha$  and  $P_m^B$  in a single group of lakes? — because only at ELA do our data cover a period longer than 5 years.

In the ELA lakes, the annual means of the photosynthesis parameters were highly variable (Figure 6). In the year with the highest parameter values, a unit of chlorophyll was on average capable of fixing three times more carbon than in the year with the lowest values. Indeed, in one year out of nine, ELA had parameter values that would be typical of SIL. Note that although there appears to be a clear trend when data from

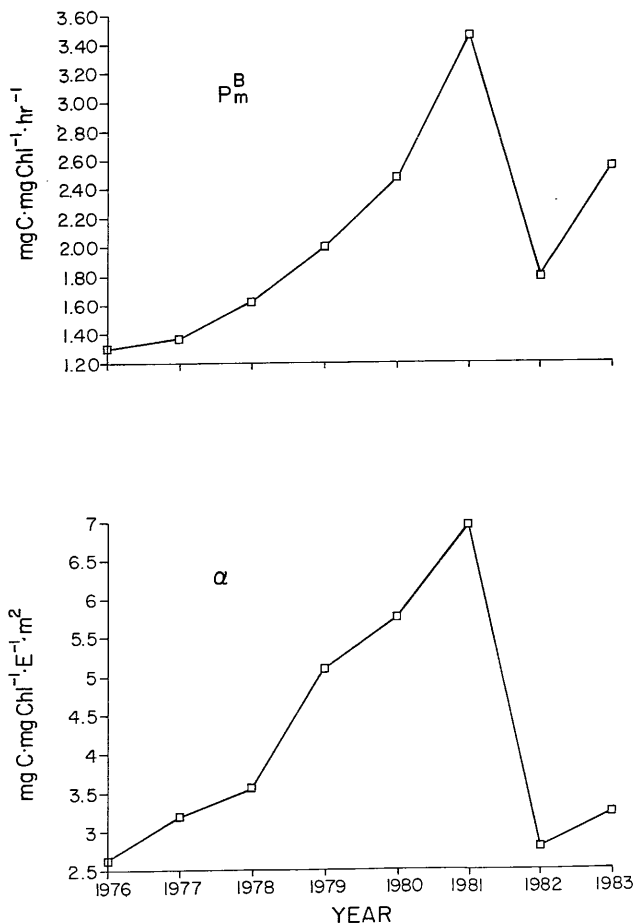


Fig. 6. The annual means of photosynthesis parameters at ELA.

all lakes are averaged (Figure 6), the pattern was not synchronous in different ELA lakes (Figure 7).

There are several potential sources of variability in the ELA data. Virtually all of the lakes that were studied experienced a major perturbation (fertilization, acidification, burning and/or logging) during the period of our study. Any of these processes could alter the availability of nutrients, which in turn is known to affect photosynthetic parameters (Curl and Small, 1965; Ichimura, 1973; Takahashi *et al.*, 1973; Eppley and Renger, 1974; Thomas and Dodson, 1972; Hecky and Guildford, 1984). However, there are two reasons why we are uncertain that these processes were responsible for the variability that we observed: (i) all of the ELA lakes that we studied demonstrated similar magnitudes of variation, regardless of whether they were acidified, fertilized, burned, logged or unmanipulated (Figure 7). (ii) None of these perturbations altered the nutrient deficiency status of ELA epilimnetic phytoplankton populations (Healy and Hendzel, 1980) — they all remained nutrient- and not light limited.



