

# Sigmoid Relationships between Nutrients and Chlorophyll among Lakes

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Previous studies of freshwater eutrophication have shown that algal biomass tends to increase with the supply of dissolved phosphorus. This concept has been condensed into empirical relationships between chlorophyll *a* and total phosphorus concentrations (convenient measures of algal biomass and phosphorus availability) which have become essential tools in theoretical and applied limnology. With few exceptions, ecologists accept the idea that chlorophyll concentration rises linearly with phosphorus concentration among lakes. Such a suggestion runs counter to Liebigian principles of fertilization however, and contradicts laboratory and field research indicating the influence of other nutrients. Our analysis of two large independent phosphorus–chlorophyll data sets from temperate-zone lakes shows that log phosphorus–log chlorophyll relationships are sigmoid in shape and that a second nutrient, nitrogen, has a significant impact on chlorophyll concentrations when phosphorus availability is high. Our new empirical relationships indicate that mechanisms regulating algal biomass change with enrichment, and suggest new management strategies for polluted lakes.

Les résultats d'études antérieures sur l'eutrophisation des eaux douces montrent que la biomasse algale a tendance à augmenter avec l'accumulation de phosphore dissous. On a exprimé ce concept par des rapports empiriques entre la chlorophylle *a* et les concentrations de phosphore total (mesures pratiques de la biomasse algale et de la quantité de phosphore disponible), qui sont devenus des outils essentiels en limnologie théorique et appliquée. À de rares exceptions près, les écologistes admettent l'hypothèse selon laquelle la concentration de chlorophylle s'accroît de façon linéaire avec celle du phosphore dans les lacs. Une telle hypothèse est cependant contraire aux principes liebigiens de fertilisation et contredit les résultats de travaux en laboratoire et sur le terrain, qui font intervenir d'autres éléments nutritifs. Notre analyse de deux importantes séries de données indépendantes sur les rapports phosphore–chlorophylle dans les lacs de la zone tempérée montre que la relation entre la courbe logarithmique du phosphore et celle de la chlorophylle *a* a une forme sigmoïde, et qu'un second élément nutritif, l'azote, a un impact significatif sur les concentrations de chlorophylle lorsque la quantité de phosphore disponible est élevée. Ces nouveaux rapports empiriques, qui indiquent que les mécanismes déterminants de la biomasse algale se modifient avec l'enrichissement, laissent entrevoir de nouvelles stratégies de gestion pour les lacs pollués.

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Average phytoplankton biomass in lakes is strongly correlated with total phosphorus (TP) concentration (Sakamoto 1966; Dillon and Rigler 1974). This relationship forms the basis for lake management techniques (Dillon and Rigler 1975), and theoretical analyses (Smith 1982) of the dependence of algal growth rates on phosphorus availability. Estimates of TP have been used extensively by limnologists to assess the degree of eutrophication of particular lakes and to predict the productivity and biomass of virtually all biological components of lakes and ponds (Peters 1986). The fact that TP concentration in lake water is correlated with so many aspects of lake biology, along with experimental result (see below), have produced the consensus that phosphorus availability sets the limit to biotic productivity in temperate zone lakes (Hutchinson 1973; Schindler 1978; Peters 1986). While some have suggested that variables other than TP might significantly affect phytoplankton biomass (e.g. Smith 1979, 1982), there have

been few detailed analyses of the shape of phosphorus–chlorophyll relationships.

The phosphorus–chlorophyll relationship presumably results from the dependence of algal growth rates on phosphorus availability. Extensive large- and small-scale experiments (Schindler 1977; Lean and Nalewajko 1979) show that phosphorus is the primary nutrient limiting algal productivity in most temperate zone lakes. The simplest nutrient-dependence hypothesis (Smith 1982) suggests that the response of algal biomass to changing phosphorus concentration might be linear. That is, a unit increase of phosphorus should yield an increment in plant biomass that is independent of the phosphorus concentration of the lake or pond. This might occur if all other plant nutrients are in infinite supply, and shifts in algal community structure or changes in the relative importance of decomposers or consumers do not systematically modify the response of plant biomass to phosphorus availability. An hypothesis that fits more closely with the classic Liebigian paradigm (von Liebig 1840; Hutchinson 1973; Droop 1974; Tilman 1982) would consider other nutrients that might limit algal growth at high levels of

