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Orthophosphate Turnover in East African Lakes

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Summary. Turnover rates of $^{32}P-PO_4$ and concentrations of orthophosphate as soluble reactive phosphorus (SRP) were measured in five East African waters. Rapid incorporation of $^{32}P-PO_4$ by the seston and orthophosphate concentrations below the limit of detectibility were found in Lakes Elmenteita, Naivasha, and Naivasha Crater Lake. Turnover was slow and orthophosphate concentration high in both Lake Nakuru and the Crescent Island Crater basin of Lake Naivasha. Further experiments in Lake Nakuru indicated that colloidal binding of orthophosphate was limited and that particles retained by an 8.0 μ filter incorporated 66% as much tracer as particles retained by a 0.1 μ filter. These experiments strengthen our conclusion that a large quantity of orthophosphate is available for algal use in Lake Nakuru.

Introduction

East African lakes are noted for their high photosynthetic rates and large standing crops of algae (Melack and Kilham, 1974), but little is known about their nutrient dynamics. Extremely high concentrations of orthophosphate have been reported from these lakes (e.g., Hecky and Kilham, 1973), and these high concentrations would suggest that orthophosphate does not limit algal growth. However, chemical analyses may not directly reflect the quantity of available nutrient.

The availability of a nutrient for algal growth depends upon biological activity and nutrient supply. Although a nutrient bioassay may be the best measure of nutrient availability, an alternative approach is to measure uptake kinetics under the assumption that turnover rate will be rapid when little nutrient is available and will be slow when a large quantity is available. Operationally, turnover rate, or the rate constant of uptake, measures the fractional accumula-

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Table 1. Location, area (km^2), mean depth (m), and conductivities (µmhos/cm, 20° C) of the Kenyan lakes

	Location	$A(km)^2$	Z(m)	K_{20} (µmho/cm)
Nakuru	0°22′S, 36°05′E	42[a]	1.4	24,000
Elmenteita	0°27′S, 36°15′E	19[a, b]	0.65	38,100
Naivasha Crater	0°47′S, 36°16′E	0.18[c]	3.8	8,700
Naivasha, main basin	0°46′S, 36°21′E	115[d]	4.6	328
Crescent Island Crater	0°46′S, 36°24′E	2.07[e]	11.1	447

[a] Nakuru, Kenya, 1:50,000 (series Y731, sheet 119/3, ed. 7-SK; Kenya Government, 1970)

[b] Gilgil, Kenya, 1:50,000 (series Y731, sheet 119/4, ed. 6-SK; Kenya Government, 1971)

[c] Survey of Kenya, 1967; photograph V13B-RAF 596 no. 116

[d] ERTS photo no. 81516071435A00, Dec. 21, 1973 (planimetry of enlargement)

[e] Kenya Ministery of Works, drawing number 44330, 1:10,000

tion of PO_4 per unit time by seston. Existing evidence suggests that lowered turnover rates reflect increased PO_4 concentrations (Levine, 1975; Peters, 1974; Rigler, 1966). Low turnover rates of $^{32}P-PO_4$ would be expected in the East African lakes if their PO_4 levels are indeed high.

In this paper, rates of ^{32}P turnover and concentrations of chemically determined orthophosphate (SRP, Strickland and Parsons, 1972) are reported for five Kenyan waters in 1974. In one of the lakes (Nakuru), experiments were performed to determine the uptake of ^{32}P by different sized particles and to determine the extent to which combination with colloids decreased the availability of orthophosphate.

Table 1 shows the location, area, mean depth, and conductivities of the lakes. Lake Nakuru, Elmenteita, and Naivasha Crater Lake are concentrated alkaline, saline lakes (Hecky and Kilham, 1973). Lake Naivasha contains fresh water (Richardson and Richardson, 1972).

Methods

Samples were collected during the day from approximately 10 cm below the surface and taken to the laboratory. Subsamples (100 ml) of whole lake water were mixed with 1 drop of 0.1 N HCl containing carrier-free $^{32}P-PO_4$ (The Radio-chemical Centre, Amersham) and 5.4 ml subsamples of this were filtered through 0.45 µ Sartorius Membranfilters at intervals from less than 2 min up to 8 h after tracer addition. Two 0.5 ml samples of unfiltered water were taken to estimate total activity. These aliquots and the filters were placed on stainless steel planchets, dried, covered with spray varnish and counted using a Nuclear Chicago gas-flow Geiger-Muller tube with end window. The data were used to plot the percentage of ^{32}P remaining in solution vs. time. Curve splitting techniques (Riggs, 1970) were then used to determine the rate constants of uptake (Lean and Rigler, 1974).

