

MASTER

RADIOACTIVE TRACER STUDIES OF SOIL
AND LITTER ARTHROPOD FOOD CHAINS

Progress Report

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ABSTRACT

This report describes progress in research on soil and litter arthropod food chains, concerning measurement of nutrient flow using radioisotope techniques and investigations of the role of soil arthropods as regulators of the ecosystem-level processes of decomposition and mineralization of nutrients. Both laboratory and field research are described. Current progress in laboratory measurement of radiotracer turnover by predaceous macroarthropods is reported, as well as status of reasearch with microarthropod turnover of radioactive tracers. Implications of results are evaluated in context of current understanding of nutrient flows along arthropod food chains. The interactions of soil fauna and mycorrhizal fungi are under field and laboratory investigation. Field work has been completed on granitic outcrop projects, and a synthesis of results is summarized. Input-output budgets revealed that granitic outcrop island ecosystems are essentially in balance as regards nutrient flows. The ecosystems showed a strong resistance component of stability, as opposed to resilience, following an applied chemical perturbation and a natural one (drought).

INTRODUCTION

This Annual Progress Report describes research on the movement of nutrient elements through soil arthropod food chains. The research projects are organized around the decomposition process, a generalized ecosystem-level process which regulates ecosystem function. Soil fauna, and particularly soil arthropods, are believed to perform a controlling function on the decomposition process itself. Radioactive tracer techniques have been an important aspect of this research, as well as systems modeling and analytical methods. Field laboratory projects are being pursued.

Soil and decomposing organic matter associated with it serve as the major nutrient reservoir in most temperate terrestrial ecosystems. Nutrients released from the decomposing organic matter become available for uptake by vegetation or loss. If decomposition is excessively rapid, mineralization of nutrients may exceed the storage capacity of exchange sites in the soil or plant uptake mechanisms, and nutrients may be leached from the system. If decomposition is slowed, rates of plant growth may be retarded. Decomposition is produced by the activities of microflora and fauna associated with the ecosystem. Microfloral blooms may immobilize nutrients and retard leaching losses. Faunal activities may influence either rates of loss from organic matter or microbial immobilization of nutrients. Other biological processes may modify nutrient availability.

External influences, including anthropogenic ones, may modify rates of decomposition, rates of leaching, or nutrient holding capacity of the

soil. These influences may range from general, widespread developments such as acid rainfall to localized processes. Planned releases of waste materials from various sources into soil systems are evidently increasing (Porter 1978). Since atmospheric, fresh water and marine disposal of many types of technological byproducts have been curtailed, soil disposal seems the only remaining alternative. The use of soil systems as a varied set of enzymes for destroying various toxic materials may become a planned activity in future technological systems. Clearly, materials must fall within the range of the ability of soil systems to immobilize or detoxify, and regulating or controlling parts of the soil system must remain functional.

The importance of soil fauna as regulators is now beginning to be accepted. Research is demonstrating that soil fauna regulate release of nutrients, either directly or in concert with microflora, and by either accelerating or retarding rates of nutrient release (Malone and Reichle 1973, Seastedt and Crossley MS). Experimental approaches including applications of pesticides have demonstrated that decomposition rates are suppressed (Witkamp and Crossley 1966, Lee 1974, Croom and Ragsdale 1976). Theoretical approaches involving systems analyses have evaluated soil arthropods in a regulatory role (Douce and Webb 1978). Interactions of biotic and abiotic parameters in decomposition regulation have been quantified, as well as demonstrations of the ability of soil fauna to enhance microbial entrapment of leachable nutrients (Seastedt 1979, Whittaker *et al.* 1979).

Radioisotope techniques have continued to be an important part of this research. The use of radioactive tracers constitutes the major method for identifying the dynamics of nutrient exchange and flow processes. Not only can pathways of movement be identified, but rates of flow may be

readily measured. Research with radioactive tracers has an additional benefit in that work adds to information about the behavior of radioactive materials in the environment. The environmental behavior of radioactive pollutants, especially fission products, has experienced a reawakening in interest. These materials and nutrients are analogs of each other, so that knowledge of nutrient flows helps to understand the movement of radioactive pollutants. And, like nutrients, the soil system may serve as a reservoir for these materials under the regulation of biological agents.

Thus, the importance of the research described in this Annual Report lies in its relation to technology, and technological impacts upon the decomposition process in general. The information is developed and described in a context of basic research, but the applications are significant in terms of providing the necessary base for intelligent decisions about technological implementations.

Results are reported under two subprojects. The first concerns the use of radioactive tracers to measure nutrient flows along soil arthropod food chains. Current results describe radiotracer retention by macroarthropods and microarthropods in laboratory experiments. Work with microfloral-faunal interactions is described, as well as field sampling for nutrient analysis of arthropod communities. The second subproject concerns field sampling for nutrient analysis of arthropod communities. The second subproject concerns field research on granitic outcrop areas, in which the small island ecosystems occurring there have been treated with perturbations. Nutrient responses of the ecosystems to perturbations have been recorded

and evaluated. This work is nearing completion.

Accompanying this Annual Report are several technical reports (manuscripts for open-literature publication) and reprints of work published during the current contract period. These materials provide further details of the research summarized here. As is customary, open literature publication is our major reporting mechanism.

Subproject (1): Radiotracer studies of nutrient element accumulation and turnover in soil-litter arthropod food chains.

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Research conducted under this subproject is concerned with several aspects of nutrient flow along soil arthropod food chains. The use of radioactive tracers to measure nutrient accumulation has been a prominent research topic, although other aspects are important: measurement of nutrient pools in fauna and substrates (Gist and Crossley 1975a, Crossley 1977a), rates of radiotracer turnover by faunal components (Nabholz and Crossley 1978), phenomena influencing food chain dynamics such as coprophagy (Webb 1977) or migration (Best et al. 1978), model development and evaluation (Webster and Crossley 1978), and refinement and development of methodologies (Seastedt and Crossley 1978). The general hypothesis guiding the research is that soil fauna regulate rates of ecosystem-level processes, and in particular, that soil arthropods regulate the general process of litter decomposition and nutrient mineralization. Assessing nutrient flow along food chains within a given system provides a means of evaluating the proportion of nutrient input which actually passes along the food chains. In some systems this amount may be significant. Gist and Crossley (1975b) estimated calcium flow through a litter arthropod food web to be about half of annual calcium release through decomposition. In other systems fauna may process less calcium (Cornaby et al. 1975, Douce and Crossley ms), and quantitative food chain passage of other elements may be lower. Indirect effects of soil fauna as catalytic agents in mineralization or regulators

of microbial immobilization of nutrients may exceed direct effects of the fauna upon the decomposition process (Crossley 1977b). In any event the accumulation and movement of nutrients in arthropod food chains can be used as a basic means of evaluating their participation in the process of litter decomposition and nutrient mineralization.

