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Excretion of Dissolved Organic Phosphorus in Tropical Brackish Waters

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Dissolved organic phosphorus (DOP) release was measured on natural populations of a brackish lagoon in Ivory Coast (West Africa). DOP mean excretion is 8% of net phosphorus absorption, and represents 1·7% h^{-1} of the biomass. Only 28% of biomass is involved in rapid uptake and excretion. Release of P is inversely proportional to the $C_p : N_p$ ratio of the seston and the dissolved inorganic phosphorus concentration.

Introduction

The uptake of dissolved inorganic phosphate by natural plankton populations can be studied by using tracers (^{32}P in this paper). But the study is complicated by the rapid exchanges between medium and cells (Rigler, 1956, 1964; Lean, 1973; Taft *et al.*, 1975; Lean & Nalewajko, 1976). A first exchange process can be considered as physical adsorption by the particles, either living or dead (Lemasson *et al.*, 1980*a*; Sebetich, 1975), with turnover times of as little as a few minutes in some cases (Lean & Nalewajko, 1976). Another process is the excretion of dissolved inorganic and organic phosphorus (DOP). In cultures Kuenzler (1970) observed excretion of up to 40% of total phosphorus; it has been objected that such excretion could be caused by the handling of cells during experiments, or could correspond to cells in poor physiological state (Watt & Hayes, 1963; Fogg, 1977; Sharp, 1977, 1978; Aaronson, 1978).

The purpose of this paper is to evaluate the importance of the excretion of dissolved organic phosphorus by natural populations in a tropical brackish lagoon (Ebrié Lagoon, Ivory Coast, West Africa; Figure 1). Experiments were made at eight stations, each one, or two, being representative of a particular zone of the lagoon, and during the 1977 main dry season when hydrological conditions are very stable (Tastet, 1974; Varlet, 1978; Pagès *et al.*, 1979).

Description of the area

The Ebrié Lagoon extends over more than 150 km, with an area of about 550 km^2. Parallel to the coast, it is relatively narrow (maximum width 5 km) and generally shallow (mean depth 3 m, with localized spots of 5 m depth); communication with the sea is made through

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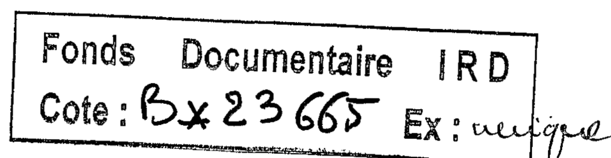

the mouth of the Comoé river, narrow and often obstructed, and through the Vridi channel in front of Abidjan. The city of Abidjan has more than one million inhabitants, and most of the city's sewage flows into the lagoon, from which it pollutes the estuary.

Phytoplankton populations in the lagoon are small, but the development of flagellates of small size (Cryptophytae, Euglenophytae, small Dinoflagellates) is favoured by the high quantity of organic matter.

Following Pagès *et al.* (1979) we have divided the lagoon into six parts for the purposes of the present study.

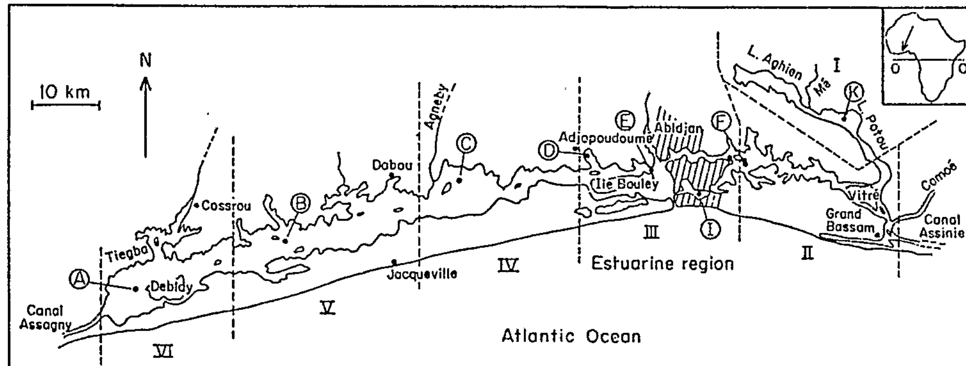

Figure 1. Station locations in the Ebrié Lagoon, Ivory Coast, West Africa. Stations (letters) are representative of a zone (roman figures).