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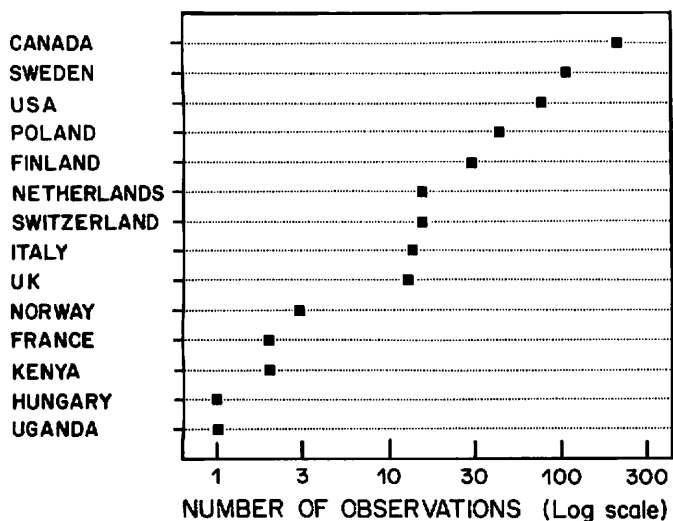


FIG. 1. Frequency of summer epilimnetic chlorophyll and summer epilimnetic total phosphorus (TP) data from 266 lakes in 14 countries, drawn from 67 published articles (reference list available on request from the authors).

ambient phosphorus. It would predict that chlorophyll should increase linearly until some other quantity (e.g. nitrogen, silicon, molybdenum, light) becomes limiting. A saturation point might thus be reached where subsequent enrichment with phosphorus would have little influence on chlorophyll concentration. Further nonlinearities might be seen if factors like competition of algae with bacteria for sparse phosphorus resources are important in lakes (Currie and Kalff 1984), or if herbivory changes systematically with enrichment (McCauley et al. 1988; Oksanen et al. 1981). These changes could alter the balance between algal growth and loss rates, and subsequently affect the equilibrium algal biomass. Relationships between TP and chlorophyll might therefore even be expected to be sigmoid in shape, and there is an ample theoretical basis to suggest that they could be nonlinear.

Despite the fact that nonlinear relationships between TP and chlorophyll among lakes are probable (Forsberg and Ryding 1980; Canfield 1983), there have been few quantitative examinations of their shape or form. A few studies (Sakamoto 1966; Dillon and Rigler 1974) have suggested that nitrogen availability modifies the chlorophyll yield per unit phosphorus, and that variation in the ratio of total nitrogen (TN) to TP could either help to explain "outliers" or reduce residual variability in phosphorus-chlorophyll relationships. Smith (1982) performed the most comprehensive analysis of phosphorus-chlorophyll relationships to date, and was the first to show that knowledge of both TP and TN concentrations could improve predictions of algal biomass. However, careful scrutiny of Smith's (1982) second figure reveals systematic lack of fit of a linear model to log TP:log chlorophyll data. This bias suggests that the fundamental relationship between TP and chlorophyll is, in fact, nonlinear. Straskraba (1985) has repeatedly argued, from a physiological basis, that the phosphorus-chlorophyll relationship is sigmoid. His limited analysis with a small data base (i.e.  $n < 30$ ) suggests that this is true at least within particular geographical regions.

Straskraba's (1985) critical analysis, reinforced by the systematic lack of fit of a linear model to Smith's (1982) data, led us to examine the form of the relationship between TP and chlo-

rophyll *a*, and to test whether nonlinearities could simply be explained by the influence of nitrogen.

## Data and Analyses

Limnologists now routinely measure chlorophyll *a*, TP, and TN concentrations, and analyses are fairly standardized: chlorophyll is measured by pigment extraction of filtered samples followed by spectrophotometry (Anon 1981); TP is determined by digestion of whole water samples followed by various modifications of the ammonium molybdate method (Murphy and Riley 1962); TN is measured as total Kjeldahl nitrogen (Anon 1981) of whole samples.

