NOTE

INTERCEPTION OF ATMOSPHERIC FIXED NITROGEN AS AN ADAPTIVE ADVANTAGE OF SCUM FORMATION IN BLUE-GREEN ALGAE[1]

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ABSTRACT

Scum formation by blue-green algae has been interpreted as a nonadaptive failure of the buoyancy control mechanism and, alternatively, as an adaptive mechanism to reduce inorganic carbon limitation. Data from Lake Valencia, Venezuela, are used to illustrate the principle that scum formers intercept significant amounts of fixed N deposited from the atmosphere at the water surface. Interception of fixed N at the surface can confer a significant selective advantage for populations that are strongly N limited, as in Lake Valencia. This additional adaptive advantage to scum formation may be alternative to or complementary to the possible relief of carbon limitation.

Key index words: blue-green algae; buoyancy; nitrogen deficiency; scums; vacuoles

Two adaptations exclusive among algae to the Cyanophyceae—nitrogen fixation and buoyancy regulation by gas vacuoles—are thought to be related to the position of blue-green algae in the seasonal successional sequence of phytoplankton and to their tendency to dominate eutrophic lakes (Reynolds and Walsby 1975). Nitrogen fixation is of obvious adaptive significance, as it provides an exclusive source of fixed nitrogen, which is often in short supply in eutrophic lakes, especially if artificial enrichment relieves phosphorus limitation (Schindler 1977). The significance of buoyancy regulation has been more difficult to unravel. Particularly intriguing is the phenomenon of scumming, also called water-bloom or breaking (Reynolds and Walsby 1975), in which the colonies come to the surface or very near the surface in large numbers under the influence of sustained buoyancy. Scumming, which is known especially in the genera *Aphanizomenon, Anabaena,* and *Microcystis,* was first explained as a nonadaptive failure of the buoyancy regulation mechanism (Reynolds and Walsby 1975). More recently, Paerl and Kellar (1979) argued that scumming is adaptive in keeping cells very near the surface where the high light demands of nitrogen fixation can be satisfied. They also suggested that CO_2 fixation and N_2 fixation are phased to optimize overall efficiency. These hypotheses are very attractive but would not apply to *Microcystis,* a non-fixer that often forms scums. Paerl and Ustach (1982) have shown, however, that

scumming in non-fixers could be a mechanism for relieving CO_2 deprivation. The present paper offers an alternative or supplementary adaptive interpretation of scumming that would apply to *Microcystis* as well as to nitrogen fixers. The alternative is based on evidence that scum formers intercept significant amounts of fixed nitrogen deposited on the lake surface from the atmosphere. Data for Lake Valencia, Venezuela, are used to illustrate the principle.

Lake Valencia is situated in Venezuela (12° N, 68° W) at 421 m above sea level (Lewis and Weibezahn 1976). The lake is well buffered (conductance, 1400 μmho/cm), has a high pH (8.5–9.5), a mean depth of 19 m, and a maximum depth of 39 m. It is stably stratified between May and November and circulates from December through March, when winds are highest and nocturnal temperatures are lowest (Lewis 1983). During stratification, the mixed layer thickness averages 13 m and chlorophyll concentrations range between 20 and 80 μg/L. The lake is artificially enriched by sewage (5 $g \cdot m^{-2} \cdot a^{-1}$ of P in 1981, see Lewis and Weibezahn 1983). As is often the case in such situations, high algal biomass leads to nutrient depletion in the upper water column during the stratification season. Depletion of soluble inorganic nitrogen is particularly evident; soluble reactive phosphorus levels remain well above those of soluble inorganic nitrogen and do not reach complete depletion. Blue-green algae dominate the algal biomass of Lake Valencia almost continually, although significant diatom populations can occur briefly. Massive scumming occurs episodically and is accounted for principally by the genus *Microcystis* (mainly *M. aeruginosa* Kütz.) and to a lesser extent also by *Anabaena* (mainly *A. spiroides* Kleb. and *A. volzii* Lemm.; see Lewis and Riehl 1982 for taxonomic details).

Precipitation of fixed nitrogen from the atmosphere with rain, dust and aerosols has been studied extensively at Lake Valencia (Lewis 1981). Major variations occur between seasons and between weeks of the same season, so averages are more meaningful than data for any short span. The data to be used here are the averages of weekly bulk collections at lakeside for two years (Lewis 1981).

