Phosphorus and Nitrogen Limitation of Phytoplankton Growth in Oligotrophic Lakes: Comment on McCauley et al. (1989)

It has proved difficult to make assessments of algal nutrient limitation in lakes based on bioassay enrichment studies (Dodds and Priscu 1990; Elser et al. 1990). Therefore, it was a valuable effort by McCauley et al. (1989) to collect a large data base on summer average chlorophyll ($\text{Chl a}$), total phosphorus (TP), and total nitrogen (TN) observations from 266 lakes and to fit a generalized linear model (sensus McCullagh and Nelder 1989) in both TP and TN to their data. Unfortunately, I think their conclusion regarding the relative role of TP and TN in limiting algal growth is an artifact of their method. They found that log TP, $(\log \text{TP})^2$, $(\log \text{TP})^3$, and the product $(\log \text{TP}) \cdot (\log \text{TN})$ had highly significant partial effects on the logarithm of chlorophyll concentration. The curves log Chl a = $f$(log TP, log TN) are represented in a log Chl a/log TP graph by a family of sigmoid curves that converged at low phosphorus concentrations. This is in contrast with results by Smith (1982), who found a family of parallel lines. The authors claim that the convergence has two implications for lake management: at low concentrations of TP ($<30 \text{ mg} \cdot \text{m}^{-3}$, e.g. in oligotrophic and mesotrophic lakes, OECD (1982) definitions of trophy) the chlorophyll concentration is little affected by TN; high concentrations of TP ($>1000 \text{ mg} \cdot \text{m}^{-3}$) have little or no effect on chlorophyll concentrations. However, based on their equations, small changes in TN and TP of the same numerical value will give about the same change in Chl a concentration for oligotrophic lakes. Typical changes, $\Delta\text{TP}$, between years in such lakes are 3–10 mg·m$^{-3}$ (Seip et al. 1990). More important, fig. 2D in McCauley et al.'s paper, which also is the basis for their conclusion, shows a striking feature. The curve Chl a = $f$(TP) for TN = 5·TP shows that Chl a decreases with increasing TP.

![Log Chl a vs. Log TP and TN](image_url)
in the regions $1 \text{ mg m}^{-3} < \text{TP} < 3 \text{ mg m}^{-3}$ and $\text{TP} > 600 \text{ mg m}^{-3}$. Their calibration region for TP is $1-14 \text{ mg m}^{-3}$ and for TN is $61-740 \text{ mg m}^{-3}$.

To explore this feature further, I depicted the response surface for Chl a to changes in both TP and TN (Fig. 1) corresponding to McCauley et al.'s equation for the version "combined model" (literature data as source). The response surface underscores the nonsigmoid particularities of the curves shown by McCauley et al. Since the author's management advice with regard to TP and TN depends upon the characteristics of the log $\text{Chl a} = f(\text{log TP, log TN})$ curves close to an apparently anomalous domain, one should probably either give a theoretical justification for the anomaly or examine if the anomalies are artifacts of the method. It is difficult to explain that for constant TN, chlorophyll may decrease with increasing TP (cf. Fig. 1 at low TN:TP ratios; the ratio between the largest TN and TP values in the data set is 0.8). However, contrary to Fig. 1 at low TN:TP ratios; the ratio between the largest TN and TP values in the data set is 0.8). However, contrary to McCauley et al. concluded that the effect of these nutrients varies depending on the level of phosphorus in the lake. This conclusion was drawn from two sets of analyses: (1) a model-free inspection of the data showing that the phosphorus–chlorophyll relationship is sigmoidal (a result independently established by Prairie et al. (1989)) and (2) a multivariate regression analysis of the influence of nitrogen and phosphorus on chlorophyll levels throughout a broad collection of lakes. Based on the parametric regression analysis, McCauley et al. found that "the effect of nitrogen is much greater at high TP concentration than at low" and that "the phosphorus–chlorophyll relationship is a family of sigmoid curves that converge at low phosphorus concentration." These conclusions differ considerably from the original interpretation

![Figure 1](image.png)

**References**


Different Effects of Phosphorus and Nitrogen on Chlorophyll Concentration in Oligotrophic and Eutrophic Lakes: Reply to Seip

