Evolution of Phosphorus Limitation in Lakes

Natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes.

D. W. Schindler

Algal physiologists have conclusively demonstrated that freshwater phytoplankton require several elements for growth and reproduction (*1*). Most limnologists have considered that all of these elements might act as potential limiting nutrients in freshwater lakes. While there is now general agreement that phytoplankton will be phosphorus-limited in the majority of lakes (*2*), eutrophication management based entirely on phosphorus control is still viewed by some as too simplistic (*3, 4*). Yet in past years evidence has mounted for an astoundingly precise relationship between the concentration of total phosphorus and the standing crop of phytoplankton in a wide variety of lakes (*5*), including many in which low nitrogen-to-phosphorus ratios should favor limitation by nitrogen. In this article, evidence from whole-lake experiments is used to reexamine the nutrient-control question, with particular attention to factors that might be missing in experiments on a smaller scale. Evidence for the two elements, carbon and nitrogen, that have received widespread attention as alternatives to phosphorus as limiting nutrients (*6*) will be considered.

Control of Phytoplankton Populations in Lakes by Carbon

Five years ago, many scientists believed that carbon might control eutrophication in some lakes (*7*). The scientific evidence for this view came largely from bioassay experiments done in small bottles (*8*), where phytoplankton were stimulated by addition of carbon, but not by phosphorus or nitrogen. This was interpreted by many as indicating that eutrophication was caused by overfertilization with carbon. Whole-lake experiments have now shown that these experiments provided misleading evidence by excluding processes occurring in natural bodies of water (*9, 10*). In experimentally fertilized lakes, invasion of atmospheric carbon dioxide supplied enough carbon to support and maintain phytoplankton populations that were proportional to phosphorus concentrations over a wide range of values (Fig. 1). Yet in bottle bioassay experiments, phytoplankton showed evidence of extreme carbon limitation throughout the period when algal populations were responding in proportion to total phosphorus concentrations. But more important, there was a strong tendency in every case for lakes to correct carbon deficiencies, maintaining concentrations of both chlorophyll and carbon that were proportional to the phosphorus concentration (Figs. 1 and 2).

Bottle bioassay experiments to test the carbon-limitation hypothesis were inadequate in two respects. First, experiments were done in small, closed or semiclosed containers, where turbulence of the water and interaction with the overlying atmosphere were restricted. Second, the proportion of alkalinity supplied by hydroxyl ions has been found to affect the rate at which carbon invades lake ecosystems (*11*), and no attempt was made in the bottle experiments to simulate such conditions (*12*).

These observations have led me to conclude that carbon control no longer deserves consideration as a method for managing eutrophication of natural waters (*13*).

Control of Phytoplankton Populations in Lakes by Nitrogen

Because of the problems our group encountered in extrapolating from small-scale experiments to whole-lake management of carbon, we designed several whole-lake experiments to investigate the nitrogen management question. Because of the important role played by atmospheric carbon, we paid particular attention to fixation of atmospheric nitrogen by algae as a supplementary source of this element.

In lake 227, the site of our first carbon experiments, the fertilizers added to the lake had contained adequate or excess nitrogen. The ratio by weight of nitrogen to phosphorus was 14. Fertilizer with this ratio was applied for 6 years, 1969 through 1974. During the entire period, phytoplankton were dominated by the green alga *Scenedesmus* and other algae incapable of fixing gaseous nitrogen. I hypothesized that by reducing the ratio of nitrogen to phosphorus in fertilizer, blue-green algae, which are capable of fixing atmospheric nitrogen, might be favored. Therefore, in a second experiment, the northeast basin of lake 226 was fertilized with a nitrogen-deficient fertilizer (*4*). The ratio of nitrogen to phosphorus by weight was only 5. In every year that this fertilizer was applied (1973 to 1975), nitrogen-fixing blue-green algae of the genus *Anabaena* dominated the lake. Fixation of nitrogen accounted for a substantial proportion of the total income of nitrogen to the lake (*14*), and the ratio of total nitrogen to total phosphorus in the lake remained similar to that in other lakes (Fig. 3).

