NUTRIENT LIMITATION OF PHYTOPLANKTON BY NITROGEN AND PHOSPHORUS:

EROSION OF THE PHOSPHORUS PARADIGM

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N vs P Limitation
The Controversy That Won't Die!

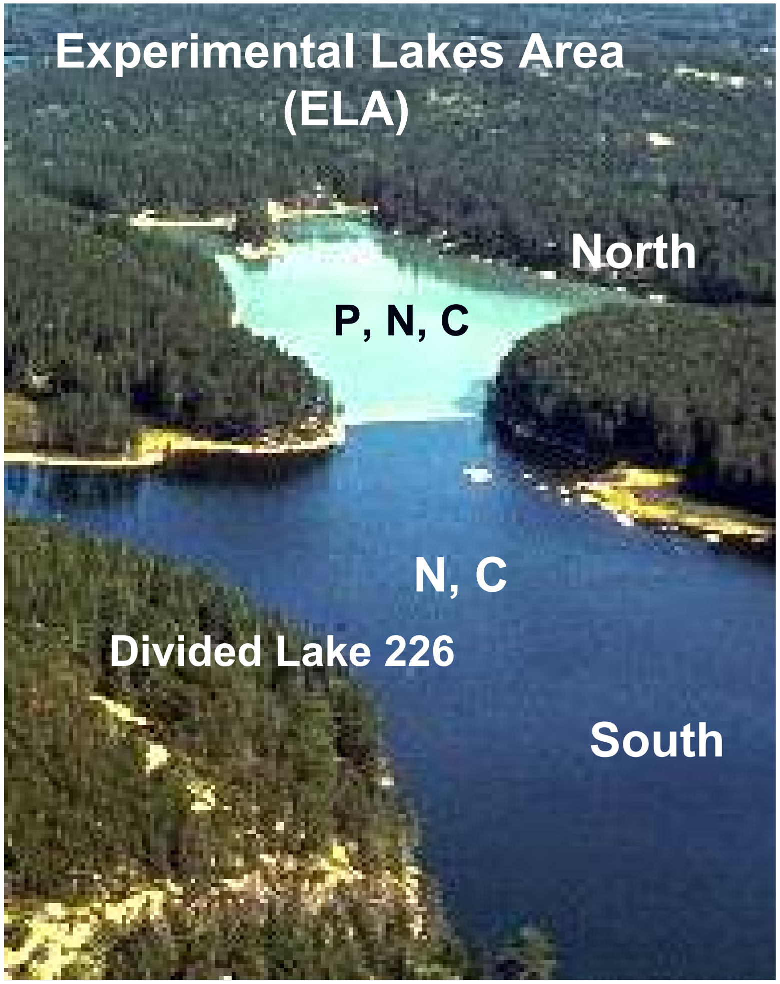
- Schindler, DW. 1977. Evolution of phosphorus limitation in lakes, Science
- Downing, JA & E McCauley. 1992. The nitrogen : phosphorus relationship in lakes. Limnology & Oceanography
- Elser, JJ et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters
- Schindler, DW et al. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. Proc. National Acad. Sci.
- Sterner, RH 2008. On the phosphorus limitation paradigm for lakes. International Review of Hydrobiology
- Lewis, WM, Jr. and WA Wurtsbaugh. 2008. Control of lacustrine phytoplankton by nutrients: Erosion of the phosphorus paradigm. International Review of Hydrobiology

One foundation of the phosphorus paradigm are whole-lake experiments suggesting that P alone controls algal biomass

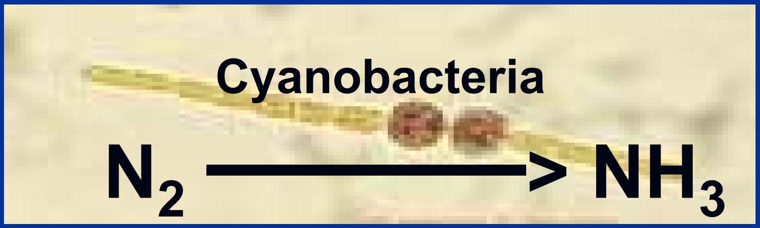
David Schindler (1977, 2008, etc.)

Concluded:
- Only phosphorus is important

- If nitrogen is in short supply, nitrogen fixation by cyanobacteria will make up the nitrogen deficit:



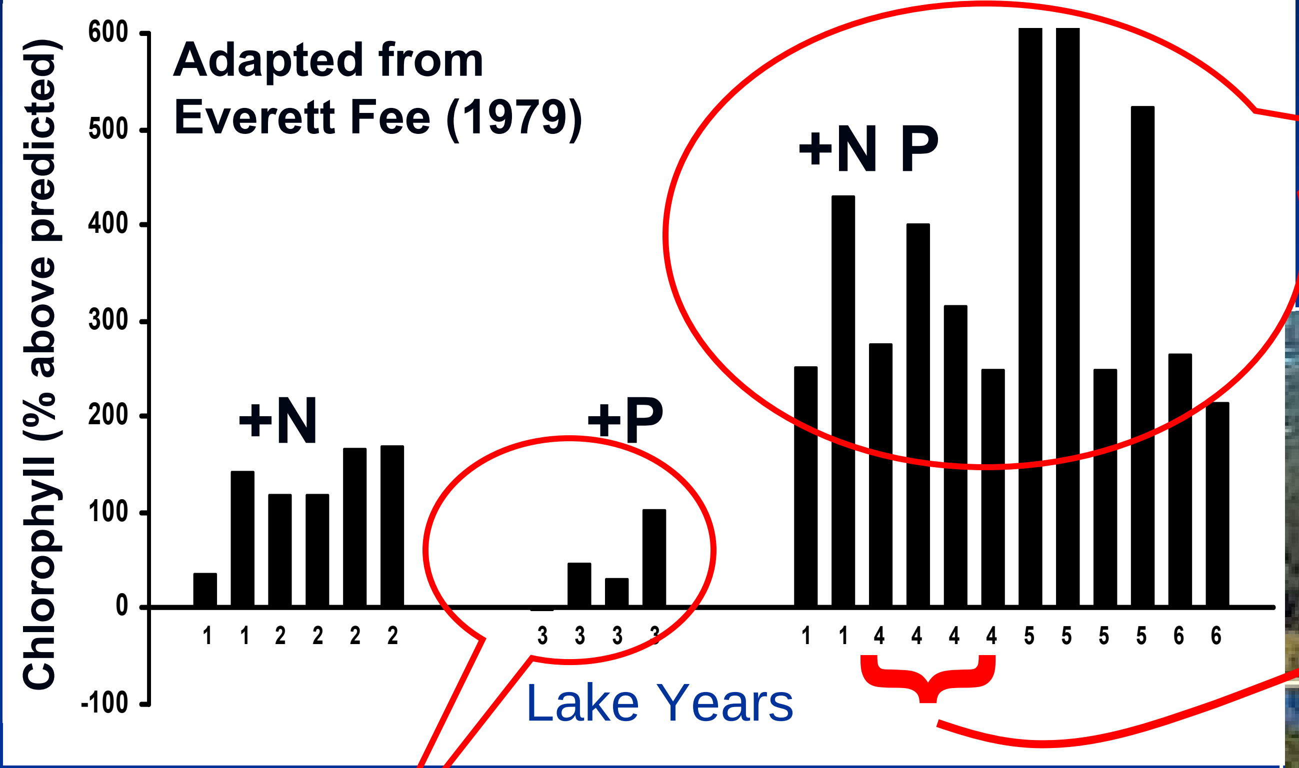
Schindler (1977) Evolution of phosphorus limitation in lakes, Science