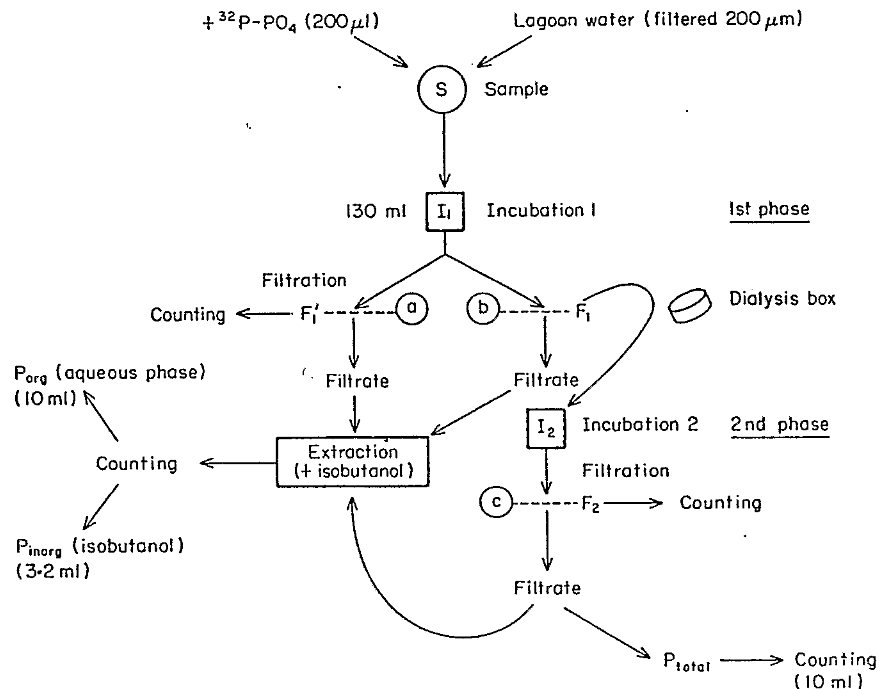

Figure 2. Flow diagram of the experiment.

Methods

The samples were filtered through a 200 μm net to retain larger particles, and distributed in 130 ml bottles; 200 μl of carrier-free $Na_2H\,^{32}PO_4$ (C.E.A., France) were inoculated, giving an activity of about 1·5 μCi. The experiments were performed generally by day and by night, and samples were carried out in triplicate (see Figure 2 for the flow chart), each result being the mean of three measurements. On filters of the first phase the mean percentage standard deviation is 6·3%, and 9·7% on dissolved organic phosphorus. Controls were sterilized by formalin (final concentration: 0·46%).

After 2 to 4 h incubation in natural light (incubation 1) the bottles were agitated and the samples divided in two halves, each of which was filtered on Whatman GF/C glass-fiber filters (45 mm diameter) with a moderate vacuum (100 Torr). One filter (a) and the corresponding filtrate were kept at −20 °C for counting. The other filter (b) was quickly transferred to a small cylindrical container made of Lucite, with sides consisting of two discs of dialysis membrane. This container was filled with about 6 ml of 200 μm-filtered lagoon water. The filter in its container was then transferred to a bottle containing about 65 ml of 200 μm-filtered natural water and incubated either in natural light or in the dark for 2 to 4 h (incubation 2). Baskett & Lulves (1974) and Prakash *et al.* (1974) have observed a satisfactory equilibrium between internal and external media with analogous set-ups. After this incubation, the contents of the dialysis box were filtered on a 25 mm glass-fiber filter [filter (c)]. The old filter (b), the dialysis membrane, the new filter (c) and the filtrate were kept at −20 °C for counting.

Environmental parameters were measured at the time when the sampling for the incubations were initiated, using standard methods (Strickland & Parsons, 1968). Photosynthesis was measured by the ^{14}C method with *in situ* incubations (Pagès & Lemasson, 1980*a*); excreted dissolved organic carbon was measured in filtrates by the customary methods (Pagès & Lemasson, 1980*b*).