Radioactive tracers have proved to be valuable aids for the measurement of nutrient turnover and retention in soil fauna. The generalized model assumes that nutrient content of fauna is the result of intakes and losses (Webster and Crossley 1978). Radioactive tracers are used to estimate rates of assimilation and biological turnover. Other methods (flame photometry, microprobe techniques) measure whole-body elemental contents. Intakes are estimates as those necessary to make up nutrient losses due to turnover and mortality. The predicted intake rates are subject to verification, using radioactive tracers (Webster and Crossley 1978). Systems modeling techniques are invaluable in extending laboratory results to field data sets.

Results of work under this subproject are routinely reported in open literature publication. Since the last contract period two publications pertinent to this subproject have been published:

Best, G. Ronnie, J. Vincent Nabholz, J. Ojasti and D. A. Crossley, Jr. 1978. Response of microarthropod populations to naphthalene in three contrasting habitats. *Pedobiologia* 18: 189-201.

Todd, Robert L., Praktison Sihanonth, D. A. Crossley, Jr. and Kermit Cromack, Jr. 1978. Elemental analysis of terrestrial microflora and fauna with an electron microbeam technique. pp. 265-274 in D. A. Adriano and I. L. Brisbin, Jr. (eds), "Environmental Chemistry

and Cycling Processes, " U. S. DOE Tech. Inform. Cent.,
Springfield, Va., CONF-760429.

Reprints of these publications accompany this Annual Report.

Two manuscripts have been prepared for publication, based on work performed under this subcontract:

T. R. Seastedt, Aruna Kothari and D. A. Crossley, Jr. A simplified gelatine embedding technique for sectioning litter and soil samples. *Pedobiologia* (in press).

Yates, Leslie R. and D. A. Crossley, Jr. Cesium-134 and Strontium-85 turnover rates in the centipede Scolopocryptops nigridia McNeill.

Copies of these manuscripts also accompany this Annual Report.

Current research progress is summarized as follows:

Radioactive tracer accumulation and turnover by soil macroarthropods.

Recent research has been concerned with radiotracer turnover by predaceous members of the larger soil fauna, in contrast to work with the saprophagous forms described in last year's Annual Report. Recently (Nabholz and Crossley 1978) we published results of experiments on turnover and retention of radiocesium by wolf spiders (Pardosa lapidicina). This year we report work with centipedes. These arthropods were found to rank second only to spiders as important predators in a forest floor system (Yates 1977). We studied ingestion, assimilation and turnover of cesium-134 and strontium-85 in the centipede Solopocryptops nigridia, an abundant species in forests of the southeastern United States.

Biological elimination of tracers was evaluated in the context of a generalized retention model described by the equation:

$$Q_t = Q_0(p_1e^{-b_1t} + p_2e^{-b_2t})$$

where Q_t is body radioactivity at any time t , Q_0 is the initial radioactivity ($t=0$), p_2 and p_1 are proportions of input either assimilated or remaining unassimilated ($p_2 + p_1 = 1$), b_1 represents the rate of loss of non-assimilated radioactivity from the gut, and b_2 represents the rate of excretion of assimilated radioactivity.

Radiocesium retention curves for three different age-classes of centipedes are shown in Figures 1, 2 and 3. Radiocesium values for parameters of the general retention model are shown in Table 1. In common with other studies of radiocesium retention by arthropods, rates for gut clearance (b_1) were much higher than rates for elimination of assimilated radiocesium (b_2). Assimilation fractions were high; p_2 suggests that more than 60% of the ingested amount of tracer became assimilated. Rates for both gut clearance and excretion of assimilated tracer decreased with age of centipede, but this is more likely a size-dependent than an age-dependent phenomenon.

Figures 4 through 6 illustrate retention of strontium-85 by the three different age classes of centipedes. Table 2 gives values for radiostrontium parameters of the general retention model described above. Again, rates of gut clearance (b_1) greatly exceeded rates of excretion (b_2). The fraction of radiostrontium assimilated ranged from 50% to 60% of the ingested amount.

The biological interpretation of the two component retention model depends upon the identification of p_2 with assimilation and b_1 with gut turnover, a point developed and argued by Webster and Crossley (1978).

Figure 1. Cesium-134 retention curve for age class 0 (less than one year old) centipedes, Scolopocryptops nigridia.

Shown are means \pm two standard errors. N = 6.

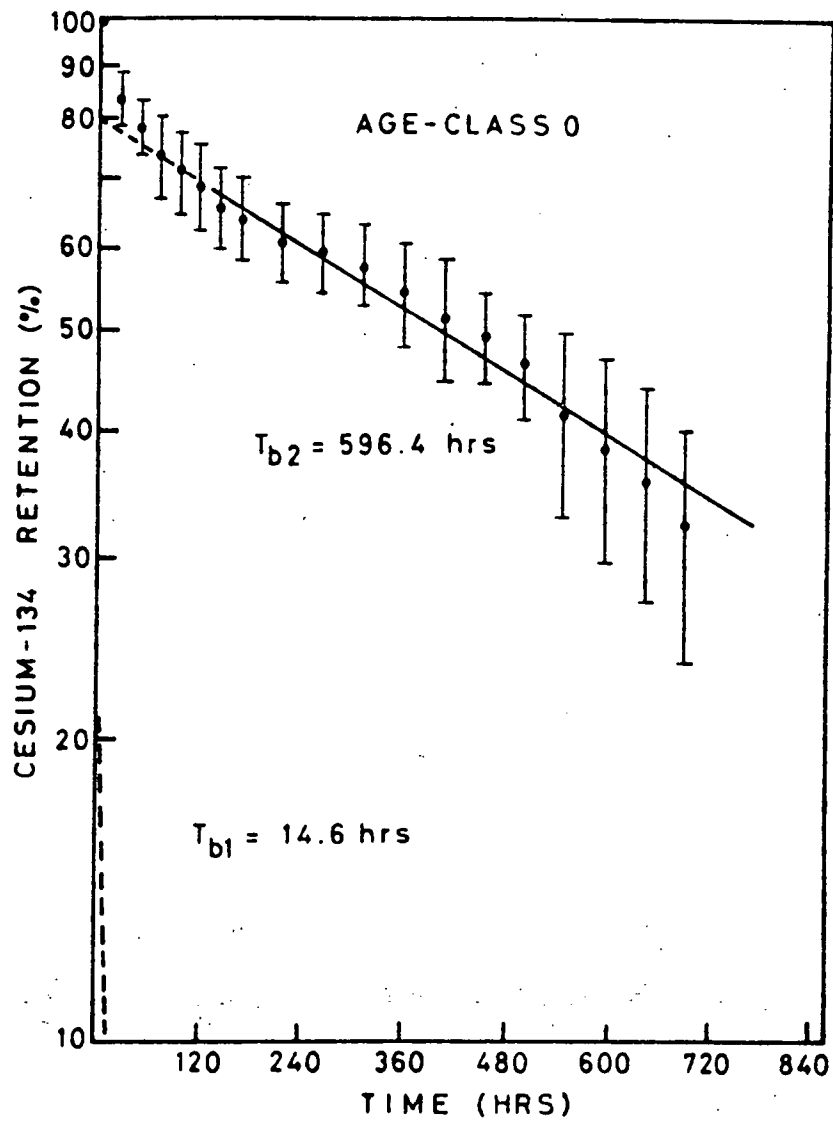


Figure 2. Cesium-134 retention curve for age class 1 (one year old) centipedes, Solopocryptops nigridia. Shown are means \pm two standard errors. N = 6.