The results for a wide range of lakes are scattered throughout the ecological literature (Fig. 1). For example, the United States Environmental Protection Agency (USEPA) has single-handedly collected comparable data on 493 lakes (Taylor et al. 1978). We thus collected two independent sets of data: data drawn from the literature (Fig. 1; including the observations from Smith 1982), and data published by USEPA. We found a total of 548 published observations representing a range of TP from 1 to 14 093  $\mu\text{g}\cdot\text{L}^{-1}$  and a range of chlorophyll concentration from a 0.2 to 265  $\mu\text{g}\cdot\text{L}^{-1}$ . Seventy percent of these observations were accompanied by summer epilimnetic total nitrogen (TN) measurements made at the same time (range of TN from 61 to 10 740  $\mu\text{g}\cdot\text{L}^{-1}$ ). USEPA (Taylor et al. 1978) data (493 lakes) included observations of summer epilimnetic chlorophyll, TP, and TN. USEPA data represented a range of chlorophyll concentration from 0.8 to 596  $\mu\text{g}\cdot\text{L}^{-1}$ , TP from 5 to 4550  $\mu\text{g}\cdot\text{L}^{-1}$ , and TN from 200 to 8204  $\mu\text{g}\cdot\text{L}^{-1}$ . Thus, the combined data include 1041 measurements of average summer epilimnetic TP and chlorophyll *a* concentration (84% accompanied by TN measurements), with which to evaluate the form of the phosphorus-chlorophyll relationship and the influence of nitrogen. This represents an almost three-fold increase in sample size over the most ambitious published study (e.g. Smith 1982). Saline lakes (e.g. Prepas and Trew 1983) were not included in our data set.

The shape of the phosphorus-chlorophyll relationship was analysed in five steps. (1) Linear regression analysis was done on logarithmically transformed values of phosphorus and chlorophyll, as is usually done in the limnological literature. Transforming the observations acts to stabilize the variance. (2) Lack-of-fit in the log-log linear fit was examined by computing the residuals of this relationship, and determining their relationship to log TP using robust, locally-weighted sequential smoothing (LOWESS: Cleveland 1979). This weighted least squares technique aids the interpretation of the form of bivariate relationships, while guarding against the influence of deviant points. (3) The actual form of the relationship between log chlorophyll *a* concentration and log TP was then determined using robust locally-weighted regression analysis (Cleveland 1979). We did not apply model-based nonlinear regression analysis at this point because we wanted to avoid a priori judgements about the exact form of the functional relationship. Parameters used in all LOWESS analyses were  $\text{delta} = 0$ ,  $n - \text{steps} = 2$ , and  $f = 0.5$ . (4) The relative roles of phosphorus and nitrogen in accounting for variation in chlorophyll concentration, and the possible role of nitrogen concentration in accounting for the nonlinearities in the log-log chlorophyll:phosphorus relationship were assessed using multiple regression analysis (Draper and Smith 1981), employing backward elimination variable selection (Hocking 1976). These multiple regression analyses were performed sep-