Another whole-lake experiment showed that this difference between lakes 226 and 227 was no accident. In 1975, the nitrogen-to-phosphorus ratio of fertilizer to lake 227 was reduced to 5, duplicating the ratio used in lake 226. For the first time in the 8 years we have studied the lake, a nitrogen-fixing blue-green alga, this time *Aphanizomenon gracile*, became dominant in midsummer (Fig. 4). Also for the first time, substantial nitrogen fixation was detected. At this time I cannot explain why different genera of nitrogen fixers should be dominant in the two lakes. This difference may be due to differences in other micronutrients or growth inhibitors and requires further investigation (*15*).

A final experiment has provided a somewhat different result. Only phosphorus fertilizer was applied to lake 261 for 3 years. No nitrogen fixers appeared in the phytoplankton, but a luxuriant

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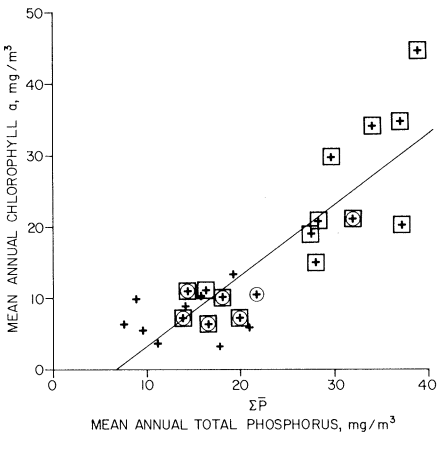
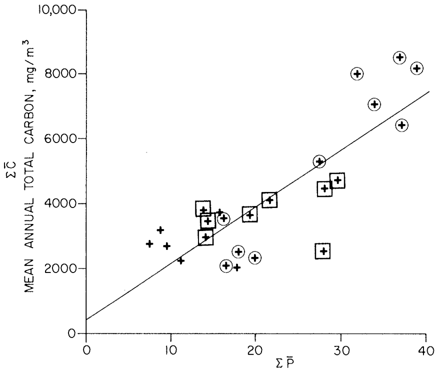
growth of attached algae (periphyton) which are capable of high fixation of nitrogen was observed (*16*). In spite of this, the phytoplankton chlorophyll increased somewhat, and the chlorophyll-to-phosphorus ratio was only slightly lower than in other lakes (Fig. 1).

Discussion

The experiments described above clearly demonstrate the existence in lakes of biological mechanisms which are capable of eventually correcting algal deficiencies of carbon and, at least in some cases, of nitrogen. It is, however, noteworthy that the ratios of carbon to phosphorus and nitrogen to phosphorus in our lakes are maintained at 174 and 31, respectively. These are much higher than the values in inputs to any of our lakes, which suggests that internal factors, as well as atmospheric compensation, may also favor high C/P and N/P ratios (*17*). No external mechanisms exist for phosphorus, which has no gaseous atmospheric cycle. Experiments in lakes 304 and 226 southwest, both phosphorus-deficient, show that there is no appreciable internal compensation in our Precambrian Shield lakes (*18*). While a sudden increase in the phosphorus input, as is common during cultural eutrophication, may cause algae to exhibit symptoms of limitation by either nitrogen or carbon or both, there are long-term processes at work in the environment which may cause the deficiencies to be corrected eventually, once again leaving phytoplankton growth proportional to the concentration of phosphorus. If our results are typical, they explain why phosphorus limitation or phosphorus proportionality is commonly observed in lakes, even where the nutrient ratios of geochemical and cultural sources might be expected to favor limitation by nitrogen or carbon. I hypothesize that only lakes which have experienced very recent increases in phosphorus input, without corresponding increases in nitrogen and carbon, or those receiving enormous influxes of phosphorus will not show the correlation between total phosphorus and standing crop.