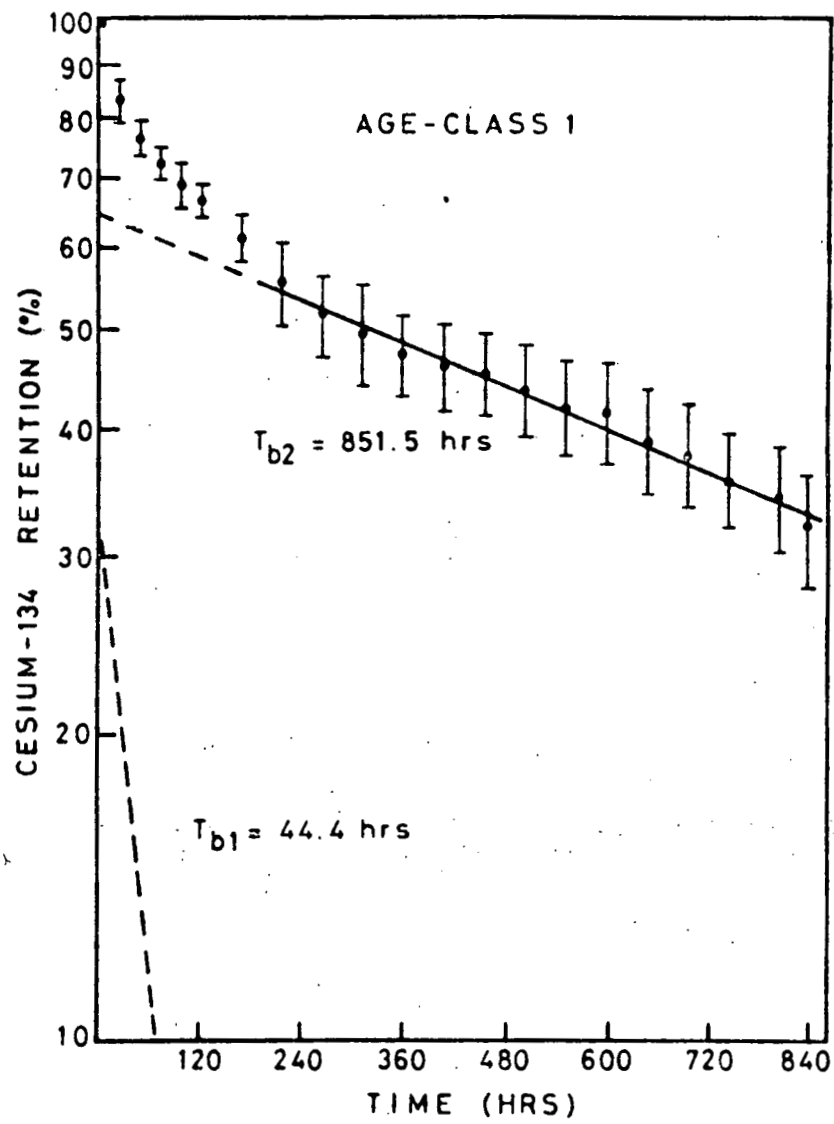


Figure 3. Cesium-134 retention curve for age class 2 (two years old or older) centipedes, Scolopocryptops nigridia. Shown are means \pm two standard errors. N = 6.

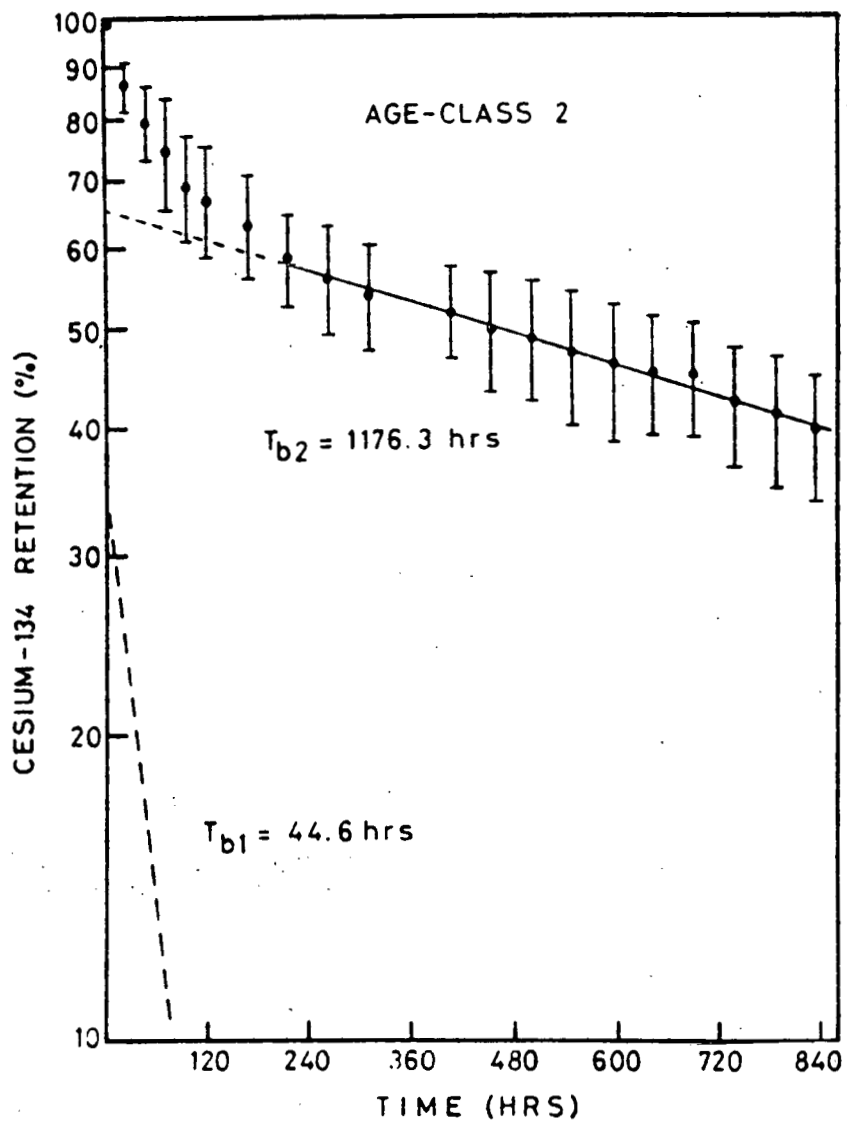


Figure 4. Strontium-85 retention curve for age class 0 (less than one year old) centipedes, Scolopocryptops nigridia. Shown are means \pm two standard errors. N = 6.