Dissolved organic phosphorus (DOP) separation

Back in the laboratory, the filtrates were thawed. The Denigès reaction (Murphy & Riley, 1958) was carried out on a 20 ml subsample; the phosphomolybdate produced was extracted by 5 ml isobutanol, after vigorous shaking and centrifuging (6000 r min^{-1} for 5 min). Only a part (3·0 to 3·2 ml, containing inorganic phosphorus) of the added isobutanol was usable for counting; the rest remained dissolved in the aqueous phase. Kuenzler (1970) has shown that only about 3% of the DOP is dissolved in isobutanol, producing a very small error.

Next, 10 ml of the aqueous phase were taken for counting; the aqueous phase contains the non-reactive phosphorus, i.e. organic phosphorus and polyphosphates, the latter contributing about 10% of the DOP value (Sakshaug & Holm-Hansen, 1977). Conversely, a portion of DOP is probably hydrolysed in inorganic P by the acid Denigès reaction.

In the second experiment the excreted inorganic phosphorus is slightly overestimated since there is probably a mineralization process of DOP by the bacterial population retained on the filter.

All count measurements were done by using the Cerenkov radiation of ^{32}P; 10 ml of extracted filtrates were used for DOP determination, and the isobutanol (after centrifugagation) for inorganic P determination. The counting was carried out by a liquid scintillation counter working on the whole spectrum by using the Cerenkov radiation (Kobayashi & Maudsley, 1974). Absorption counts were corrected from adsorption counts given by controls (Lemasson *et al.*, 1980*a*).

Table 1. Symbols and units

j	1 and 2 for 1st and 2nd phase	
DIP	dissolved inorganic phosphorus	μmol l^{-1}
*DIP	initial activity of the DIP fraction	ct min^{-1}
$(DIP_j)_{ex}$	excreted DIP	μmol l^{-1}
DOP	dissolved organic phosphorus	μmol l^{-1}
$*DOP_j$	activity of the DOP fraction	ct min^{-1}
$(DOP_j)_{ex}$	excreted dissolved organic phosphorus	μmol l^{-1}
TDP	total dissolved phosphorus	μmol l^{-1}
E_j	excretion rate relative to microbial biomass	h^{-1}
$Ex\text{-}P_j$	excretion rate	μmol l^{-1} h^{-1}
$\Sigma*P_1$	activity of the gross uptake in phase 1: $(*P_{p1}+*DOP_1+(*DIP_1)_{ex})$	ct min^{-1}
$\Sigma*P_2$	activity of biomass at start of phase 2, calculated by adding particulate and aqueous phases (organic and inorganic) activities at the end of phase 2	ct min^{-1}
$P_{pj} = P_p$	particulate phosphorus	μmol l^{-1}
$*P_p$	activity of the particulate fraction	ct min^{-1}
C_p, N_p	particulate C and N	
t_j	incubation time interval	h
r_S	rank correlation coefficient of Spearman; significance level: +: 0·05% ++: 0·01% +++: 0·001%	

Results

The two types of evaluation of the excretion are very different since in the first case tracer is in the medium, and in the second case it is the microbial biomass which is labelled. In addition excretion is proceeding from organisms for which radioactive P-uptake is stopped through lack of $^{32}P\text{-}PO_4$ in the substrate. Allowing that bacterial biomass is negligible compared with phytoplankton (Lemasson *et al.*, 1980*b*) we can compare phytoplankton P-excretion rate to PO_4-P uptake rate, and get the P-excretion rate relative to microbial biomass which is evaluated by particulate phosphorus (P_p). P_p is a good evaluation of biomass because detrital P_p is low (Lemasson *et al.*, 1980*b*).

By using the usual hypothesis made in experiments with tracers, that the various compartments of the cell are in isotopic equilibrium, we have the following equations (index 1 and 2 respectively for the first and the second incubation phase). The explanation of the symbols is given in Table 1 and the detailed results are in Table 2.