Several additional tracer experiments were performed on water from Lake Nakuru. On July 17, 1974, the role of particles of different sizes in the incorporation of phosphate was examined by using filters of four different porosities (0.1, 0.45, 1.2, and 8.0 µ). On July 18, the availability of tracer in solution after 24 h of incubation with tracer was determined by adding 0.45 µ filtrate to whole lake water and following incorporation of the label. Attempts to measure PO_4 concentration with a radio-bioassay technique (Rigler, 1966) were fruitless because PO_4 turnover was relatively insensitive to the additions of orthophosphate used.

Orthophosphate concentrations were measured using Vogler's (1965) method modified to reduce silica interference (MacIntyre, in prep.).

Results and Discussion

Calculated turnover rates and SRP concentrations are presented in Table 2. Figure 1 presents uptake curves from Lakes Elmenteita and Nakuru. Concentrations of SRP in surface waters ranged from 2,000 μg P/l to less than 3 μg/l.

Table 2. Rate constants of orthophosphate incorporation (k, in fraction/min), PO_4-P concentrations (μg/l), and sampling times of the Kenyan lakes

Lake	Date	k (min^{-1})	PO_4-P (μg/l)
Elmenteita	28/6/74	1.5	<3
Naivasha, main basin	26/6/74	1.0	<3
Naivasha Crater	27/6/74	0.20	<3
Nakuru	24/6/74	0.0029	23
	25/6/74	0.0014	
	30/6/74	0.0010	
	17/7/74	0.0039	7
Crescent Island Crater	26/674	0.000	117

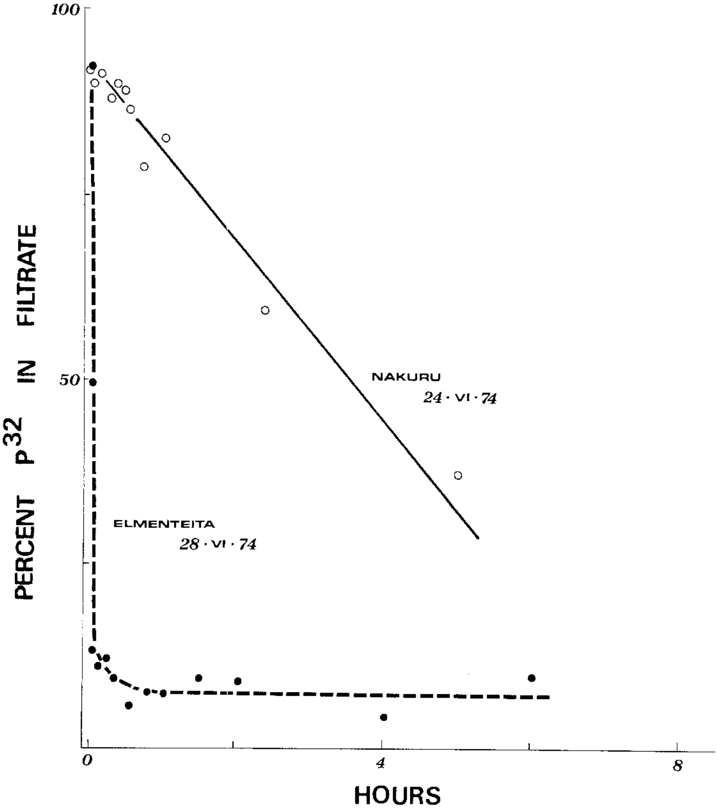

Fig. 1. The proportion of $^{32}P-PO_4$ which passes a 0.45 μ membrane filter at intervals after addition of tracer to samples of surface water from two East African lakes

