Measuring Nutrient Spiralling in Streams[1]

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Nutrient cycling in streams involves some downstream transport before the cycle is completed. Thus, the path traveled by a nutrient atom in passing through the cycle can be visualized as a spiral. As an index of the spiralling process, we introduce spiralling length, defined as the average distance associated with one complete cycle of a nutrient atom. This index provides a measure of the utilization of nutrients relative to the available supply from upstream. Using ^{32}P as a tracer, we estimated a spiralling length of 193 m for phosphorus in a small woodland stream.

Key words: downstream transport, nutrient cycling, phosphorus, spiralling, stream

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Le cycle des éléments nutritifs dans les cours d'eau comporte un certain transport en aval avant que le cycle soit complété. On peut donc concevoir comme une spirale le chemin parcouru par un atome de nutriment durant ce cycle. Comme indice du processus, nous introduisons la longueur du trajet en spirale, définie comme la distance moyenne associée avec un cycle complet d'un atome de nutriment. Cet indice est une mesure de l'utilisation des éléments nutritifs par rapport à la quantité disponible en amont. Avec le ^{32}P comme marqueur, nous estimons que dans un petit cours d'eau traversant un boisé, la longueur du trajet en spirale du phosphore est de 193 m.

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NUTRIENTS, such as nitrogen and phosphorus, are critical to the maintenance of ecosystem function. Their cycling affects the ability of an ecosystem to withstand and recover from perturbations (Webster et al. 1975; Bormann and Likens 1979). Webster (1975; Webster and Patten 1979) pointed out that nutrients in a stream do not cycle in place, but are displaced downstream as they complete a cycle. He described this coupling of transport and cycling as "spiralling" and suggested that the ability of a stream to utilize nutrients is associated with the "tightness" of the spirals. Other workers have referred to the concept of spiralling (Wallace et al. 1977; Naiman and Sedell 1979; Meyer 1979; Benke and Wallace 1980), or recognized the importance of spatially dependent reutilization of nutrients (Ball and Hooper 1963; Short and Maslin 1977) and organic matter (Fisher 1977). In this paper we introduce an index of nutrient spiralling and report a field measurement of this index.

To develop the index, we assume that a nutrient atom "cycles" through three generalized compartments (water, particulates, and consumers) of a stream ecosystem (Fig. 1). Each compartment is continuously transported downstream, so that the path of the nutrient describes an imaginary spiral. We can quantify this path in terms of spiralling length (S) (Fig. 1a), defined as the average distance required to complete one loop of the spiral. The three components of spiralling length are the average distance a nutrient atom moves in the water compartment (S_W), in the particulate compartment (S_P), and in the consumer compartment (S_C). The shorter the spiralling length, the more efficiently the nutrient is utilized, i.e. the more times a nutrient atom is recycled within a given reach of stream.

Methods — The experiment involved releasing 370 MBq each of ^{32}P (as carrier-free $K_2{}^{32}PO_4$) and ^{3}H (as tritiated water) in July 1978 in the West Fork of Walker Branch, a small woodland stream on the Department of Energy Reservation (Curlin and Nelson 1968) in Oak Ridge, Tennessee, USA. Water samples for radioassay were taken from 11 stations at 3- or 6-min intervals as the 30-min release slug passed through the 120-m reach. Total passage of ^{32}P past a station was estimated by integrating the concentration vs. time curve and applying dilution corrections obtained from the ^{3}H data. Radioactivity in sediments, seston, and biota was monitored for several weeks thereafter.

Results and discussion — The first component of spiralling length, S_W, was estimated from uptake of ^{32}P from water to particulates. As Ball and Hooper (1963) observed, uptake of

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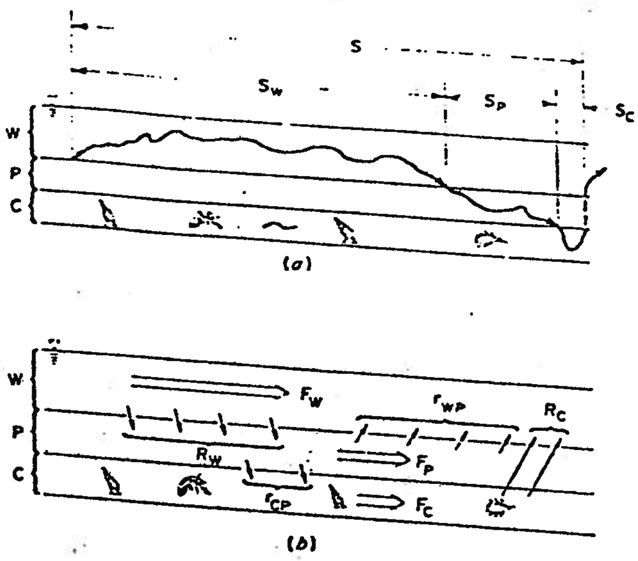

