the central nervous system is based on relative sparing of functions following early brain damage. Paradoxically, the cases with orbital lesions presented here, in which initially orbital functions fail to be spared, may turn out to be stronger models for developmental plasticity than cases in which the immediate result is lack of impairment. In the latter case, it would be necessary to show that deficits do not appear with increasing age before absence of impairment could be interpreted as recovery of function.

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References and Notes

1. Some evidence for this is reviewed in *The Neuropsychology of Development*, R. Isaacson, Ed. (Wiley, New York, 1968).
2. K. Akert, O. S. Orth, H. F. Harlow, K. A. Schiltz, *Science* **132**, 1944 (1960); H. F. Harlow, A. J. Blomquist, C. L. Thompson, K. A. Schiltz, M. K. Harlow, in *The Neuropsychology of Development*, R. Isaacson, Ed. (Wiley, New York, 1968), pp. 79–120; H.-L. Teuber, in *Physical Trauma as an Etiological Agent in Mental Retardation*, C. R. Angle and E. A. Baring, Eds. (Department of Health, Education, and Welfare, Washington, D.C., 1970), pp. 7–28; T. J. Tucker and A. Kling, *Brain Res.* **5**, 377 (1967).
3. D. Bowden, P. S. Goldman, H. E. Rosvold, R. Greenstreet, *Exp. Brain Res.* **12**, 265 (1971); P. S. Goldman, H. E. Rosvold, M. Mishkin, *J. Comp. Physiol. Psychol.* **70**, 454 (1970); *Exp. Neurol.* **29**, 221 (1970).
4. P. S. Goldman, *Exp. Neurol.* **32**, 366 (1971).
5. ———, *Acta Neurobiol. Exp.* **32**, 495 (1972); ——— and H. E. Rosvold, *Brain. Res.* **43**, 53 (1972).
6. Supported in part by NIMH postdoctoral fellowship MH 43167 to E.A.M.
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Carbon Dioxide and pH: Effect on Species Succession of Algae

The report of Shapiro (*1*) raises a number of perplexing questions regarding the role of inorganic carbon in the eutrophication process. Although there is considerable circumstantial evidence (*2*) to support Shapiro's hypothesis that blue-green algae predominate at high *p*H levels ($pH > 9$), it is difficut to accept his or King's (*3*) conclusion that the predominance of blue-green algae results from a lowering of the CO_2 (aqueous) concentration as the *p*H rises in natural waters. Thus, the implication from their work is that blue-green algae have a higher affininty for CO_2 (aqueous) than green algae.

I contest this point on several grounds. First, I know of no evidence in the literature that the growth rate of algae is controlled solely by the CO_2 (aqueous) concentration. Rather, as I have demonstrated (*4*), algal growth rates in an inorganic carbon–limited growth situation are controlled by the total inorganic carbon concentration ($C_T = CO_2 + H_2CO_3 + HCO_3^- + CO_3^{2-}$) regardless of the *p*H. As I pointed out (*4*), on the basis of the established values of the rate constant for the dehydration of H_2CO_3, only in the most dense algal cultures (for example, stabilization ponds or controlled laboratory cultures) would such a high demand be placed on the C_T reservoir that the rate reaction for the dehydration of H_2CO_3 to CO_2 (aqueous) would become a limiting step for algal growth. In reality for most natural waters, regardless of the *p*H, it is not the CO_2 (aqueous) concentration that controls algal growth rates, but rather the C_T concentration.

In addition, if the dehydration of H_2CO_3, or, more accurately, the direct conversion of HCO_3^- to CO_2 (aqueous) at high *p*H ($pH > 10$), is not a rate-limiting step, then from an ecological point of view it should make little difference what form of inorganic carbon is directly taken up by algae. As an example, it has been suggested by a number of researchers that certain species of both green and blue-green algae can utilize HCO_3^- directly (*5*). Because in the *p*H range from 10 to 11 HCO_3^- and CO_3^{2-} are the major forms of inorganic carbon, it could be argued that at high *p*H algal species capable of using HCO_3^- directly would be able to win out in competition with species that use only CO_2 (aqueous). It can easily be shown (*4*), on the basis of a few simple calculations, that for practically all natural waters the rate at which CO_2 (aqueous) is supplied from HCO_3^- via chemical reactions is still considerably greater than the rate at which it is assimilated by algae. Thus, at high *p*H, regardless of what form of carbon an algal species uses, only the C_T concentration is of importance.

