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MAT-WATER PHOSPHORUS EXCHANGE IN AN ACID BOG LAKE¹

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Abstract. The exchange of phosphorus between a bog lake and its surrounding *Sphagnum* mat and the fate of mat phosphorus entering the limnetic zone of a lake were studied by means of a series of mat-labeling experiments using ³²P, and by an analysis of water budgets of the lake and mat.

A ³²P solution applied directly to the *Sphagnum*, so as to simulate phosphorus input from rainfall, produced a labeled soluble but biologically refractory phosphorus fraction which persisted in the lake at the initial concentration level for >16 d. Labeling the interstitial water of the mat directly with ³²P produced a labeled particulate fraction which was biologically active and was quickly concentrated in the limnetic food web. Heavy rainfall flushed both labeled components into the lake.

The pathway phosphorus takes to enter the lake from the mat was determined by temperature gradients in the mat and the degree of decomposition of the mat material. In early spring, with low water temperatures, phosphorus moves along isotherms from the mat directly to the hypolimnion and bypasses the thermocline. In late spring movement is to the epilimnion and thermocline. The maximum phosphorus concentrations in the mat were above a compacted zone at the 2-m depth. This maximum coincided with an open-water phosphorus maximum at 2 m, which indicated that there were frequent inputs of mat phosphorus to this stratum.

The direction of net phosphorus movement was largely controlled by the water balance of the system. During periods of high precipitation, low temperatures, and low evapotranspiration, as was found in early spring, net phosphorus movement was toward the lake. During midsummer high evapotranspiration of the mat vegetation increased the storage capacity of the mat. This reduced phosphorus flow toward the lake so that net flow was often toward the mat.

Key words: atmospheric phosphorus; bog mat; groundwater movement; lake mat exchange; nutrient cycle; phosphorus; *Sphagnum*.

INTRODUCTION

Bog lakes differ from other standing water systems because of the unique way the *Sphagnum* mat and the surrounding vegetational complex interact with the limnetic habitat. In earlier reports (Koenings and Hooper 1973, 1976, Koenings 1976) we have identified a number of organic phosphorus fractions occurring in the *Sphagnum* mat and open water of North Gate Lake in Michigan's Upper Peninsula. We have described the relationship of these compounds to iron and followed their transformation in the aerobic and anaerobic strata of the lake. In this report we describe hydrological studies and labeling experiments designed to (1) identify the location and mechanism of phosphorus interchange between the mat and the open lake water, (2) measure the net flux of phosphorus between the mat and water during seasonal changes in evaporation and precipitation, and (3) determine the extent to which the phosphorus leachates and particulates from the mat are utilized in primary and secondary production of the lake.

The groundwater of perched, undrained bog systems in the Great Lakes area is typically highly colored, with a pH from 3.5 to 4.6 and a conductivity of

between 10 and 46 μ S (Bay 1967). Although this water is low in alkaline earth cations, it may be high in non-ionic phosphorus and iron compounds (Koenings and Hooper 1973). In North Gate and other bogs in the northern Michigan study area, the dissolved organic phosphorus content of the mat water may exceed 1400 μ g/L, and the total dissolved iron content 1200 μ g/L (Koenings 1977). Such large concentrations of dissolved phosphorus and iron are unique in unpolluted waters in the Great Lakes area; the groundwaters adjacent to these bog lakes have phosphorus resources comparable to highly eutrophic systems. North Gate and other bog lakes in this study area (cf. Stross and Hasler 1960) therefore present a biological paradox: they are lakes of low productivity within ecosystems rich in phosphorus. The low productivity of lakes of this type arises in part from their low transparency (Hasler et al. 1951); however, this does not fully explain the anomalous relationship between phosphorus and productivity. We have addressed this problem by labeling experiments that simulated input of inorganic phosphorus to the bog mat by rain and by groundwater. We have then observed the fate of these labeled materials from the mat upon entering the lake.

STUDY AREA

North Gate Lake is one of a number of bog lakes located within the University of Notre Dame Environmental Research Area in Gogebic County, Michigan,

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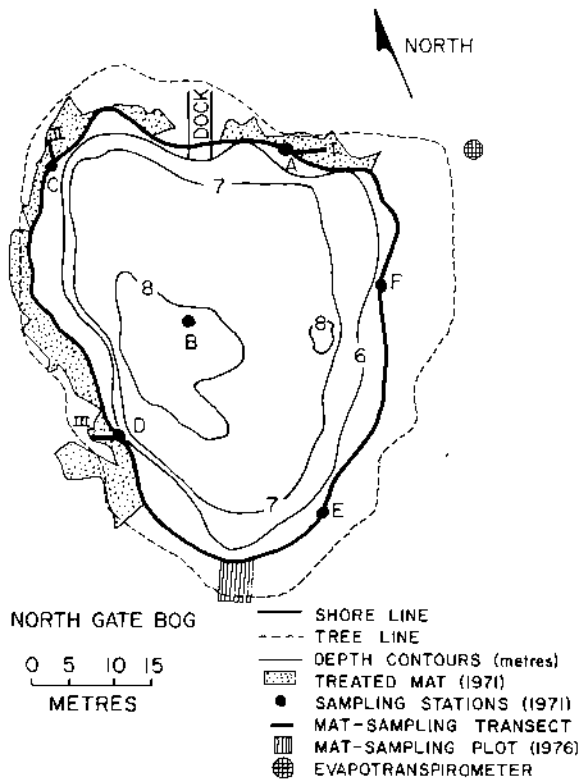


FIG. 1. Hydrographic map of North Gate Lake and adjacent bog, showing mat area labeled, sampling sites, and transects.

USA (Township 45N, Range 42W, Section 36). The lake has a surface area of 0.40 ha and a maximum depth of 8 m (Fig. 1). The shallow thermocline of the lake (Fig. 2) together with the large ratio of depth to

surface area leads to an incomplete spring overturn each year (Hooper and Imes 1971). This gives a di-chothermal temperature curve (i.e., with minimum temperature above the bottom) with a chemocline varying in depth between 4 and 7 m. Similar morphometry and chemical conditions have been noted in other small bog lake of the University of Notre Dame tract (von Ende 1979).