FIG. 1. Nutrient spiralling in a stream ecosystem. (a) The three components of spiralling length, S. The nutrient atom travels an average longitudinal distance, S_W, dissolved in the water compartment, W, plus an average distance, S_P, in the particulate compartment, P, plus an average distance, S_C, in the invertebrate consumer compartment, C, before returning to the water. (b) Downstream nutrient fluxes, F ($g \cdot s^{-1}$), and exchange fluxes, R ($g \cdot s^{-1} \cdot m^{-1}$), of nutrients between compartments. The total release from the particulate compartment, R_P, consists of the sum of the release to the water, r_{WP}, and the uptake by consumers, r_{CP}.

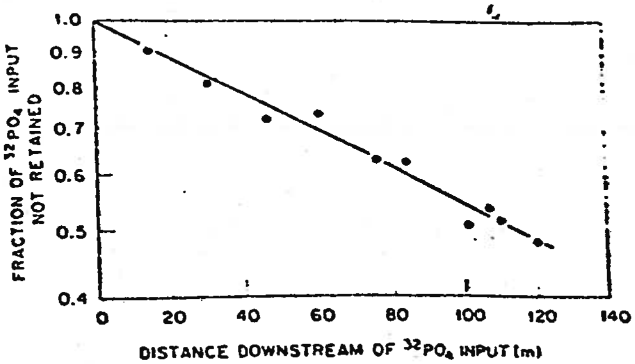

FIG. 2. Proportion of total ^{32}P input remaining in the water versus distance downstream from the point of release. Points represent time-integrated values for ^{32}P transport. Line is the function $A(x) = \exp(-k_w x)$, where $k_w = 0.0060\ m^{-1}$.

^{32}P at each point downstream is proportional to the ^{32}P remaining in the water at that point. Therefore, the proportion $A(x)$ of ^{32}P remaining in the water x metres downstream from the point of release decreases exponentially with distance downstream; i.e. $A(x) = \exp(-k_w x)$, where k_w is the distance rate constant (m^{-1}). Then, the average distance traveled downstream by a ^{32}P atom, calculated as the cumulative distance traveled by all of the ^{32}P atoms divided by the number of ^{32}P atoms initially present, is given by $S_W = 1/k_W$ (Overman and Clark 1960, p. 288).

Uptake of ^{32}P in Walker Branch conformed to the exponential model (Fig. 2), giving an estimate for k_W of 0.0060 m^{-1}, or a value of 167 m for S_W. If significant release (i.e. cycling) of ^{32}P from particulates occurred during the passage of the tracer slug (which approached 90-min duration at 120 m), S_W would be overestimated by this approach. As the tracers left the reach, however, water concentrations of both ^3H and ^{32}P dropped simultaneously to below detection limits, indicating that release rates of ^{32}P were too small to interfere with the uptake esitmate.

We can interpret S_W and the other two components of spiralling length in terms of the supply and utilization rates of dissolved P. We define F_i as the supply rate or downstream flux of phosphorus in compartment i; it is the amount of phosphorus passing through a given cross section of stream per unit time. We define R_i as the utilization rate or exchange flux of phosphorus from compartment i; it is the amount of phosphorus per unit time lost from compartment i per unit length of stream bottom. As the downstream flux (F_i) travels a unit length of stream bottom, a proportion of this flux, R_i/F_i, is lost from compartment i. If we trace the downstream rate of disappearance of phosphorous atoms without interference from replacement fluxes from other compartments, the rate of disappearance of the tracer over distance is a direct measure of this ratio, R_i/F_i. Thus, the distance rate constant (k_i) equals R_i/F_i, and the average distance or average number of unit lengths of stream bottom a phosphorus atom moves downstream in compartment i is given by $1/k_i = S_i = F_i/R_i$. In terms of the nutrient fluxes shown in Fig. 1b, the first component of spiralling length can be calculated as $S_W = F_W/R_W$, where F_W is the downstream flux ($g \cdot s^{-1}$) of dissolved nutrient in the water, and R_W is the uptake flux per unit length of stream bottom ($g \cdot s^{-1} \cdot m^{-1}$) from water to particulates and associated microbes.