$$\frac{*DOP_1}{(DOP_1)_{ex}} = \frac{*DIP}{DIP} \text{ in the first phase,} \tag{1}$$

$$\frac{*DOP_2}{(DOP_2)_{ex}} = \frac{\Sigma*P_2}{P_p} \text{ in the second phase} \tag{2}$$

and the organic excretion rates, in μmol l^{-1} h^{-1}:

$$Ex-P_1 = \frac{*DOP_1}{*DIP} \cdot DIP \cdot \frac{1}{t_1}, \tag{3}$$

$$Ex-P_2 = \frac{*DOP_2}{\Sigma*P_2} \cdot P_p \cdot \frac{1}{t_2}. \tag{4}$$

TABLE 2. Excretion rates and chemical characteristics at the studied stations

	Station										
	A 11 Jan		B 1 Feb		C 15 Feb	D 22 Feb	E 8 Jan	F 8 Feb	I 4 Jan	K 25 Jan	
	D[a]	N	D	N	D	D	D	D	N	D	N
DIP (μmol l^{-1})	0·39	0·13	0·48	0·36	0·22	0·10	0·72	0·50	2·95	0·57	1·08
P_p (μmol l^{-1})	1·39	1·50	1·15	1·24	0·71	0·87	0·83	0·65	2·07	0·63	0·71
S (‰)	4	4	4	4	7	12	24	15	22	0	0
$C_p : P_p$	297	320	168	183	113	129	72	77	71	250	181
Net P-uptake $P_p^{-1}\ t_1^{-1}$ (h^{-1})	0·018	0·006	0·033	0·019	0·058	0·011	0·096	0·079	0·053[b]	0·110	0·134
$*DOP_1/\Sigma *P_1$	0·069	0·103	0·071	0·096	0·068	0·082	0·067	0·080	—	0·080	0·130
E_1 ($10^{-3}\ h^{-1}$)	1·4	0·9	2·9	2·9	2·8	1·2	7·0	7·7	—	12·6	29·0
$(*DOP_2/\Sigma *P_2)\ t_1\ t_2^{-1}$	0·077	0·017	0·057	0·017	0·049	0·023	0·100	0·122	0·056	0·051	0·064
$*DOP_2/(*DIP_2)_{ex}$	0·56	0·48	0·75	0·34	0·54	0·47	(2·52)	0·73	—	0·45	0·53
E_2 ($10^{-3}\ h^{-1}$)	21	9	16	9	14	5	29	30	21	17	19
$Ex{-}P_1$ (10^{-3} μmol $l^{-1}\ h^{-1}$)	2·0	1·3	3·4	3·6	2·0	1·0	5·8	5·0	—	8·0	20·7
$Ex{-}P_2$ (10^{-3} μmol $l^{-1}\ h^{-1}$)	29·0	13·5	18·4	11·1	9·9	4·3	23·9	19·5	43·5	10·8	13·6

[a]D: day, N: night
[b]Uptake estimated from another experiment.

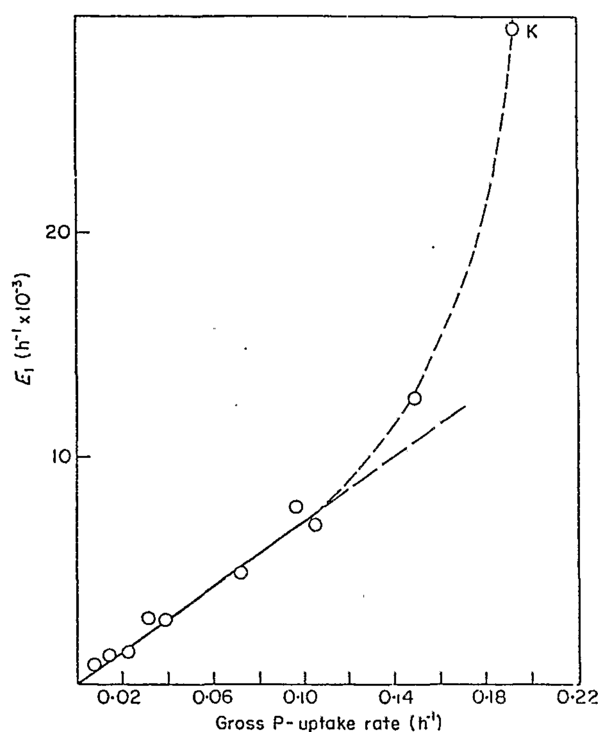

Figure 3. Gross P-uptake rate per unit of biomass (h^{-1}) *vs.* E_1 (h^{-1}); r_S=0·98. Each point represents three experiments.

