

# Trophic relationships and phosphorus budget of an old-field soil ecosystem

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Middendorf, Peggy A. (Rutgers U., New Brunswick, N.J.) Trophic relationships and phosphorus budget of an old-field soil ecosystem. Hutcheson Memorial Forest Bull. 2(4):6-14. 1971. An exploratory study was made of the food web relationships and phosphorus budget of an old-field soil ecosystem utilizing radioisotopes. Phosphorus<sup>32</sup> was injected into the dominant forb, ragweed (*Ambrosia artemisiifolia*). Subsequently its movement through the copious external stem flow of ragweed and various soil faunal groups was recorded.

The radioisotope was detected in macroarthropods and earthworms but not in microarthropods. Large but consistent variability occurred in radioisotope uptake by the fauna. A complex of environmental and physiological factors contributed to this variability which has only infrequently been reported for such studies. Differences in radioisotope uptake curves of the various soil animal groups were used to hypothesize their trophic relationships.

Stem flow may add significant amounts of phosphorus to the soil as compared to the total amounts found in the soil fauna populations. After six weeks, however, the bulk of the isotope still resided in the ragweed tissues.

Integrated studies of terrestrial ecosystems are essential to an ultimate understanding of their dynamics under natural and disturbed conditions. Basic work on the structure and functional processes of ecosystems, however, is far from complete. Most research has been done on segments of ecosystems dealing with such aspects as primary productivity (Whittaker and Woodwell 1968), floral diversity (Whittaker 1965), and energy flow (Odum, Connell, and Davenport (1962)). The advent of radionuclide tagging techniques has greatly facilitated studies of mineral cycling (Olson, Peters, and Anderson 1969) and food web relationships (Wiegert, Odum, and Schnell 1967). These studies have rarely dealt with detritus-based ecosystems such as the soil. However, since primary consumption of net productivity is relatively small (Bray 1961, 1964), most of the organic matter produced each year ultimately enters the soil system (Malone and Swartout 1969). The soil also is a reservoir for vast quantities of essential nutrients (Peters, Olson, and Anderson 1969). Consequently, the soil ecosystem plays a major role in energy and mineral flow. This is a preliminary study of certain functional aspects of the soil ecosystem.

Comprehensive research on the soil food web has only infrequently been tried (Reichle and Crossley 1965). Trophic relationships of detritus-feeding organisms have largely been inferred from direct observation of the feeding patterns of individual groups (Wallwork 1958; Engelmann 1961). Yet, radionuclide tagging techniques have yielded much more information on food web structure than direct observation alone. Their use in broad trophic studies has been

largely restricted to above-ground systems (Odum and Kuenzler 1963; de la Cruz and Wiegert 1967; Rose, Monk, and Wiegert 1969). Since the efficiency and versatility of this technique is now recognized (Wiegert and Odum 1969), its usefulness in an integrated trophic study of soil organisms is strongly suggested.

The first objective was to test the adaptability of the radionuclide tagging technique in delineating a soil food web with phosphorus <sup>32</sup>. Organisms of various trophic levels appear to exhibit characteristic radioisotope uptake curves as shown by previous studies in autotroph-based food complexes. Such uptake curves were calculated here for a soil ecosystem and utilized in interpreting trophic positions of the particular faunal groups involved.

Secondly, I made a brief examination of a phosphorus budget in an old-field soil system. Entire mineral cycles are defined in terms of the paths of movement of the mineral, storage reservoirs, and rates of transfer between various ecosystem compartments (Rice 1965). My objective, however, was simply to evaluate the importance of several broad routes of P<sup>32</sup> movement in the soil-ragweed system of an old field. Observations by Shure (1969) revealed that a great quantity of moisture collects on the stem surfaces of ragweed (*Ambrosia artemisiifolia* L.), a dominant forb of the study area, and flows down the stem. This stem flow contains dew, transpiration moisture, extrametabolites, and various minerals exuded by the plant. The role of stem flow in the mineral and hydrological cycle of an old field is as yet little understood. Consequently, the magnitude of P<sup>32</sup> in the stem flow relative to that in the soil fauna and ragweed plants was measured.

In short, the objective of this study was to examine the following functional characteristics of an old-field soil ecosystem: 1) trophic relationships of the soil food web using radioisotope methodology; 2) distribution of the radionuclide in the soil-ragweed system.

## Materials and methods

### PREPARATION OF THE STUDY AREA

The study area as described by Shure (1969) was located in a field adjacent to the William L. Hutcheson Memorial Forest in East Millstone, New Jersey. In early spring of 1969, a 30.5 x 30.5 m area of this field was cultivated to a depth of 15 cm and abandoned. Subsequently, a dense growth of ragweed (*Ambrosia artemisiifolia* L.) dominated the vegetation. This common annual is a pioneer species invad-

ing fields the first year after disturbance (Bard 1952) In early July four plots 2m<sup>2</sup> were chosen for uniformity of ragweed density. Metal sheets were placed at the boundaries to a depth of about 25 cm to reduce migration of the soil animals in and out of the plots.

The radioisotope P<sup>32</sup> was applied to the ragweed, utilizing the "stem well method" (Wiegert and Lindborg 1964) modified by Shure (1969). On August 1, 1969, twenty-eight ragweed plants were randomly selected in each plot and individually labeled with 25 uCi of P<sup>32</sup> as Na<sup>2</sup>HP<sup>32</sup>O<sub>4</sub> in aqueous solution. The day was sunny, and P<sup>32</sup> activity throughout the plants indicated that the plants absorbed the isotope very rapidly. A total of 168 plants was labeled over an area of 12 m<sup>2</sup>. That is, 4200 uCi were applied or 350 uCi/m<sup>2</sup>.

Two randomly selected plots were utilized as controls. The other two plots were used to measure the quantity and P<sup>32</sup> concentration of the stem flow. In order to intercept this liquid, large plastic tape wells (volume 15 cc) were applied to the tagged ragweed stems. They were placed above the "labeling wells" to prevent contamination.

#### SOIL FAUNA SAMPLING

Samples of the fauna were collected on days 5, 12, 19, 26, and 39 after labeling. On each date annelids, macroarthropods and microarthropods were removed using one of two types of samples. Each technique sampled a specific category of organisms as follows.

