

Factors Affecting the Relation Between Phosphorus and Chlorophyll *a* in Midwestern Reservoirs¹

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The mean chlorophyll *a* (mg/m³) yield per unit of total phosphorus (mg/m³) (P–C relation) in 96 midwest reservoirs and the variance about this yield was similar to relations for natural lakes reported in the literature. The remaining error term for this relation could not be reduced by adding variables for nitrogen, zooplankton abundance, or hydrologic flushing rate. In reservoirs with ratios of total nitrogen to total phosphorus of less than 10, nitrogen accounted for the same amount of variance in chlorophyll *a* as did phosphorus. Using partial regression path analysis, we found that when the concentration of phosphorus was held constant, increasing the concentration of inorganic suspended solids (mg/L) significantly decreased chlorophyll *a*. The following multivariate equation was developed to account for the effect of inorganic solids on the P–C relation:

$$\log \text{chlorophyll } a = -0.47 + 1.13 \log \text{ total phosphorus} \\ - 1.03 \left(\frac{\text{inorganic suspended solids}}{\text{total phosphorus}} \right).$$

This equation accounted for 7% more variance than the univariate equation and the 95% predictive confidence interval, at an average phosphorus concentration, was reduced by 10%. This equation should be useful for predicting chlorophyll *a* in lakes with inorganic turbidities. When Secchi transparency data were regressed on both chlorophyll *a* and inorganic suspended solids, they accounted for 42% more variance in transparency than did chlorophyll *a*.

Key words: lake trophic state, nitrogen, zooplankton, flushing rate, suspended solids, reservoirs

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Le rendement moyen en chlorophylle *a* (mg/m³) par unité de phosphore total (mg/m³) (relation P–C) dans 96 réservoirs du Midwest et la variance par rapport à ce rendement sont identiques aux relations mentionnées dans les travaux publiés pour les lacs naturels. Il a été impossible de réduire l'erreur résiduaire dans cette relation par additions de variables à l'azote, l'abondance du zooplancton et le taux de vidange hydrologique. Dans des réservoirs dont le rapport azote total:phosphore total est inférieur à 10, l'azote est responsable de la même variance dans la chlorophylle *a* que le phosphore. Une régression de parcours partielle a permis de constater que, lorsque la concentration de phosphore est maintenue constante, une concentration accrue de solides inorganiques en suspension (mg/L) cause une diminution significative de chlorophylle *a*. L'équation multivariable suivante explique l'effet des solides inorganiques sur la relation P–C :

$$\log \text{chlorophylle } a = -0,47 + 1,13 \log \text{ phosphore total} \\ - 1,03 \left(\frac{\text{solides inorganiques en suspension}}{\text{phosphore total}} \right).$$

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Cette équation explique 7 % plus de variance que l'équation univariable, et l'intervalle de confiance prévisionnel à 95 % à une concentration de phosphore moyenne est réduit de 10 %. L'équation devrait être utile pour prédire la chlorophylle dans les lacs à turbidités inorganiques. Une régression de la transparence au disque de Secchi à la fois sur la chlorophylle *a* et les solides inorganiques en suspension explique 42 % plus de variance dans la transparence que ne le fait la chlorophylle *a*.

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DURING the past decade research on eutrophication has demonstrated that phosphorus is the major nutrient limiting algal biomass in most lakes. Using data from natural lakes covering a wide range of limnological conditions, investigators have described a strong relation between total phosphorus concentrations (spring or summer) and summer algal biomass as measured by chlorophyll *a* (Sakamoto 1966; Dillon and Rigler 1974; Jones and Bachmann 1976; Carlson 1977). The relation is weaker in reservoirs (Canfield and Bachmann 1981), but many reservoirs have algal levels in agreement with the phosphorus-chlorophyll *a* (P-C) relation. Differences in the concentration of total phosphorus among water bodies account for most of the variability in phytoplankton biomass. For this reason lake managers have attempted to control phosphorus as a method of regulating algal biomass.