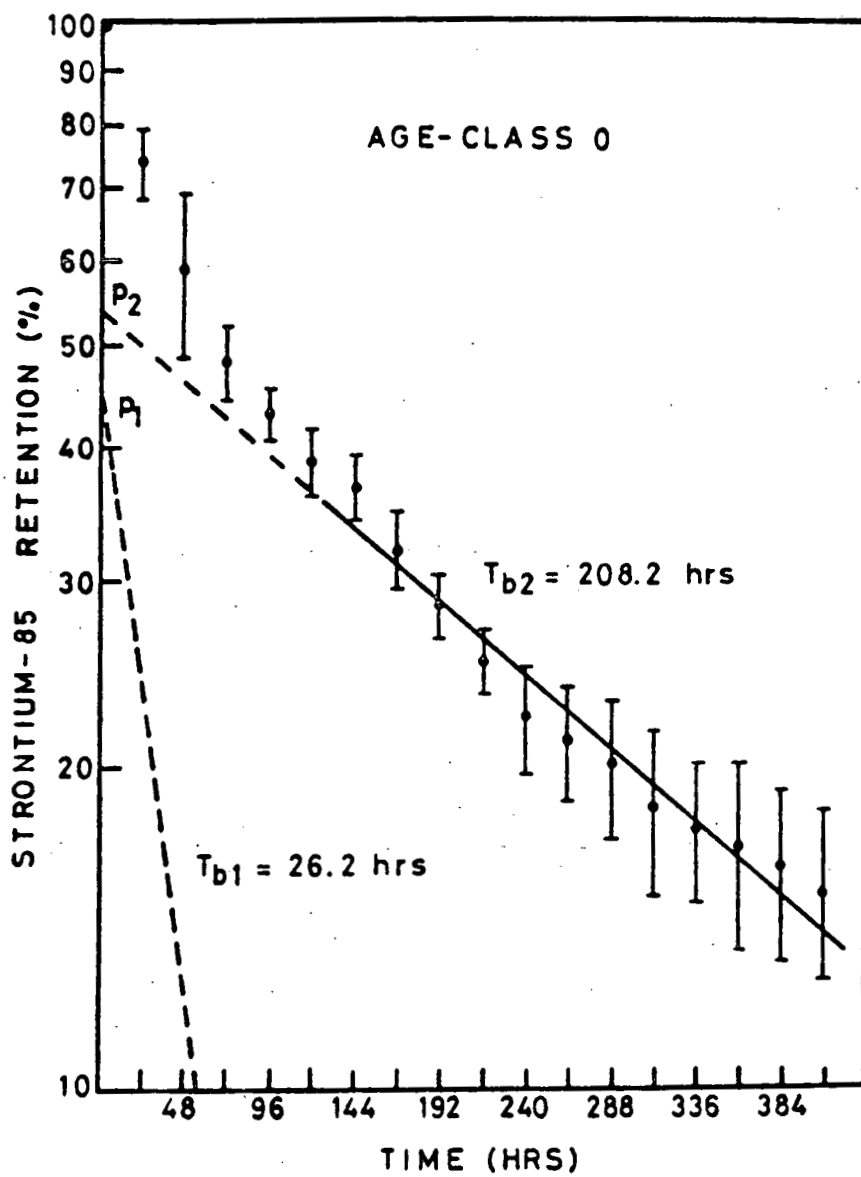


Figure 5. Strontium-85 retention curve for age class 1 (one year old) centipedes, Scolopocryptops nigridia. Shown are means \pm one standard error. N = 6.

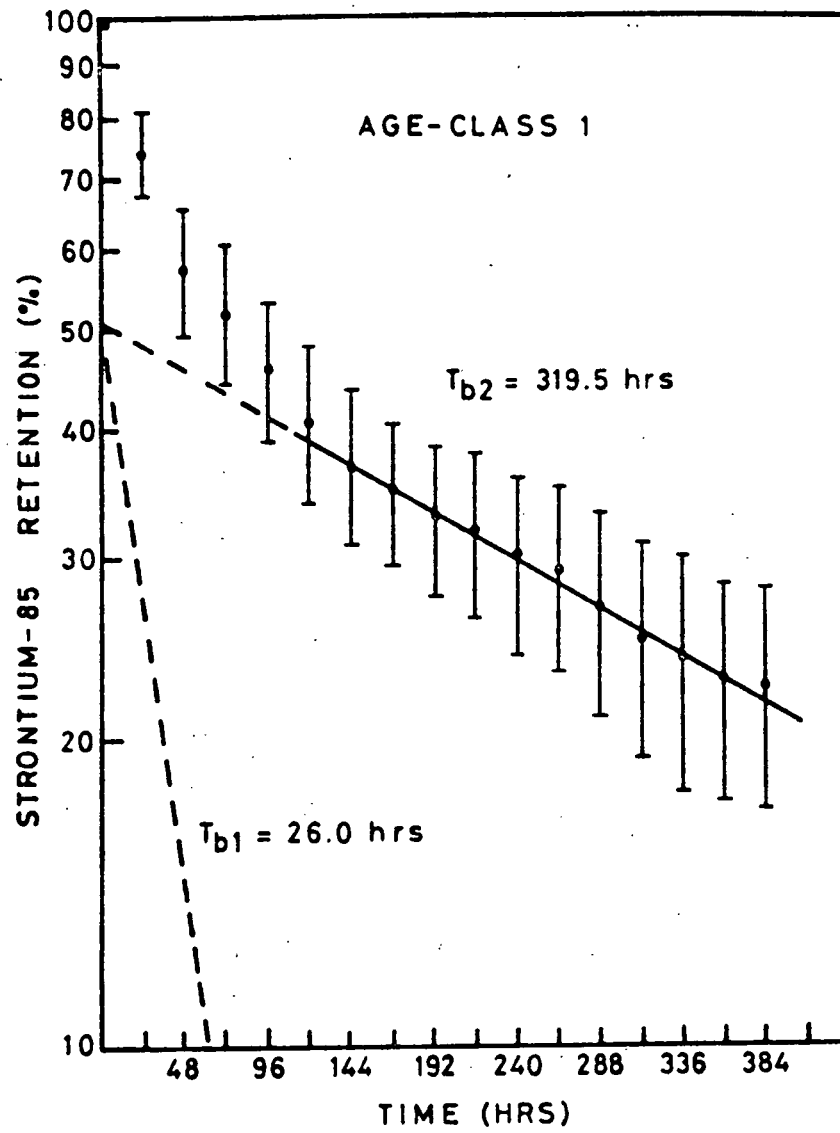


Figure 6. Strontium-85 retention curve for age class 2 (two years or older) centipedes, Scolopocryptops nigridia. Shown are means \pm two standard errors. N = 6.