$N_2 \longrightarrow NH_3$

However, median N-fixation as a proportion of the total N necessary to support primary production is less than 5% (Howarth et al. 1988) – Cyanobacteria rarely make up the deficit

However, response to nutrient additions in <u>all</u> of the ELA Lakes suggest a different conclusion



Adapted from Everett Fee (1979)

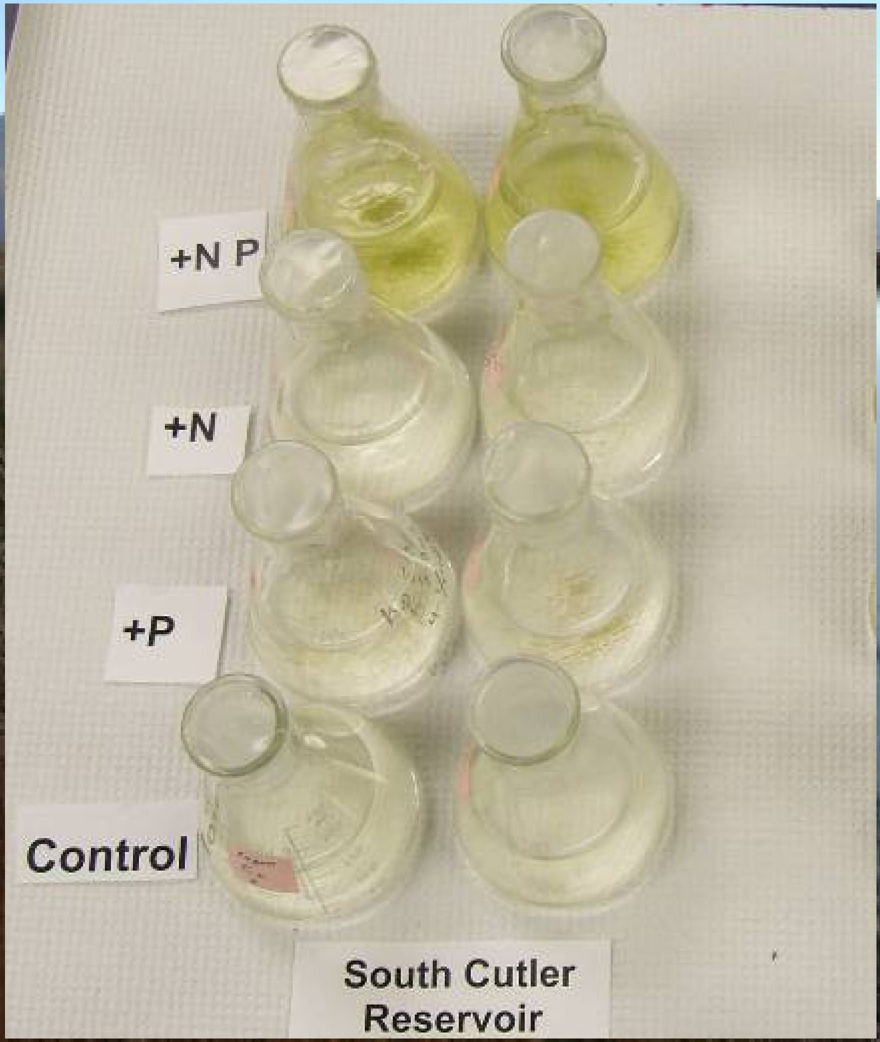
Planktonic N-fixation in most of these eutrophic lakes

<u>No</u> nitrogen fixation in plankton, but important in epiphytic periphyton

(D. Schindler, personal communication)

Small-scale bioassays also shed doubt on the phosphorus paradigm

Cutler Reservoir, Utah (Sept. 2008)