The slope and intercept values from the log-normal regressions of chlorophyll *a* on total phosphorus in the literature are surprisingly consistent, despite differences among the data sets. However, deterministic predictions of chlorophyll *a* based on a change in lake phosphorus concentration are not always useful to lake managers because of variations in the relation. The 95% predictive confidence interval of chlorophyll *a* at a given phosphorus concentration is broad (Dillon and Rigler 1974). For example, a lake with 20 mg/m³ total phosphorus could have a chlorophyll *a* concentration ranging from 2 to 15 mg/m³. On the basis of Likens' (1975) criteria for classifying lake trophic status, this lake could be classified from oligotrophic to eutrophic. Predictions are even less reliable in reservoirs with nonalgal turbidities (Jones and Novak 1981). Consequently, it is difficult to estimate how phosphorus-control projects will affect algal biomass. More precise models are needed to determine the potential benefits of such projects.

Although the chlorophyll *a* content of algal cells, methodology, and other factors contribute to the variance in P-C relations (Kalff and Knoechel 1978; Nicholls and Dillon 1978), recent hypotheses suggest that nitrogen concentration (Sakamoto 1966; Smith 1979), zooplankton abundance (Shapiro 1979), flushing rate (Dickman 1969; Dillon 1975), and inorganic suspended solids concentrations (Canfield and Bachmann 1981; Jones and Novak 1981) may account for a significant part of the variance. The objective of the present study was to determine the effect of these variables on the P-C relation in midwestern reservoirs. Because most P-C relations have been developed on the basis of data from natural lakes, and because natural lakes and reservoirs can differ in morphological and hydrological characteristics (Baxter 1977), another objective was to determine if the P-C relation

for the reservoirs in this study was similar to the relation in natural lakes.

Materials and Methods

Surface waters of 96 reservoirs in Missouri and Iowa were sampled between May and September 1978-81. Limnological characteristics of these reservoirs are summarized in Table 1. Collections were made at 0.5 m in acid-cleaned Nalgene bottles at three midreservoir locations on at least three (up to 10) sampling dates during a given season. Six highly variable stations in Lake of the Ozarks (Jones and Novak 1981) were considered as independent water bodies, as were two stations in Table Rock Reservoir and four stations in Truman Reservoir. Reservoirs were sampled for one to four seasons, thus providing data for 157 seasonal means. A seasonal mean is here considered as the mean of all samples collected from a water body during a given season. (A copy of our data may be obtained from the Fish and Wildlife Reference Service, 3840 York Street, Denver, CO 80205, by requesting "Supplementary data for factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs" by M. V. Hoyer and J. R. Jones.)

Chlorophyll *a* (mg/m³) was determined by filtering water through Gelman type A-E glass fiber filters. We determined concentrations by using the method of Yentsch and Menzel (1963) and the equations of Parsons and Strickland (1963). Values were not corrected for pheophytin. Total phosphorus (mg/m³) was determined by using the procedures of Murphy and Riley (1962) with a persulfate oxidation (Menzel and Corwin 1965).

Total nitrogen (mg/m³) was determined for 125 seasonal means by using an automated block digestion (Wall and Gehrke 1975).

Concentrations of total, organic, and inorganic suspended solids (mg/L) were determined for 82 seasonal means. Total suspended solids were determined by filtering water through precombusted (550°C), preweighed, Whatman 934 AH glass fiber filters. Filters were weighed after drying at 103°C for 1 h. Inorganic suspended solids were determined after combustion at 550°C for 1 h. Organic suspended solids were determined by differences. Appropriate corrections were made for blanks.

Flushing rates were determined for 54 seasonal means. Water inputs were calculated from watershed areas and runoff from the nearest United States Geological Survey Station. Water inputs from May through August were divided by lake volume to obtain summer hydraulic flushing rates. Lake

TABLE 1. Mean, standard deviation (SD), and range of limnological characteristics in 96 reservoirs in Missouri and Iowa.

Variable	<i>n</i> (seasonal means)	\bar{x}	SD	Range
Total phosphorus (mg/m ³)	157	38.4	27.8	5.2–265.3
Chlorophyll <i>a</i> (mg/m ³)	157	17.0	17.6	0.7–142.2
Secchi transparency (m)	157	1.4	0.9	0.2–4.6
Total nitrogen (mg/L)	125	0.7	0.5	0.3–3.4
Inorganic suspended solids (mg/L)	82	6.1	7.3	0.3–45.2
Hydrologic flushing rate (d)	54	92	44.4	7.6–12 000
Zooplankton (individuals/L)				
Cladocerans	21	141	223	3–1052
Copepods	21	90	80	12–277
Rotifers	21	317	456	16–2043

evaporation was assumed to equal precipitation on the lake surface; groundwater influences were not considered.