Macroarthropods and earthworms were hand sorted from a 25 cm<sup>2</sup> by 5 cm deep soil sample removed from each plot. The animals were killed immediately in 10% formalin, poured into an ultra-fine sieve (270 meshes/inch; 53 micron opening) to be washed with 0.1 N HCl and individually placed in numbered planchets. The acid wash was used to remove any P<sup>32</sup> adsorbed to body surfaces.

Microarthropods were extracted using the Berlese funnel method. Three soil cores were taken from each plot (volume 115 cc, height 5 cm) with a cylindrical steel corer (Southwood 1966). The samples were contained in polyethylene cylinders which fit both into the corer and the extractor.<sup>1</sup> The latter was modeled after a small funnel extractor with an air conditioning unit described by Macfadyen (1961). A constant temperature-humidity gradient was maintained. Air above the cores was kept at 35°C and 0% relative humidity, below the cores 15°C and 95% relative humidity. The collecting jars beneath the funnels were partially filled with 10% formalin in which the animals were collected, killed, and fixed. The cores were kept for one week in the Berlese apparatus to assure efficient extraction of microarthropods. The organisms were then washed with acid and stored in 70% alcohol until sorted. They were identified and counted with the aid of a binocular microscope and placed into numbered tared planchets.

<sup>1</sup> Built by Dr. H. T. Streu and associates, Department of Entomology and Economic Zoology, Rutgers—The State University, New Brunswick, New Jersey.

Hand and Berlese samples were taken from every labeled ragweed plot as well as nearby non-labeled soil on each sampling date. The radioactivity of these latter samples served to differentiate tagged from untagged samples.

All samples, once in planchets, were oven-dried for 24 hours at 100°C. The samples were then counted in groups of 50 in a gas flow detector (Nuclear Chicago—Model =1049) with an automatic planchet changer and printout. The instrument was operated in the Geiger-Muller region using Q gas (1.3% butane, 98.7% helium) and a micromil window with a density less than 150 g/m<sup>2</sup>. All samples were counted once for 10 minutes and subsequently weighed using an Oertling balance (Model R20) sensitive to 0.1 mg.

Counts were corrected for background, efficiency, and physical decay to day 0. They are expressed as activity densities in disintegrations per minute per milligram oven-dry weight (dpm/mg). Self-absorption corrections were not made. Most of the samples were equal to or less than 10-12 mg/cm<sup>2</sup> in thickness. Because P<sup>32</sup> has such a high energy particle, self-absorption at these thicknesses is generally less than 5% (Wang 1969). Geometry differences in samples were also ignored.

Three ragweed plants were removed on days 5 and 26, and the leaves, flowers, stems and roots of each weighed separately. Three subsamples of each of these organs from each plant were dried, weighed, and assayed for radioactivity.

Stem flow was collected from the stem well plots early in the morning on thirteen days throughout the study period. A hypodermic needle was used to extract the liquid from the stem wells. Stem flow from seven plants was consolidated into one sample, making four samples per plot. Filter paper was used to remove coarse debris from the liquid and the volume of the sample recorded. A 4-cc subsample of each was pipetted into a planchet, evaporated with an infrared lamp, and the residue assayed for radioactivity.

## Results

### UPTAKE OF P<sup>32</sup> BY THE SOIL FAUNA

#### *Proportion of each population tagged*

Sufficient isotope was introduced into the plants to insure that at least some proportion of the earthworm, and macroarthropod populations eventually became labeled (Figures 1 and 2).

Increasing proportions of earthworm, Hymenoptera, and Chilopoda populations were tagged over time. However, the percentage labeled of Diplopoda and Coleoptera (adults and larvae) was more erratic throughout the study. Hemiptera (nymphs) were the only macroarthropod group that was consistently not labeled. Likewise, no radioactivity was detected in the microarthropods including Acarina, Collembola, Thysanura, Symphyla, and small Diptera (larvae). While occasional samples would have some radio-

activity, it was never very far above normal background counts or of consistent enough occurrence that any discussion or conclusions could be made. The density of these populations is shown in Tables 1 and 2.