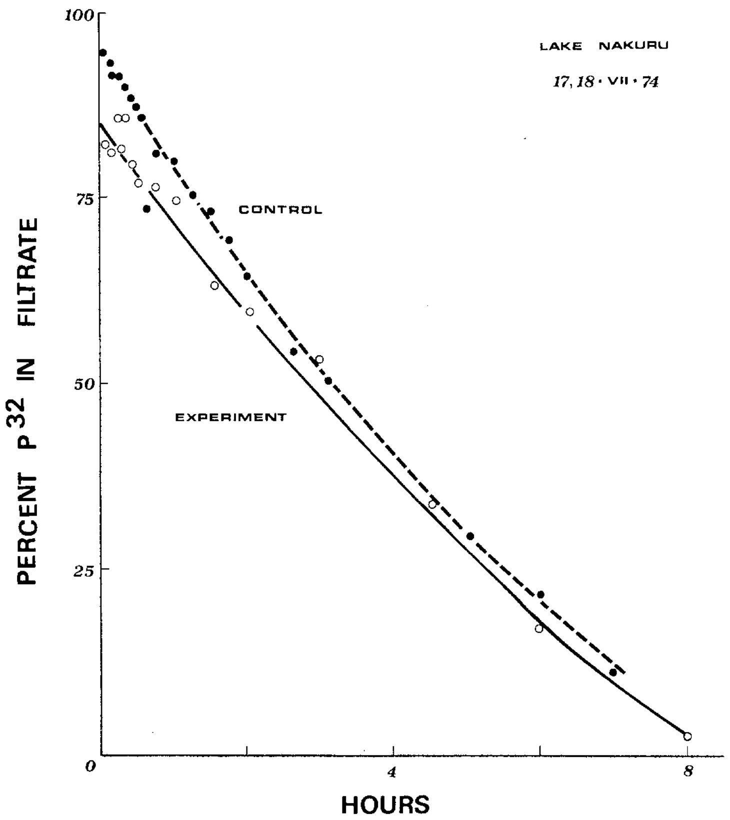

Fig. 2. The sestonic incorporation of tracer in the filtrate of lake water equilibrated with $^{32}P-PO_4$ for 24 h (experiment) and a $^{32}P-PO_4$ control

Lake Elmenteita and the main basin of Lake Naivasha had turnover rates which compare with the fastest rates in North America: more than 50% of the tracer was removed by the filter in less than 1 min and no further change in tracer distribution was measured after 4 min. The turnover rate in Naivasha Crater Lake was only slightly lower. The remaining lakes had much lower turnover rates. The average rate in Lake Nakuru was 0.0023 min^{-1} and no significant uptake was observed in the Crescent Island Crater basin of Lake Naivasha.

These data suggest that orthophosphate is in very short supply in three of the five water bodies. Two further experiments support the contention that a large quantity of orthophosphate is available for algal growth in Lake Nakuru.

When unfiltered lake water from Canadian lakes is equilibrated with $^{32}P-PO_4$ and then membrane filtered much of the tracer in the filtrate does not behave like $^{32}P-PO_4$ (Lean, 1973a; Lean and Rigler, 1974). A substantial proportion, termed "refilterable solids" by Chamberlain (1968), is retained on refiltration and that remaining in the filtrate is incorporated much more slowly than $^{32}P-PO_4$. Lean (1973a, b) believes this indicates that much of the "dissolved P" in lake water is colloidally bound and therefore not readily available to the plankton. If much of the dissolved P is orthophosphate then

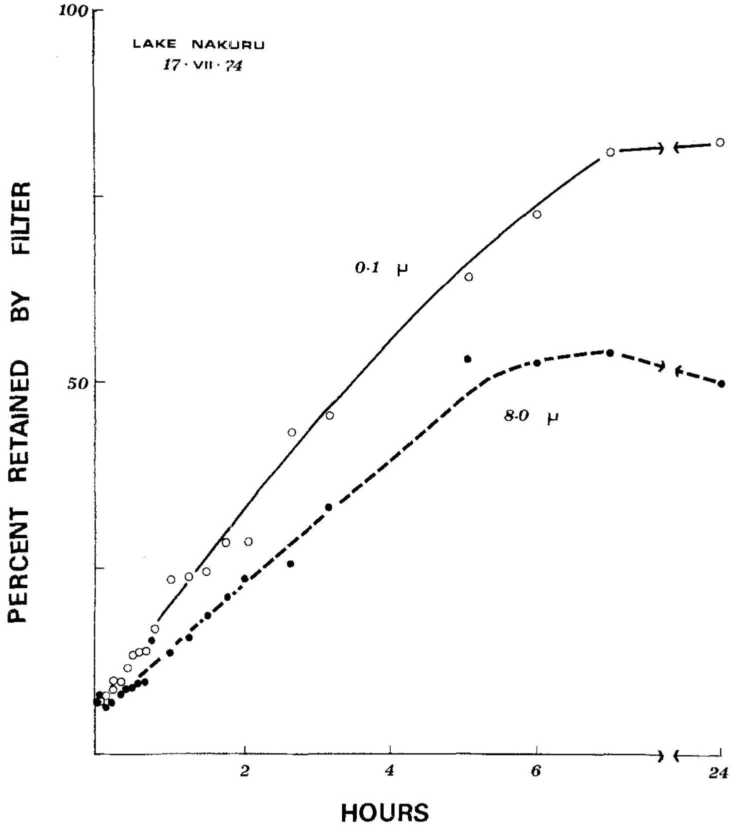

Fig. 3. The incorporation of $^{32}P-PO_4$ by two sestonic size fractions. 8.0 μ filters retained 70 μg dry weight of seston l^{-1} and 0.1 μ filters retained 220 μg l^{-1}

