COMMENT

Limnol. Oceanogr., 33(1), 1988, 151–154
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Phytoplankton exudation of organic matter: *Why* do healthy cells do it?[1]

Since Sharp (1977) forwarded the provocative question: "Excretion of organic matter by marine phytoplankton—do healthy cells do it?," most of the accumulated data have supported the replying statements of Mague et al. (1980, p. 262): "Extracellular release is a normal function of healthy cells," and of Fogg (1983, p. 11): "The answer to Sharp's question . . . is surely yes."

Beside the direct determination of phytoplankton exudation by fractionated measurements of ^{14}C assimilation (e.g. Fogg et al. 1965; Derenbach and Williams 1974; Larsson and Hagström 1979), several methodologically independent approaches for assessing bacterioplankton secondary production have suggested high bacterial activity, also in situations where phytoplankton exudation is likely to be the major source of substrate, i.e. where release of dissolved organic matter facilitated by grazing ("sloppy feeding") or lysis can be considered of minor importance (e.g. Fuhrman et al. 1980; Larsson and Hagström 1982; Bell and Kuparinen 1984).

Although the reality of exudation from active phytoplankton cells seems to be generally accepted, understanding the physiological mechanism behind it is still lacking. Exudation has been implicitly interpreted as the active release of excess photosynthates that accumulate when carbon fixation exceeds incorporation into new cell material (Fogg 1983).

[1] Contribution 445 from the Freshwater Biological Laboratory. This work was supported by the Danish Natural Science Research Council. O. Geertz-Hansen, J. Gomme, E. Hviid-Larsen, L. M. Jensen, C. Barker Jørgensen, J. B. Larsen, M. Olesen, K. Richardson, B. Riemann, and K. Sand-Jensen provided discussions, references, and comments on the manuscript.

Phytoplankton exudates are rapidly used by planktonic bacteria (Iturriaga and Hoppe 1977) which are able to take up inorganic nutrients more efficiently than phytoplankton (Taylor 1982; Azam et al. 1983). If exudation served as an overflow of carbon during nutrient limitation, it would lead to an apparently paradoxical situation in which phytoplankton actively stimulated its competitors (Azam et al. 1983; Bratbak and Thingstad 1985). In that situation other possible mechanisms for uncoupling photosynthesis, such as changed pigmentation, decreased photosynthetic efficiency, and pseudocyclic photophosphorylation (Radmer and Kok 1976; Falkowski 1984), seem less unfavorable to the phytoplankton.

Furthermore, exudates from actively growing phytoplankton are often dominated by a wide range of low molecular weight (LMW) compounds, including amino acids with high amounts of nitrogen (Watt 1969; Mague et al. 1980; Søndergaard and Schierup 1982).

An alternative mechanism for exudation could be passive permeation through the cell membrane. Permeability is defined for specific compounds and membrane systems as

$$P = \frac{J}{G_m} \quad (1)$$

where P is permeability (cm s^{-1}), J is the flux (mol cm^{-2} s^{-1}), and G_m is the concentration difference (mol cm^{-3}) across the membrane. This simplified approach does not include the effects of water or cell motion (cf. Csanady 1986). The background permeability through the lipid bilayer, which accounts for most of the cell surface, is determined by the size and hydrophily of the

permeant molecules (Stein 1967; Diamond and Wright 1969). Glucose permeabilities of about 10^{-10} cm s^{-1} have been measured on artificial bilayer lipid membranes (Wood et al. 1969; Jung 1971; Brunner et al. 1980). Scarcer data on permeabilities for amino acids and other metabolic intermediates indicate permeabilities $>10^{-9}$ cm s^{-1} (Raven 1984).

The concentration difference across the membrane might be diminished by the existence of a boundary layer around the cell. However, a diffusivity (D) of 10^{-5} cm^2 s^{-1} for small organic molecules (*Handbook of Chemistry and Physics* 1975) and a boundary-layer thickness (L) of 100 μm will imply a "permeability" ($D \times L^{-1}$) of the boundary layer of 10^{-3} cm s^{-1}—10^6 times the permeability of the membrane. At steady state, the fluxes through the membrane and boundary layer must be equal, so the concentration difference across the boundary layer will be only 10^{-6} of the difference across the membrane (Eq. 1). Analogously, the presence of a porous cell wall will not inhibit permeation of LMW compounds.