The open water of North Gate Lake is surrounded by a mat of sedges, *Sphagnum*, and shrubs (Fig. 1), which extends into a black spruce-tamarack lowland ≈ 10 ha in area. In early spring the water table of the mat and the lake level normally are high. With heavy rain large areas of the mat may be flooded, but no surface drainage from the basin has been observed, although it may occur during years of exceptionally high water.

At the edge of the open water the mat consists of a surface layer of sedges and mosses covering living or dead undecomposed mosses and recognizable plant material which extends to a depth of ≈ 15 cm. This layer is exceptionally porous. Shoreward, the mat material becomes increasingly consolidated so that 4 m into the forest the surface layer of living mosses is underlain by black, well-decomposed peat, and the plant remains are unrecognizable.

METHODS AND PROCEDURES

Chemical and radiological methods

We analyzed three components of the stable phosphorus in the lake water and in the interstitial water of the adjacent mat. These components were (1) soluble reactive phosphorus (SRP), here defined as the phosphorus that passes through a $0.45\text{-}\mu\text{m}$ filter and reacts with ammonium molybdate upon acidification

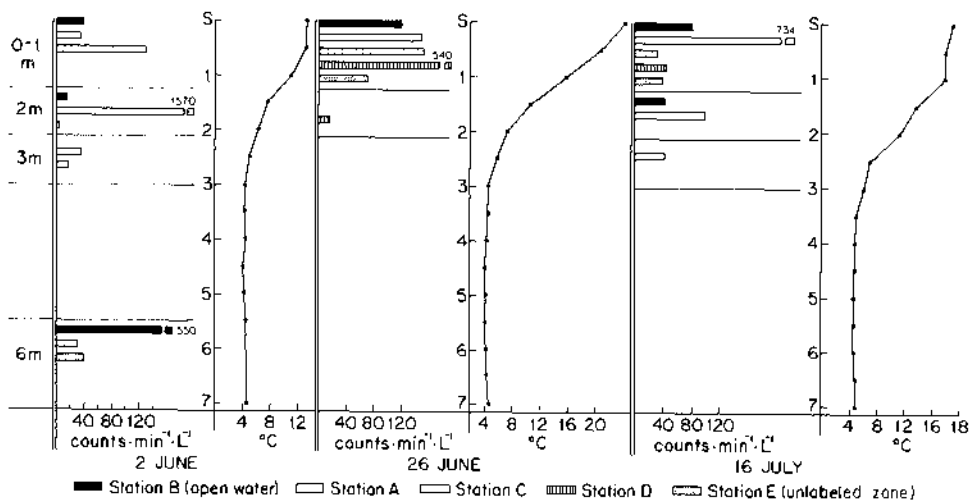


FIG. 2. Vertical temperature profiles and ^{32}P activity entering the water column in 1971 at various lake sites, after *Sphagnum* labeling (2 June), after mat interstitial water labeling (26 June), and after flushing of mat by 3.5 cm of rainfall (16 July).

to form a blue complex, (2) soluble unreactive phosphorus (SUP), defined as the phosphorus that passes through a 0.45- μm filter but reacts with molybdate only after acid digestion, and (3) particulate phosphorus (PP), which is defined as the phosphorus retained by a 0.45- μm membrane. Lake samples analyzed for PP included all water particulates, but samples analyzed from the bog mat were filtered by a 173- μm screen placed in the water-sampling tubes. Total phosphorus (TP) is the sum of the above three components. Chemical procedures used in the analysis of the above phosphorus components followed closely the outline given by Strickland and Parsons (1972). In all cases, the samples were collected and analyzed in duplicate.

In the labeling experiments, we monitored water ^{32}P by evaporating filtered 10-mL samples to dryness on a 50-mm planchet and counting on a low-background beta counting system. To measure the activity associated with the total phosphorus, we plated on planchets 5-mL aliquots of solutions previously digested with perchloric acid. We then evaporated the sample to dryness and counted. To identify the activity associated with the three stable phosphorus components mentioned above, it was necessary to employ separation techniques which differentiate between reactive and unreactive ^{32}P activity. To do this we extracted the molybdate blue complex produced in the orthophosphorus procedure with hexanol, using the technique outlined by Stephens (1963). This extract was then dried on a planchet and counted to give an estimate of the reactive ^{32}P activity. Subtraction of this activity from that obtained from evaporation of 0.45- μm filtered samples gives the activity associated with the SUP component.

After labeling, we monitored biological uptake of ^{32}P components in the lake system using the following procedures. We collected 10 L of lake water from the surface and from a 2-m depth at station B. Water was filtered first through 153- μm and then through 10- μm Nytex netting. We used the material retained by 153- μm Nytex for measurement of zooplankton activity, and that retained by the 10- μm Nytex as the measure of seston. These fractions were transferred to a 0.45- μm membrane; the membrane was then digested with perchloric acid, dried, and counted.

To collect *Chaoborus*, we made vertical hauls at night with a closing net between 3 m and the surface. These samples were filtered onto a 0.45- μm membrane, which was digested, dried, and counted. To measure activity of the mudminnow *Umbra* we collected fish in minnow traps placed at five stations near the lake margin and at one station near the center (station B). A sample of trunk muscle was removed from a fish collected at each of these six stations. Samples were digested, dried, and counted. In addition, the intestinal tract was removed from a sample fish from each of the six collecting stations. The contents of the

intestine were removed, their mass was determined, food items were identified, and the activity of a small aliquot of material was measured. All of the above activity measurements were made at 4-d intervals after each mat labeling.

Since small amounts of radioactivity (fallout) existed in the bog system prior to these labeling experiments, the background activity of all components of the system was monitored 10 d prior to the first experiment. Activity measurements of all components were made as described above. In subsequent experiments, we considered activity to be above background if it exceeded the activity of 95% of the background samples processed and counted in an identical manner. In processing the radiological data of labeling experiments all activity values were corrected for decay to the date of field application.