Establishing the role(s) of the many nutrients that might affect the observed biomass and production of phytoplankton throughout the natural domain of lakes is a daunting task. Results from manipulation experiments along with evidence gathered from natural variation in levels of nutrients and chlorophyll provide key pieces of the puzzle. While Elser et al. (1990) synthesized and criticized experimental results on phosphorus (TP) and nitrogen (TN) limitation, McCauley et al. (1989) evaluated the relative role of the two nutrients by examining their empirical relationship with chlorophyll concentration among lakes throughout the Northern Hemisphere, thereby extending the initial work of Smith (1979). Seip has questioned one of the conclusions presented in McCauley et al. regarding the asymmetrical effect of phosphorus and nitrogen in lakes of different trophic status. McCauley et al. concluded that the effect of these nutrients varies depending on the level of phosphorus in the lake. This conclusion was drawn from two sets of analyses: (1) a model-free inspection of the data showing that the phosphorus–chlorophyll relationship is sigmoidal (a result independently established by Prairie et al. (1989)) and (2) a multivariate regression analysis of the influence of nitrogen and phosphorus on chlorophyll levels throughout a broad collection of lakes. Based on the parametric regression analysis, McCauley et al. found that "the effect of nitrogen is much greater at high TP concentration than at low" and that "the phosphorus–chlorophyll relationship is a family of sigmoid curves that converge at low phosphorus concentration." These conclusions differ considerably from the original interpretation.
of Smith (1979) that the relationships consist of a parallel series
of lines.

Seip questions only the validity of the interpretation of the
parametric model presented by McCauley et al. for oligo-
trophic lakes and suggests that we failed to replicate Smith's
family of parallel relationships between TP and chlorophyll due
to the particular quadratic model that we chose. We disagree
with Seip that our original interpretation is incorrect, and we
support our original conclusion in two ways: (1) by showing
that the asymmetrical effect of nitrogen and phosphorus is pres-
ent in the contour plot presented by Seip based on our para-
metric model and (2) by examining the raw data themselves
without model fitting to provide evidence that our findings result
from the data and not from our choice of statistics.

Before proceeding, however, it is important to recognize that
the predictions of the regression model must be examined only
over the range of the independent variables. Clearly, models
can often predict spurious (and often ludicrous) results if applied
outside the range of data from which they were derived. There-
fore in the analyses presented below, we restrict the contour
plots to the realistic range of log TP and log TN values.

Figure 1A shows the contour plot of predictions of chloro-
phyll concentration from our combined model when limited to
the range of natural variation of log TN and log TP. Once the
contour plot is restricted to the range of data present in the
original analysis, the asymmetrical effect of phosphorus and
nitrogen on chlorophyll is readily apparent from the asymmetry
in the isoclines at both low and high phosphorus levels. A nearly
identical response to nitrogen and phosphorus is seen in a sim-
ple contour plot of the data (Fig. 1B). To illustrate this asym-
metry at low phosphorus levels, consider an oligotrophic lake
with log TP (micrograms per litre) = 0.5. Lakes with this level
of phosphorus have an average of 308 μg TN-L⁻¹ or log TN =
2.48 as determined from our original dataset. If you locate this
point on the log TN - log TP surface (Fig. 1) and then ask what
effect does a unit change in log TP or log TN have on the esti-
mate of chlorophyll a, you observe that the change in log TP
predicts an increase in chlorophyll response from the 0–0.5
range to the 0.5–1.0 range whereas a unit change in log TN
still predicts chlorophyll levels within the original range of
0–0.5. In both Fig. 1A and 1B, isoclines of chlorophyll a con-
centration are nearly vertical at low phosphorus concentrations,
but nearly horizontal at high phosphorus concentrations. Chlo-
rophyll concentration therefore appears to vary little with TN
in oligotrophic lakes but varies greatly with TN in eutrophic
lakes. Chlorophyll concentrations are very sensitive to variation
in phosphorus concentration in oligotrophic lakes, and insen-
sitive to variation in phosphorus concentration in eutrophic
lakes. These predictions are consistent with the conclusions
presented in McCauley et al. and are independent of statistical
fitting methods.

The polynomial equation presented in McCauley et al. are
one of many models that could describe the same result. No
matter what model is chosen, the result is the same: TP con-
centration is correlated differently with chlorophyll at different
combinations of phosphorus and nitrogen. Chlorophyll con-
centration covaries primarily with TP in oligotrophic lakes and
primarily with TN in eutrophic lakes — Edward McCauley,
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References

nitrogen limitation of phytoplankton growth in the freshwaters of North

MCCAULEY, E., J. A. DOWNING, AND S. WATSON. 1989. Sigmoid relationships
Sci. 46: 1171–1175.

PRAIRIE, Y. T., C. M. DUARTE, AND J. KALFF. 1989. Unifying nutrient–chlo-