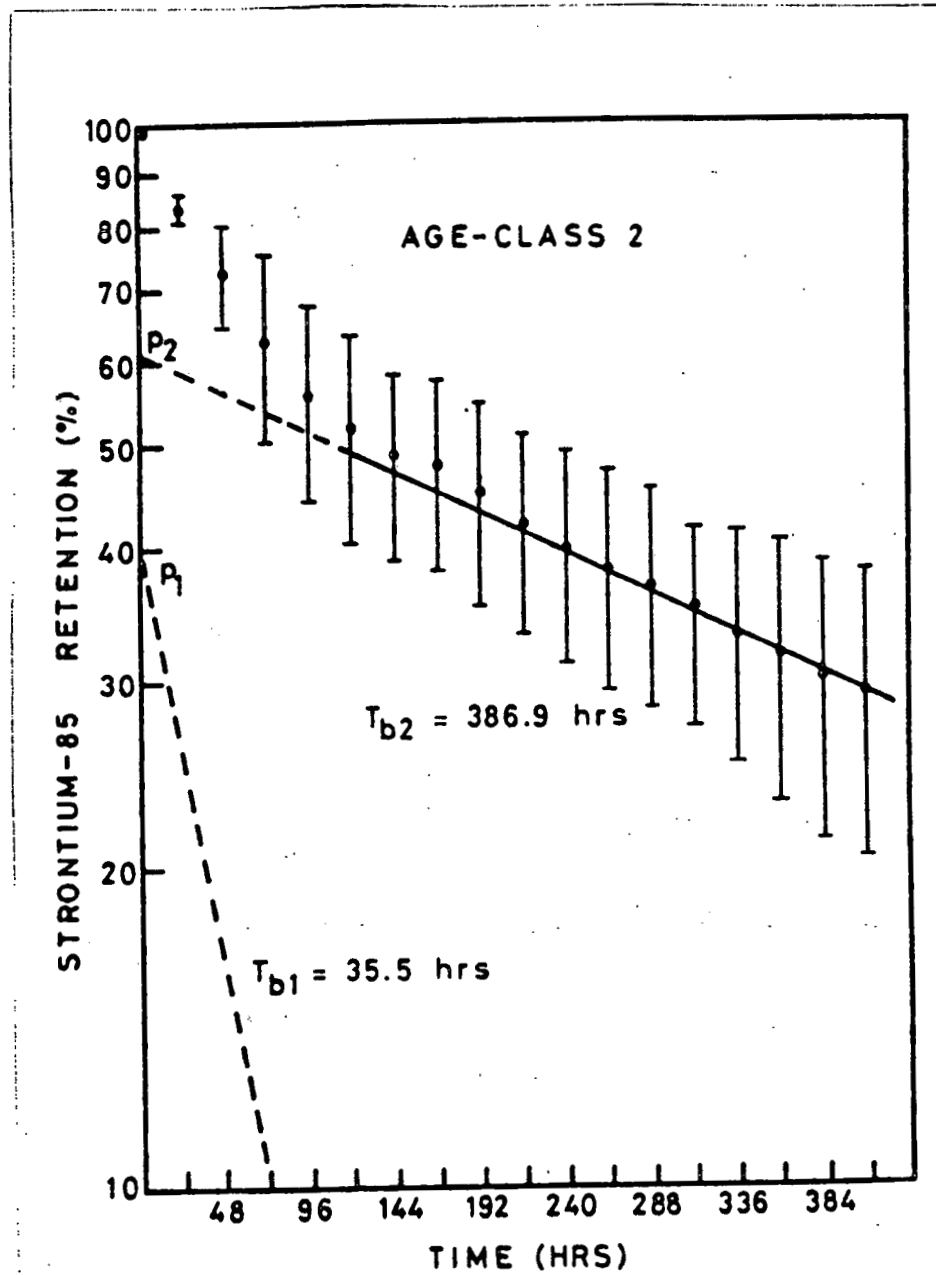


Table 1. Radiocesium values for parameters of the general two-component retention model for three age classes of Scolopocryptops nigridia. Means \pm standard errors. (Symbols explained in text).

	AGE-CLASS 0	AGE-CLASS 1	AGE-CLASS 2
b_1 (hrs ⁻¹)	0.047 \pm 0.0120	0.0156 \pm 0.0020	0.0155 \pm 0.0010
p_1 (%)	20.4 \pm 2.07	32.5 \pm 2.11	34.0 \pm 1.02
b_2 (hrs ⁻¹)	0.0016 \pm 0.000046	0.00081 \pm 0.000055	0.00059 \pm 0.000025
p_2 (%)	79.6 \pm 1.234	65.5 \pm 1.90	65.3 \pm 0.91
r^2	0.99	0.99	0.99

Table 2. Radiostrontium values for parameters of the general two-component retention model for three age classes of Scolopocryptops nigridia. Means \pm standard errors. (Symbols explained in text).

	AGE-CLASS 0	AGE-CLASS 1	AGE-CLASS 2
b_1 (hrs ⁻¹)	0.026 \pm 0.00278	0.027 \pm 0.0018	0.019 \pm 0.0016
p_1 (%)	46.0 \pm 2.97	49.5 \pm 1.88	39.6 \pm 2.01
b_2 (hrs ⁻¹)	0.0033 \pm 0.00021	0.0022 \pm 0.00014	0.0018 \pm 0.00011
p_2 (%)	53.9 \pm 2.94	50.4 \pm 1.81	60.9 \pm 2.04
r^2	0.99	0.99	0.99

A strong argument for the interpretation of b_1 as gut turnover rate includes the observation that, for a given arthropod species, radiotracers with widely varying p_2 and b_2 exhibit similar rates for b_1 (Van Hook and Crossley 1969). Thus we would expect that the rates b_1 for radiostrontium and radiocesium in S. nigridia would be similar, at least within age classes. Tables 1 and 2 show that this is not the case; the rates b_1 seem more characteristic of radiotracer than of age class. Thus it would appear that radiotracer is being voided with feces at rates which differ for the two types of tracers. Alternatively, assimilation mechanisms or internal physiological properties may differ for these elements, enough that the two-component model is less adequate.