We can define the excretion rates per biomass unit, in h^{-1}:

$$E_1 = \frac{Ex—P_1}{P_p}, \tag{5}$$

$$E_2 = \frac{Ex—P_2}{P_p} \tag{6}$$

In equation (5), P_p is measured at the beginning of phase 1 (P_{p1}), whereas in equation (6) P_p is measured at the beginning of phase 2 (P_{p2}). This second value is unknown and slightly higher than P_{p1} since there was a production of particulate matter during phase 1. However we shall consider that the two values are equal: $P_{p1}=P_{p2}$, and E_2 will be slightly overestimated.

The $(DIP_2)_{ex}$ measured in the second experiment is about twice as high as the organic excretion, except at Station E where it is very low. Without this station the following relationship is obtained:

$$\frac{*DOP_2}{(*DIP_2)_{ex}} = 0{\cdot}54 \pm 0{\cdot}10 \text{ (95\% confidence level).}$$

We shall use this result to evaluate $(DIP_1)_{ex}$ in the first experiment. This interpretation is based on the hypothesis that the specific activities of intracellular DIP and DOP are equal.

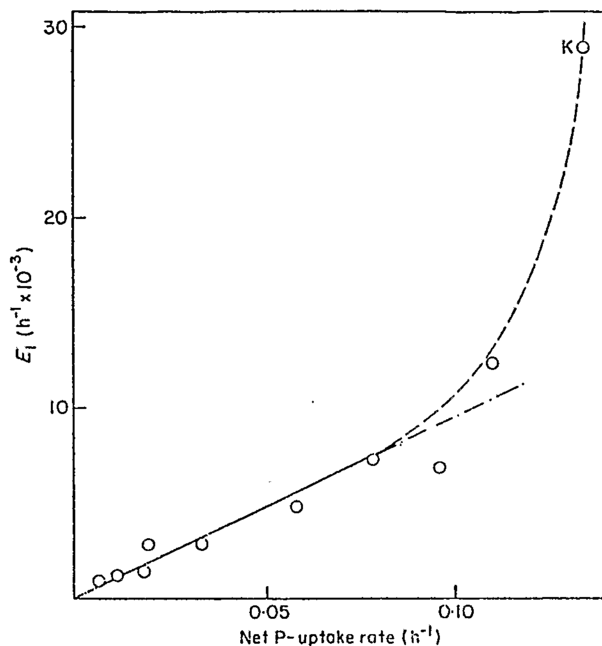

Figure 4. Net P-uptake rate per unit of biomass (h^{-1}) *vs.* E_1 (h^{-1}); $r_S=0{\cdot}95$. $E_1=0{\cdot}099$ net uptake (without station K night); with station K (night), equation of the fitting curve is ln ($E_1 \times 10^{-3}$)$=23{\cdot}23\times$(net uptake)$+0{\cdot}036$. Each point represents three experiments.

Excretion

(a) In the first experiment, excretion rate E_1 (Table 2) shows lower values at Station A ($0{\cdot}9\times10^{-3}$ and $1{\cdot}4\times10^{-3}$ h^{-1}) and Station D ($1{\cdot}2\times10^{-3}$ h^{-1}), and higher values at Station K ($12{\cdot}6\times10^{-3}$ to 29×10^{-3} h^{-1}).

There is a very highly significant correlation ($r_S=0{\cdot}98^{+++}$, Figure 3) in the linear regression between excretion rate E_1 and gross uptake rate, without the last point (Station K at night); then the slope of the principal axis is

$$\frac{{}^*\mathrm{DOP}_1}{\Sigma^*\mathrm{P}_1} = 0{\cdot}08.$$

This means that organic excretion represents 8% of gross uptake. If we take into account the last point, then the fitting curve is logarithmic ($r_S=0{\cdot}98$).

The regression is also linear between E_1 and net P-uptake ($r_S=0{\cdot}95^{+++}$) without Station K at night; if we take account of this point, the fitting curve is logarithmic. In the first case with the slope of the principal axis, the excretion is 9·9% of the net uptake (Fig. 4).

(b) In the second experiment, the excretion should be equal to that of the first series, since the considered biomasses are, ideally at least, identical. This is not the case however, and the excretion rates are about four times higher than E_1, except for Station K where organic excretions are similar in the two cases. The following hypotheses can be proposed:

(1) We have an experimental artifact. The handling of the cells could be the main and artificial cause of organic excretion (Sharp, 1977). The incubations were necessarily long to have sufficient counts (about 3 to 4 h for the incubations); the filtration, although under low vacuum, could also play a role.