In 1981, zooplankton abundance (individuals/L) was determined weekly in 14 Missouri reservoirs. Three mid-reservoir vertical tows from 0.3 m above the bottom to the surface were made with a 70- μ m Wisconsin net with a mouth diameter of 12 cm. Samples were preserved in 90% alcohol. Weekly samples from a given reservoir were combined and zooplankters were enumerated as cladocerans, copepods, and rotifers (Elliott 1977). Cladocerans were divided into three size groups: small (<0.5 mm), medium (\geq 0.5 and <1.5 mm), and large (\geq 1.5 mm). We calculated abundance by using the epilimnetic volume of the tow as the water volume and by assuming 100% net efficiency. Zooplankton and other limnological data from seven Iowa reservoirs (Noonan 1979) were included with our data set yielding zooplankton data from 21 seasonal means.

Before statistical analyses, data were transformed to base 10 logarithms to meet the requirements of parametric statistical analysis. Statistical analyses were performed by using the Statistical Analysis System (1979) computer package. Unless stated otherwise, statements of statistical significance imply $P \leq 0.05$.

Results and Discussion

COMPARISON OF P-C RELATIONS IN NATURAL LAKES AND RESERVOIRS

Six percent of our reservoir data were outside the 95% predictive confidence limits of Jones and Bachmann's (1976) P-C relation for natural lakes (Fig. 1), and we found no significant difference between the regression equations for these two data sets. We used this P-C relation because our data were collected by the same sampling and analytical techniques. Use of the same P-C relation eliminated variation caused by different methodologies (Nicholls and Dillon 1978), making a more robust comparison. Consequently, we suggest that the mean chlorophyll yield per unit of total phosphorus and the variance about this yield are similar in many natural lakes and reservoirs. Because of this, we assume that the factors and mechanisms controlling variation are similar in both lake types.

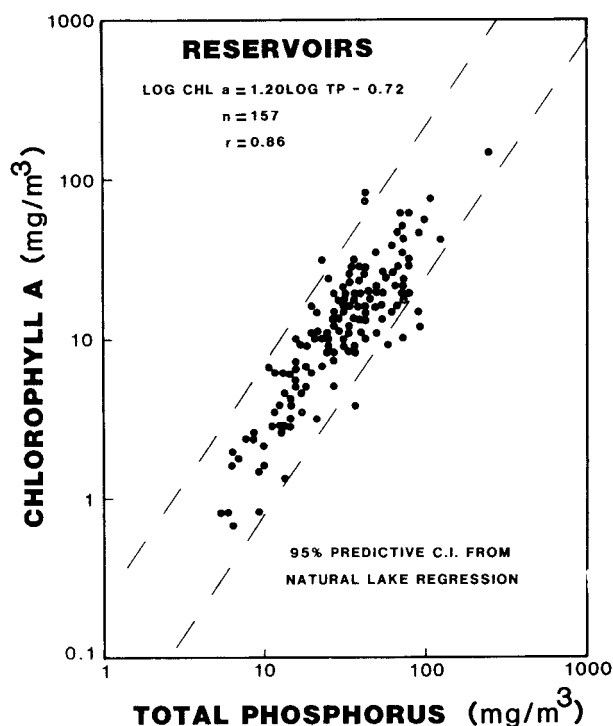


FIG. 1. Relation between summer mean chlorophyll *a* and total phosphorus concentrations for 157 seasonal means from midwest reservoirs. Broken line is the 95% predictive confidence interval for natural lake data (Jones and Bachmann 1976).