Furthermore, since intracellular concentrations of LMW compounds are in the millimolar range and extracellular concentrations are in the nanomolar range (Mopper and Lindroth 1982; Fuhrman and Bell 1985), the concentration difference across the membrane is dominated by the intracellular concentration (C, mol cm^{-3}). Accordingly, Eq. 1 can be approximated by

$$P \simeq \frac{J}{C}. \tag{2}$$

The leakage rate E (mol s^{-1}) is the product of flux and surface area (A, cm^2) (Eq. 3), and the intracellular pool (S, mol) of a permeating compound is the product of concentration and cell volume (V, cm^3) (Eq. 4):

$$E = J \times A, \tag{3}$$

and

$$S = C \times V. \tag{4}$$

From Eq. 2–4 the leakage rate in proportion to the intracellular pool can be expressed as the product of permeability and the surface-to-volume ratio:

$$\frac{E}{S} \simeq P\frac{A}{V}. \tag{5}$$

Equation 5 is valid for single compounds or for groups of compounds with similar permeability. A phytoplankton cell of 10-μm diameter has a surface-to-volume ratio of 6×10^3 cm^{-1}. If we assume a permeability for LMW organic compounds of 10^{-9} cm s^{-1}, the daily loss will be 50% of the intracellular pool.

This value represents a gross permeation loss which could be counteracted by active "reuptake." However, several studies on the uptake of radiolabeled compounds by natural plankton assemblages have shown bacterioplankton to be responsible for the entire uptake of LMW organic compounds (Williams 1970; Azam and Hodson 1977). This observation is as expected if the exudates are rapidly dispersed, because bacteria account for most of the overall cell surface in natural planktonic communities (Williams 1981).

On the assumption that LMW organic compounds make up about 10% of phytoplankton cell carbon (Terry et al. 1983; Cuhel and Waterbury 1984; Smith and Geider 1985), the loss rate of 50% d^{-1} from the LMW organic pool can be converted into a loss rate of about 5% of carbon biomass per day.

Unfortunately, most workers have expressed exudation exclusively in proportion to total carbon fixation, with only a few allowing calculation of exudation rates in proportion to phytoplankton biomass. However, diel bacterial consumption rates of 3–6% of phytoplankton biomass have been estimated from both marine and freshwater environments (Fuhrman et al. 1980; Bell and Kuparinen 1984) as well as in vitro (Bratbak and Thingstad 1985).

The calculation for a 10-μm phytoplankton cell indicates that passive diffusion could be responsible for all of the observed release of LMW organic compounds from healthy phytoplankton. If so, we should expect continued exudation at night, better correlation of exudation to phytoplankton biomass than to primary production, and relatively higher exudation from small cells. On the other hand, if exudation is primarily an overflow

mechanism for carbon fixation, we should expect exudation to cease at night and better correlation of exudation to primary production than to biomass. Continuous exudation has been observed from phytoplankton incubated in light–dark cycles (Huntsman 1972; Fogg 1983; Berman and Kaplan 1984). Constant exudation rates in proportion to biomass have been found when carbon fixation rates were varied in chemostats (Bratbak and Thingstad 1985) or by manipulating the concentration of dissolved inorganic carbon (Smith and Wiebe 1976). Thus, there is evidence supporting passive diffusion rather than overflow.

Nearly all studies on phytoplankton exudation have expressed the release as percentage of total carbon fixation. This representation, together with the extensive use of the differential filtration approach (Derenbach and Williams 1974; Larsson and Hagström 1979), has predetermined the interpretation of exudation as an integral part of photosynthesis, i.e. as an "income tax" to phytoplankton. In contrast, the arguments presented here suggest that exudation can be interpreted as a continuous loss from phytoplankton biomass, i.e. as a "property tax." Planktonic bacteria, by steadily assimilating the exudates and thereby depleting the extracellular concentration of LMW organic compounds, thus act as ectoparasites rather than as mutualists.

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