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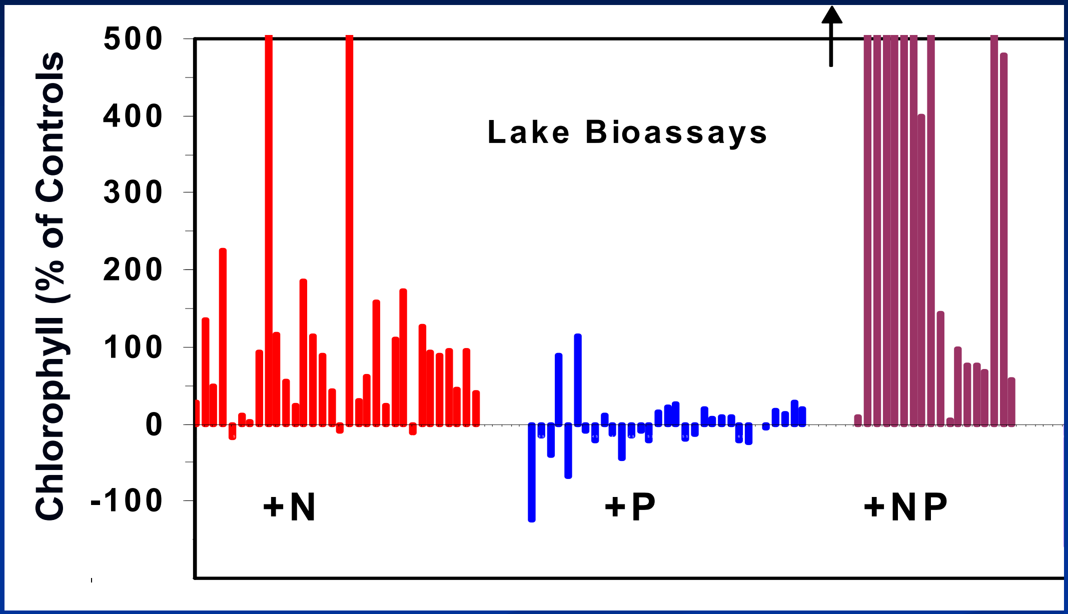
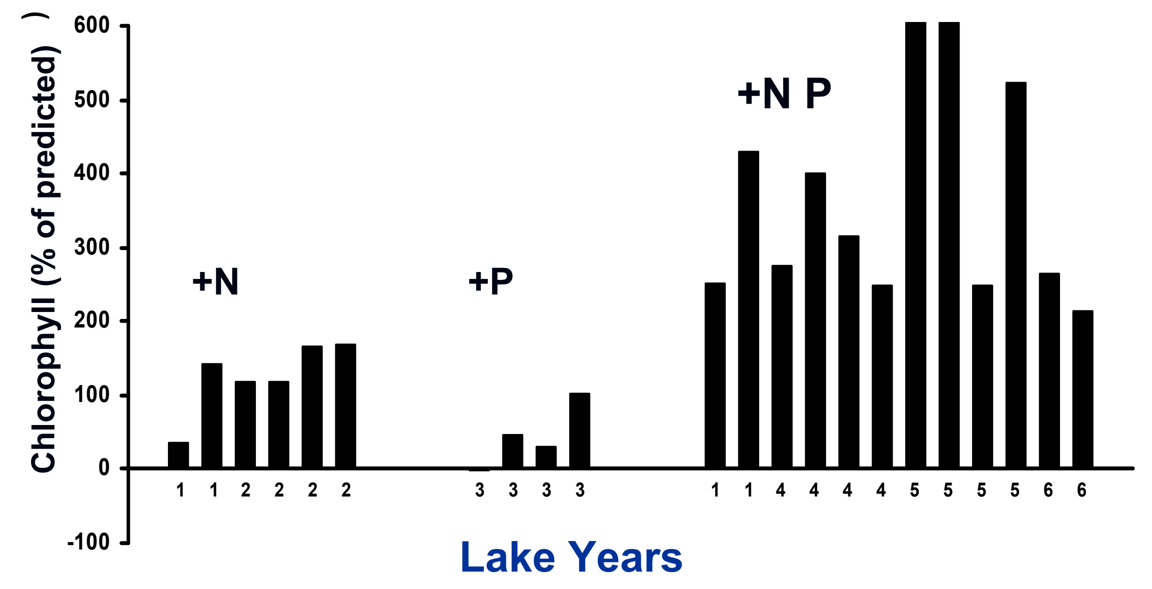
Many lakes show N- or NP-limitation

Summary of 32 Bioassays in 8 Widely-different Lakes in western US, Spain, Peru (W. Wurtsbaugh)

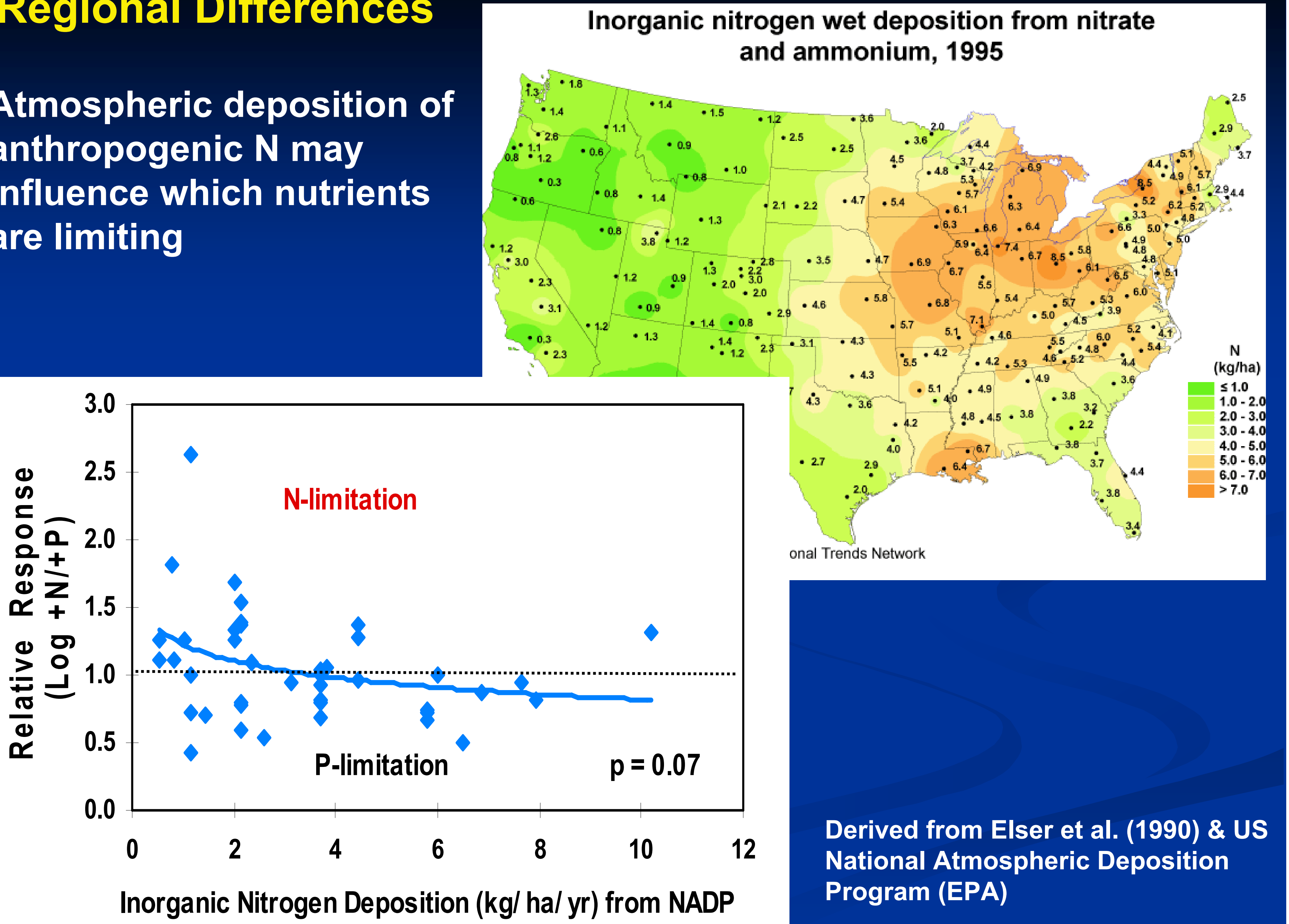


Experimental Lakes Area of Canada (adapted from Fee 1979)