Weather data

Daily observations of wind direction, temperature, and cloud cover were made. We put rain gauges on a raft in the center of the lake, and the volume of rainfall was recorded daily. Maximum and minimum air temperatures were obtained from records at the United States Forest Service Weather Station at Watersmeet, Michigan, which is located ≈ 32 km east.

1971 tracer experiments

In 1968 and 1969 we noted that rainfall samples collected in the center of the lake contained large concentrations of SRP. We frequently found concentrations in excess of 100 $\mu\text{g/L}$. Similar rainout of atmospheric phosphorus has been reported by Gorham (1976). From these observations we hypothesized that the sources of phosphorus input to the large pool of soluble unreactive phosphorus (SUP) and particulate phosphorus (PP) within the mat and lake must be rain and groundwater from the watershed. Of course, watershed phosphorus would be transformed chemically during passage through the mat. To trace phosphorus supplied to the lake in these two ways, we devised the following two labeling experiments, using ^{32}P .

To simulate phosphorus entering the mat via rainfall, we prepared a labeled phosphorus solution by mixing 5.9 GBq of ^{32}P (as PO_4^{-3}) with 150 L of lake water in an oil drum. We tested an aliquot of the mixture before application and found that essentially all activity was in the form of SRP. On 30 May we applied the label to the surface of the mat vegetation, using 2-L sprinkling cans. Approximately half of the open mat was labeled (Fig. 1). The rate of application (≈ 0.5 L/m 2) was so low that little of the label reached the water table at the time of the application but was absorbed by the surface vegetation. However, after a light rainfall 12 h later, sampling tubes in the water table of the labeled area recorded a high level of ac-

tivity, and traces of activity were recorded in the open lake adjacent to the labeled zone (station A).

A second labeling experiment on 24 June was designed to assess the fate of phosphorus carried through the mat into the lake without direct contact with the surface of the bog vegetation. To apply the tracer, we used plastic funnels with stems ≈ 18 cm long and 2 cm in diameter. Funnel stems were forced through the surface vegetation, and the tracer solution was poured directly into the uppermost saturated layer of the mat. These injections were made at 0.5-m intervals on a grid pattern (416 injections), gave approximately the same application rate as in the first labeling (0.5 L/m^2), and were applied to the same area. The same quantity of labeling solution was used, but there was an increase in total activity applied (7.4 vs. 5.9 GBq). Approximately 2 h after labeling, we sprayed the labeled area with surface lake water which was pumped through a garden hose. We calculated that the volume of water sprayed was equivalent to ≈ 2 cm of rainfall. Earlier trials in which ^{32}P was added to the mat interstitial water had shown that the label was taken up by particulates, chiefly bacteria, within 2 h. Thus spraying with lake water served to flush the labeled mat water into the lake after it had interacted with particulates.

Before and after labeling we monitored activity in the mat by installing three transects of sampling tubes across the mat from the open water to the tree zone (Fig. 1). The three transects differed somewhat in their relationship to surrounding upland areas from which surface drainage might be anticipated. Transect I crossed a section of mat adjacent to an upland area where a maximum input of surface drainage might be expected. Transect III crossed the mat adjacent to a lowland area where a minimum input of surface drainage was expected. Transect II was intermediate to the other two sites in its hydrological relationship.

To monitor inputs of activity to the lake following labeling of the mat we established lake-mat interface stations adjacent to the mat at five locations (Fig. 1). Stations A, C, and D were at the edge of the mat adjacent to mat-sampling transects I, II, and III, respectively. Stations E and F were on the side of the lake that was not labeled. At these interface stations we monitored activity of water at depths of 1, 2, 3, and 6 m. A vertical profile of water activity was obtained at the same depths at station B, which was located in the center of the open water. Following labeling, samples were collected and analyzed for activity at 4-d intervals (Fig. 3). Duplicate samples were collected and processed from each station at each depth on each date. We measured activity of filtered and unfiltered samples, as described above, to determine activity associated with SRP, SUP, and PP fractions. We were never able to identify activity in the SRP component of samples collected from the open lake.

Mat phosphorus movement

In studying phosphorus movement between the lake and the mat, we collected three sets of data. In 1974 we measured total phosphorus concentration of the interstitial water at a series of depths at two locations in the mat. These measurements allowed us to compare changes in concentration in the mat phosphorus with concentration of phosphorus in the adjacent lake during spring and summer and during periods of varying weather conditions. In 1975 we used ^{32}P to trace phosphorus movement within this area. In 1976 we attempted to correlate phosphorus flow data with an analysis of water flow between the mat and lake made by measuring lake evaporation, rainfall, lake level changes, mat water level changes, and evapotranspiration of the mat.

To sample the mat for phosphorus and to make temperature measurements at depths below the surface, we installed water-sampling tubes in the mat. Sampling tubes consisted of sections of 5.08-cm polyvinyl chloride (PVC) pipe which contained on the inside a section of 0.64-cm Tygon tubing with a funnel attached to its lower end. Perforations at the lower end of the PVC pipe allowed water to enter at the desired level. The lower end of the pipe was covered with 173- μm screen, and the upper end was stoppered. Tubes were inserted at desired depths of the mat by opening a hole with a 5-cm wooden point and forcing the sampling tubes into this opening. Mat temperatures were measured by lowering a temperature probe into the sampling tubes. To remove water samples, the Tygon tubing was connected to a sample flask, which in turn was connected to an evacuated 20-L glass carboy, which provided suction. Sampling tubes were installed at depths of 0.15, 0.5, 2, and 4 m at locations that were 1 and 3 m from the open water, in the vicinity of Transect I (Fig. 1). These depths were selected because it had been previously determined that the maximum phosphorus concentration in the mat was at ≈ 2 m depth and that beyond a 4-m depth there was little change in concentration.