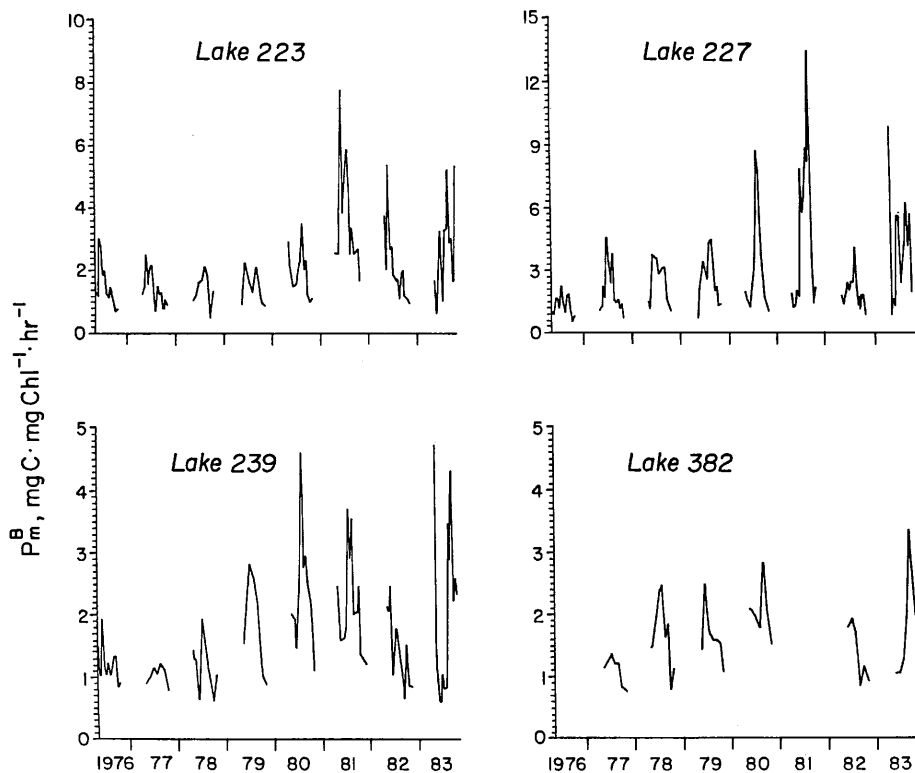


Fig. 7. Variations of  $P_m^B$  in fertilized, acidified and burned ELA lakes. Lake 223 received additions of sulfuric acid starting in 1977. Lake 227 has been fertilized with phosphorus and nitrogen since 1971. Lake 239 was burned in 1974 and 1980. Lake 382 was partially burned in 1978.

Neither annual mean temperature nor total surface light changed appreciably in the ELA region during the period when  $P_m^B$  and  $\alpha$  were measured. There were changes in annual rainfall totals but they did not correlate with the observed changes in photosynthetic parameters. Water transparencies changed in a similar fashion to the curve in Figure 6 (J.A. Shearer, unpublished data). However, we do not believe that these events are linked causally because they are in the opposite sense from the changes that occurred in SIL, where the lower mean light values that resulted from flooding were correlated with higher values of  $P_m^B$  and  $\alpha$ . The pattern observed at SIL is physiologically plausible (Hecky and Guildford, 1984) while the sign of the correlation observed at ELA is not.

Another factor that could lead to high variability in ELA lakes is their small size. It is reasonable to expect that variability will be greater in small lakes. ELA lakes have rapid nutrient turnover times [0.5–2.4 years for phosphorus (Schindler, 1985)] and consequently the influence on the plankton community of nutrient perturbations can be seen almost immediately (Schindler *et al.*, 1971). Except in unusual circumstances, larger water bodies have longer nutrient turnover times [1.5–15 years for phosphorus in the Laurentian Great Lakes (calculated from data in International Joint Commission, 1969, 1977 a,b,c), and 69 000 years for phosphorus in the ocean (Broecker and

Peng, 1982)]. Large lakes will therefore be less responsive to year-to-year fluctuations of nutrient inputs. Further, as the size of the drainage basin increases, the less likely it becomes that the entire basin will be subject to a disturbance such as a forest fire or clear cutting.

Of course, it may be that these parameters have an inherently high variability in all water bodies. If this is true then the type of year-to-year differences that were observed at ELA will be found in lakes of all sizes. Extensive and careful observations are needed from a variety of locales to resolve this question.

Color sensors mounted in satellites and aircraft are now being used to measure chlorophyll concentrations in the mixed layers of lakes and oceans. To date, remotely sensed chlorophyll data have been used primarily as water mass tracers (Gordon *et al.*, 1982, 1983; Feldman *et al.*, 1984; McLain *et al.*, 1984; Barale *et al.*, 1984; Gower, 1984) but there are widespread expectations that they can eventually be used to estimate rates of phytoplankton production in the mixed layers of water bodies. As a first step towards this goal Smith *et al.* (1982); Platt *et al.* (1983) and Eppley *et al.* (1985) showed that chlorophyll data derived from satellites correlate well with direct measurements of phytoplankton production in the sea. The next logical step in this work is to use remotely sensed chlorophyll data as input to deterministic productivity models. If these models can be shown to give reliable results, information on photosynthetic carbon fluxes could be efficiently gathered. Such techniques would be especially useful for work on very large water bodies like the Laurentian Great Lakes and the oceans. However, until the spatial and temporal variability of  $P_m^B$  and  $\alpha$  is better known, very broad confidence intervals will have to be placed around primary production estimates derived from remotely sensed chlorophyll data and the extrapolation of photosynthesis parameter values from other sites or times.

## Acknowledgements

Over the years, many people at ELA, SIL and SAQ assisted in this work. Permanent staff who were directly involved were John Shearer, Doug DeClercq and Ed DeBruyn at ELA, Stephanie Guildford at Southern Indian Lake and Jean Legault and Larry DeMarch at SAQ.

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*Received February 1985; accepted December 1986.*