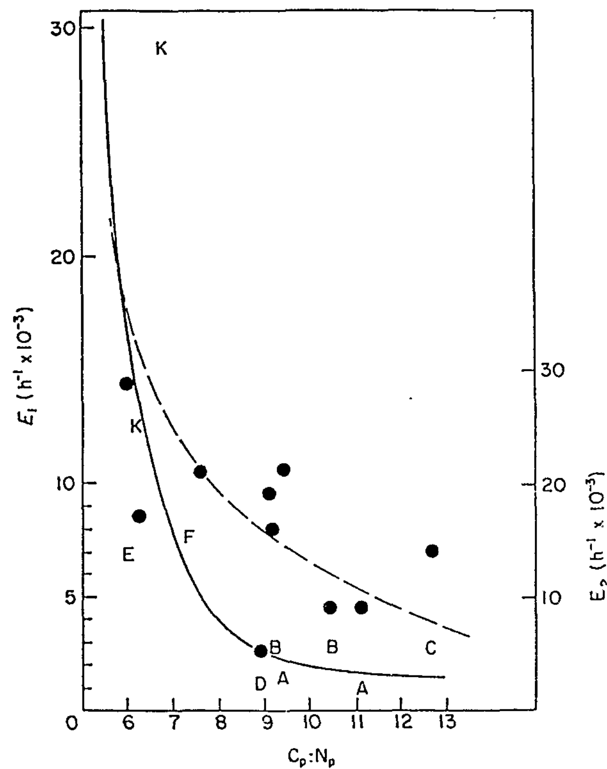

Figure 5. E_2 (h^{-1}) *vs.* ($C_p : N_p$) (●); $r = -0{\cdot}71$; $E_2 = -1{\cdot}45 \times (C_p : N_p)^{-1{\cdot}21}$. E_1 *vs.* ($C_p : N_p$) (letters); $r = -0{\cdot}67$; $E_1 = 7{\cdot}92 \times (C_p : N_p)^{-3{\cdot}04}$.

(2) The cells are not uniformly labelled and the absorbed P is more easily exchangeable. Only a part of P_p is labelled so that the value of P_p in the calculation of E_2 leads to overestimation of this since there are several excretion compartments. Indeed, we must have $E_1 = E_2$ theoretically, and $Ex-P_1 = Ex-P_2$,

$$\frac{*DOP_1}{*DIP} \, . \, (DIP) \, . \frac{1}{t_1} = \frac{*DOP_2}{\Sigma *P_2} \, . \, (k \, . \, P_p) \, . \, \frac{1}{t_2},$$

where k represents the proportion of living matter of the excretion compartment, and then we have:

$$E_1 = k \, . \, E_2. \tag{7}$$

The linear regression E_1 *vs.* E_2 gives $r_S = 0{\cdot}74$ and the principal axis slope is $m = 0{\cdot}278$. Then the part of P_p playing an 'active' role in excretion is 27·8% of total P_p.

We have a further hint of the possible isotopic imbalance of the compartments. Considering the excreted labelled P percentage during the same time interval,

$$\frac{*DOP_1}{\Sigma *P_1} \quad \text{and} \quad \frac{*DOP_2}{\Sigma *P_2} \, . \, t_1 . \, t_2^{\ -1},$$

we observe that the values are not very different, being, respectively, 0·085 and 0·058 (mean values). The lower second term could be explained by isotopic dilution in the second

phase. Since the suppression of the role of P_p almost leads to the suppression of the discrepancy, this observation confirms our hypothesis that on the one hand the P_p pool is really not uniformly labelled and on the other hand the phosphorus recently uptaken is first excreted. If we consider the whole biomass (P_p), E_2 excretion rate is $17{\cdot}3 \times 10^{-3}$ h^{-1} ($\pm 1{\cdot}5 \times 10^{-3}$ at 95% confidence level).

Relations with external factors

The excretion rates E_1 and E_2 decrease with increasing $C_p : N_p$ ratios (Figure 5); there is a positive regression E_1 *vs.* total dissolved phosphorus (TDP), ($r_S = 0{\cdot}83^+$; Figure 6). No relationship can be observed between excretion rates and either dissolved organic phosphorus of the medium or dissolved organic carbon excretion.

