MODELLING MINERAL CYCLING BY PERIPHYTON IN A SIMULATED STREAM SYSTEM*

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Introduction

The energetics of most small streams are basically driven by allochthonous primary production. Although the periphyton community usually provides a relatively small percentage of photosynthetically produced organic matter, it is an important food base for many organisms and thus of interest in studies of food web dynamics.

Radioisotopes have been used in a variety of ways in ecological studies of periphyton including productivity estimates (ELWOOD & NELSON 1972, WETZEL 1963), biomass estimates (NELSON, KEVERN, WILHM, & GRIFFITH 1969), gross radionuclide accumulation data (NEAL, PATTEN, & DePOE 1967; CUSHING 1967; WATSON, CUSHING, COUTANT, & TEMPLETON 1971), and cycling of nutrients (CUSHING & ROSE 1970, CUSHING & WATSON 1973) to mention a few. Few studies have been concerned with attempting to devise models to aid in quantifying mineral cycling in periphyton communities. McINTIRE (1973) presented a simulation model of periphyton dynamics in laboratory streams; mineral cycling, however, was not included and it is this aspect with which our research is concerned.

Methods

The experimental microcosm used in these studies was described by CUSHING & PORTER (1969) and CUSHING & ROSE (1970); details will not be repeated here. It should be emphasised that the system, despite its small size in relation to

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natural streams and the relatively brief time period of the experiments, does approximate many of the natural conditions in terms of flow, light, temperature, and the use of natural periphyton communities. Therefore, it is a useful tool to provide mechanistic data leading to hypotheses on mineral cycling that can be tested in either larger artificial systems or natural streams. Results from such a microcosm are useful for modelling for two reasons: (1) because subsequent system manipulations suggested by results are possible, and (2) a more precise assessment of statistical validity of models can be made when nearly continuous data points are recorded.

Results

Earlier work with this microcosm has provided the basis from which the current modelling efforts have evolved. Using ^{65}Zn , CUSHING & ROSE (1970) concluded that the cycling of this element by periphyton (1) is basically adsorptive rather than absorptive, (2) is directly related to the initial ambient concentration, and (3) involves competition for divalent cation adsorption sites with other divalent cations such as Mg^{++} . These results were generally consistent with the findings of previous studies by others who studied the uptake of radionuclides by algae. BACHMANN & ODUM (1960), however, reported that ^{65}Zn uptake by marine benthic algae was proportional to the gross oxygen production and accumulated in proportion to the net oxygen production. This would indicate an absorptive, rather than adsorptive, mechanism. The complex process by which an element is sorbed by algae involves not only the method of sorption (which may well be a combination of the two), but also pH, light, chemical form of the element, etc. [see CUSHING & ROSE (1970) for a more detailed discussion and references]. With the data available, we have attempted to devise models to provide further insight into these mechanisms.

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An initial assessment of the system resulted in the simple model illustrated in Fig. 1. Solution of the appropriate differential equations led to the two exponential expressions listed (Fig. 1). The experimental results from each test run in the microcosm allowed two ways of calculating μ_1 : (1) from observation on the community, expressed as counts per minute (CPM), as measured and recorded during the uptake phase of each experiment, and (2) from observations on the decreasing ambient concentration (nCi/ml) of ^{65}Zn during an experiment measured in periodic water samples. Five sets of experimental data were fit by non-linear least squares using the equations in Fig. 1. In addition, the retention rate (μ_2) was estimated independently by fitting an exponential decay model to data obtained when unspiked river water was circulated through the system after completion of the uptake phase of the experiment. The fitted curves for the CPM data are shown in Fig. 2 and for the ambient water concentration data in Fig. 3. Subsequent calculations using the ambient equation and definitions in Fig. 1 gave estimates of μ_1 , the uptake fraction, which ranged from 0.021 to 0.148 hr^{-1} . Estimates of μ_1 from the CPM data could not readily be compared to the estimates obtained from the ambient data because of the two modes of measurement (CPM and nCi/ml) and questions concerning geometry of the counting device and community mass. Estimates of μ_2 , based on ambient data, were from 0.008 to 0.012 hr^{-1} , suggesting remarkable consistency. However, independent estimates of μ_2 based on retention slopes ranged from 1/2 to 1/8 of the corresponding values obtained in the uptake phase. Because of this difference and the definite pattern of deviations of the observed data from the calculated lines (Fig. 2), we decided to attempt to use a different model.