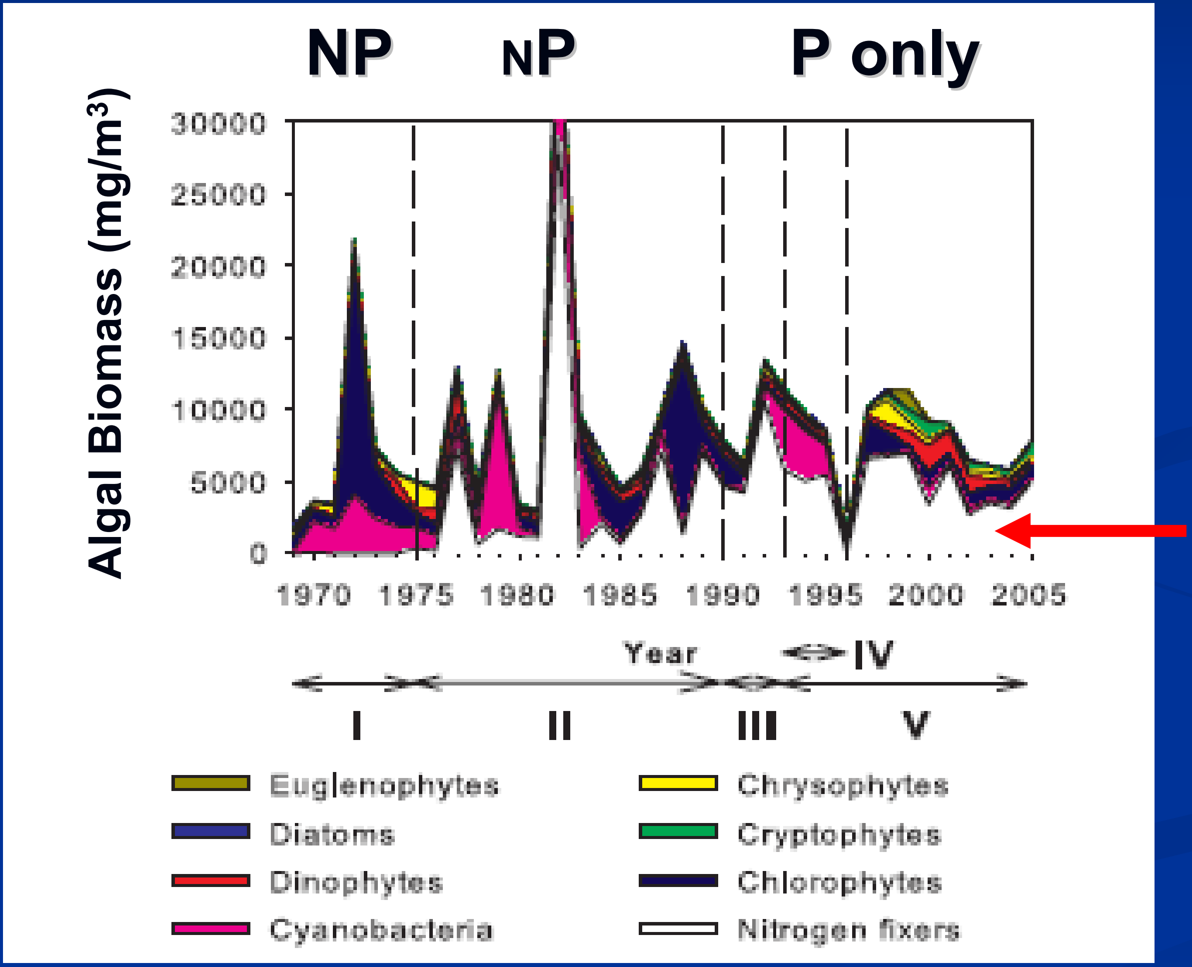
Regional Differences

Atmospheric deposition of anthropogenic N may influence which nutrients are limiting



Derived from Elser et al. (1990) & US National Atmospheric Deposition Program (EPA)

37-Year Whole-Lake Bioassay Experiment (Schindler et al. 2008)