The second component of spiralling length can be calculated in an analogous manner as $S_P = F_P/R_P$, where F_P (Fig. 1b) is the downstream flux ($g \cdot s^{-1}$) of nutrient in the particulate phase, and R_P is the release flux per unit length of stream bottom ($g \cdot s^{-1} \cdot m^{-1}$) from the particulates. This release consists of loss to the water (r_{WP}) plus loss to consumers (r_{CP}). For a stream in steady state, release flux from particulates equals uptake flux from water to particulates (i.e. $R_P = R_W$). Therefore

$$S_P = F_P/R_W = (F_P/F_W)\, F_W/R_W = (F_P/F_W)\, S_W.$$

Thus, under these conditions, S_P can be determined from S_W if F_P/F_W is known. In July–August 1978, soluble reactive phosphorus (SRP) (Chamberlain and Shapiro 1969) averaged 4.1 µg/L and total phosphorus in suspended particulates averaged 1.9 µg/L. Laboratory equilibration experiments, however, showed that only 34% of the particulate P is exchangeable with the dissolved P pool in Walker Branch (Elwood et al. 1981). Considering only the exchangeable portion of the particulate P, we obtain $F_P/F_W = 0.16$. From the equation given above, $S_P = 0.16\, S_W = 26$ m. The soluble reactive phosphorus analysis may have overestimated the available P in the water (Rigler 1966; Stainton 1980), but the error would have produced a compensating overestimate of exchangeable pool size in particulates, because the latter estimate also incorporated a chemical determination of SRP in Walker Branch water.

Once a nutrient atom enters the consumer compartment, its expected travel distance is F_C/R_C, where F_C (Fig. 1b) is the downstream flux ($g \cdot s^{-1}$) of nutrient in the consumer compartment, and R_C is the release flux ($g \cdot s^{-1} \cdot m^{-1}$) from the consumers by excretion to the water compartment. However, only the fraction (b_C) of nutrient that passes through the consumer compartment, rather than returning directly from particulates to water, actually contributes to the total spiralling length. Therefore, the third component of spiralling length can be given by $S_C = b_C\,(F_C/R_C)$. At steady state, release flux from consumers is a constant fraction of release flux from particulates, and $R_P = R_W$. Therefore $b_C = R_C/R_P = R_C/R_W$, and S_C can be written in terms of S_W and downstream fluxes:

$$S_C = F_C/R_W = (F_C/F_W)\,S_W.$$

Phosphorus in drift, on a volume basis, was 0.002 μg/L, all of which was assumed exchangeable. Therefore, $F_C/F_W = 5 \times 10^{-4}$, and $S_C = 0.08$ m. Downstream transport in consumers contributes negligibly to the total spiralling length, $S = S_W + S_P + S_C = 193$ m.

From the relations developed above, total spiralling length can be expressed as the ratio of total downstream flux of nutrient (F_T) to R_W:

$$S = F_W/R_W + F_P/R_W + F_C/R_W = F_T/R_W.$$

The importance of this ratio is that spiralling length provides a relationship between nutrient utilization (R_W) and total nutrient supply (F_T). If nutrient utilization in a stream is to increase, S must decrease. Adaptations and functions that reduce downstream transport (e.g. holdfast devices and filter feeding) will tend to shorten the spiral. While the definition of spiralling length as the expected distance to complete one cycle does not depend on whether the stream is at steady state, both our calculations and the interpretation in terms of total nutrient fluxes apply only to the steady state. An alternate approach to the calculation of S_P and S_W that does not depend on the steady-state assumption will be considered in a future publication.

Upstream–downstream comparisons of ^{32}P loss demonstrate that spiralling occurred. Figure 3 shows that ^{32}P loss from leaf detritus (≥1 mm), which accounted for ~ 60% of ^{32}P uptake, was slower downstream (open circles) than upstream (closed circles). This indicates that some of the ^{32}P released upstream was resorbed downstream.

A simple model for transport and exchange of ^{32}P in the stream is given by:

$$\frac{\partial Q_W}{\partial t} = D\,\frac{\partial^2 Q_W}{\partial x^2} - v\,\frac{\partial Q_W}{\partial x} - \frac{v}{S_W}\,Q_W + k\,Q_P, \text{ and}$$

$$\frac{\partial Q_P}{\partial t} = \frac{v}{S_W}\,Q_W - k\,Q_P,$$

where D is longitudinal dispersion and v is water velocity (both estimated from ^{3}H tracer data), $Q_W(x,t)$ is ^{32}P concentration in water, $Q_P(x,t)$ is ^{32}P concentration in particulates, and k is the turnover of ^{32}P associated with particulates. Because S_P is small relative to S_W, the transport of particulates is neglected in this model. With S_W set at the measured value of 167 m, k was estimated by fitting the model to the 20-m data (broken line in Fig. 3). With no further fitting, the model predicted the curve shown through the data from 120 m. Other values of S_W, over the range $130 < S_W < 200$ m, produced poorer but acceptable fits. The ability of the model to predict this reutilization of ^{32}P provides a rough validation of our estimate of spiralling length. In lakes, a significant amount of regenerated phosphorus may be associated with large molecules and unavailable for immediate re-uptake (Lean 1973). Our result suggests that, in Walker Branch, the availability of regenerated P is not very different from that of orthophosphate.