Growth response to fixed nitrogen was tested on a bloom occurring in the week of 15 September 1981. A 100 L sample was taken of the top 5 m with an integrating sampler (Lewis and Saunders 1979)

TABLE 1. *Response of the bloom-forming algae of Lake Valencia to nutrient enrichment. Initial chlorophyll was 41 $\mu g/L$. Only the N and N + P treatments are statistically distinguishable from the control (P < 0.001).*

Treatment	Chlorophyll a ($\mu g \cdot L^{-1}$)		
	$\bar{x}$	$s_{\bar{x}}$	Change
No additions, 48 h (control)	38.9	4.3	—
P only, 48 h	37.5	5.0	−1.4
N only, 48 h	114.5	4.3	+75.6
N + P, 48 h	108.1	8.0	+69.2

TABLE 2. *Supply of soluble fixed nitrogen by precipitation to the surface of Lake Valencia (computed from data in Lewis 1981).*

Form	Mean annual loading ($kg \cdot ha^{-1} \cdot a^{-1}$)	Concentration in rain, rainy season mean ($\mu g \cdot L^{-1}$)
NO_3^--N	1.28	305
NH_4^+-N	2.43	154
Dissolved organic N	1.33	148
Total	5.04	607

at a time when the wind had just mixed the scum-forming algae into the upper water column. The sample was divided into treatments receiving N enrichment, P enrichment, N + P enrichment and no enrichment (control). Three replicates each of the four treatments were incubated for 48 h at a depth of 1.2 m. This depth was selected because it placed the sample below the zone of light inhibition, but still high enough in the water column to produce light saturation of photosynthesis near midday (ca. 150 $\mu E \cdot m^{-2} \cdot s^{-1}$). Each of the replicates was enclosed in a 10 L soft plastic container along with a 0.5 L air pocket. Response of the air pocket to water currents and to the bobbing of the floats kept the contents dispersed within the container. Nitrogen treatments received a spike of 1000 $\mu g/L$ N as KNO_3; P treatments received 150 $\mu g/L$ P as KH_2PO_4. The N + P treatments received both the N and P spikes. Chlorophyll a was measured before and after the incubation by hot methanol extraction (Talling 1974).

The results of the enrichment are shown in Table 1. Growth response to N was very high; P gave no response beyond the control. The N + P treatment reacted as though only N had been added. This plus the depletion of inorganic N in situ indicate that the algae of the upper water column were N-limited. Enrichment on three other dates spread over the stratification period produced very similar results.

Large amounts of nitrate, ammonium, and soluble organic N are deposited on the surface of Lake Valencia with bulk (dry and wet) precipitation (Table 2). The wet fraction of precipitation is typically responsible for most of the atmospheric N deposition (e.g. Grant and Lewis 1982: >75%). Nitrate and ammonium are obviously available for uptake by phytoplankton at the surface. Soluble organic N is here considered as potentially available to the blue-green algae in view of their known capacity for photoheterotrophy (Fogg et al. 1973, Wolk 1973). Particulate N is considered unavailable and is excluded from Table 2. The nitrogen loading of Lake Valencia from the atmosphere as shown in Table 2 is not unusually high by comparison with other temperate and tropical locations (Lewis 1981). Any conclusions that can be reached from the Lake Valencia data may thus be of general importance.

If distributed throughout the water column, the

atmospheric fixed N deposited on the surface of Lake Valencia or of any other productive lake would be nutritionally minor by comparison with internal cycling and would thus be of no obvious importance to the competitive balance of species. However, if this source is intercepted at or near the surface exclusively by a taxonomically select group at a time when N is severely depleted, it may be important in sustaining that group preferentially. This is best shown by the last column of Table 2 in the context of the nutrient enrichment studies summarized in Table 1. During the rainy season, when the bloom occurred, rain falling on algae at the surface would have a concentration of fixed N approaching that of the nitrogen-enriched treatments that produced very high growth. Since lacustrine N fixation by blue-greens is typically below 15 $\mu g \cdot L^{-1} \cdot d^{-1}$ (Fogg et al. 1973), and the mean concentration of N in rain is more than an order of magnitude higher, ability to intercept even part of the atmospheric fixed N may be as important an adaptation as N fixation. From this viewpoint, scumming takes on the appearance of an adaptive property originating from selection pressures associated with nutrient depletion.

There seem to be presently three possible evolutionary explanations for scumming that could apply either to fixers or nonfixers of nitrogen: (1) scumming is nonadaptive, (2) scumming is adaptive because it relieves carbon limitation, (3) scumming is adaptive because it relieves nitrogen limitation. Either of the two adaptive explanations seems more parsimonious than the nonadaptive one, as the nonadaptive explanation requires an additional hypothesis to explain why the scum formers have not evolved a mechanism to deflate their vacuoles so that they sink when they come too near the surface. The two adaptive explanations will be difficult to separate; they may be complementary rather than alternative. Increased buoyancy under carbon stress as demonstrated by Paerl and Ustach (1982) seems to suggest that carbon is the key. In the Valencia experiments, however, the scum formers were isolated from atmospheric carbon (the small air pocket can be ignored, as it contained less than 4% of the algal carbon). Even so, the algae grew rapidly if supplied with N. The results thus indicate that the algae in Lake Valencia were not limited by inorganic carbon.

The adaptive function of scum formation could clearly differ from one lake to another, or from one time to another. Either of the two possible adaptive advantages of scumming would only be available to relatively large growth forms (10 000–100 000 μm^3), as minor density variations of the cells have much less effect on the vertical position of very small forms (Fogg et al. 1973, Reynolds and Rogers 1976). The special ability of large buoyant forms to use the nitrogen source at the surface may be a means by which large growth forms offset the kinetic advantages of small forms when nitrogen is scarce.

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