VARIANCE ABOUT THE P-C RELATION

Nitrogen — Part of the variable yield of chlorophyll *a* per unit of phosphorus has been attributed to nitrogen concentration (Smith and Shapiro 1981). For our data there was no strong relation between nitrogen and chlorophyll *a* ($R^2 = 0.18$). Thus, there was no reduction in the error sum of squares when nitrogen was regressed with total phosphorus against chlorophyll *a* (Table 2A). We expected this lack of improvement and fit because the reservoirs in our data set

TABLE 2. Regression models relating chlorophyll *a* (mg/m³) to total nitrogen (mg/m³) and total phosphorus (mg/m³) alone and together, (A) 125 seasonal means; (B) 11 seasonal means with nitrogen-to-phosphorus ratio (N:P) less than 10.

Model	R ²	F	P
A. 125 seasonal means			
Log chlorophyll <i>a</i> = -0.83 + 1.28 log phosphorus	0.75	367.7	0.0001
Log chlorophyll <i>a</i> = 1.31 + 0.83 log total nitrogen	0.18	27.7	0.001
Log chlorophyll <i>a</i> = 1.19 + 1.23 log phosphorus + 0.15 log total nitrogen	0.75	182.6	0.0001
B. 11 seasonal means with N:P < 10			
Log chlorophyll <i>a</i> = 1.65 + 1.70 log phosphorus	0.71	24.4	0.0006
Log chlorophyll <i>a</i> = 3.50 + 1.81 log total nitrogen	0.73	27.7	0.0004
Log chlorophyll <i>a</i> = 3.04 + 0.49 log phosphorus + 1.31 log total nitrogen	0.74	12.9	0.002

TABLE 3. Regression models relating chlorophyll *a* (mg/m³) to cladoceran, copepod, and rotifer abundance (individuals/L) and total phosphorus (mg/m³) alone and together, for 21 seasonal means.

Model	R ²	F	P
Log chlorophyll <i>a</i> = -0.49 + 1.10 log phosphorus	0.79	74.3	0.0001
Log chlorophyll <i>a</i> = -0.69 + 1.04 log phosphorus + 0.10 log cladoceran abundance	0.81	40.2	0.0001
Log chlorophyll <i>a</i> = -0.69 + 1.01 log phosphorus + 0.13 log copepod abundance	0.80	39.3	0.0001
Log chlorophyll <i>a</i> = -0.02 + 1.03 log phosphorus - 0.12 log rotifer abundance	0.82	42.0	0.001
Log chlorophyll <i>a</i> = -0.23 + 0.99 log phosphorus + 0.06 log cladoceran abundance + 0.02 log copepod abundance - 0.10 log rotifer abundance	0.83	42.7	0.0001

are nitrogen-rich. Only one seasonal mean had a nitrogen-to-phosphorus ratio (N:P) below 7, which is the ratio in aquatic plant tissues (Valentyne 1974), and only 11 seasonal means (9% of our data) had N:P ratios less than 10, the ratio below which Sakamoto (1966) suggested that nitrogen rather than phosphorus limits algal biomass. However, in our reservoirs with N:P ratios less than 10, nitrogen accounted for the same amount of variance in chlorophyll *a* as did phosphorus ($R^2 = 0.73$ and $R^2 = 0.71$, respectively; Table 2B). This observation supports the importance of nitrogen in lakes with N:P ratios less than 10, and suggests that nitrogen might reduce some of the remaining error sum of squares if a greater number of reservoirs with low N:P ratios were included in the data set.

Zooplankton — Kalff and Knoechel (1978) and Shapiro (1979) suggested that zooplankton grazing can reduce the yield of chlorophyll *a* per unit of phosphorus in lakes. However, when we regressed seasonal mean abundances of cladocerans (range 0–1316/L), copepods (range 3–439/L), and rotifers (range 1–6054/L) together and separately with phosphorus against chlorophyll *a*, there was no significant reduction in the error term compared with that indicated by phosphorus alone (Table 3). This lack of reduction could be due to the small data set (21 seasonal means) or to the relatively small size of zooplankters in these reservoirs. Only five of our reservoirs had large (>1.5 mm) cladocerans, and two of these had large cladocerans on only one sampling date. J. Shapiro (personal communication) suggested that large

cladocerans especially *Daphnia* sp. would have a greater effect on the P–C relation than smaller zooplankters.