We assumed μ_2 was an expression of "average" loss from the periphyton community composed of a mixture of dead organic material, heterotrophic organisms,

and the dominant autotrophs-all having a wide range of individual masses. This supposition led to the derivation (EBERHARDT & NAKATANI 1969) of the following equation when the loss rates of individual components are assumed to be from a gamma distribution:

$$Y = D (1+T/E)^{-F} \quad (1)$$

We have used Equation (2) for fitting uptake but have not yet obtained a mathematical derivation wholly in accord with the experimental condition of these experiments or Equation (1).

$$Y = [1-(1 + T/E)^{-(F-1)}] \quad (2)$$

Fig. 4 illustrates the results obtained when these equations were used and also shows some cyclic deviations around predicted values. The fitted curves developed from Equations (1) and (2) offer a considerable improvement over those obtained from the equations used in Fig. 2. Our current efforts in modelling these data are directed toward assessing the usefulness of the parameters in estimating rates, devising appropriate expression(s) for ambient concentration, and demonstrating the validity of Equation (2) or a counterpart.

Discussion

The work described above emphasizes the value of modelling as a tool to help ecologists understand controlled microcosm studies which may in turn lead to a better understanding of natural ecosystems. The initial models suggested that (1) additional measurements of ambient decline were needed to obtain more reliable rate estimates, (2) community mass and/or growth measurements may be needed, (3) a way of reconciling two kinds of measurements of μ_1 , was needed, and (4) estimates of μ_2 were markedly different during uptake and retention. While the additional mathematical treatment has not as yet resulted in rate estimates which can be shown to be more meaningful for predictive uses, we have provided quantitative

evidence that the very simple uptake and retention models are not adequate for mineral cycling in periphyton. We believe the important questions have to do with adsorption vs. absorption (and think that adsorption dominates) and the varied sizes (or masses) of community components. Our model is thus as yet mainly descriptive but does provide the basis for formulating hypotheses and/or tests in larger scale experiments (see CUSHING & WATSON 1973) or in field situations, and suggests some additional questions for study with other minerals or perturbations in the microcosm.

The chemical similarities between cesium and potassium makes it attractive to use ^{137}Cs as an analog for studying potassium kinetics. DAVIS (1963) discussed their relationship in detail; however, NELSON (1969) presents data which shows that ^{137}Cs to K ratios are untenable for predictive purposes in fish. To explore these relationships, we have begun a series of experiments using the microcosm and ^{137}Cs as the tracer. In addition, we have used both ^{65}Zn and ^{137}Cs with repetitive spikes to study saturation kinetics and adsorption using inert substrates. We also will use photosynthetic inhibitors and antibiotics to partition the autotrophic and heterotrophic components of the community.

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$$\text{AMBIENT (nCi/ml)} = Y_1 = A + B \cdot e^{-CT}$$

$$\text{UPTAKE (CPM)} = Y_2 = B[1 - e^{-CT}]$$

WHERE:

$$A = \lambda \mu_2 / (\mu_1 + \mu_2)$$

$$B = \lambda \mu_1 / (\mu_1 + \mu_2)$$

$$C = \mu_1 + \mu_2$$

$$\lambda = \text{THE INITIAL SPIKE (nCi/ml)}$$

$$\mu_1 = \text{INSTANTANEOUS RATE OF TRANSFER OF } ^{65}\text{Zn FROM WATER TO PERIPHYTON}$$

$$\mu_2 = \text{INSTANTANEOUS RATE OF TRANSFER OF } ^{65}\text{Zn FROM PERIPHYTON TO WATER}$$