In 1975 five surface (0.15-m) holes were made 2 m from the open water, midway between two groups of sampling tubes. After monitoring of temperature and background activity, the five holes were each labeled with 74 MBq of ^{32}P . Every 3rd d 100-mL water samples were taken from each sampling tube and from the open water at 1-m intervals. Samples were dried at low temperatures and counted.

In 1976, 20 water-sampling tubes were installed in a 3×4 m plot in the mat at the south end of the lake. These tubes were randomly located and sampled at a variety of depths from the surface to 3 m. They were used to follow the flow of phosphorus from the mat after labeling a central point. Before additions of the label, we monitored temperature and background activity at all depths in these sampling tubes. On 19 July

at a central location, we added a label to an opening in the mat 1 cm in diameter and 1 m deep. During the remainder of the summer, we followed movement of the label by removing 50-mL samples from the sampling tubes. Samples were then dried at a low temperature and counted.

An evapotranspirometer similar to that described by Bay (1966) was installed in an open area on the east side of the bog. The evapotranspirometer was constructed of 1.27 mm thick (18-gauge) sheet metal which was rolled into a cylinder 2.44 m in diameter. The joint of the sheet metal was bolted and sealed and the cylinder was driven into the peat to a depth of 0.61 m. At this depth a consolidated peat layer effectively sealed the inside of the cylinder from the surrounding groundwater. The groundwater level within the cylinder was measured every 3 d. This measurement monitored the combined changes due to evapotranspiration and rainfall.

To measure water table fluctuation in the mat adjacent to the evapotranspirometer, we installed four surface-sampling tubes at locations that were 7 and 9 m north and south of the evapotranspirometer. These surface-sampling tubes consisted of sections of 5.08-cm PVC pipe perforated at the lower end with 1.91-cm holes. These openings allowed the groundwater to flow into the tubes from the mat. The tubes were sealed at the top with a stopper when not in use. The water level inside the tubes was recorded at 3-d intervals. To monitor the lake level, we fastened a vertical gauge to a horizontal bar that extended to the lake from a tree near the open water. The water level was recorded at 3-d intervals. Lake evaporation was measured by anchoring a child's hard plastic swimming pool 80 cm in diameter and 20 cm deep in the open lake (Fig. 1). The pool was filled with lake water so that it was partially submerged in the lake. This minimized temperature differences between the lake and the evaporating water. A plastic 125-mL graduated cylinder perforated at its lower end was cemented to the bottom of the pool and was used to gauge water evaporation loss. The pool was filled to a fixed level after the water level was recorded every 3 d.

RESULTS

1971 labeling experiments

After ^{32}P was applied directly to the mat vegetation to simulate input from rain, the activity entering the lake was entirely SUP. Particulate activity was never significantly above background until after the second experiment in which the mat interstitial water was labeled (Fig. 3).

Major inputs of SUP activity into the lake basin were first recorded on 2 June (Fig. 2). At shallow depths at the edge of the mat adjacent to the labeled area, samples had much higher levels of activity than in the open water ($t = 3.7$; $\alpha = .01$). Activity above

background was encountered at 2- and 3-m depths at station A. Samples from station B at the 6-m depth contained $550 \text{ counts} \cdot \text{min}^{-1} \cdot \text{L}^{-1}$, which indicated that there had been considerable subsurface inflow of phosphorus to the basin. Since these samples were collected below the thermocline, movement through unconsolidated portions of the mat to the hypolimnion must have taken place. Water temperature was 6.2°C at the 2-m depth. The minimum air temperature on 31 May was 7.8° and on 1 June was 2.4° . At this time the water table was high, locally exposed to the atmosphere, and subjected to advective and radiational cooling. With these thermal gradients, inflow from the mat to the lake is possible at a variety of depths depending upon local temperature, hydrological conditions, and the porosity of various sections of the mat.

There was no significant change in water activity levels (corrected for decay) at successive sampling dates from 6 June through 22 June (Fig. 3); thus, no further mat input to the lake was indicated. Mat inputs might have been expected during this period because there was rainfall of 2 cm on 7 June and 1 cm between 12 and 13 June. This rain, however, followed a dry period when the air temperature exceeded 30° ; thus, the rainfall replaced transpiration losses and did not provide runoff to the lake.

The procedures used in the interstitial-water labeling on 24 June brought a more rapid flow of the label to the lake than when the label was applied to the vegetation. Samples collected 48 h after treatment showed a large input of activity. With this labeling procedure a much smaller fraction of activity was retained in mat-sampling tubes than when vegetation was labeled. Except for a single 2-m sample at station D, the only activity input above background was at the surface (Fig. 2). In contrast to the first labeling, the entire input to the lake as well as the ^{32}P activity increase in mat-sampling tubes was PP (Fig. 3). The small increase of SUP shown in Fig. 3 at the surface is largely an artifact created by using 24 June instead of 30 May as the date for calculating decay of the residual SUP from the first treatment.

On 29 June a storm added 3.5 cm of rain to the watershed, flooded the mat, and further increased particulate activity (PP) in the surface water ($t = 2.39$; $\alpha = .05$) but did not increase SUP significantly. A significant decrease in PP occurred between 30 June and 1 July ($t = 2.39$; $\alpha = .05$), but there was no change in SUP. Between 1 and 12 July there was no significant change in the quantity of either phosphorus fraction. On 13 July a heavy rainfall (3.6 cm) again flooded the mat. Rain, strong winds, and cool weather continued for 3 d. This brought about mixing and deepened the epilimnion from 0.5 to 1 m. The precipitation brought labeled SUP into the lake. This input, recorded on 16 July, was highest at station A, and entered the basin at the surface and at the 2- and 3-m depths (Fig. 2). Particulate activity decreased during this period. From