Results of these experiments are discussed in greater detail in a manuscript (Yates and Crossley) accompanying this Annual Report.

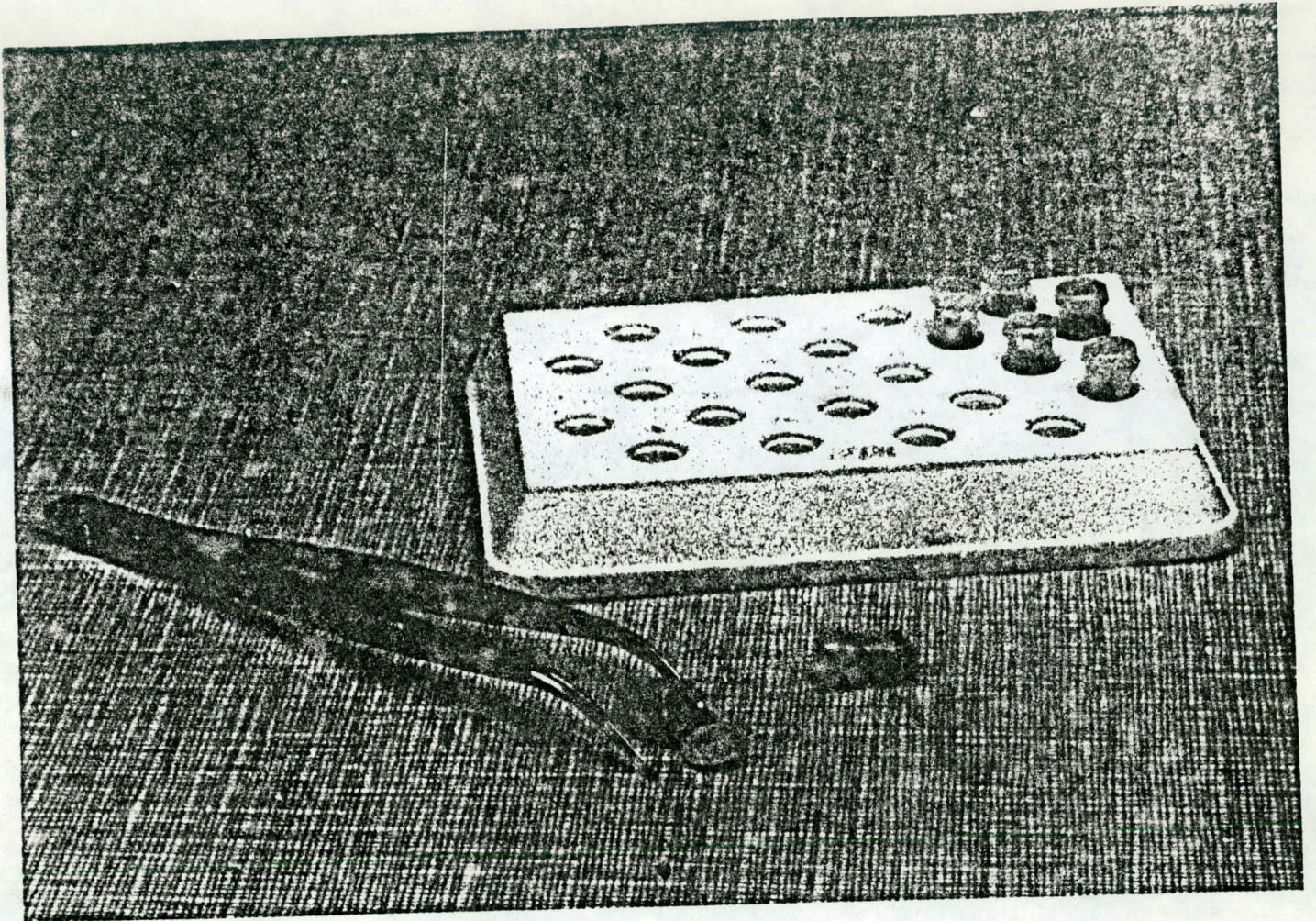
Radiotracer retention by microarthropods. The microarthropods of soil-litter systems, particularly mites and collembolans, maintain impressive population sizes. Earlier soil ecologists (e.g. Jacot 1940) ascribed considerable importance to microarthropods in directly and indirectly affecting decomposition rates. Experimental work with these arthropods has proven to be difficult to perform and results are difficult to verify. Most assessments have been based on attempts to construct energy budgets (Englemann 1966, Mitchell and Parkinson 1976). These assessments tend to fall short because of inadequate information about energy transformations in soil systems. Often workers ascribe almost all CO_2 evolution from soil to the respiration of microbes, leaving little to be derived from roots or from fauna. Nutrient budgets, in contrast, show that

fauna consume a considerable portion of the annual disappearance of litter inputs and associated microflora. Further experimental evidence about the significance of microarthropods is derived from exclusion experiments, in which microarthropod populations are reduced with chemical treatments (Kurcheva 1964, Witkamp and Crossley 1966, Lee 1974, Best et al. 1978, Douce and Crossley ms). Often such experiments demonstrate significant shifts in disappearance of litter or mineralization rates, suggesting that soil fauna are performing a major regulatory role.

We are attempting to develop data on nutrient turnover by microarthropods, following the same general procedures as used for macroarthropods. Earlier we (Kowal and Crossley 1971) and others (McBrayer and Reichle 1971) reported results of experiments in which arthropods were allowed continued access to radioactive tracers, and model parameters were evaluated from uptake curves. Data required that arthropods be sacrificed sequentially. Such experiments yielded large variations in results, due to several factors difficult to control. Better techniques follow the procedures used for macroarthropods, that is, single feedings upon radioactive food with subsequent repeated measurements of the same individuals. Single-tagging experiments have the advantage that model parameters can be later validated in uptake experiments (Webster and Crossley 1978).

The technique we are now using continues to yield good results. Microarthropods are allowed access to food materials tagged with high concentrations (mCi/mg rates) of radioactive tracers. For maintenance and counting, individual microarthropods are kept in BEEM capsules (small plastic capsules) lined with a moistened plaster of Paris-charcoal (9:1)

Figure 7. BEEM Capsule.



mixture (Figure 7). Food materials are added and the capsules with microarthropods are maintained in environmental chambers. At the time of counting, microarthropods are transferred to fresh BEEM capsules. In this manner changes in radioactivity of individual microarthropods are easily followed.