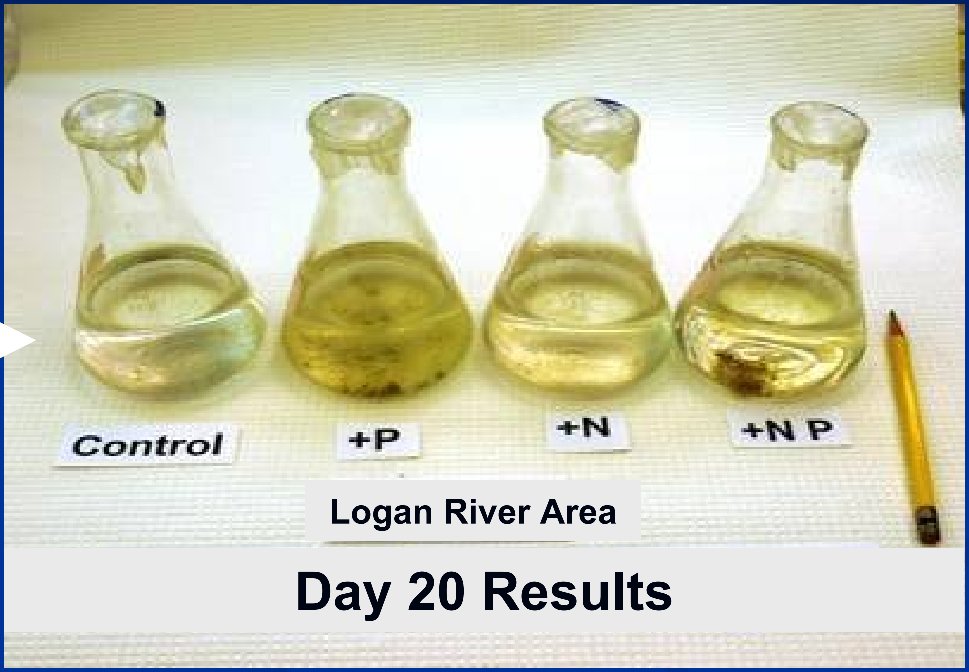


Once eutrophic, adding only P has maintained high algal levels for 12 yr

Lake 227, ELA

“Long-term” Bioassay Results

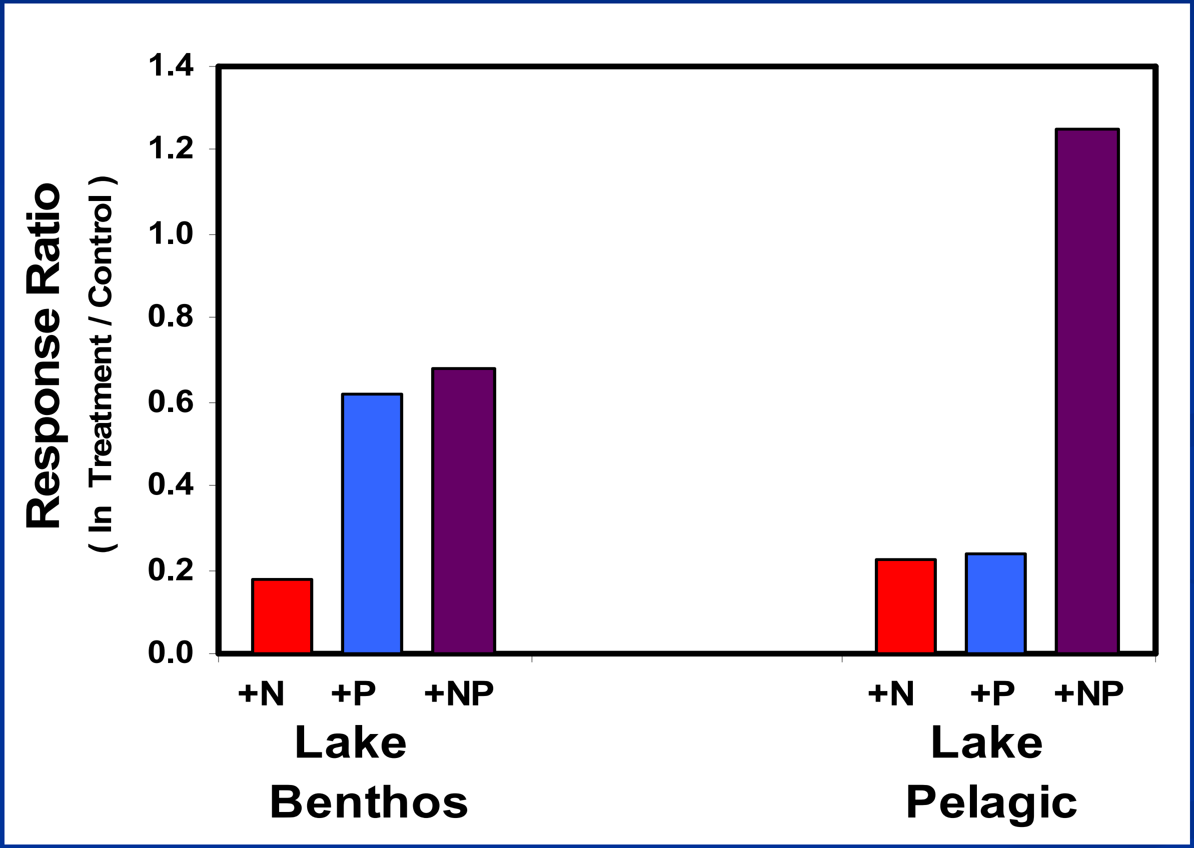
Day 4 Results



Day 20 Results

Cyanobacteria (*Anabaena*) associated with “benthic” walls of flasks

Meta-analysis of Elser et al. (2007) also indicates that periphyton respond better to P-alone additions than do the algae in pelagic zones



Is strong response to P limited primarily to eutrophic lakes & "eutrophic" biofilms?

Conclusions

- Both N and P can be important in controlling eutrophication: We need a more <u>balanced</u> and integrated approach for understanding eutrophication whether we're studying freshwaters or marine ecosystems.

- Pelagic nitrogen-fixing cyanobacteria are limited by more than just phosphorus, but we still do not have a good understanding of this process in either freshwaters, estuaries or the oceans

Conclusions

- **P may be more effective in promoting N-fixation in eutrophic situations:**
  - **Eutrophic lakes**
  - **“Eutrophic” benthic areas of lakes (or flasks)**

- **If so, control factors for *eutrophication* and *oligotrophication* may not be symmetrical:**

N and P necessary

Oligotrophic -----------→ Eutrophic

Remove only P?

Oligotrophic <------------- Eutrophic

Conclusions

- Management of eutrophication must consider:
  - Current limiting nutrient in system
  - Cost-effectiveness of removing P, N
  - May be most efficient to make a nutrient limiting by removing it from effluent, even though it might not initially be limiting