This "evolution" of appropriate nutrient ratios in freshwaters involves a complex series of interrelated biological, geological, and physical processes, including photosynthesis, the selection for species of algae that can utilize atmospheric nitrogen, alkalinity, nutrient supplies and concentrations, rates of water renewal, and turbulence. It is impossible to





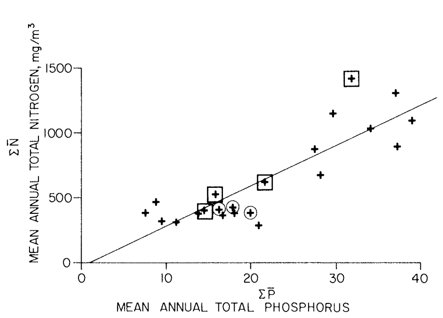


Fig. 1 (top). Relationship between mean annual concentrations of total phosphorus and chlorophyll a in lakes of the Experimental Lakes Area. All averages are weighted for morphometry of the lakes. Both fertilized and unfertilized lakes are included. (○) Data for fertilized lakes where nutrients supplied by fertilizer, precipitation, and runoff were deficient in nitrogen ($N/P < 8$ by weight). (□) Data for lakes where nutrients from the same three sources were deficient in carbon ($C/P < 50$ by weight). Points (+) without either circles or squares represent lakes where C/P and N/P ratios in inputs are either natural or higher than natural. The linear regression equation chlorophyll $a = 0.987\Sigma\bar{P} - 6.520$ fits the points with the correlation coefficient $r = .86$. Fig. 2 (middle). Mean annual total carbon and total phosphorus concentrations in fertilized lakes of the Experimental Lakes Area, illustrating how the carbon content of these lakes has increased because of addition of phosphorus. Total carbon includes seston, dissolved inorganic carbon, and methane, but excludes dissolved organic carbon (DOC). Concentrations of DOC have not changed as a consequence of eutrophication. (○) Data for lakes that received no carbon with fertilizer. (□) Data for lakes that received low fertilizations with sucrose (C/P ~ 6 by weight in lake 226, ~ 14 in lake 304, and ~ 85 in lake 226 southwest). Points without circles or squares represent lakes with either natural or higher than natural C/P inputs. The regression equation $\Sigma\bar{C} = 173.6\Sigma\bar{P} + 420.3$ fits the points with $r = .83$. Fig. 3 (bottom). Mean annual concentrations of total nitrogen and total phosphorus in fertilized lakes, illustrating that the nitrogen content of a lake increases when phosphorus input is increased, even when little or no nitrogen is added with fertilizer. (○) Data for lake 261, which received only natural nitrogen. (□) Data for lakes 226 northeast and 227. The N/P in input to lake 226 northeast in 1973 to 1975 and lake 227 in 1975 was less than 8. Points without circles or squares represent lakes with N/P equal to or greater than the natural ratio. The regression equation $\Sigma\bar{N} = 30.9\Sigma\bar{P} - 29.3$ fits the points with $r = .86$.