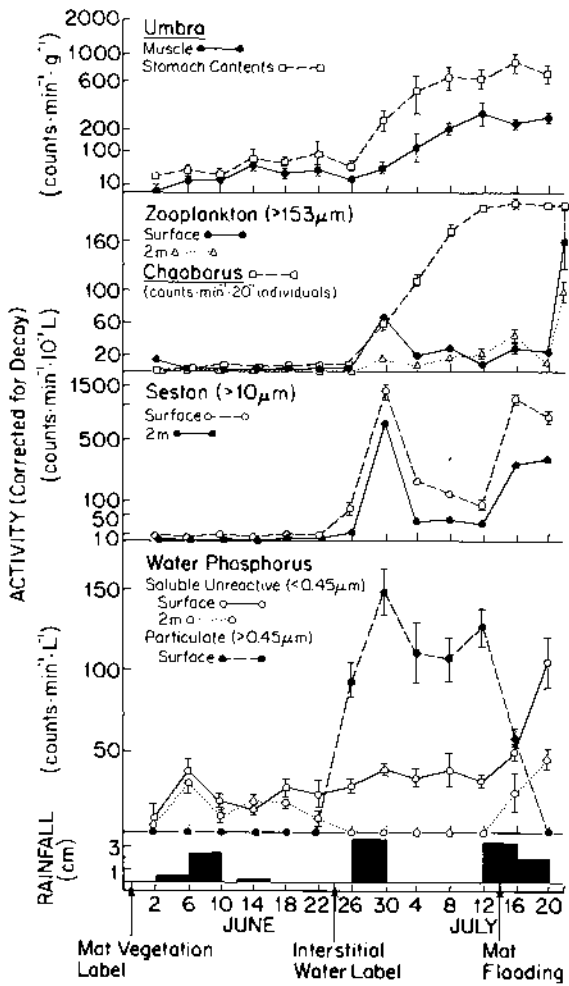


FIG. 3. Rainfall, activity of lake water fractions, and activity of components of the biota following application of ^{32}P to surface vegetation (*Sphagnum*) and to the mat interstitial water in June 1971. Each vertical line equals ± 1 SD.

16 to 20 July the weather remained cool and rainy, and input of labeled SUP and loss of PP continued. By 20 July particulate phosphorus had fallen to background level, but SUP had increased to >100 counts·min $^{-1}$ ·L $^{-1}$ at the surface and 40 counts·min $^{-1}$ ·L $^{-1}$ at 2 m (Fig. 3).

Source of phosphorus compounds entering the lake

These experiments indicate that inorganic phosphorus entering the mat from the atmosphere or from groundwater is transformed into either organic or particulate form before being flushed into the lake by rainfall. When flushed into the lake basin, the labeled SUP fraction remained at approximately the same concentration for at least a 16-d period. It may have persisted longer, but the second labeling on 24 June made interpretation of data difficult because of uncertainty of the decay corrections. The long residence time of SUP

indicates that the organic phosphorus compounds produced by the mat vegetation were refractory and were not utilized by the biota of the open lake. The SUP that entered the lake on 16 July could have been SUP from the first mat treatment or PP from the second treatment that was converted into SUP by the mat biota. With flooding, the water table in the mat was exceptionally high, and this SUP input may have been labeled SUP from a remote section of the mat that was carried to the lake by strong lakeward flow.

The depth of input of these phosphorus compounds into the lake seems to be controlled by temperature gradients in the interface zone. In the first experiment, when mat temperatures were low, labeled mat phosphorus entered the bottom of the basin. This took place in early spring when the surface mat water was cooler than the surface lake water. With this thermal gradient, flow was along isotherms within the mat and led to an increase in the SUP in the deeper strata. The second labeling showed that exchanges between the mat and lake later in the summer take place in shallower strata. At this season weather changes cool and deepen the epilimnion and make possible exchange with subsurface layers of the mat complex.

Fate of mat phosphorus fractions in the limnetic habitat

Although the lake retained an average of 20 counts·min $^{-1}$ ·L $^{-1}$ of SUP activity for at least 16 d following labeling of surface vegetation, only traces of activity appeared in the biota. Prior labeling experiments demonstrated that when added as PO_4^{3-} , a much lower concentration of ^{32}P than used in this experiment gives high activity levels in the limnetic food chain (Hooper and Imes 1971). Thus while this quantity was sufficiently high for biological uptake, its form (SUP) appears to have restricted entry into the food chain. A small but significant amount of activity appeared in *Umbra*, and traces appeared in zooplankton and *Chaoborus* on 30 May (Fig. 3). This may indicate that the lake received labeled P that did not pass through the mat vegetation; however, this input to the water must have been small since no trends in incorporation in the food chain were observed. *Umbra* feeds at night in the mat-lake interface zone and may have fed upon invertebrates of the mat that were labeled directly.

On the first sampling date following labeling of the interstitial water and after input of mat PP to the lake, activity was detected in seston, zooplankton, *Chaoborus*, and *Umbra*. Activity was much higher than that observed at any time after labeling the vegetation. Water, seston, and zooplankton reached peaks in activity on 30 June, but species with a longer phosphorus turnover (*Chaoborus* and *Umbra*) continued to accumulate activity for an additional 8–12 d. Seston and zooplankton at 2 m showed accumulation patterns similar to those at the surface, even though we did not detect an input of particulate activity at 2 m. Activity