Merci

- Didn’t present the following slides

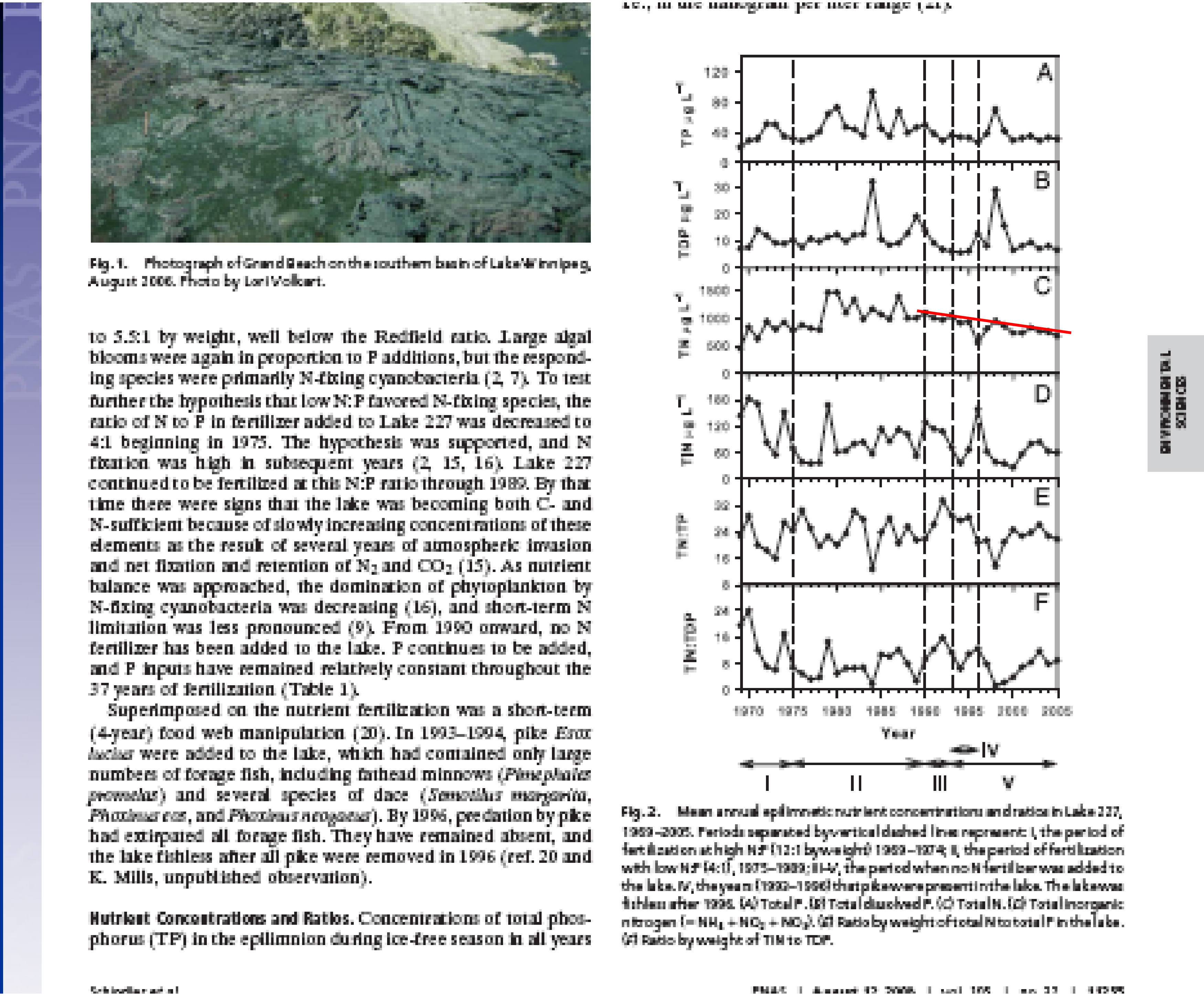


Fig. 1. Photograph of Grand Beach on the southern basin of Lake Winnipeg, August 2006. Photo by Lori Volkart.

to 5.5:1 by weight, well below the Redfield ratio. Large algal blooms were again in proportion to P additions, but the responding species were primarily N-fixing cyanobacteria (2, 7). To test further the hypothesis that low N:P favored N-fixing species, the ratio of N to P in fertilizer added to Lake 227 was decreased to 4:1 beginning in 1975. The hypothesis was supported, and N fixation was high in subsequent years (2, 15, 16). Lake 227 continued to be fertilized at this N:P ratio through 1989. By that time there were signs that the lake was becoming both C- and N-sufficient because of slowly increasing concentrations of these elements as the result of several years of atmospheric invasion and net fixation and retention of N_2 and CO_2 (15). As nutrient balance was approached, the domination of phytoplankton by N-fixing cyanobacteria was decreasing (16), and short-term N limitation was less pronounced (9). From 1990 onward, no N fertilizer has been added to the lake. P continues to be added, and P inputs have remained relatively constant throughout the 37 years of fertilization (Table 1).

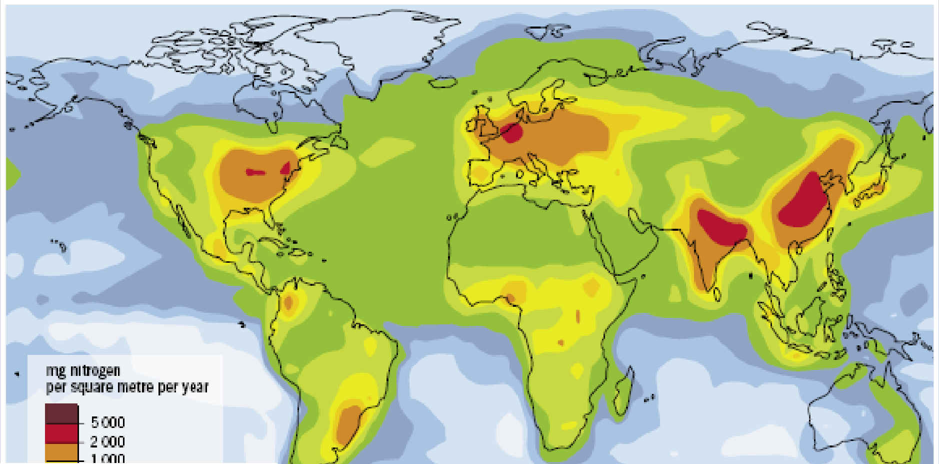
Superimposed on the nutrient fertilization was a short-term (4-year) food web manipulation (20). In 1993–1994, pike *Esox lucius* were added to the lake, which had contained only large numbers of forage fish, including fathead minnows (*Pimephales promelas*) and several species of dace (*Semotilus margarita*, *Phoxinus eos*, and *Phoxinus neogaeus*). By 1996, predation by pike had extirpated all forage fish. They have remained absent, and the lake fishless after all pike were removed in 1996 (ref. 20 and K. Mills, unpublished observation).

Nutrient Concentrations and Ratios. Concentrations of total phosphorus (TP) in the epilimnion during ice-free season in all years

L⁻¹, in the nanogram per liter range (21).

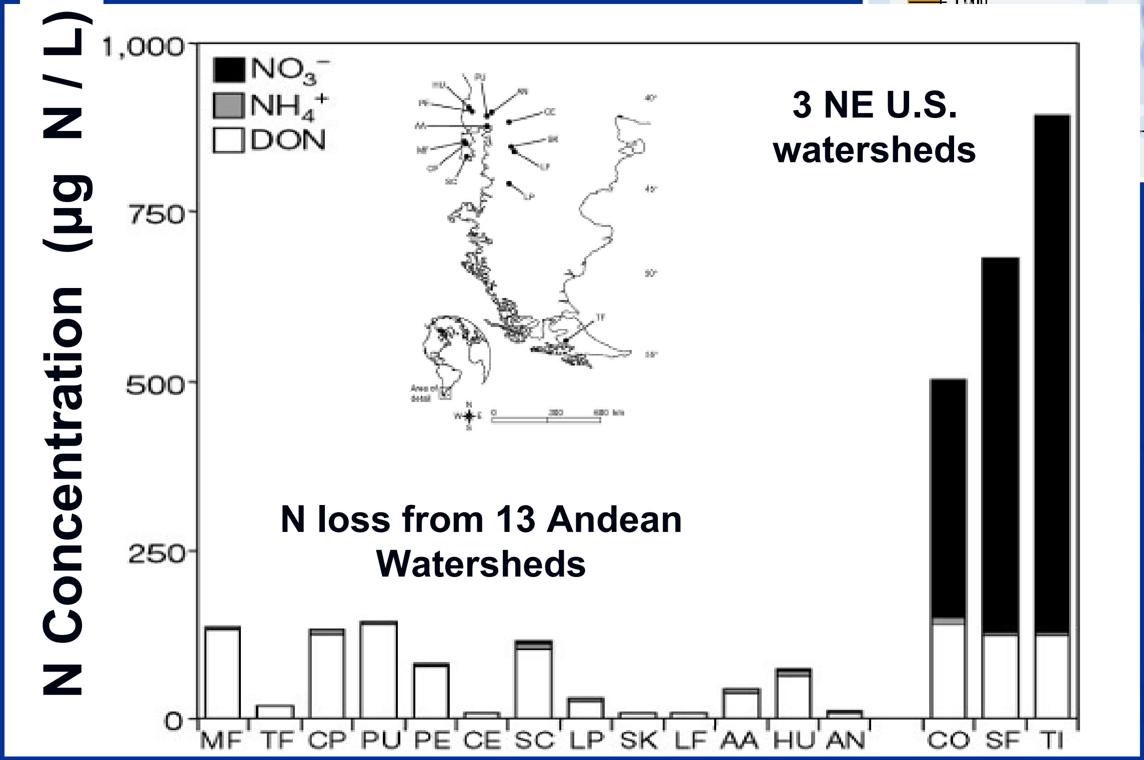
Fig. 2. Mean annual epilimnetic nutrient concentrations and ratios in Lake 227, 1969–2005. Periods separated by vertical dashed lines represent: I, the period of fertilization at high N:P (12:1 by weight) 1969–1974; II, the period of fertilization with low N:P (4:1), 1975–1989; III–V, the period when no N fertilizer was added to the lake. IV, the years (1993–1996) that pike were present in the lake. The lake was fishless after 1996. (A) Total P. (B) Total dissolved P. (C) Total N. (D) Total inorganic nitrogen (= $NH_4 + NO_2 + NO_3$). (E) Ratio by weight of total N to total P in the lake. (F) Ratio by weight of TIN to TDP.