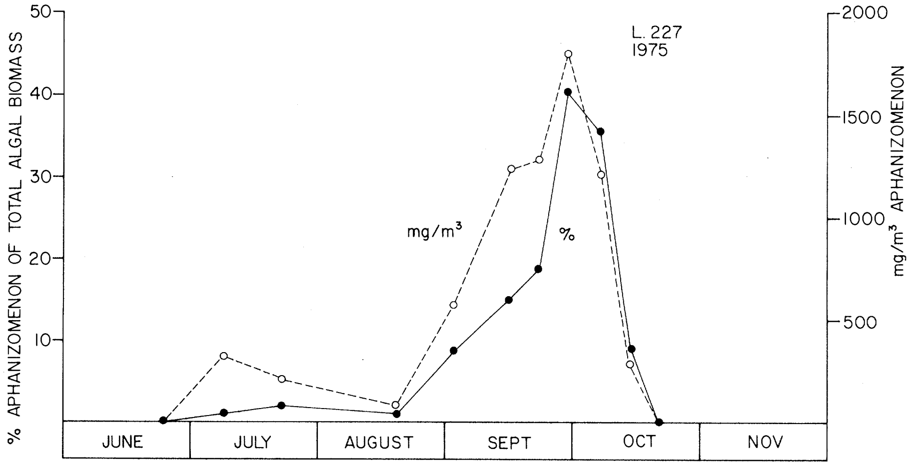


Fig. 4. Summer population of *Aphanizomenon* in lake 227 in 1975, after the N/P ratio in fertilizer had been cut back to 5 by weight. The genus had not been observed in quantifiable numbers in any of the six previous years, when an N/P ratio of 15 had been used in fertilizer. High fixation of atmospheric nitrogen accompanied the bloom of this species.

visualize a laboratory bioassay experiment that could realistically represent all of these parameters.

On the basis of data from several studies of the carbon, nitrogen, and phosphorus cycle, I hypothesize that schemes for controlling nitrogen input to lakes may actually affect water quality adversely by causing low N/P ratios, which favor the vacuolate, nitrogen-fixing blue-green algae that are most objectionable from a water quality standpoint. Conversely, when phosphorus control causes an increase in the N/P ratio, the resulting shift from "water bloom" blue-green algae to forms that are less objectionable may be as important as quantitative decreases in algal standing crop. Several authors have observed such species shifts with changing N/P ratios (*19*).

It is clear that management decisions on nutrient control measures must be based on controlled field tests as well as simple laboratory bioassays.

References and Notes

1. For a summary of these, see J. Vallentyne, *Can. Fish. Mar. Serv. Misc. Spec. Publ. No. 22* (1974), p. 162.
2. The general assemblies of both the International Limnological Congress and the International Ecology Congress unanimously passed resolutions recommending widespread phosphorus control as a solution to eutrophication. Almost all of the freshwater scientists in the world were represented.
3. For example, see J. W. G. Lund [*Nature (London)* **249**, 797 (1974)] for a critique of phosphorus control, including my report of the same year (*4*).
4. D. W. Schindler, *Science* **184**, 897 (1974).
5. P. Dillon and F. Rigler, *J. Fish. Res. Board Can.* **32**, 1519 (1975); R. A. Vollenweider, *Schweiz. Z. Hydrol.* **37**, 53 (1975); D. W. Schindler, *Limnol. Oceanogr.*, in press.
6. See papers in G. E. Likens, Ed., *Am. Soc. Limnol. Oceanogr. Spec. Symp. No. 1* (1972).
7. For example, see articles in *Can. Res. Dev.* **3**, 19 (1970).
8. For example, W. Lange, *Nature (London)* **215**, 1277 (1967); *J. Phycol.* **6**, 230 (1970); M. Sakamoto, *J. Fish. Res. Board Can.* **28**, 203 (1971); A. Christie, *Ont. Water Resour. Comm. Res. Publ. No. 32* (1968).
9. D. W. Schindler, G. Brunskill, S. Emerson, W. Broecker, T-H. Peng, *Science* **177**, 1192 (1972); D. W. Schindler (*10*); S. Emerson, W. Broecker, D. W. Schindler, *J. Fish. Res. Board Can.* **30**, 1475 (1973).
10. D. W. Schindler, *Int. Ver. Theor. Angew. Limnol. Verh.* **19**, 3221 (1975).
11. ——— and E. Fee, *J. Fish. Res. Board Can.* **30**, 1501 (1973).
12. S. Emerson [*Limnol. Oceanogr.* **20**, 743 (1975); *ibid.*, p. 754] showed that gas exchange is roughly proportional to the square of the wind velocity at the lake surface. He also reported that chemical enhancement of gas exchange in softwater lakes may yield values five to ten times higher than unenhanced values, once nutrient additions have caused depletion of inorganic carbon, so that alkalinity is dominated by hydroxyl ions.
13. These views are summarized by D. W. Schindler (*10*).
14. In lake 226, nitrogen fixation contributed 38 percent of the total nitrogen income in 1974 and 19 percent in 1975 (R. Flett, University of Manitoba, thesis, 1976).
15. For example, T. P. Murphy, D. R. S. Lean, and C. Nalewajko [*Science* **192**, 900 (1976)] showed that *Anabaena* requires iron for fixation of atmospheric nitrogen and that this genus can suppress the growth of other species of algae by excretion of a growth-inhibiting substance.
16. M. Turner and R. Flett, unpublished data. As yet no quantitative estimates of nitrogen fixation for an entire season are available. G. Persson, S. K. Holmgren, M. Jansson, A. Lundgren, and C. Anell [in *Proceedings of the NRC-CNC (SCOPE) Circumpolar Conference on Northern Ecology* (*Ottawa, 15 to 18 September 1975*)] reported similar results for a lake in Sweden that was fertilized with phosphorus.
17. Possible additional mechanisms are outlined by D. W. Schindler [in *Environmental Biogeochemistry*, J. O. Nriagu, Ed. (Univ. of Michigan Press, Ann Arbor, 1976), pp. 647–664]. In particular, nitrogen appears to be more efficiently recycled from sediments than phosphorus.
18. Whole-lake experiments with phosphorus-deficient fertilizations in lakes 226 southwest and 304 have confirmed the lack of either biological or geochemical mechanisms for enhancing inputs of phosphorus.
19. For example, see P. Sze, *Phycologia* **14**, 197 (1975); M. Michalski and K. Nicholls, *Phosphorus Removal and Water Quality Improvements in Gravehurst Bay, Ontario* (Ontario Ministry of Environment, Rexdale, Ontario, 1975); M. Michalski and N. Conroy, *Proc. 16th Conf. Great Lakes Res.* (1973), p. 934; W. T. Edmondson, *Verh. Int. Ver. Limnol.* **18**, 284 (1972). Other members of our staff have recently been able to cause shifts in dominance from blue-green to green algae in hypereutrophic lakes by adding nitrogen (J. Barica and H. Kling, personal communication).
20. My thanks to T. Ruszczynski, who performed the calculations for Figs. 1, 2, and 4, to D. Findlay, whose plankton identifications and counts allowed these interpretations, and to J. Prokopowich for chemical analyses. The critical comments of K. Patalas, R. Flett, and E. Fee are greatly appreciated.