The factor that is important, however, is the relative affinities for C_T of green and blue-green algae, as represented by their respective half saturation coefficients (K_s) for C_T-limited growth. As I have shown (*4*), in the *p*H range from 7.1 to 7.6 the K_s values for C_T-limited growth of two typical green algae were 0.2 to 0.6 mg/liter (*Scenedesmus quadricanda*) and 0.4 to 1.3 mg/liter (*Selenastrum capricornutum*), and the K_s values increased with increasing *p*H. It might be possible that blue-green algae have even lower K_s values for C_T-limited growth, particularly at high *p*H; this would explain their predominance in some situations. This explanation, however, would be valid only for conditions of C_T-limited growth. Many researchers, including Shapiro and I, are of the opinion that carbon is not limiting in most natural waters (*6*). The ability of blue-green algae to thrive at high *p*H must then be explained by other factors. Shapiro's evidence that low CO_2 concentrations (that is, high *p*H) resulted in the predominance of blue-green algae, and that through the addition of 100 percent CO_2 and a concomitant reduction in the *p*H green algae succeeded blue-green algae must be considered highly circumstantial.

My second line of reasoning to counter Shapiro's claims concerns the effect of *p*H on the availability of several algal nutrients. At high *p*H levels the solubility of such essential nutrients as phosphorus, iron, and many trace elements is very low (*7*). The possibility that blue-green algae have a higher affinity for one or more of these nutrients could explain their predominance at high *p*H values. Shapiro (*1*) actually alluded to this possibility by suggesting that blue-green algae have a greater affinity (that is, lower K_s value) than green algae for phosphorus. Therefore, is it not possible that, as the *p*H rises as a result of algal growth, the phosphorus concentration in a sample of natural water decreases through chemical precipitation, and phosphorus, if it is not already the limiting nutrient, becomes limiting? Then could not blue-green algae, because of their ability to utilize lower concentrations of phosphorus, acquire an ecological advantage over green algae? In view of the fact that the chemistry of phosphates and other sparingly soluble compounds is extremely complex and so influenced by *p*H, it is crucial that this point be clearly defined and investigated in any experiments dealing with the effect of *p*H on species succession.

Third, most enzyme systems have a pH optimum (8). The difficulty in separating the effects on algal metabolic activity of pH from the effects of inorganic carbon or other nutrients has plagued many researchers. This factor is particularly complex, as little is known about the mechanisms by which nutrients are transported across the outer cell membranes of algal cells. As several researchers have pointed out (9), most cell enzymes are surface-bound and immobilized. Although the internal cell pH may be well buffered and not greatly affected by external pH variations, the activity of those enzymes in the outer cell membranes or acting extracellularly and that are involved in nutrient transport may be significantly influenced by external pH changes. Shapiro's results do little to resolve this problem, as there is no evidence to contest the implication that blue-green algae predominated at the high pH values in his experiments because they can tolerate low hydrogen ion concentrations better than green algae. Obviously, if pH is to be eliminated as a variable, it will be necessary to conduct experiments with noncarbon buffer systems and to vary CO_2 (aqueous) and C_T concentrations at several fixed pH values over the entire pH range in which algae grow.

The idea that pH plays a major role in determining species succession in natural waters is not a new one (2). To date, however, hardly any definite conclusions can be reached concerning the actual mechanisms governing the pH dependency of algal species succession in natural waters.