Regional Differences Clearly Evident



Nitrogen Deposition
(mg m^{-2} y^{-1})

From Galloway et al. 2004

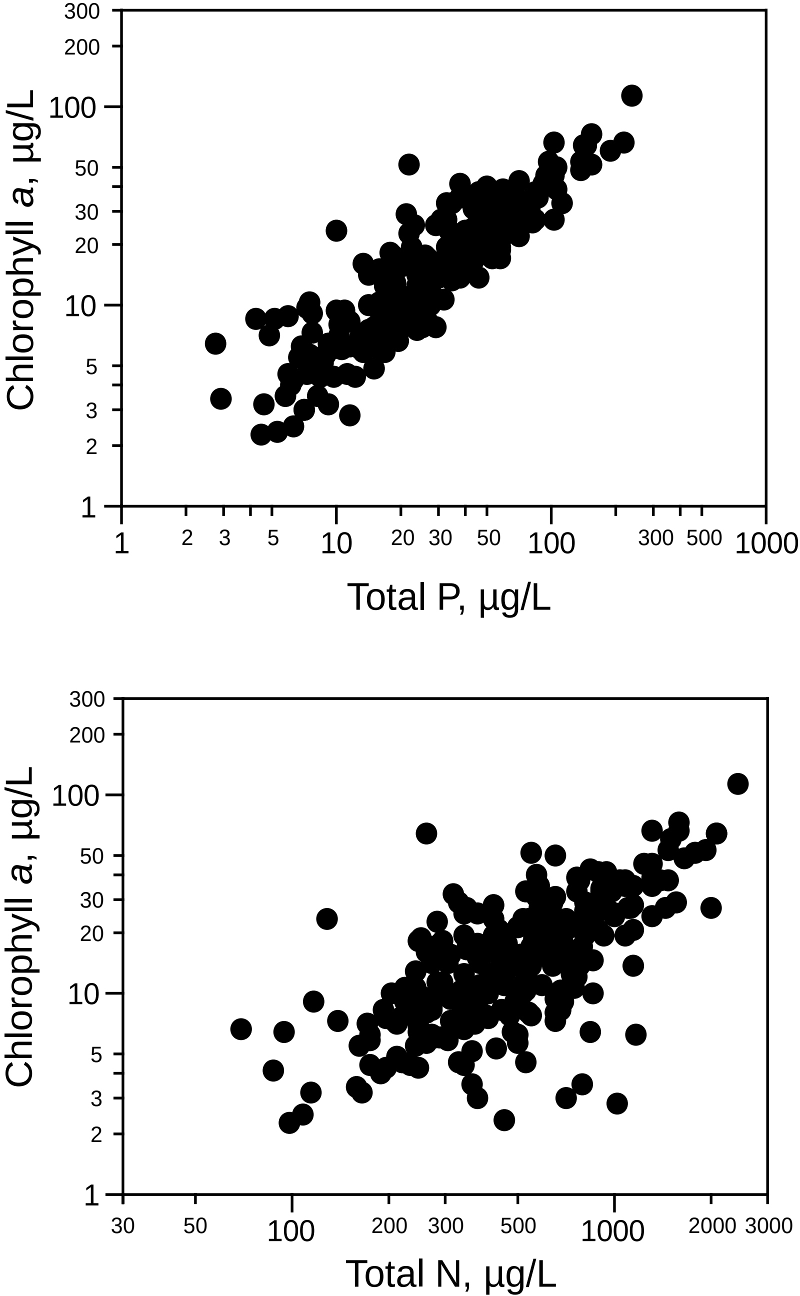


3 NE U.S. watersheds

N loss from 13 Andean Watersheds

Perakis, S.S. and L.O. Hedin. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds Nature 415, 416-419.

A foundation of phosphorus paradigm is the stronger correlation between TP and algal biomass in suites of lakes