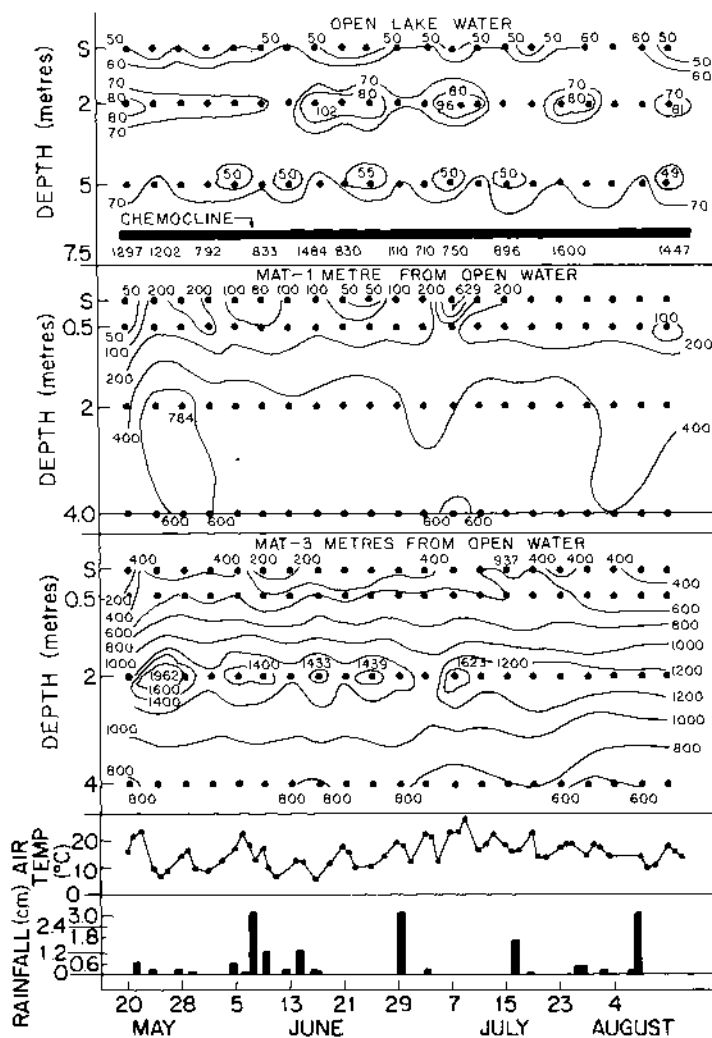


FIG. 4. Total phosphorus concentration ($\mu\text{g/L}$) of mat water and open lake water, air temperature, and rainfall during spring and summer 1974. Samples were collected from undisturbed mat.

in seston decreased from 30 June through 12 July, but a second increase in activity was observed after the mat flooding and mixing that occurred with the change in weather pattern between 13 and 16 July.

These experiments indicate that limnetic production is sustained by particulate phosphorus entering from mat groundwater but not by organic phosphorus leachates from the mat vegetation. Our data do not identify the form of PP entering the lake. In the filtration procedures used, filters were rinsed with dilute acid, which would free absorbed ^{32}P . Thus PP activity when collected in the lake was probably incorporated into bacteria. The concurrent increase in seston activity, however, indicates that entering PP was rapidly made available by excretion by bacteria and/or zooplankton.

Distribution and movement of mat phosphorus

The vertical distribution of total phosphorus in the lake-mat interface zone varied only slightly during the

summer of 1974 (Fig. 4). The persistent pattern in the open water and at the 3-m mat station was a maximum concentration at a depth of ≈ 2 m. This overall pattern persisted throughout the summer, but variations seemed to be related to weather patterns. There was an increase in total phosphorus with increasing distance from the open water at all depths within the peat profile. At the site 3 m from open water, concentrations at the 2-m depth ranged from 1200 to 1900 mg/L and exceeded the high concentration encountered below the chemocline (Fig. 4).

Weather-induced fluctuations were temporary. A wet, cool period between 5 and 13 June coincided with a decreased surface phosphorus concentration at both the 1- and 3-m sites. These results agree with measurements of mat phosphorus made in July 1973 when a heavy rain reduced surface concentration from 500 to 212 mg/L at a station 0.6 m from the open water and from 1123 to 688 mg/L at a station 2.4 m from the

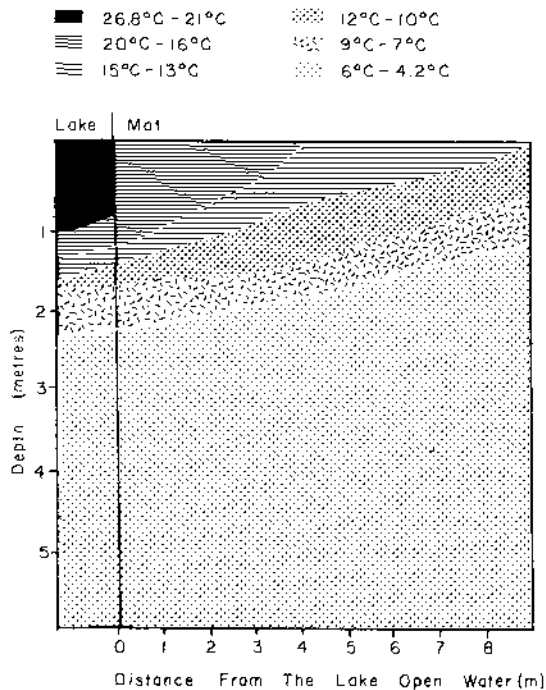


FIG. 5. Temperatures of mat and adjacent lake water, 14 August 1975.

open water. In 1973 some dilution of phosphorus occurred at depths of 0.5 and 2 m at the 0.6-m station, but at the 2.4-m station the only significant change was at the surface. On 29 June and 17 July 1974 precipitation occurred following a period of drought. Rain was absorbed by the mat, and there was very little horizontal movement. The elevated air temperatures and lack of precipitation between 7 and 10 July 1974 increased surface phosphorus at both the 1- and 3-m sites and suggest that during periods of high evapotranspiration, phosphorus may be carried upward from the deeper strata of the mat to the surface.

The depth of the maximum concentration of total phosphorus (2 m) in the mat reflects the level of the zone of compacted peat. This zone reduces vertical movement and shunts flow horizontally. Our finding that this maximum extends into the open water of the lake (Fig. 4) indicates considerable exchange with the open water at this depth, as labeling experiments described above demonstrated.