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References and Notes

1. J. Shapiro, *Science* **179**, 382 (1973).
2. D. F. Jackson, in *Proc. 19th Ind. Waste Conf.* (1964), p. 402; O. Holm-Hansen, in *Environmental Requirements of Blue-Green Algae: Proceedings of a Symposium* (U.S. Department of the Interior, Corvallis, Ore., 1967), p. 87.
3. D. L. King, *J. Water Pollut. Contr. Fed.* **42**, 2035 (1970).
4. J. C. Goldman, thesis, University of California, Berkeley (1972).
5. The entire question of direct HCO_3^- utilization by certain algae is in the realm of controversy, as no methods have been developed to allow a distinction to be made between CO_2 (aqueous) and HCO_3^- uptake. An extensive review of previous work in this area has been given by J. A. Raven [*Biol. Rev. Cambridge* **45**, 167 (1970)].
6. D. W. Schindler, *J. Phycol.* **7**, 321 (1971); J. C. Goldman, D. B. Porcella, E. J. Middlebrooks, D. F. Toerien, *Water Res.* **6**, 637 (1972); G. E. Likens, Ed., *Nutrients and Eutrophication: The Limiting-Nutrient Controversy* (American Society of Limnology and Oceanography, Lawrence, Kansas, 1972).
7. W. Stumm and J. J. Morgan, *Aquatic Chemistry* (Interscience, New York, 1970), pp. 514–563.
8. M. Dixon and E. C. Webb, *Enzymes* (Academic Press, New York, ed. 2, 1964), pp. 116–144.
9. A. D. McLaren and L. Packer, *Advan. Enzymol.* **33**, 245 (1970); E. Katchalski, I. Silman, R. Goldman, *ibid.* **34**, 445 (1971).

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When I submitted my report (1) to *Science*, I justified it by pointing out that, although it was short on data, it was long on speculation. Therefore, I am grateful to Goldman for picking up the gauntlet.

Goldman's objections are three: (i) that algal growth is not controlled by free CO_2 concentrations, (ii) that the pH can affect the availability of nutrients other than CO_2, and (iii) that the result of changing the pH may be through its effects on algal enzymes that may be involved in nutrient transport.

On the first point Goldman attacks with that deadliest of weapons—the unpublished thesis—and declares that algal growth rates in carbon-limited systems are controlled by the total inorganic carbon concentration (C_T). Therefore, in a system that is not carbon-limited, the pH should not favor one alga over another. He also discounts the possibility that superior kinetics for the uptake of C_T can favor one alga over another in a system that is not carbon-limited. However, the data presented by King (2), showing that photosynthesis can occur at lower free CO_2 concentrations in mixed systems than in quiescent ones, suggest that "carbon limitation" may occur in a system that is "not carbon-limited" (probably through the depletion of carbon in the medium around the cell), and that superior kinetics could thus be of value to an alga even in a system supposedly not carbon-limited. Even if we accept Goldman's assertion of C_T being the key factor, the addition of CO_2 and thus an increase in C_T could benefit algae with poorer carbon uptake kinetics—in this case presumably the green algae. This would be especially true where excess nitrogen and phosphorus were added, as seems to be necessary in order for the shift from one algal species to the other to occur. Clearly, the definitive experiment would be one in which C_T were increased without any change in pH, or one in which the CO_2 concentrations were increased without any change in pH—harder but perhaps possible in a system highly buffered with organic compounds.

I do not feel that Goldman's second objection of the lesser solubility of nutrients at higher pH is significant. For example, more iron can be held available at high pH than at low (3), but certainly the kinetics for the uptake of phosphate suggest that blue-green algae would gain an edge as the phosphate concentration falls. Furthermore, my (alas) as yet unpublished data suggest that, as the pH rises, the K_s for phosphate uptake by green algae increases at a more rapid rate than that for blue-green algae, so that green algae would become progressively more disadvantaged as the pH rises.

With regard to Goldman's third objection, certainly enzymes do have pH optima. My (alack) as yet unpublished results on phosphate uptake show, however, that the mechanisms transporting one nutrient, phosphate, into blue-green and green algae both behave similarly toward pH; that is, both have an inverted U-shaped curve, with significantly lower rates of transport at low and high pH values and with similar optimum pH values.

Well, these are not really arguments. Certainly, Goldman is correct—there are several possible explanations for the species succession observed. What I did was to say, "If King is right, then, if I add CO_2, the populations should change." He may be, because I did and they did. What I would like to defend is the possible management significance of this phenomenon, regardless of mechanism. It is easily reproducible: a 15-year-old boy in Colorado repeated the experiment and got the same results. (He also won eight awards in the State Science Fair.)

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References

1. J. Shapiro, *Science* **179**, 382 (1973).
2. D. L. King, *J. Water Pollut. Contr. Fed.* **42**, 2035 (1970).
3. J. Shapiro, *J. Amer. Water Works Ass.* **56**, 1062 (1964).

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