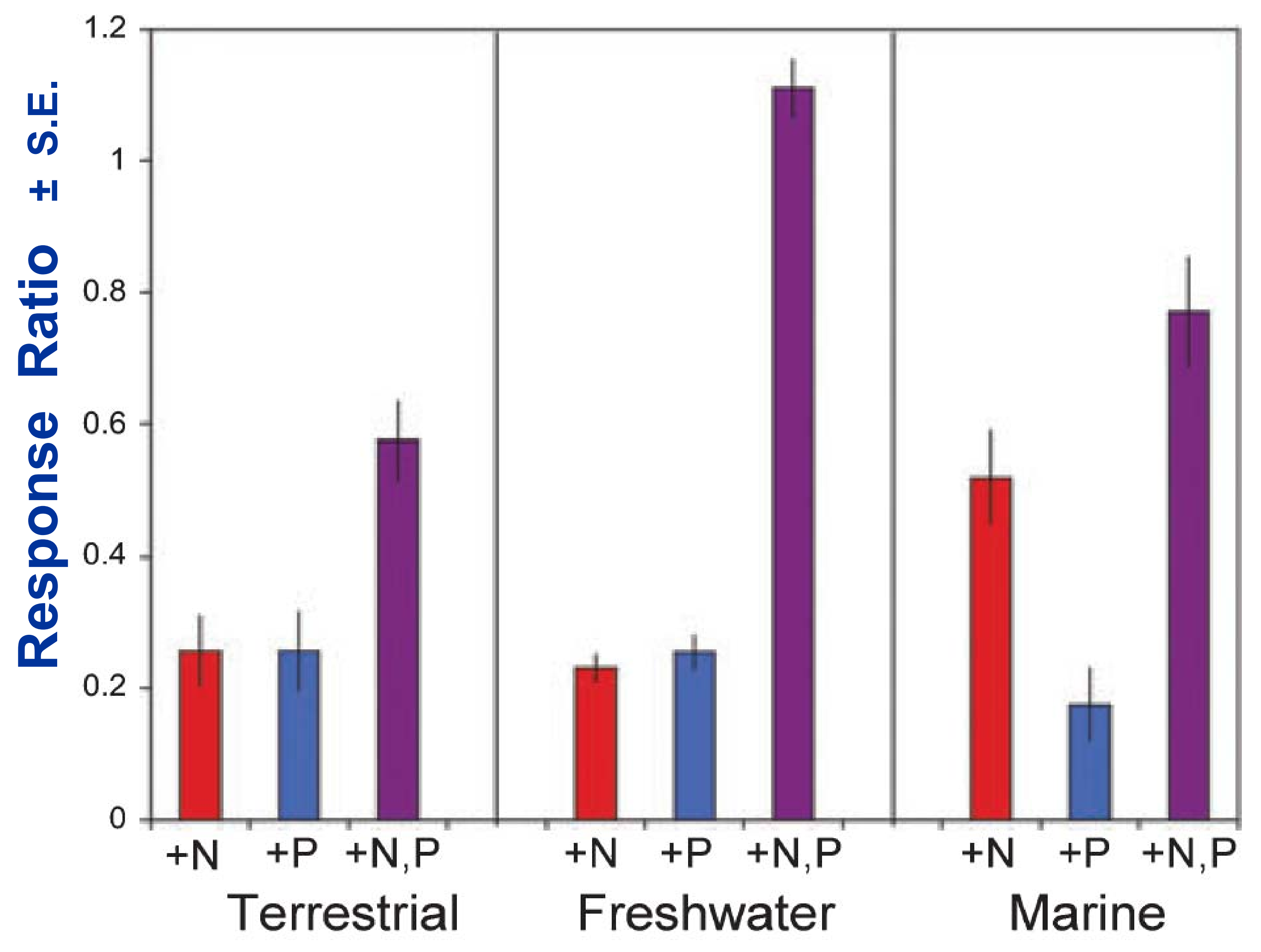


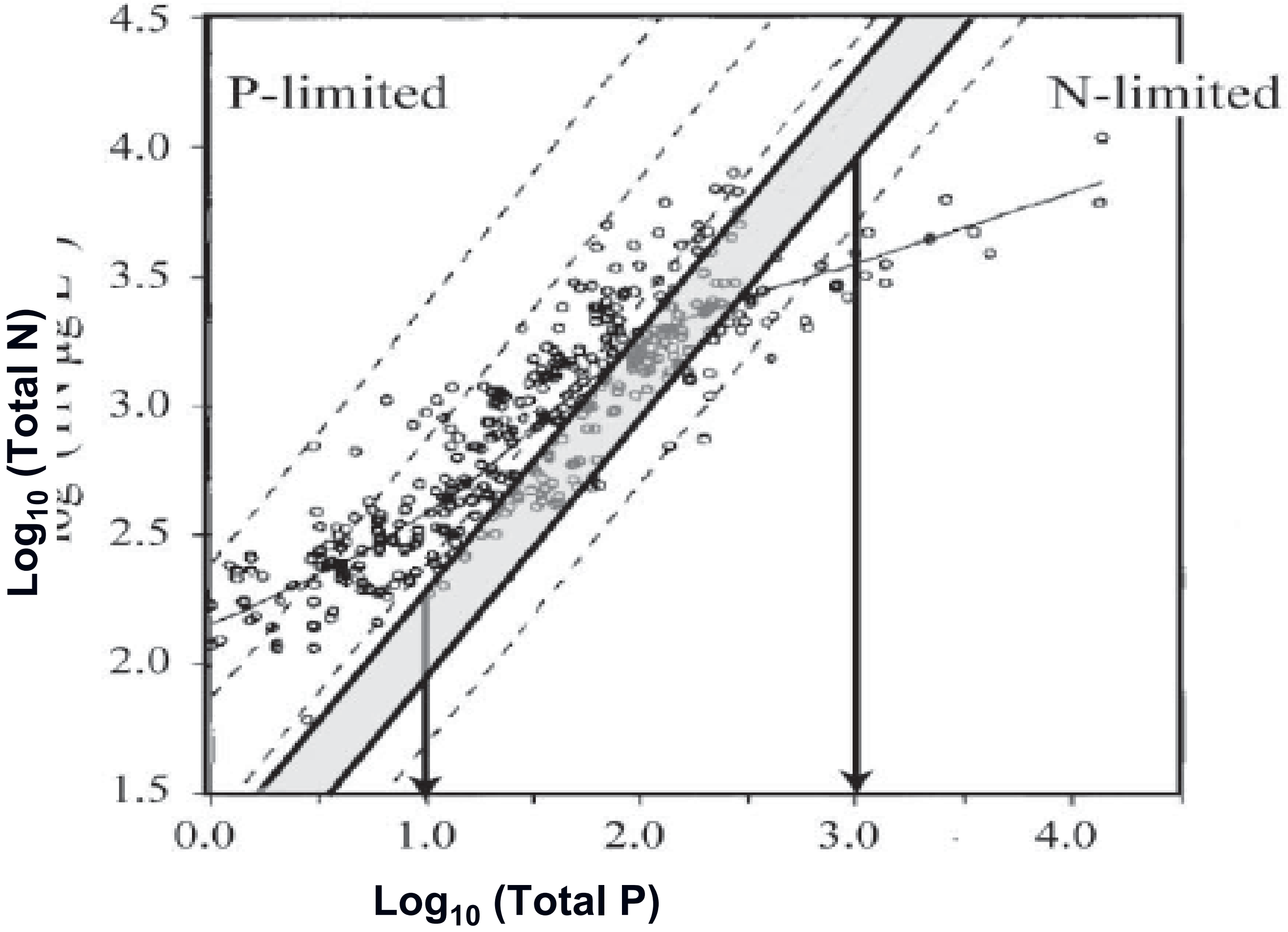
-The simulated data at right shows a situation when the cell quota of of the N:P in algae was set at 16:1 such that neither nutrient was more limiting than the other, but with reasonable assumptions concerning the concentrations of DON, DOP, DIN and SRP.

-In this case the natural variability of the relatively non-available DON causes a much high scatter in the TN-chlorophyll relationship

Elser et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems.

Ecology Letters 10: 1-8





Sterner 2008

Can nitrogen fixing cyanobacteria make up the N-deficiency?

For eutrophic lakes showing N fixation in the plankton, the median contribution to total load that could be attributed to N fixation is near 22%, and the median fixation as a proportion of the total N necessary to support primary production is less than 5%, according to the data compiled by HOWARTH et al. (1988). -- Lewis & Wurtsbaugh (2008)

- Limited by some other nutrient
  (e.g. Fe, Wurtsbaugh and Horne 1983)
- Light limitation (energetic constraints)
- Turbulence
- Grazing losses