Several other factors also influence the effect of zooplankton on the P–C relation, including planktivorous predation on zooplankton, zooplankton feeding on detritus and bacteria, zooplankton filtering rate, and type of planktonic algae (Crowley 1973; Haney 1973; Gliwicz 1975; Weers and Zaret 1975; Porter 1975, 1977; Anderson et al. 1978; Threlkeld 1979). Using data from three Missouri reservoirs, we showed how cladoceran abundance and chlorophyll *a* concentrations were directly related, inversely related, or unrelated over time (Fig. 2). Until zooplankton dynamics within individual lakes are better understood, the variance in the P–C relation that is caused by zooplankton cannot be accounted for easily.

Flushing rate — Flushing rate may potentially affect variation in the P–C relation by washout or removal of phytoplankton before the standing crop reaches the level determined by the concentration of the limiting nutrient (Dickman 1969; Dillon 1975). This effect becomes increasingly important as the rate at which cells are flushed from a system approaches the cell growth rate (Herbert 1969). In our reservoirs ($n = 54$ seasonal means) the mean retention time was 92 d (range 7.6–12 000 d). Flushing rate and total phosphorus, however, did not account for significantly more variance in chlorophyll *a* than did total phosphorus alone. Figure 3 illustrates this with a plot of flushing rate and retention time against residual chlorophyll *a* [log-observed chlorophyll *a* minus log-predicted chlorophyll *a* calculated

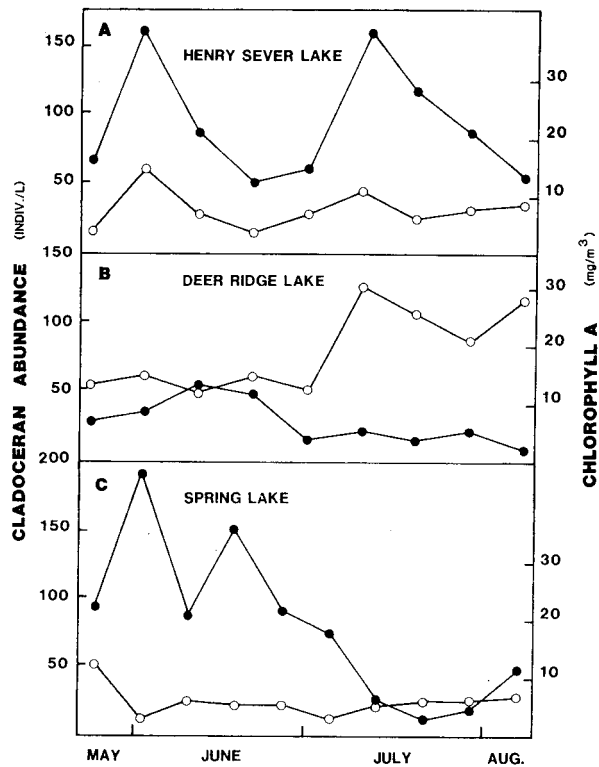


FIG. 2. Differences in the relation between weekly chlorophyll *a* and cladoceran abundance in three Missouri reservoirs over time, May–August 1982: Henry Sever Lake (direct relation between log chlorophyll *a* and log cladoceran abundance, $r = 0.70$, $P < 0.05$), Deer Ridge Lake (inverse relation, $r = -0.66$, $P < 0.05$), and Spring Lake (no relation, $r = 0.22$, $P = 0.5$).

using the P–C relation of Jones and Bachmann (1976)]. If flushing rates were affecting the P–C relation, the residual chlorophyll *a* would be negative at high flushing rates — not the case for our data.

Inorganic suspended solids — Hergenrader and Hammer (1973) and Jones and Novak (1981) found that reservoirs with high concentrations of inorganic suspended solids may have as little as 10% of the chlorophyll that would be predicted for a given total phosphorus concentration. Consequently, we expected to find a negative correlation between inorganic suspended solids and chlorophyll in our reservoirs. The simple correlation coefficient, however, was positive and significant, as were the correlation coefficients among summer mean inorganic suspended solids, total phosphorus, and chlo-