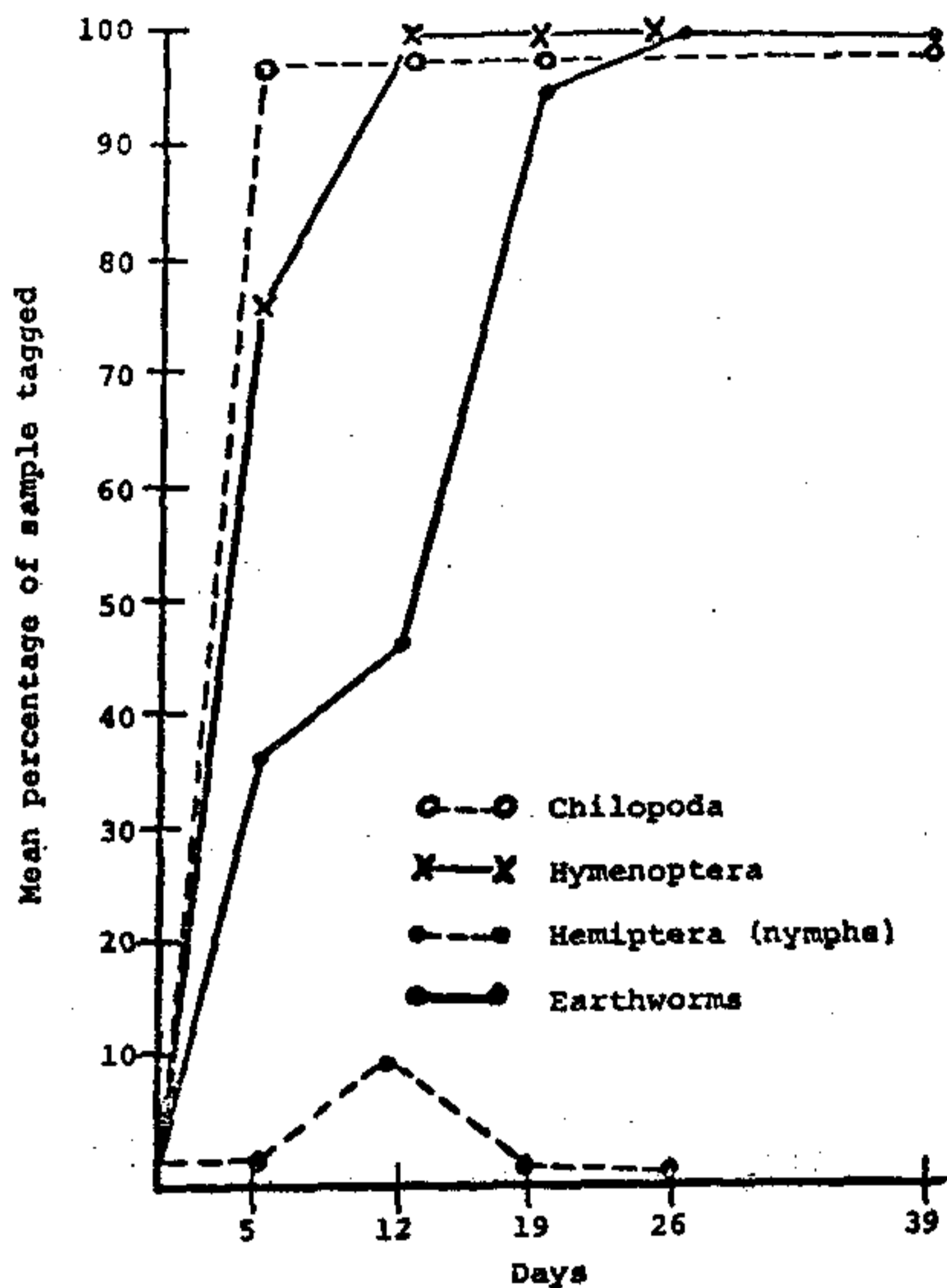


Figure 1. Percentage of total invertebrates collected that were labeled with  $P^{32}$  on a given sampling day.

Table 1. Numbers per meter<sup>2</sup> of soil invertebrates in experimental plots. Data for handpicked samples.

Taxonomic group	Day				
	5	12	19	26	39
Earthworms	112	67	22	13	352
Coleoptera (larvae)	13	22	16	29	16
Coleoptera (adults)	8	16	26	22	3
Hymenoptera	16	67	10	282	23
Chilopoda	13	26	22	13	4
Diplopoda	21	27	10	13	13

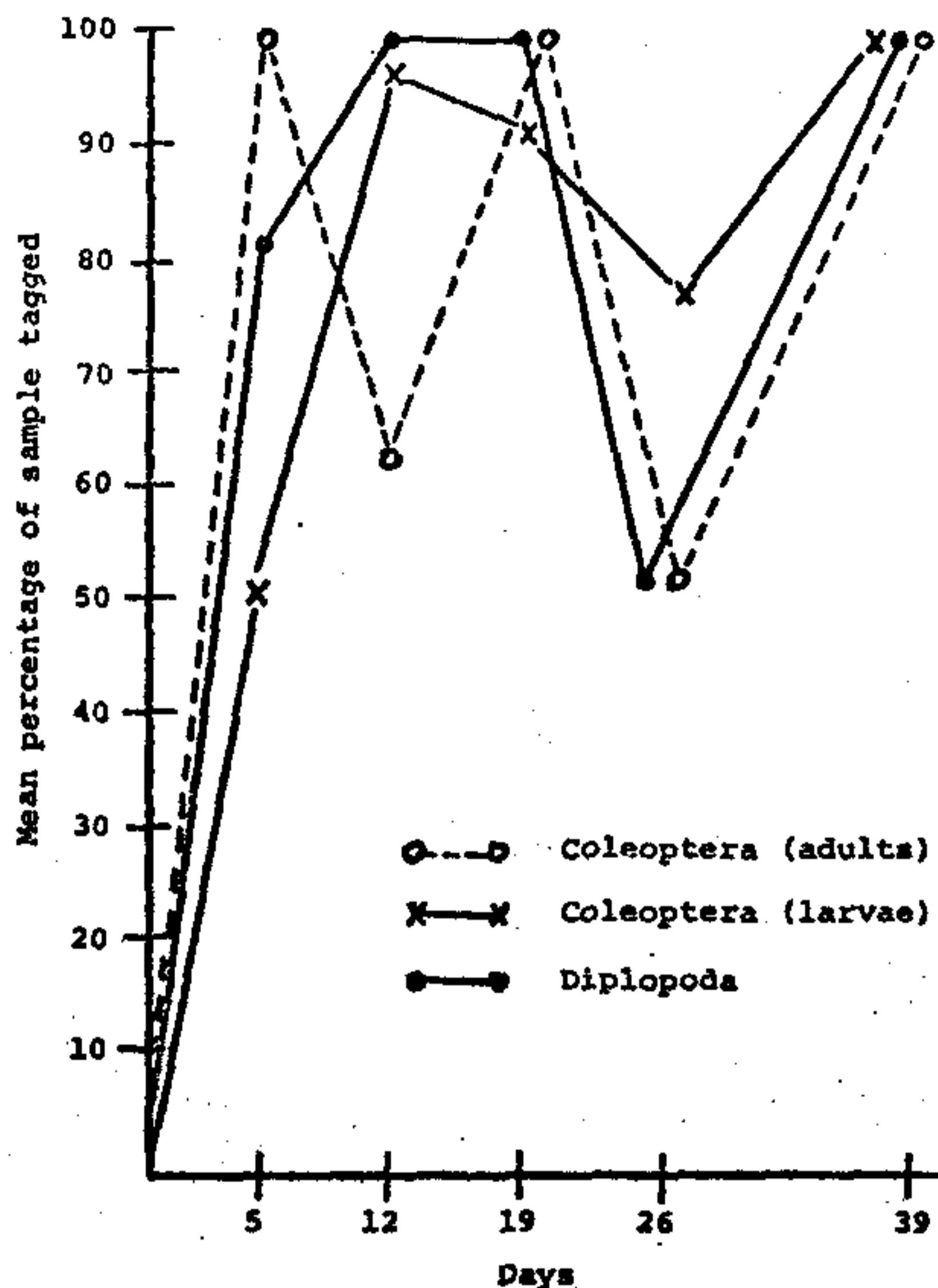


Figure 2. Percentage of total invertebrates collected that were labeled with  $P^{32}$  on a given sampling day.