filtrate of lake water equilibrated with tracer should contain label which will be as rapidly incorporated by particles as a $^{32}P-PO_4$ control.

Figure 2 shows the results of such an experiment for Lake Nakuru. Although the amount initially retained on the filter was increased by approximately 10%, tracer uptake over time is very similar. The rate constants of uptake of the $^{32}P-PO_4$ control and the 24 h filtrate ^{32}P were 0.0039 min^{-1} and 0.0037 min^{-1} respectively. This similarity suggests that most of the unincorporated tracer remained as orthophosphate.

Rigler (1956) found that most of the ^{32}P uptake in Canadian lakes could be attributed to bacteria and other ultraplankton. Rhee (1972) found that bacteria were more effective in utilizing low PO_4 concentrations than were algae, but bacterial utilization is saturated by lower PO_4 concentrations than algal utilization. If the physiologies of algae and bacteria in Lake Nakuru are similar to those of the alga and bacterium studied by Rhee, and if the PO_4 concentrations are elevated, one would expect the incorporation of tracer by larger particles to be more significant in Lake Nakuru than in Canadian lakes.

Figure 3 shows that particles retained by an 8.0 μ filter incorporated about 66% as much tracer as all particles retained by a 0.1 μ filter. The rate constants of uptake were $0.0025\,\mathrm{min}^{-1}$ for particles retained by an 8.0 μ filter and $0.0038\,\mathrm{min}^{-1}$ for particles which are caught by a 0.1 μ filter. The rate constants determined using 0.45 μ ($0.0039\,\mathrm{min}^{-1}$) and 1.2 μ ($0.0028\,\mathrm{min}^{-1}$) filters were similar to those obtained with 0.1 μ and 8.0 μ filters respectively. The importance of large particles in P uptake in Lake Nakuru thus gives further, if circumstantial, evidence for high PO_4 values in that lake.

Membrane filters are not good fractionating systems (Sheldon and Sutcliffe, 1969; Sheldon, 1972); however, Figure 3 shows that the smallest porosity filters consistently retained more tracer than the largest porosity filters. This differential retention is further evidenced by estimates of dry weight of seston retained on filters of different porosity (0.1 μ=0.22 mg/l; 0.45 μ=0.13 mg/l; 1.2 μ= 0.083 mg/l; 8.0 μ=0.068 mg/l). The simplest explanation for these differences is to suppose an effective size fractionation which is reflected by the porosity of the filters, although there is no indication that these fractions correspond directly with the stated porosities.

Final Discussion

The appropriateness of SRP analyses in the determination of the levels of dissolved inorganic PO_4 depends upon the phosphorus pools within a lake and, in Canadian lakes, the measurement is held in disrepute (Rigler, 1966, 1968). In lakes where SRP values are high and $^{32}P-PO_4$ turnover rates are low, SRP may be an appropriate measure of dissolved inorganic PO_4 concentrations. In these Kenyan lakes, the chemical analyses and orthophosphate turnover rates concur in the ranking of lakes in terms of PO_4 availability. This concurrence and the apparently low level of colloids in Lake Nakuru suggest that the molybdenum blue method is a useful tool for describing orthophosphate levels in some African lakes. In lakes with low colloid levels phosphate movements between algae and lake water may differ from the scheme proposed by Lean (1973a, b); this difference may contribute to the high productivities measured in those African lakes.

Rapid rates of ^{32}P turnover have been reported for the summer months in epilimnetic waters of North America (Rigler, 1956, 1964; Lean et al., 1975), in central European lakes (Peters, 1975), and in subtropical Lake Kinneret (Hallman and Stiller, 1974). Among these East African lakes two showed a PO_4 turnover as rapid as any previously measured, but the highly productive Lake Nakuru (Melack and Kilham, 1974) had low turnover rates which imply that the quantity of orthophosphate present exceeded algal demand.

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