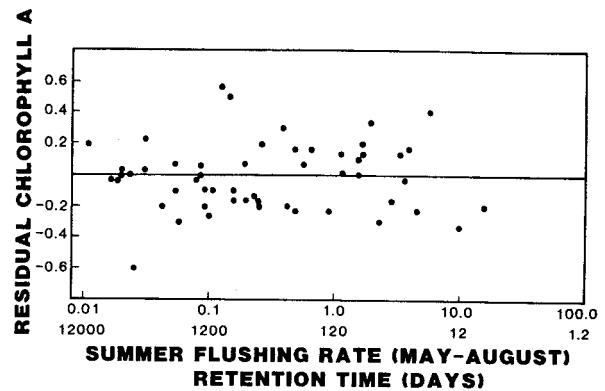


FIG. 3. Relation between summer mean observed chlorophyll *a* minus predicted chlorophyll *a* [after the P–C relation of Jones and Bachmann (1976)] and summer flushing rate or retention time.

rophyll concentrations (Table 4). A positive relation between inorganic solids and chlorophyll was not expected. Therefore, we hypothesized that this relation was probably due to the high degree of intercorrelation among these variables. We analyzed further the individual effect of inorganic solids and total phosphorus concentrations on chlorophyll *a* in reservoirs by using path analysis and partial correlation procedures (Systems Regression Procedures in Statistical Analysis System 1979). The standard partial regression path coefficient (1.06) of chlorophyll *a* on total phosphorus, when the concentration of inorganic solids was held constant, was significantly positive (Fig. 4). The standard partial regression path coefficient of chlorophyll *a* on inorganic solids when total phosphorus was held constant, however, was negative (-0.31) and significant. This relation suggests that if the phosphorus concentration of a lake is held constant, an increase in the concentration of inorganic suspended solids will decrease the chlorophyll concentration.

We found a significant negative correlation between residual chlorophyll *a* and the ratio of inorganic suspended solids to total phosphorus (I:TP) ($r = -0.36$). We used this ratio to estimate the effect of inorganic solids on chlorophyll *a* at a given phosphorus concentration. The mean I:TP ratio for our data was 0.13. Most reservoirs with an I:TP ratio greater than this value had less chlorophyll than would be predicted from their phosphorus concentration, and reservoirs with low I:TP ratios generally had a higher yield of chlorophyll per unit of phosphorus than predicted. This negative effect of inorganic suspended solids on chlorophyll yield per unit of phosphorus was consistent over a wide range of trophic states (Fig. 5).

The interactions among phosphorus–inorganic solids and chlorophyll *a* can also be seen in Lake of the Ozarks, a

TABLE 4. Correlation coefficients (r) among total phosphorus (mg/m^3), chlorophyll *a* (mg/m^3), and inorganic suspended solids (mg/L) for 82 seasonal means.

	r	F	P
Log phosphorus \times log chlorophyll <i>a</i>	0.84	195.0	0.0001
Log phosphorus \times log inorganic solids	0.70	78.7	0.0001
Log inorganic solids \times log chlorophyll <i>a</i>	0.44	52.0	0.0001

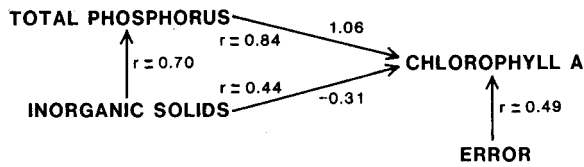


FIG. 4. Path analysis diagram, with standard partial regression path coefficients and simple correlations (r) among summer mean total phosphorus (mg/m^3), inorganic suspended solids (mg/L), and chlorophyll *a* (mg/m^3). These variables were measured on 82 seasonal means from midwest reservoirs.