Discussion

Origin of the excreted phosphorus

We have seen that E_2 is much higher than E_1. This can stem either from a mechanical damage to the cells or can be due to the mode of calculation. We shall examine both possibilities.

(a) *Damage to the cells.* Since the first description of dissolved organic matter excretion by phytoplankton (Fogg, 1952; Fogg & Westlake, 1955), this process has often been considered as an experimental artifact and the debate is still going on (Sharp, 1978). Most authors consider that mechanical damage may be avoided through a minimum of precautions during filtration and handling of the filter (Smith & Wiebe, 1976; Harris & Piccinin, 1977; Aaronson, 1978). In our experiments the magnitudes of the excreted activity during first and second phase ($*DOP_1$ and $*DOP_2$) are not very different. This shows that no important mechanical damage was sustained by the cells during filtration and subsequent handling. Moreover, the slightly smaller value of $*DOP_2$ corresponds to the expected effect of suppressing the tracer in the environment during phase 2.

(b) *Mode of calculation.* If we admit that P_p is approximately constant during the whole experiment, the relationship between E_1 and E_2 may be rewritten from (7):

$$\frac{*DOP_1 \,.\, (DIP)}{*DIP} = k \,.\, \frac{*DOP_2 \,.\, P_p}{\Sigma * P_2}$$

(for the same incubation time interval).

The factor k has the value 0·278 as seen above. Among the various factors of the above expression, P_p is the only one for which a hypothesis was made, i.e. that the specific activity of the excreted DOP was equal to that of P_p. Then we must admit that the P_p compartment is not homogeneous, and that only a fraction ($k \,.\, P_p$) is active in the excretion processes.

Value of the excretion and relations with other factors

Excretion rates E_1 ($0{\cdot}9$ to 29×10^{-3} h^{-1}) are of the order of magnitude of the results of Lean & Nalewajko (1976) who, working on cultures with incubations of up to 235 h, observed rates of 3 to 6×10^{-3} h^{-1} (*Chlorella pyrenoidosa*) up to 15 to 524×10^{-3} (*Anabaena flosaquae*). The ratio of excretion E_1 to gross uptake, equal to 8%, is in good agreement with the value observed in open sea (8·7%) by Ketchum & Corwin (1965). Our values are surprisingly constant at the various stations.

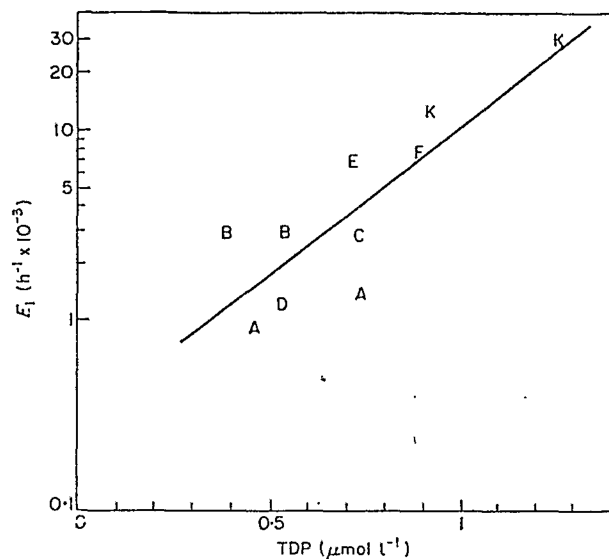

Figure 6. E_1 (log) *vs.* total dissolved phosphorus (TDP) at the beginning of the first incubation; $r=0{\cdot}83$; $\ln(E_1 \times 10^3)=3{\cdot}577 \times \text{TDP}-1{\cdot}226$.

The good correlation between excretion and P-uptake is interesting because of the analogous relationship between dissolved organic carbon excretion and photosynthetic C-uptake found at the same stations in the Ebrié lagoon (Pagès & Lemasson, 1980*b*) and in seawater (Smith *et al.*, 1977).

Since high $C_p : N_p$ ratios (higher than 7) are characteristic of aging or nutrient-depleted populations (Moal *et al.*, 1977) our observations agree with the hypothesis of Fogg (1971) who, reviewing DOP-excretion literature, concluded that organic excretion is maximum with maximum growth, i.e. when $C_p : N_p$ ratio is lowest. The linear regression E_1 *vs.* total dissolved phosphorus (TDP), ($r_S=0{\cdot}83^+$; Figure 6) strengthens this hypothesis, as $C_p : N_p$ ratios are the lowest in waters which have the highest TDP concentrations (Lemasson *et al.*, 1980*b*).