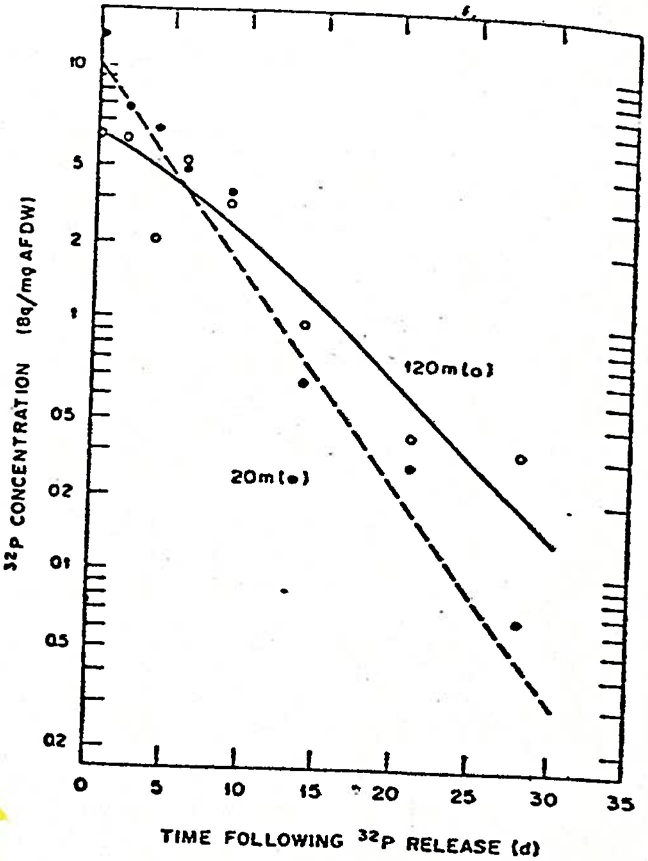

FIG. 3. Mean concentrations of ^{32}P (Bq/mg ash-free dry weight) in leaf detritus (≥1 mm) from Walker Branch at two locations downstream after a 30-min release of $^{32}PO_4$ as a function of time following the release. Broken line shows model calibration to data from 20 m; solid line is model prediction for 120 m.

The spiralling concept provides a basis for considering the role of ecosystem structure in governing nutrient utilization. Travel distance in the water (S_W) dominated the spiralling length, indicating that uptake from the water may be the primary constraint on increased nutrient utilization. The small value for the consumer component, S_C, does not imply that the role of consumers in spiralling is negligible, but it indicates that downstream drift of consumers does not significantly limit nutrient utilization. The indirect influence of consumers may be important. Feeding activities of grazers and shredders (Cummins and Klug 1979) decrease organic particle sizes, which can increase the surface area available for sorption and microbial activity (Hargrave 1977). In addition to increasing nutrient uptake from water, which would reduce S_W, consumers may also reduce particulate turnover length, S_P, by preventing buildup and sloughing of the aufwuchs community and reducing particulate flux, F_P.

Abiotic factors clearly would have a major influence on spiralling. For example, we would expect spiralling length to increase with increasing streamflow, and we would expect physical, rather than biological, explanations to dominate comparisons of spiralling length in streams of very different morphometry. An index such as uptake per unit area (R_W/stream width), which can be calculated for a field measurement of S_W and F_W, may be appropriate for purely biotic comparisons. Storms and seasonal variations can have a major influence on the phosphorus budgets of streams (Meyer and Likens 1979; Rigler 1979), and they undoubtedly affect spiralling length. Analysis of these variations in terms of their effect on spiralling may help to elucidate the relations between biotic and abiotic factors controlling nutrient utilization.

Spiralling length, then, is an index of the utilization of nutrient supplied from the surrounding watershed. The concept incorporates both reuse and retention, and it provides an approach for relating downstream fluxes to instream metabolic activity. Spiralling length is analogous to a recycling index (Finn 1976; Richey et al. 1978), but it explicitly considers the longitudinal dependence of nutrient recycling in the stream.

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