#### Variability of activity densities

The activity densities of labeled individuals of populations from the handpicked samples were not randomly distributed (Table 3). The high degree of variability involved in these skewed distributions was measured by a coefficient of variation (C.V.):

$$C.V. = \frac{s}{y} (100\%) \text{ where } y = \text{mean} \\ s = \text{standard deviation}$$

None of the C.V. means among populations (Table 4)

Table 2. Numbers per meter<sup>2</sup> of soil invertebrates in experimental plots. Data for Berlese samples.

Taxonomic group	Day				
	5	12	19	26	39
Acarina	3196	5344	2655	4786	6360
Collembola	860	885	1114	557	2163
Thysanura	327	819	983	459	491
Symphyla	163	32	0	0	131
Hemiptera (nymphs)	459	524	327	360	327

Table 3. List of activity densities of individuals from major soil invertebrate populations.<sup>a</sup> Activity densities are arranged in sequence.

Taxonomic group	Activity density (dpm/mg)	Taxonomic group	Activity density (dpm/mg)
<i>Earthworms</i>	6	<i>Hymenoptera</i>	161
	8		222
	17		504
	17		522
	20		691
	20		774
	27		796
	38		843
	39		887
	73		887
	99		909
	113		1,296
	146		1,365
	344		1,935
	346		6,517
<i>Coleoptera</i> (larvae)	23	<i>Chilopoda</i>	111
	54		371
	89		491
	222		600
	293		677
	11,995		812
<i>Coleoptera</i> (adults)	26		1,205
	79		8,886
	187	<i>Diplopoda</i>	4
	425		5
	566		19
	1,532		38
	2,282		77
	3,387		

<sup>a</sup>Data presented for earthworms, *Coleoptera* (larvae), *Coleoptera* (adults), and *Chilopoda* were collected on day 19; for *Hymenoptera*, day 12; for *Diplopoda*, day 5.

are significantly different ( $t = .74, P > .50$ ), indicating that although the variability is large, it is fairly constant.

An analysis of variance (ANOVA) was performed on the  $\log_{10}$  of the individual activity densities of a particular taxonomic group for each sample day and plot treatment. Frequently the greatest source of variability was due to plot-to-plot variation. In some cases these differences were even greater than those expected due to chance alone. Inadequate sample size in handpicked samples also occurred with less abundant groups and populations that migrated from the top few inches of the soil during periods of environmental stress associated, for instance, with too much or too little moisture. This accounts for missing data of particular groups on certain sample days.

*P<sup>32</sup> uptake curves of the tagged soil fauna*

Six major taxonomic groups dominated the hand-picked samples. To analyze differences in their up-

Table 4. Mean coefficients of variation (C.V.)<sup>a</sup> for activity densities of individuals from major soil invertebrate populations.

Taxonomic group	Mean C.V. for group (C.V. $\pm$ s) <sup>b</sup>	Number of observations
<i>Earthworms</i>	1.55 $\pm$ .48	146
<i>Coleoptera</i> (larvae)	1.36 $\pm$ .35	27
<i>Coleoptera</i> (adults)	1.44 $\pm$ .49	15
<i>Hymenoptera</i>	1.28 $\pm$ .26	93
<i>Chilopoda</i>	1.04 $\pm$ .81	19
<i>Diplopoda</i>	1.07 $\pm$ .10	17
Mean C.V. for all groups throughout study (C.V. $\pm$ s) <sup>b</sup>	1.29 $\pm$ .43	317

<sup>a</sup>Coefficient of variation (C.V.)  $s/y$  where  $y$  = mean activity density of group on a particular day and  $s$  = one standard deviation of the mean.

<sup>b</sup>Where  $s$  = one standard deviation of overall average C.V.

take of the isotope, the  $\log_{10}$  of the activity densities of the tagged individuals in each taxonomic category was grouped according to the days on which they were collected. A randomized unbalanced ANOVA (Steel and Torrie 1960) with three sources of known variability (days, groups-within-days, and organisms-within-groups) was performed, Table 5 shows there were significant differences over time and between groups.

The expected differences over time reflect the gradual influx of P<sup>32</sup> into the soil fauna. Of greater interest are the differences between the groups at each time period. These differences can be used to infer the actual trophic position of the particular animal. From these uptake curves (Figure 3) several major differences are notable.

*Hymenoptera* became very highly labeled many times faster than all other groups. They initially acquired a heavy concentration of P<sup>32</sup>, continued to accumulate the isotope throughout the study, and at

Table 5. Analysis of variance table of  $\log_{10}$  activity densities of major soil invertebrate populations collected on successive sampling days.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value
Total	317	264.31		
Days	4	86.04	21.51	8.62**
Groups (days)	25	62.41	2.50	6.23**
Organisms (groups [days])	289	115.86	.40	

\*\*Significant at .005 level.