Nonetheless it has been shown that the inverse effect can occur; Kuenzler (1970) observed anomalously high excretion during low growth, but on pure cultures, and for certain cultures Watt & Hayes (1963) observed that DOP originates from dead organisms. Organic excretion seems then to be related to the physiological condition of cells, but is as yet unexplained. We have been led to admit the existence of a separate compartment at isotopic equilibrium as the main source of excreted matter. Its average importance is 28% of P_p.

Storch & Saunders (1975) hypothesized an analogous phenomenon for excreted dissolved organic carbon (DOC); they showed there were several excretions pools of dissolved organic C, excreted by phytoplankton. Either excretion products with high molecular weight come from a compartment smaller than the one containing total proteins, or DOC comes from both compartments in isotopic equilibrium and compartments not in equilibrium. Calculating for our carbon results the equivalent rates E_1 and E_2, we obtain an average figure of 29% of the particulate carbon involved in excretion processes (Pagès & Lemasson, 1980*b*). The similarity of the figures is surprising considering the differences between C and P pathways; the values of E_1/E_2 for C and P show no mutual relationship.

DOP utilization

The utilization of excreted DOP remains a problem. In algal cultures, Perry (1976) observed a small DOP excretion, and that the main part of this DOP is not used. On the contrary, in oligotrophic waters of the Central North Pacific with very low PO_4–P concentrations, hydrolysable DOP is rapidly cycled through high alkaline phosphatase activity (Perry, 1972). Further instances of phosphatase activity have been observed in other bodies of PO_4–P depleted waters (Berman, 1970; Jansson, 1977) allowing DOP hydrolysis and utilization. Kuenzler (1970) observed a DOP regeneration and uptake of up to 75% in 2 h. Such a rapid recycling could even mask the excretion during incubations (Lean & Nalewajko, 1976). The same process could exist in the P-depleted waters of the Ebrié lagoon, particularly in the westernmost part. In the whole lagoon, DOP concentrations are uniformly low, ranging from 0·04 µmol l^{-1} P (Station B) to 0·52 µmol l^{-1} P (Station I), (Pagès *et al.*, 1979). There are no marked variations during the day. These facts suggest that there is a balance between DOP excretion and its rapid remineralization. A further indication of this rapid remineralization of DOP may appear in the atomic ratio of the 'refractory' part of dissolved organic matter (DOM). Correlations between dissolved organic parts of C, N and P (Lemasson *et al.*, 1980*b*) give for residual DOM a C : N : P ratio of 1200 : 50 : 1.

We have seen that DIP excretion appears to be about twice the amount of DOP excretion. DIP may be excreted as such; another possible origin is, as seen above, a partial remineralization of DOP during the time interval of incubation. A third explanation is to be sought in isotopic exchanges. Adsorption phenomena have been observed in several instances (Taft *et al.*, 1975; Lemasson *et al.*, 1980*a*) and could be due, at least partly, to isotopic exchange; the reverse process has been shown to exist (Sebetich, 1975). A possible way of distinguishing the origin of DIP would be to observe the time course of DIP release; the adsorption–desorption rates are much higher than the purely biological ones (Lean & Nalewajko, 1976). Successive labelling (Berman & Skyring, 1979) could probably distinguish between DOP hydrolysis and DIP excretion.

Conclusion

The mode of calculation of the excretion rates is of prime importance. As stressed by Saunders (1972) and Storch & Saunders (1975) for C excretion, the true value is unattainable and only upper and lower limits can be defined. Up to now, we do not know of any possible method for obtaining a better approximation.

In the case of the populations studied here, the excreted DOP represents at least 8% of gross P-uptake. This is not negligible and would justify a closer study. We can imagine two ways of excretion; the first would correspond to the physiological condition of the cell, and involve a compartment readily exchangeable with around 28% of the biomass, while the second would involve a compartment more closely linked to internal metabolism.

In relation to the analogy between the problems arising with both C and P, it would be interesting to try and extend excretion studies to nitrogen and to develop a general approach usable on the three major elements C, N and P.

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