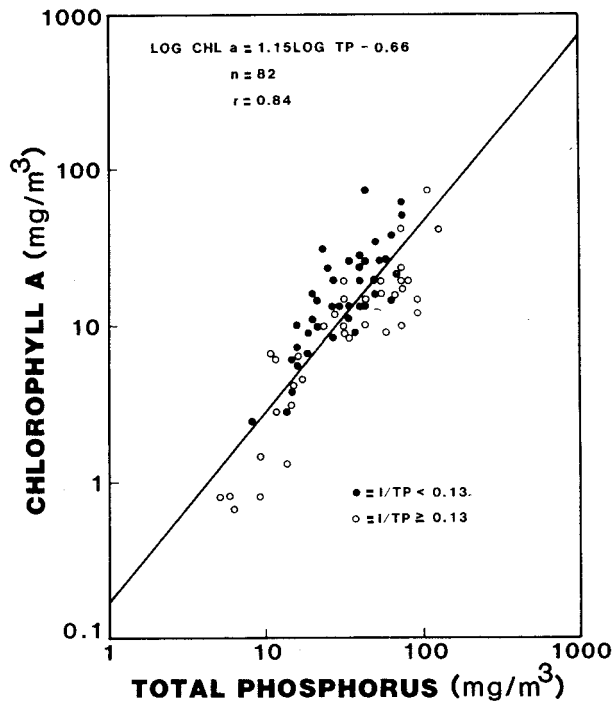


FIG. 5. Relation between summer mean chlorophyll *a* and total phosphorus concentration for 82 seasonal means from midwest reservoirs. Symbols represent the range of inorganic suspended solids to total phosphorus ratio (I:TP) — < 0.13 or ≥ 0.13 .

50-yr-old reservoir (Table 5). In a relatively clear arm of the reservoir (station 1), phosphorus and chlorophyll concentrations decreased from 1979 to 1980 and generally followed the P-C relation. There was no significant difference between years in the I:TP ratio at this station. In the upper end of the reservoir (stations 5 and 6) phosphorus concentrations decreased but chlorophyll concentrations increased concurrently with a significant decrease in I:TP ratios. We believe that the yield of chlorophyll per unit of phosphorus increased, in part, because of a proportional decrease in the concentration of inorganic suspended solids.

To account for the effect of inorganic solids on the P-C relation, we developed a multivariate model regressing chlorophyll *a* on total phosphorus and I:TP ratios (Table 6). The model accounts for 7% more variance in our data than the

TABLE 5. Summer mean total phosphorus (mg/m^3), chlorophyll *a* (mg/m^3), and inorganic suspended solids to total phosphorus ratio (I:TP) \pm SD for stations 1, 5, and 6 in Lake of the Ozarks.

Station and year	Total phosphorus	Chlorophyll <i>a</i>	I:TP
<i>Ozark 1</i>			
1979	27.6 ± 1.0	15.3 ± 3.8	0.9 ± 0.001
1980	15.1 ± 3.2	7.3 ± 0.5	0.7 ± 0.042
<i>Ozark 5</i>			
1979	57.0 ± 23.5	9.2 ± 4.0	0.19 ± 0.093
1980	28.9 ± 3.9	13.8 ± 3.7	0.07 ± 0.018
<i>Ozark 6</i>			
1979	70.9 ± 18.6	9.8 ± 6.5	0.38 ± 0.024
1980	54.7 ± 11.8	19.4 ± 6.9	0.17 ± 0.062

univariate equation, and the 95% predictive confidence interval is reduced by 10%.

Several hypotheses have been proposed to explain how inorganic solids reduce summer mean chlorophyll yield per unit of phosphorus. Fitzgerald (1970), Stumm and Lechic (1971), and Edzwald et al. (1976) suggested that, because of phosphate adsorption reactions, inorganic solids could decrease the biologically available phosphorus in a lake. Inorganic suspended solids could also decrease light available for photosynthesis (Marzolf and Osborne 1972), thus reducing algal biomass.

Our data showed a direct relation between inorganic suspended solids and total phosphorus (Fig. 6). We do not, however, have information that would enable us to quantify the amount of phosphorus bound to inorganic solids or to determine its availability to algae. Because Cowen and Lee (1976) showed that 45–92% of the particulate phosphorus in urban runoff was unavailable in algal cultures, and Cunningham (1979) showed that algal cultures produced 20–50% less algal biomass when phosphorus in the media was associated with sediments rather than dissolved, we believe that part of the reduced chlorophyll yield per unit of phosphorus can be explained by the binding hypothesis. We also have no data to determine if inorganic suspended solids in our reservoirs were limiting light for photosynthesis. Our Secchi transparency data, however, were negatively related to inorganic solids. When these data were regressed on both chlorophyll *a* and inorganic solids, they accounted for 42% more variance in transparency than did chlorophyll *a* alone (Table 7). Therefore, as the concentration of inorganic solids increases in a lake, water clarity decreases. This reduction in light may also function to reduce the average yield of chlorophyll *a* per unit of phosphorus.