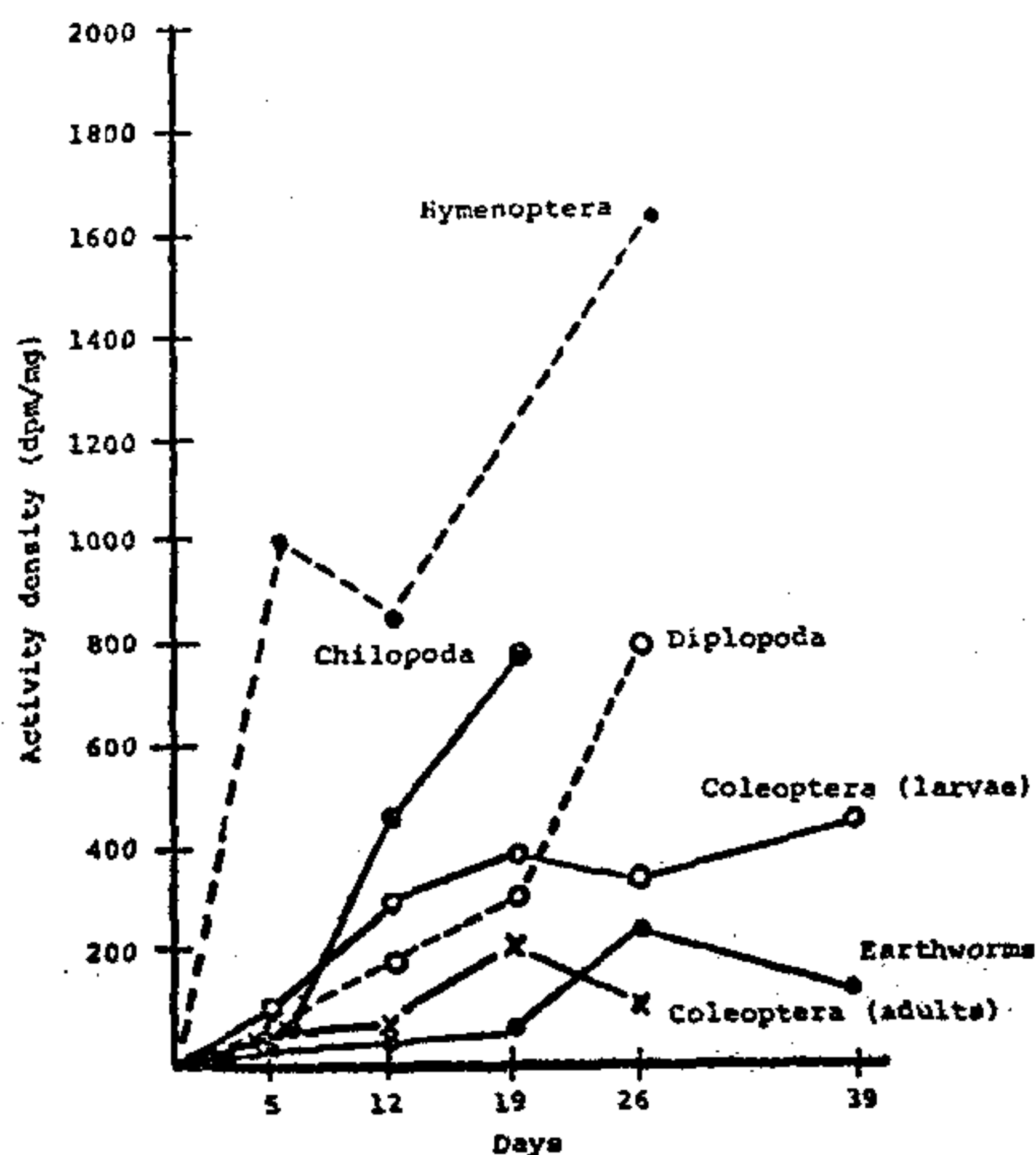


Figure 3. Average activity density (dpm/mg) of major soil invertebrate populations on five sampling days. Number of observations for each population on a particular day is variable.

all times maintained activity densities an order of magnitude greater than all other groups. Earthworms, Coleoptera (adults), and Diplopoda maintained relatively low population levels of the isotope and tended to peak later in the study. The uptake curve for Coleoptera larvae was higher than the adult curve, and the larval population reached its maximum concentration later than the adults.

#### *Addition of P<sup>32</sup> to the soil by stem flow*

Radioactivity of stem flow in terms of dpm/microliter was highly dependent upon the amount of rainfall that occurred 24 hours preceding collection. In order to eliminate the covariant effect of rain dilution, an analysis of the P<sup>32</sup> concentration of the stem flow included data for rainless days only. Significant decreases occurred over time in the isotopic concentration of this liquid (Figure 4).

Of greater interest is the impact of the P<sup>32</sup> in this liquid on the soil system. Figure 5 contrasts the P<sup>32</sup> levels of several of the animal groups in control versus stem well plots. The results of these comparisons are not clear-cut; however, there are several points of interest. In two situations when sample size happened to be exceptionally large, the control plot levels were significantly higher than in the stem well plots (earthworms on day 5, Hymenoptera on day 26). Also the radioactivity body burdens were higher in many cases in control plots than those in the stem well plots although not significantly so. This trend indi-