Ongoing research is currently utilizing a species of acarid mite, Tyrophagus longior as an experimental species. Figures 8 and 9 and Table 3 illustrate some current results. In these experiments mites were fed dried activated yeast tagged with strontium-85 or chromium-51. Untagged dried activated yeast was used as a standard food source in BEEM culture capsules. Experiments were maintained in environment chambers at 30° C. Counting was performed with the aid of a 3 x 3 in. NaI (TI) well crystal detector connected to a Packard 410A gamma spectrometer. Results for strontium showed (Figure 8) a two-component retention system yielding parameters which can be interpreted in the context of the general retention model given for macroarthropods. Assimilation values were high (above 60%) and rates were satisfactorily measured. Retention experiments with chromium-51 yielded less satisfactory information (Figure 9). Previously (Van Hook and Crossley 1969, Webster and Crossley 1978) we have shown that chromium is virtually unassimilated in crickets. In those insects the turnover rate for chromium-51 approximated the gut clearance rate (b_1) for other radioactive tracers. Such a similarity exists for ^{85}Sr and ^{51}Cr in Tyrophagus longior (Table 3) but the data for radiochromium show large variation. These experiments are continuing. Eventual validation may be performed by analysis of Ca content of mites

and yeast. Knowledge of turnover rates for radiotracers and elemental content of yeast should yield a prediction of elemental contents of the mites, which can then be compared with measured values.

Figure 8. Retention of Strontium-85 by mites (Tyrophagus longior). Values shown are means \pm two standard errors.

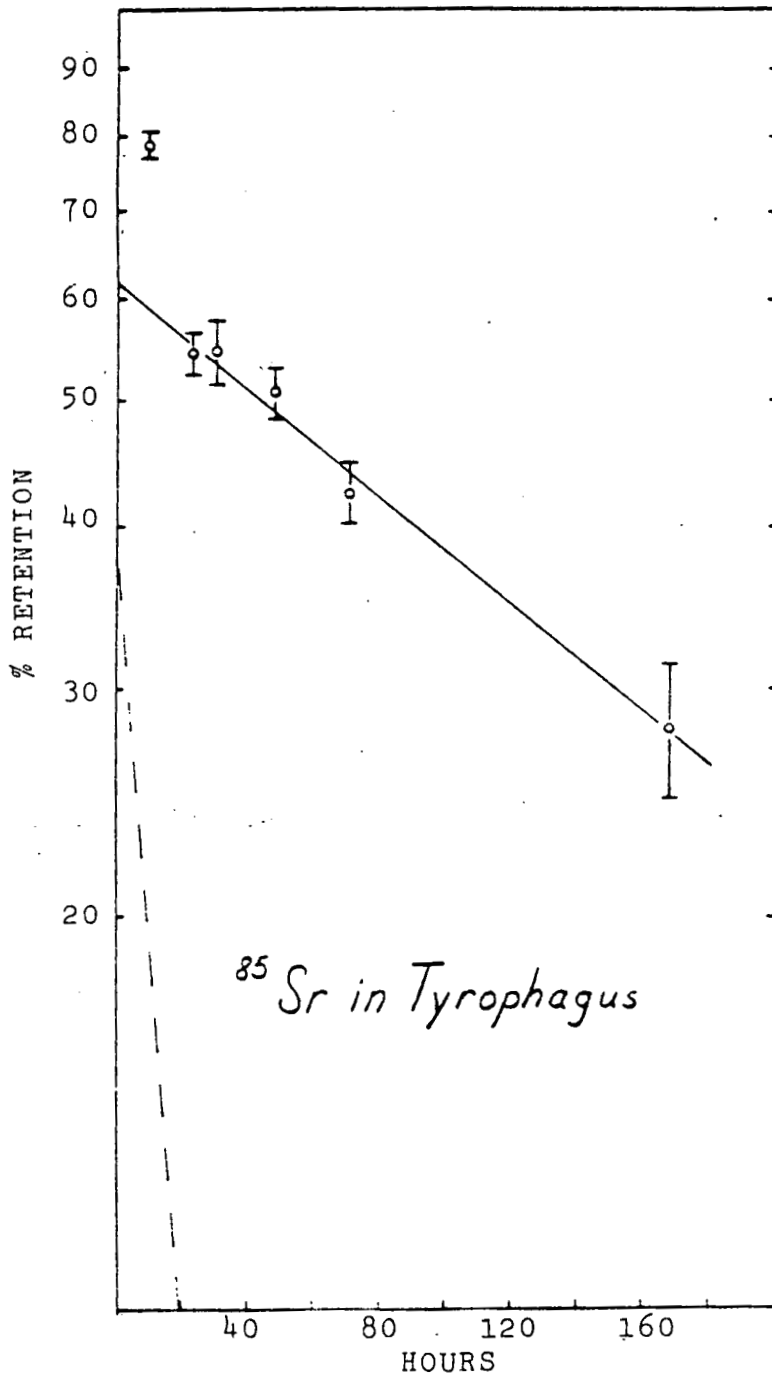


Figure 9. Retention of Chromium-51 by mites (Tyrophagus longior). Values are means \pm two standard errors.