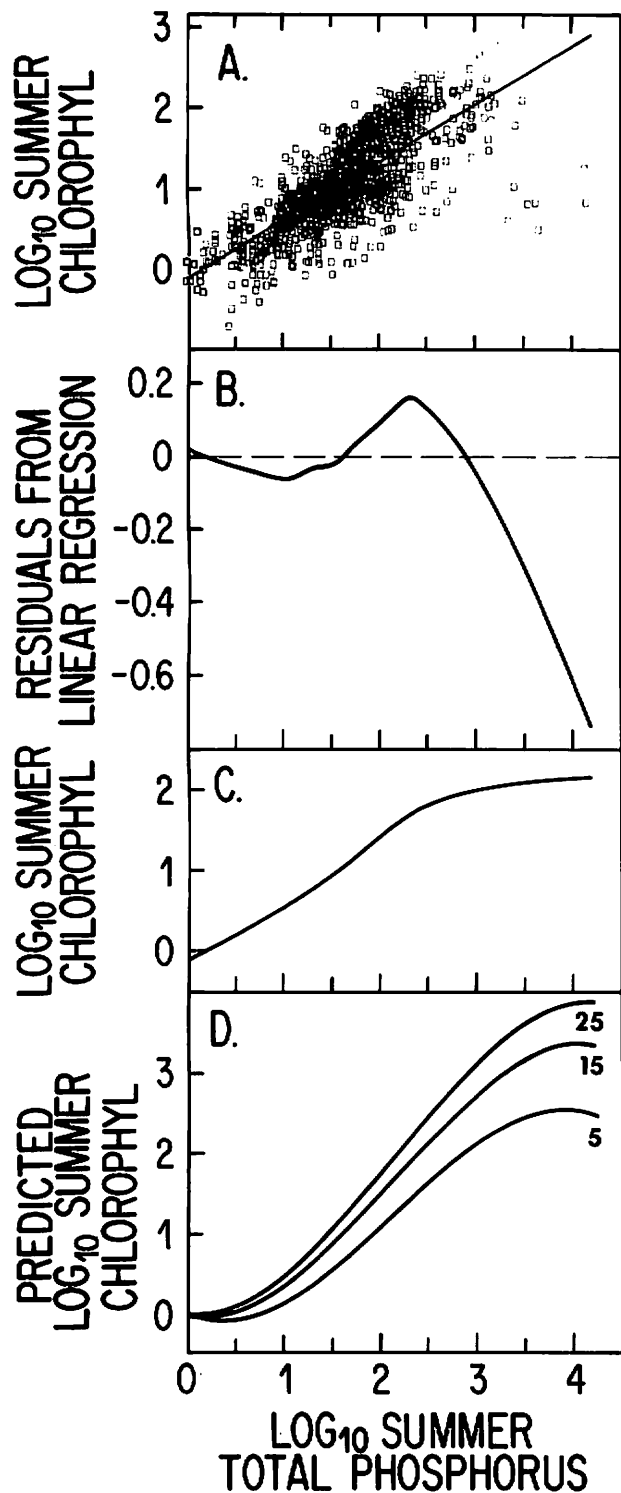


FIG. 2. Relationship between summer epilimnetic chlorophyll *a* concentration and summer epilimnetic total phosphorus (TP) concentrations in the world's lakes. (A) Combined observations from the data sources listed in the legend of Fig. 1. The line shows the linear regression obtained from a least squares analysis of the data. (B) The trend in residuals of a linear regression model fitted to the data in panel (A). Trends are estimated by locally weighted robust sequential smoothing (Cleveland 1979). (C) The overall trend in the relationship between chlorophyll and TP estimated by locally weighted robust sequential smoothing (Cleveland 1979). (D) Relationships between lake TP and chlorophyll concentrations predicted from regression models (combined model, data source-literature) presented in Table 1 for TN:TP ratios (by mass) of 5, 15, 25.

TABLE 1. Partial regression coefficients for effects of variables on  $\log_{10}$  summer chlorophyll *a* concentration (micrograms per litre) found by least squares regression analysis. Variables were the logarithms of summer TP (log TP) and TN (log TN) concentrations (micrograms per litre), the square and the cube of the logarithms of these variables, the product of log TN and log TP, and, in the combined analysis of both data sets, a dummy variable signifying the source of the data (0 = published literature, 1 = USEPA). <sup>a</sup> indicates that the coefficient is not significantly ( $p < 0.01$ ) different from zero. The number of observations (*n*), coefficient of determination ( $r^2$ ), and the overall *F*-value are presented for each analysis.