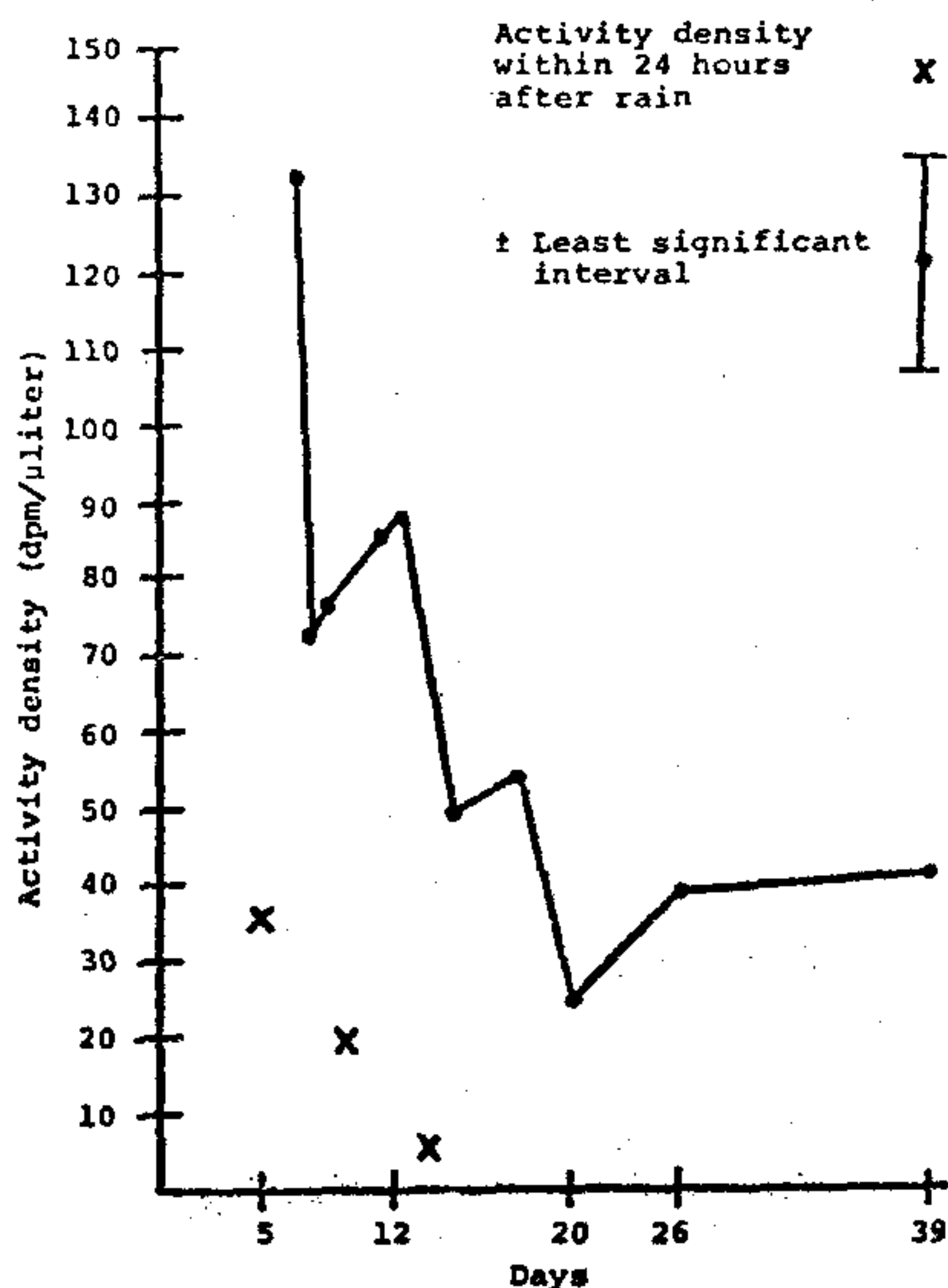


Figure 4. Average activity density (dpm/uliter) of stem flow removed from stem well plots of 13 days throughout the study. Each point represents the mean of eight samples.

cates that stem flow may have an important role in addition of phosphorus to the soil mineral pool, perhaps augmenting the amount available to the fauna. Although the data are not conclusive, employment of a more extensive sampling program could easily determine the reality of these trends.

#### *P<sup>32</sup> budget and dispersal*

A budget for the instantaneous distribution of P<sup>32</sup> in various compartments of the old field soil system is presented for days 5 and 26 (Figure 6). Most of the original isotope remained within the plants on both days; however, a deficit of 16% existed by day 26. That is, approximately 1/6 of the P<sup>32</sup> was unaccounted for at this time, presumably lost mainly to the soil sink and somewhat to above-ground herbivory.

Stem flow and soil fauna fractions contained a relatively minute amount of the total P<sup>32</sup> in the study area. A rather large increase occurred in three weeks within these fractions, but they still contained less than 1% of the total P<sup>32</sup> injected into the system. The stem flow, interestingly enough, contained a larger portion of the isotope than the overall faunal fraction. This observation supports the suggestion that stem flow may carry fairly large amounts of phosphorus into the soil.

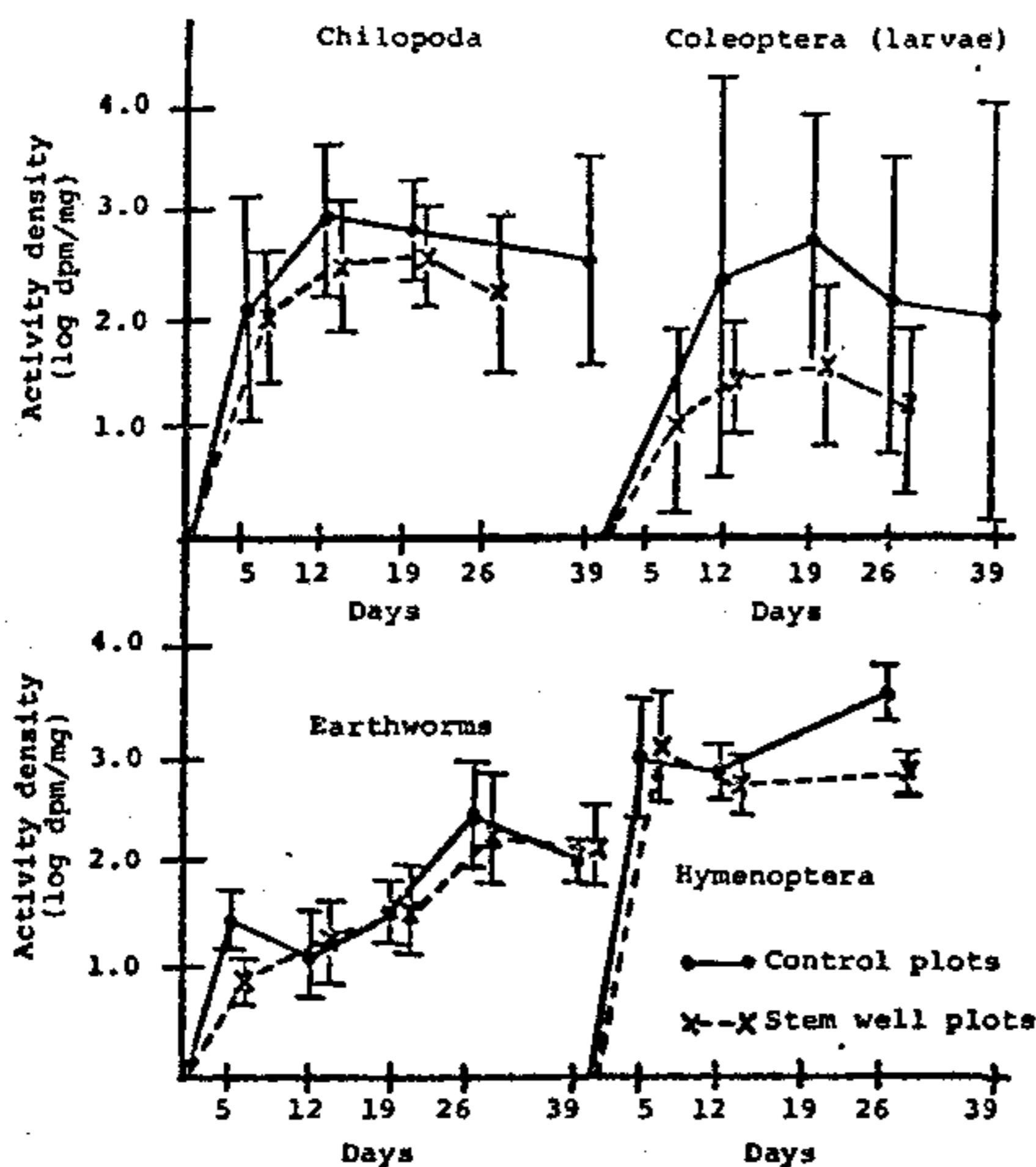


Figure 5. Average activity density (log dpm/mg) of four invertebrate populations removed from control and stem well plots on five sampling days. Number of observations for each point is variable. Least significant interval (LSI) around each mean.