Assessment — The following multivariate relation describes how concentrations of inorganic suspended solids in a lake affect the chlorophyll *a* yield per unit of phosphorus.

$\text{Log chlorophyll } a = -0.47 + 1.13 \text{ log total phosphorus} - 1.03 \text{ I:TP}$. Because the relation among phosphorus, inorganic suspended solids, and chlorophyll *a* is a continuum, the multivariate model should be especially useful for predicting chlorophyll in lakes with high inorganic turbidities. This relation should also be useful when phosphorus management is associated with reducing the total sediment load to a lake. In

TABLE 6. Comparison between phosphorus–chlorophyll *a* and a multivariate model used to predict chlorophyll *a* concentrations. Both models were developed using summer mean values from 82 seasonal means. I:TP is the ratio of inorganic suspended solids (mg/L) to total phosphorus (mg/m³).

Model	R ²	95% predictive confidence interval at geometric mean ^a
Log chlorophyll <i>a</i> = -0.66 + 1.15 log phosphorus	0.70	3.6–34.7
Log chlorophyll <i>a</i> = -0.47 + 1.13 log phosphorus - 1.03 I:TP	0.77	4.1–31.9

^aMean values 11.3 mg/m³ chlorophyll *a*, 30.9 mg/m³ total phosphorus, 0.13 I:TP. Confidence interval for the multivariate model exhibited similar reduction over the entire range.

TABLE 7. Regression model relating Secchi depth (m) to inorganic suspended solids (mg/L) and chlorophyll *a* (mg/m³) alone and together, for 82 seasonal means.

Model	R ²	F	P
Log Secchi depth = 0.46 - 0.38 log chlorophyll <i>a</i>	0.42	57.7	0.001
Log Secchi depth = 0.53 - 0.19 log chlorophyll <i>a</i> - 0.47 log inorganic suspended solids	0.84	550.9	0.0001

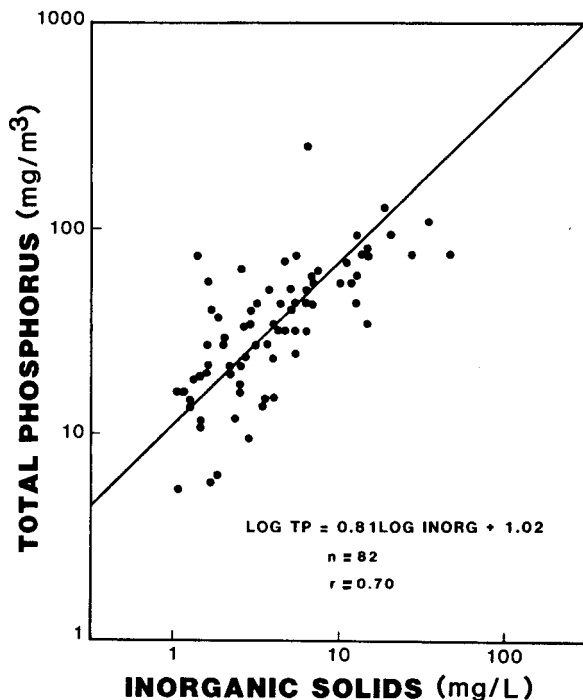


FIG. 6. Geometric mean fit (Ricker 1973) between summer mean concentrations of inorganic suspended solids and total phosphorus for 82 seasonal means from midwest reservoirs.

such situations, phosphorus concentration may decrease but algal biomass may increase because the concentration of inorganic suspended solids is reduced, as exemplified by data

from Lake of the Ozarks (Table 5).

For a wide range of midwest reservoirs, a significant part of the variance in the P–C relation could not be attributed to the concentration of nitrogen, zooplankton abundance, or flushing rate. Other investigators, however, have shown that these factors can significantly affect the chlorophyll concentration in individual lakes. Therefore, the future of P–C relations may be in developing relations for homogeneous groups of lakes that are affected by unique factors (Lorenzen 1981). This systematic improvement in empirical P–C relations should eventually lead to the development of accurate predictive capabilities for lake managers.

Acknowledgments

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