Variable	USEPA	Literature	Combined
log TP	-2.93	-0.77	-0.83
(log TP) <sup>2</sup>	1.21	0.59	0.34
(log TP) <sup>3</sup>	-0.24	-0.16	-0.12
(log TP) · (log TN)	0.45	0.31	0.43
Data source	—	—	-0.08
Intercept	1.46	0.03 <sup>a</sup>	0.03 <sup>a</sup>
<i>n</i>	493	382	875
$r^2$	0.61	0.80	0.71
<i>F</i> (overall)	191	375	431

arately for each of the two independent data sets (literature and USEPA). Candidate variables in both analyses were the logarithms of summer TP (log TP) and TN (log TN) concentrations (micrograms per litre), the square and cube of the logarithms of these variables to account for possible nonlinearities in the response, and the product of log TP and log TN to seek possible interactions between phosphorus and nitrogen concentrations. Initially all candidate variables were entered in the regression analysis, then variables were eliminated stepwise, based on their partial *F*-significance, until only the variables remained that had a partial *F*-significance of  $\alpha < 0.01$ . (5) Finally, a global multiple regression analysis was performed on the combined literature and USEPA data sets. The analysis was performed exactly as in step (4) above, except that an apparent systematic underestimation of chlorophyll concentration in the USEPA data necessitated the addition of a dummy variable (Gujarati 1978) signifying the source of the data (0 = published literature, 1 = USEPA). (A complete set of tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ontario.)

## Results and Discussion

Contrary to several previous analyses (Sakamoto 1966; Dillon and Rigler 1974; Nicholls and Dillon 1978; Smith 1982), we found a nonlinear relationship between the logarithm of chlorophyll concentration and the logarithm of TP concentration (Fig. 2 a-c). Figure 2a shows the results of a linear fit to the log TP:log chlorophyll relationship. The inadequacy of this linear relationship is visually apparent: chlorophyll concentration is overestimated at low phosphorus levels (2–50  $\mu\text{g}\cdot\text{L}^{-1}$ ) and underestimated at higher phosphorus levels (50–1000  $\mu\text{g}\cdot\text{L}^{-1}$ ). Figure 2b illustrates the precise form of the lack-of-fit by examining the relationship between the residuals of the linear regression and the logarithm of TP using LOWESS procedures (Cleveland 1979). Finally, analysis of the data by locally-weighted sequential smoothing (Cleveland 1979) reveals that the form of the relationship between log chlorophyll and log TP approximates a sigmoid curve (Fig. 2c). It is important to note that this nonlinearity occurs in the log-log relationship

between chlorophyll and phosphorus (Fig. 2a,c). The increment in the logarithm of chlorophyll concentration per unit change in log TP appears to increase over the range of 1–50  $\mu\text{g}\cdot\text{L}^{-1}$  TP, and above approximately 50  $\mu\text{g}\cdot\text{L}^{-1}$  TP the increments decrease in magnitude. These results support Straskraba's contention that the phosphorus–chlorophyll relationship is sigmoidal.

Polynomial regression analysis of two independent data sets (Table 1) shows that both  $(\log \text{TP})^2$  and  $(\log \text{TP})^3$  have highly significant partial effects on the logarithm of chlorophyll concentration. The sign and significance of effects are the same in both data sets providing independent corroboration of a curvilinear relationship. Higher order terms of log TP failed to enter significantly into the multiple regression model. The curvilinearity is highly significant even when data with  $\text{TP} > 1000 \mu\text{g}\cdot\text{L}^{-1}$  are excluded from the analysis. In addition, we have found (S. Watson et al., unpubl. data) that the relationship between algal biomass, estimated by cell volume, and TP among lakes is also nonlinear using logarithmically transformed observations. Thus, the nonlinearity is not due to variation in chlorophyll per cell with enrichment.