The budget is presented for these days only since ragweed data were collected at these two times. An average value for the ragweed at all times would be inaccurate, since activity densities in the plant tissue change significantly over time (Shure and Pearson 1969).

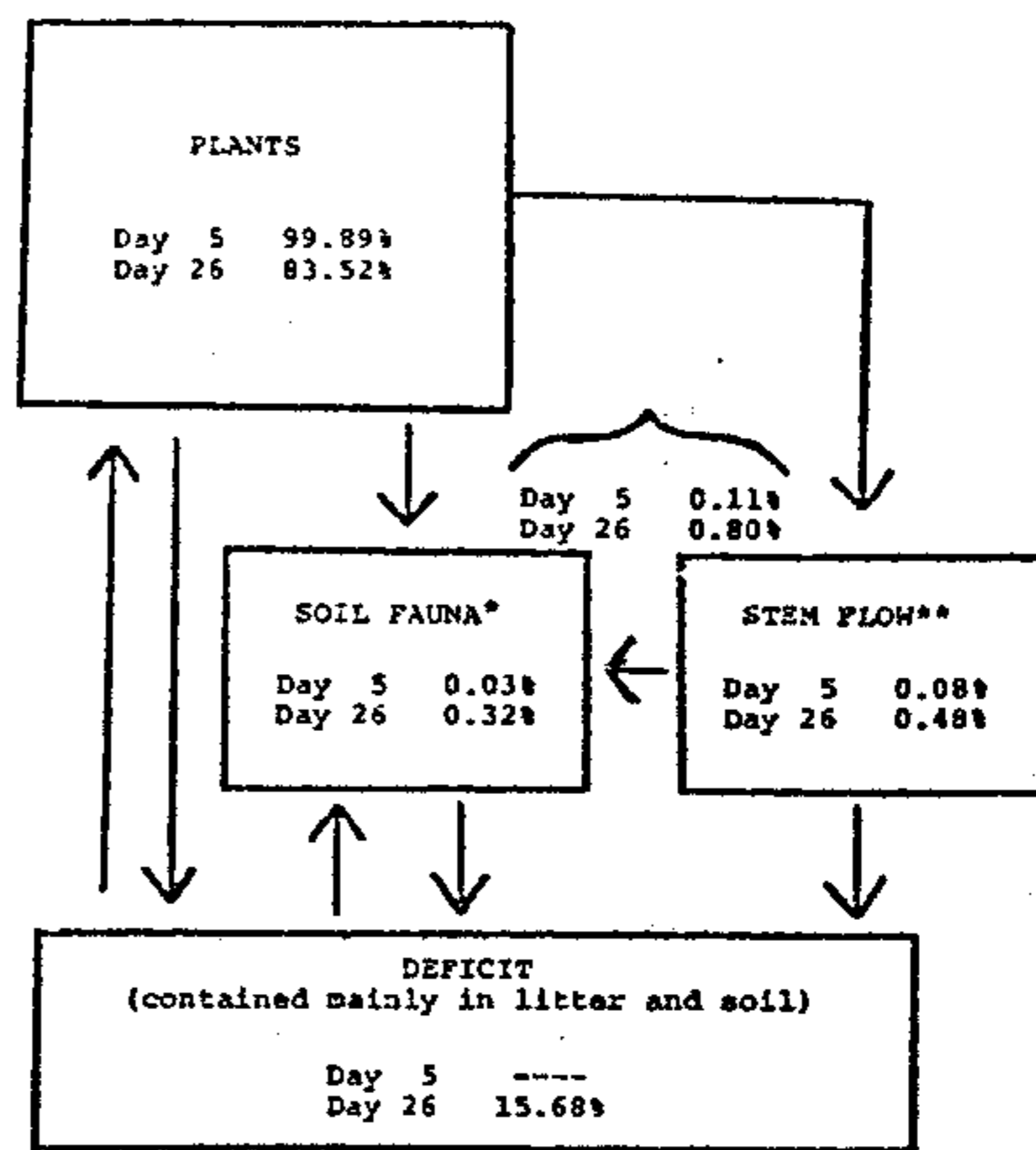
The several components of this ecosystem have characteristic ranges of isotope concentration per mg of body tissue (Table 6). The large differences between individual fractions of the system primarily reflect dilution of the isotope as it moves through various trophic levels of the soil system. Reduction in P<sup>32</sup> concentration was recorded in movement to soil-inhabiting herbivores such as ants as well as in transfer to the saprovores component. Dilution of P<sup>32</sup> as it is cycled through saprovores and predator levels has been observed elsewhere (Wiegert et al. 1967; Shure 1969).

## Discussion

### UPTAKE OF P<sup>32</sup> BY THE SOIL FAUNA

#### Variability in uptake and body burdens

Many factors governed P<sup>32</sup> uptake by soil fauna from the environment. Consequently, only a percentage of some populations was tagged and within the labeled part of the populations much individual variability in P<sup>32</sup> concentration was observed.



\*Based on control plot data only.

\*\*Day 26 stem flow value based on total accumulation to that day.

Figure 6. Percentage of the total P<sup>32</sup> present in the individual ecosystem compartments on days 5 and 26.

Entire populations or individuals within a population may not be tagged for the following reasons:

1. *Insufficient isotope in the soil system:* During the earlier part of the study, many soil animals remained untagged (Figures 1 and 2) until P<sup>32</sup> gradually became available from additions by stem flow, root exudation, and dying ragweed leaves and roots.