Flow of phosphorus in the mat should take place along isotherms, provided there is no increase in density from the dissolved solutes in the interstitial water. A high concentration of filterable iron and phosphorus in the mat water at 4 m gave a conductivity of $65 \mu\text{S}/\text{cm}$ compared to a value for the surface lake water of $20 \mu\text{S}/\text{cm}$; hence, some nonisothermal flow would be anticipated in deeper strata. However at 0.5 m and at the surface, solute effects would be small. At the end of the summer, isotherms slope downward toward the

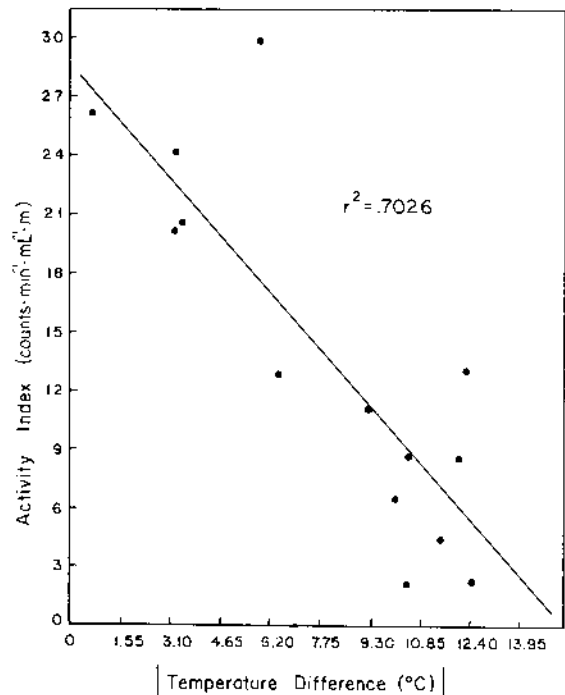


FIG. 6. Regression of activity index on the absolute value of the temperature difference between samples collected at the labeling site and samples collected from other locations in the mat after mat labeling experiment in 1975.

open lake water (Fig. 5) and reflect (1) the insulation qualities of *Sphagnum* and (2) water movements, which in turn depend upon the porosity and decomposition of peat (Dooge 1972).

The 1975 labeling experiments with ^{32}P tested the hypothesis that the phosphorus flow is along isotherms within the mat. If the phosphorus flows along mat aquifers, its movement would be confined by the compacted and decayed peat of the deeper horizons, and we would expect to find the isotope dispersed along isotherms. An activity index was calculated by multiplying ^{32}P activity by the distance in metres between the sampling tubes and the line where the label was introduced. This index takes into account reduction in activity from dispersion during movement away from the source. The sum of activity index values from each tube was compared with the differences in temperature between the peat at the labeling site and each tube (Fig. 6). The coefficient of determination of the linear regression was .70.

At North Gate during August, *Sphagnum* at the edge of the lake was warmer at all depths than at similar depths in the forest (Fig. 5). The degree of decomposition is less at the edge of the lake than at the same depth in the forest, allowing water to flow faster near the lake than at the same depth in the forest. This pattern may allow rapid water movement at the peat surface and in the undecomposed layers.

TABLE 1. Net ^{32}P movement from "marginal" and "forest" group samplers (1976). Positive values indicate runoff to the lake; negative values indicate uptake of lake water by the mat.

Dates	No. days in sample period	^{32}P activity sampled in marginal-mat group (counts \cdot min $^{-1}$ \cdot mL $^{-1}$) (m/d)	^{32}P activity sampled in forest mat group (counts \cdot min $^{-1}$ \cdot mL $^{-1}$) (m/d)	Net ^{32}P (marginal-mat group - forest mat group) (counts \cdot min $^{-1}$ \cdot mL $^{-1}$) (m/d)	Net water movement 0.5[(LL + LE) - (ML + ME)] (cm/d)
16-22 July	6	0.00	0.00	0.00	0.0610
22-25 July	3	2.57	3.16	-0.59	-0.3980
25-28 July	3	19.00	11.18	7.82	0.4138
13-21 August	8	1.11	2.20	-1.09	-0.1438
21-24 August	3	0.56	0.00	0.56	0.0805
24-30 August	6	7.60	0.48	7.12	0.3986

Phosphorus flushing from the mat should be related to the net water balance of the mat-lake system. To test this hypothesis we attempted to correlate net ^{32}P movement with net water movement over short periods of time. Net ^{32}P movement is defined as the difference between ^{32}P movement toward the lake and ^{32}P movement toward the forest. If all activity had an equal chance of being sampled at any sampling tube, subtracting all activity lakeward of the labeling point from all the activity sampled toward the forest would be an appropriate way of calculating net ^{32}P movement. The 1975 study showed that ^{32}P movement occurs along isotherms (Fig. 6). Therefore some samples should have more activity than others. The water table was exceptionally low at times, and samples could not always be collected from all sampling tubes.

To calculate net ^{32}P movement, two groups of samplers were selected: marginal-mat samplers and forest mat samplers. Marginal-mat samplers were those located lakeward of the labeling point and included: (1) open-water lake samplers at the surface and at 2 m, (2) samplers located at the edge of the mat 2 and 3 m deep, and (3) samplers 0.75 m from the edge at depths of 3 and 1.5 m. These marginal-mat samplers were compared to forest mat samplers, which were samplers located: (1) 1.5 m from the open water, 0.5 and 1.5 m deep, and (2) 3 m from the open water, 2 and 3 m deep. To determine whether or not these two groups of samplers received comparable amounts of activity over the entire sampling period, the activity of the two groups was compared using the Mann-Whitney U test of medians (Sokal and Rohlf 1969). For the entire period sampled, the activity of the two groups was not significantly different ($\alpha = .1$).

To estimate net water movement between the mat and the open water, change of lake level (LL), change of mat water level (ML), lake evaporation (LE), mat evapotranspiration (MET), and rainfall (R) were measured. Rainfall that occurred between sampling periods was subtracted from the change in each measurement from one sampling period to the next.