Our analysis shows that nitrogen has an unexpected effect on the relationship between TP and chlorophyll concentrations (cf. Smith 1982). TN concentration only accounted for significant variability in chlorophyll concentration as an interaction term with TP (Table 1). This term accounted for significant ( $p < 0.0001$ ) variability in chlorophyll concentration in both independent sets of data (Table 1). Simply put, the effect of nitrogen on the phosphorus–chlorophyll relationship is not “a family of parallel lines whose position is a function of the TN:TP ratio” (Smith 1982). In reality, the effect of nitrogen is much greater at high TP concentration than low (Fig. 2d). The so-called phosphorus–chlorophyll relationship is a family of sigmoid curves that converge at low phosphorus concentration. Our analysis shows that the correlation between TP and chlorophyll concentrations is little affected by TN at low TP concentrations, but that chlorophyll concentration rises sharply with TN at high TP concentrations. Apparently, chlorophyll concentrations in the world's lakes are influenced both by phosphorus and nitrogen, with the latter playing a more dramatic role in phosphorus-rich lakes (Ahlgren 1980). Our observations suggest that covariation among lakes in phosphorus and nitrogen concentrations might determine features of the plateau in chlorophyll concentrations in lakes with high phosphorus levels (J. A. Downing et al., unpubl. data).

These findings influence current concepts of lake management. It was formerly assumed that a decrease in phosphorus loading of any water body would decrease the TP concentration and thus bring about a proportionate decrease in chlorophyll concentration, thereby improving water clarity (Dillon and Rigler 1974, 1975; Nicholls and Dillon 1978). Figure 2 shows that the rate of change in chlorophyll concentration with change in TP concentration varies with both TP and TN. At low TP concentrations (e.g.  $< 50 \mu\text{g}\cdot\text{L}^{-1}$ ) lakes are particularly sensitive to phosphorus loading because increases in TP concentration tend to accelerate the rate of change in chlorophyll concentration per unit change in TP concentration. Variation in TN concentration in oligotrophic systems has little, if any, consequence to algal biomass. In hypereutrophic conditions ( $\text{TP} > 1000 \mu\text{g}\cdot\text{L}^{-1}$ ), lake management by phosphorus effluent abatement would have little or no effect on chlorophyll concentration (Fig. 2c), whereas changes in nitrogen loading might bring about order-of-magnitude variations in algal biomass (Fig.

2d; Table 1). This agrees with experimental evidence from diversion experiments (Ahlgren 1980). Such treatment would not be without its costs, however, as reductions in nitrogen loading, without a reduction in TP concentration would decrease TN:TP, potentially driving the algal community structure toward noxious blue-green algae (Smith 1986).

Our analysis raises questions concerning how processes that influence the average algal biomass present in lakes, might vary with enrichment of phosphorus and nitrogen. If the temporal average of summer chlorophyll concentrations reflects the equilibrium algal biomass, then the shape of the phosphorus–chlorophyll relationship (Fig. 2c) indicates that the balance between average growth and loss rates of algae must vary systematically with lake enrichment. For example, increments of algal biomass per unit change in log TP increase, over the range of 1–50  $\mu\text{g}\cdot\text{L}^{-1}$  TP, suggesting a nonlinear increase in the difference between growth and loss rates. This would occur if changes in growth rates accelerate with increased phosphorus, or changes in loss rates decelerate, or both. Accelerating algal growth rates could arise from changes in algal community structure to competitively superior species moving from ultra-oligotrophic to oligotrophic lakes, or from shifts in the competitive balance between phytoplankton and bacteria. Loss rates imposed by herbivores, such as zooplankton, might not increase linearly because of the progressive establishment of carnivore communities affecting herbivore abundance. Similarly, the tendency of phosphorus–chlorophyll relationships to reach a plateau (i.e. decreasing increments in algal biomass over the TP range of 50–1000  $\mu\text{g}\cdot\text{L}^{-1}$ ), the elevation of which is correlated with TN concentration, suggests that nitrogen or some other factor is modifying the relationship between algal growth or loss rates and phosphorus.

Existing experiments cannot yet differentiate among these hypotheses. The challenge for theoretical ecology is therefore to elucidate the biological mechanisms that change with enrichment to produce the nonlinear response. McCauley et al. (1988) have used equilibrium predictions from simple predator–prey models in an attempt to provide mechanistic explanations for variation in plankton densities with enrichment. Perhaps the next step in the analysis of the relationship between algal biomass and nutrients would be a more detailed description of whether the nonlinear changes in algal biomass with enrichment can be attributed to variation in certain taxonomic or functional groups of phytoplankton. These observations might help to identify more precisely the processes changing with enrichment.

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