2. *Food habits:* Hemiptera (nymphs) were consistently untagged, suggesting that they did not feed on the tagged plants or organic matter of the system.

Table 6. Range of activity densities recorded throughout the study for various components of the ecosystem.

Ecosystem component	Range of activity density (dpm/mg)
Ragweed plants	10 <sup>3</sup> -10 <sup>4</sup>
Soil fauna	
Herbivores (arthropods)	
Predators	10 <sup>2</sup> -10 <sup>3</sup>
Nematodes	
Saprovores (arthropods and earthworms)	10 <sup>1</sup> -10 <sup>2</sup>
Stem flow	10 <sup>1</sup> -10 <sup>2</sup>

3. *Insufficient sample size:* For less abundant groups, sample size was usually small. The chance exists of sampling several unlabeled animals from these non-randomly distributed populations. Erratic curves of percentage of population labeled (Figure 2) were therefore observed in certain groups.

4. *Effect of small biomass:* Microarthropods did not appear to be tagged. If in fact they were labeled, their biomass weighed in micrograms (Block 1966; McBrayer, Reichle, and Shanks 1969) would still contain only a small amount of radioactivity. Background noise would render the Geiger-Muller detector insensitive to such low levels.

Variability in activity density among labeled portions of the populations was probably due to a few additional factors.

5. *Non-random distribution of the isotope in the soil system:* High levels of  $P^{32}$  occur mainly within the vicinity of the labeled plant roots and litter. Phosphorus is relatively immobile, however (Devlin 1966), and the isotope probably did not diffuse randomly throughout the entire soil system of the plots.

6. *Distribution of animals relative to  $P^{32}$  distribution:* The animals are usually not randomly distributed and their area of movement and feeding relative to the differential distribution of the isotope probably greatly affects the ultimate concentration in their tissues.

These last two factors contribute to the microenvironmental variability found between plots in this study.

7. *Variation in individual metabolic rates:* Uptake and excretion rates for radionuclides are dependent upon many factors including body size, age (Eberhardt and Nakatani 1969), and the physiological state of the animal (Breymer and Odum 1969).

Large but constant variability in radionuclide uptake and retention has been reported for several plant and animal populations exposed to fallout. However, the coefficients of variation are lower than those reported here (Eberhardt 1964). Although sample size was frequently very small in this study, the coefficient of variation is not reduced in the few cases where sample size was quite large. Thus the factors listed above probably contributed largely to the great variability of the individual activity densities. Eberhardt and Nakatani (1969) have studied sources for variability observed in radionuclide body burdens in nature and found that microenvironmental variability is greater than variability among individuals and the latter larger than experimental error. The plot-to-plot variability observed here supports this hypothesis.

#### TROPHIC RELATIONSHIPS OF THE SOIL FAUNA

Soil organisms may have become tagged by ingestion of labeled roots, tagged detritus, tagged soil and

humus, another tagged animal or its feces.

The uptake curves for tagged organisms of various taxonomic groups reflect their trophic positions. The very heavy  $P^{32}$  concentration found in the Hymenoptera suggests that most of them were feeding directly on exudations, living vegetative parts, or fallen leaves of the labeled ragweed. Earthworms, Coleoptera (adults), and Diplopoda displaying lower levels and delayed peaks in  $P^{32}$  concentration were probably feeding on a source not immediately labeled, that is, the organic detritus and soil particles. Earthworms and Diplopoda are well known for their role in fragmentation of organic matter (Blower 1955; Raw and Lofty 1963; Hoffman and Payne 1969). However, the feeding patterns of beetles are varied. A majority of beetles collected were the large darkling beetles (Tenebrionidae). Most species of this family are described as scavengers of decaying vegetable matter (Comstock 1930; Imms 1934; Ross 1965). Elateridae (click beetles), Curculionidae (weevils), and Staphylinidae (rove beetles) were also found. Species of the former two families are phytophagous while those of the latter are scavengers, although some are said to be predators (Imms 1934; Swain 1948; Ross 1965). These three groups were relatively uncommon, and the Coleoptera (adult) uptake curve seems most strongly influenced by the saprovores of this order.

Coleoptera (larvae) are also quite varied in their food habits. They frequently have food preferences similar to the adults, although they may utilize a different species or a different part of the food source (Ross 1965). However, many are predaceous as larvae, becoming saprovores or herbivores after metamorphosis (Imms 1934; Swain 1948). Differences were observed in the uptake curves for larvae and adults. Since so little taxonomic separation of families was done here, only a preliminary hypothesis for these differences can be offered. Assuming that many of the larvae were predators, the differences between the uptake curves of adults and larvae may reflect changes in trophic position occurring with metamorphosis. Centipedes are also predators (Fenton 1947) and, because they concentrated the radioisotope to such a degree, may have been utilizing the highly labeled Hymenoptera as a major food source.

#### $P^{32}$ MOVEMENT THROUGH THE SOIL-RAGWEED SYSTEM

The results here suggest that stem flow may be an important mechanism for transport of minerals and water in a ragweed field. The distribution of phosphorus in the soil by stem flow however is not random. Because of the immobility of phosphorus, it probably tends to accumulate where it is deposited in the vicinity immediately surrounding the ragweed plants.

Stem flow is generally not an important route in movement of elements in forested ecosystems (Waller and Olson 1967; Thomas 1969). Various paths in a mineral cycle probably change significantly as succession occurs, and stem flow may be of decreasing

importance in mineral transport during the later stages of succession.

The significance of the bodies of the soil fauna in the maintenance of elements in upper soil layers has been suggested (Nielson 1949; Shaw 1968). The results, however, tend to dispute this hypothesis since only a negligible amount of P<sup>32</sup> resided in the entire faunal population. Similarly, Crossley (1963) found only minute amounts of Cs<sup>137</sup> and Sr<sup>90</sup> in the soil fauna relative to the total amount in the medium. Witkamp and Frank (1969) demonstrated that millipedes maximally accumulated a mere 0.7% of the total Cs<sup>137</sup> content of a soil-litter microcosm. Most likely the soil fauna are of much greater importance in the breakdown and decomposition of organic matter than in mineral storage.

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