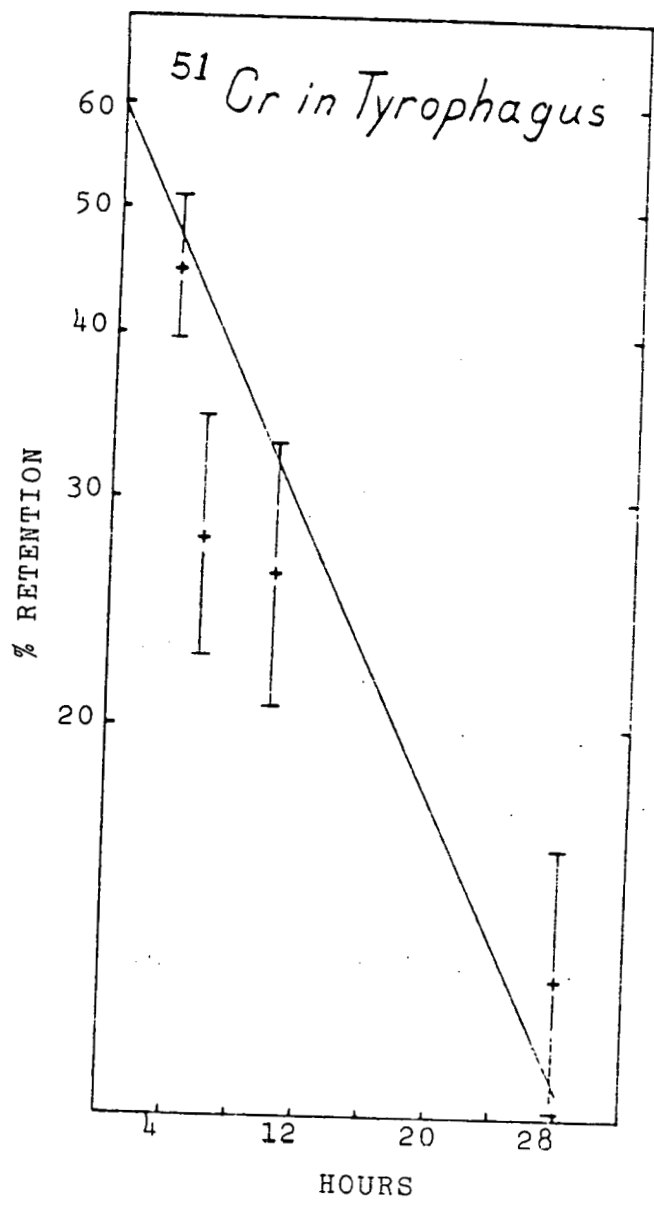


Table 3. Values for parameters of the general retention model for Chromium-51 and Strontium-85 in the mite Tyrophagus longior. Value are means.

Parameter	Strontium-85	Chromium-51
p_1 (proportion)	0.38	0.60
k_1 (days ⁻¹)	1.673	1.490
p_2 (proportion)	0.62	--
k_2 (days ⁻¹)	0.115	--
r (correlation coefficient)	0.80	0.76

Nutrient relations between soil fauna and mycorrhizae. Last year we began investigations on attempts to measure nutrient transfer between mycorrhizal fungi and soil arthropods. Mycorrhizal fungi are plant symbionts, literally "fungus roots", which have been demonstrated to have great importance in plant nutrition (Marx et al. 1970). Plants whose roots possess mycorrhizal associations perform markedly better in nutrient-poor soils. In reforestation projects, inoculations with mycorrhizae may effectively be used as substitutes for fertilization programs. Mycorrhizae receive carbohydrates from plants, and in turn increase nutrient uptake by plants. The amount of primary production shunted to mycorrhizae is not well known, but minimal estimates now suggest that about 30% of primary production appears in fungal growth. Ecologists who use the harvest method to estimate net PP in forests thus may be underestimating PP by a considerable amount (Biever, pers. comm.). Recently, small mammals have been shown to consume mycorrhizal fruiting bodies, and probably act as vectors of spores (Maser et al. 1978). If soil fauna feed upon the hyphae of mycorrhizae, they may regulate nutrient uptake by plants. Last year we reported experimental tagging of fungal hyphae of mycorrhizal species, using radiostrontium and radiocesium tracers. This research is still proceeding.

We have also begun looking at in situ microflora and fauna in soil sections, with a view to demonstrating specific interactions between microflora and fauna. A manuscript (Seastedt, Kothari and Crossley) accompanying this Annual Report describes refined and simplified methods for embedding and sectioning soil cores. Application of the technique has suggested that the calcium-rich exoskeletons of dead oribatid mites are

rapidly invaded by fungal hyphae. The observation has prompted some new research on decomposition and nutrient loss by arthropod remains. Details of the sampling device and first results are given in the accompanying manuscript (Seastedt et al.).

Reassessment of arthropod data sets. We have begun a set of field collections to update and extend existing data sets on arthropod communities in soils and in vegetation. During last year's review an external reviewer noted that efforts in this project were devoted primarily to measurements of rates. He questioned that budgets could be done for nutrients unless nutrient pools could be measured as well. We responded that we still have access to previous data sets on herbivores (Crossley et al. 1975, Duke and Crossley 1975) and soil fauna (Gist and Crossley 1975a), and further, we have access to data sets developed on other projects. Still, the criticisms have merit and accordingly, we have begun accumulating new data sets on soil arthropod communities. These sets will consist of individuals per species, weights of individuals, and nutrient contents, together with appropriate collection data. They will be accumulated over a two-year period.

Collections of arthropods in vegetation began last year with attempts to evaluate effectiveness of insecticide applications in the granitic out-crop project described below. Questions were raised about rates of reinvasion of treated island ecosystems. We devised a set of obstacle traps ("bumper traps") to sample flying insects above the island ecosystems. Catches were encouraging and we are expanding usage of the technique.

(Forest entomologists have used window sash traps, suspended in trees

as a method for collecting flying insects for many years. Disadvantages of the traps are that collections are relative, not absolute, and they are expensive to construct and maintain (Coulson *et al.* 1970). We have overcome these difficulties by (1) using inexpensive plastic parts and (2) sampling in lower vegetation where catches are more readily compared to the actual arthropod community on vegetation).

Quantification of the bumper trapping technique requires a relatively large expanse of uniform vegetation. Such an area is available in a set of agroecosystem experiments at the Horseshoe Bend facility, operated by the Institute of Ecology at the University of Georgia campus. We are operating traps in that area, and making simultaneous D-Vac collections of arthropods in vegetation. Details of the trapping procedures, and results of trapping, will be given in later Reports.

Soil arthropod communities are being sampled with high-efficiency extractor methods (Merchant and Crossley 1970, Seastedt and Crossley 1978) for microarthropods. The macroarthropod data set is being developed with pitfall trapping methods (Gist and Crossley 1973).

We are reassessing procedures for nutrient analysis of arthropod collections. Currently, analysis is based upon flame photometry or atomic absorption spectrometry. If feasible, we intend to use the inductively coupled plasma emission spectrograph (ICP) housed in the Institute of Ecology at the University of Georgia for future analysis of macroarthropod samples. At present, we are comparing methods of digestion and analysis for the ICP with the procedures used for AA or flame photo-

metry. For microarthropods, the microprobe (an energy dispersive X-ray analyzer) will continue as the method of choice, as described in a recent publication (Todd et al. 1978).

Subproject (2): Mineral element cycling and trophic dynamics
in granitic outcrop systems.

D. A. Crossley, Jr. and J. Vincent Nabholz

The objectives of this work have centered around the use of the small depression communities on granitic outcrops as small, island ecosystems. Initially we studied radioactive fallout and nutrient element movement through food chains in these systems (Crossley et al. 1975, Duke and Crossley 1975). We have completed a set of field experiments examining functional properties of these ecosystems. Perturbations were used to evaluate systems stability characteristics (resistance to perturbation and resilience following perturbation).

This year we have synthesized results, in the form of two manuscripts for open-literature publication:

The nutrient budgets of rock outcrop ecosystems and their response to selected perturbations. J. Vincent Nabholz and D. A. Crossley, Jr.
An inexpensive weir and proportional sampler for miniature watershed ecosystems. J. Vincent Nabholz, D. A. Crossley, Jr. and G. Ronnie Best.

Copies of these manuscripts accompany this Annual Report.

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