Changes in LL that remained after accounting for precipitation and LE indicate either runoff to the lake (when the number is positive) or uptake of lake water

by the mat (when the number is negative). Changes in ML after accounting for the MET and R could also indicate increase from the surrounding watershed or lake, or loss to the watershed or lake. Therefore net water movement (NWM), which can be considered runoff or influx of water to the mat, can be evaluated:

$$(\text{ML} + \text{MET}) + \text{NWM} = (\text{LL} + \text{LE}) - \text{NWM} \quad (1)$$

$$\text{NWM} = 0.5 [(\text{LL} + \text{LE}) - (\text{ML} + \text{MET})] \quad (2)$$

Net water movement and net ^{32}P movement are closely associated ($r^2 = .7693$). Although values for LL after accounting for R and LE (LL + LE) are never negative (Table 2), there is a range of positive values from 0.0375 to 0.4942. After accounting for R and MET (ML + MET), values for ML are both negative and positive. Any negative values of NWM are then the result of (ML - MET) values being greater than the positive (LL + LE) values. Both net ^{32}P movement (marginal-mat group activity - forest mat group activity) and net water movement, $0.5 [(\text{LL} + \text{LE}) - (\text{ML} + \text{MET})]$, showed both negative and positive values (Tables 1 and 2). Net water movement was toward the lake between 25 and 28 July and between 24 and 30 August but toward the mat between 22 and 25 July and between 13 and 21 August. Lake and mat movement of water were nearly equal between 16 and 22 July and between 21 and 24 August. Net ^{32}P movement was highly correlated with this pattern.

Time of P input to the lake seems to be in part regulated by the water storage capacity of the mat system. During early spring when the water table is high, more P should flush from the mat into the lake as a result of lack of storage capacity. The increase in P concentration at 2 m in the open water after the rainy period between 5 and 13 June 1974 (Fig. 4) occurred after a period when air temperatures were low, which indicates that evapotranspiration rates would be low. These conditions meet the requirements for an input of phosphorus from forested areas. As evaporative losses increase, less phosphorus from the surrounding watershed is flushed into the lake. The amount of water and phosphorus draining from the mat may differ at various sites along the margin as well as at dif-

TABLE 2. Net water movement variables (1976).

Dates	No. days in sample period	Lake level (LL) (cm/d)	Lake evaporation (LE) (cm/d)	Mat level (ML) (cm/d)	Mat evapotranspiration (ME) (cm/d)	Net movement (NWM) $0.5[(LL + LE) - (ML + ME)]$ (cm/d)
16-22 July	6	-.2138	.5857	.0667	.1833	0.0610
22-25 July	3	-.5292	.5667	-.8333	1.6667	-.3980
25-28 July	3	-.1058	.6000	-.8333	.5000	0.4138
13-21 August	8	-.2375	.4500	-.4375	.9375	-.1438
21-24 August	3	-.1058	.2667	-.5000	.5000	0.0855
24-30 August	6	-.1157	.5795	-.7295	.3961	0.3986

ferent distances from the margin. More phosphorus is present in the more-decomposed layers, but more drainage will occur from the less-decomposed layers.

DISCUSSION

Movement of phosphorus in the system is regulated to a large degree by decomposition profiles, water balance, and water density. Decomposition regimes and water density regulate the depth of movement, but water balance dynamics regulate time of phosphorus movement and the distance it moves to and from the open water. These movements in effect regulate the amount of P input to the lake. In early spring mat water temperatures are low, and phosphorus will enter deeper strata (hypolimnion and monimolimnion). Temperature profiles at this season indicate that flow to the lake is downward to the compacted peat layer at 2 m, then horizontal to the lake-mat interface zone, and then downward as a density current along the basin slope. Such a flow could account for the similarity in phosphorus concentration between the mat 2-m layer and the monimolimnion (Fig. 4). Later in the summer as the mat water warms, flow will be to the warmer strata of equivalent density. The maxima in total phosphorus in both the mat and lake at 2 m (Fig. 4) indicate that this is a zone of frequent phosphorus input to the water column. This is also the zone with the highest bacteria counts in the basin (Koenings 1977), which suggests that mat inputs bring in a component of phosphorus from mat bacteria. In midsummer, evapotranspiration of marginal plants reverses the direction of net transport. As the water-retaining capacity of the mat increases there is less opportunity for the drainage from areas rich in phosphorus to reach the lake, thereby reducing phosphorus inputs to the limnetic zone.

Loss of water during high evapotranspiration concentrates the SUP within the mat but at the same time creates a flow of lake water low in phosphorus into the mat. At increasing distances from the lake, dilution of SUP by lake water becomes progressively less, and there appears to be some upward flow of the phosphorus-rich water from deeper strata of the mat (Fig. 4). Thus a gradient in phosphorus concentrations is

established within the mat adjacent to the lake by evapotranspiration. Phosphorus concentrated in this way by evapotranspiration is again diluted and moved lakeward by rainfall; thus, over an extended period an equilibrium in phosphorus exchange may exist between mat and lake.

The fates of inorganic phosphorus entering the bog system from the atmosphere and from groundwater appear to be quite different. Atmospheric inputs to the mat vegetation enter the water table and lake as refractory organic phosphorus with a long turnover time in the lake basin and probably also in the mat. The labeled SUP fraction that persisted in the limnetic zone was probably identical to the filterable but non-dialyzable fraction of high molecular mass that was isolated by Koenings (1977) and had a turnover time in excess of 6.5 mo. The principal chemical environment in the bog lake system which frees SRP from this organic component appears to be the monimolimnion, and re-formation of refractory SUP takes place upon transport of the SRP to the aerated layers of the mat or lake (Koenings and Hooper 1976). A major fraction of the total phosphorus of the bog system is made up of these refractory SUP components with a long turnover time. This may account for the anomalous situation of low biological productivity of these bog lakes in the face of high concentrations of total phosphorus. Anthropogenic contributions to atmospheric phosphorus (Gorham 1976) would increase this refractory fraction if contaminated rain falls upon the vegetational complex of the mat. On the other hand, inputs of SRP from groundwater at the edge of the mat could behave as a labile phosphorus component and would be cycled rapidly into the food chain if delivered to the lake as PP.

Modification of the littoral zone brought about by the development of a *Sphagnum* mat not only strongly modifies phosphorus flow patterns, but also creates phosphorus storage and high concentrations of phosphorus at a variety of sites within the lake basin and mat. Thus compared to nonbog lakes, bog-lake systems exhibit greatly reduced recycling of phosphorus because of (1) reduced biological transformations and (2) storage, which reduces physical recycle.

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