The Biosphere Reserve Program in the United States

A program has been developed to select key sites for environmental research and monitoring.

Jerry F. Franklin

Biosphere reserves are major elements in Unesco's "Man and the Biosphere" (MAB) program and in the U.S.–U.S.S.R. Environmental Agreement. They are part of an international system of reserves with the primary objectives of conservation of genetic diversity, environmental research and monitoring, and education.

The scientific community must be aware of the existence and potential of the biosphere reserves if they are to fulfill their intended functions. I will outline the conceptual development of the Unesco effort, the philosophy guiding its implementation in the United States, and the utilization and expansion of U.S. biosphere reserves expected in the future. The views presented are those of the U.S. National Committee for Man and the Biosphere.

Development of the Biosphere Reserve Concept

The concept of biosphere reserves was developed as a major element of Project 8, *Conservation of Natural Areas and of the Genetic Material They Contain*, in the Unesco-sponsored Program on Man and the Biosphere (*1*). This project, which emerged as an important component early in the MAB planning, was initially considered in detail by an expert panel, which met in Morges, Switzerland, in September 1973. Establishment of a worldwide network of biosphere reserves was this panel's first recommendation. A task force with the responsibility of defining "criteria and guidelines for the selection and establishment of biosphere reserve" (*2*, p. 9) met in Paris in May 1974. The task force report is the source of the following information on the international program.

Biosphere reserves have three basic purposes or objectives: (i) conservation or preservation—"to conserve for present and future use the diversity and integrity of biotic communities of plants and animals within natural ecosystems, and to safeguard the genetic diversity of species on which their continuing evolution depends" (*2*, p. 6); (ii) research and

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