RESOURCE PARTITIONING IN LEAF-LITTER FAUNAS FROM HARDWOOD AND HARDWOOD-CONVERTED-TO-PINE FORESTS

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ABSTRACT

The structure and function of litter faunas were measured from the forest floors of two forest watersheds: mature hardwood (reference) and adjacent white pine, once hardwood (experimental) forests. The biomass of some 18 combined taxa of litter animals was about one-third lower, numerical abundances were about one-half lower, and standing crops of calcium and potassium were also lower in the pine plantation than in the hardwood system. These data were synthesized as models of the cryptozoans' food webs. In the hardwood watershed, 11% of the calcium and 3% of the potassium from annual leaf-litter input were processed by the litter animals. By contrast, 2% of the calcium and 28% of the potassium from annual litter input entered the food webs of the litter fauna in the white pine watershed.

As much as 90% of the net primary production in forests does not pass through herbivore food chains before it is deposited on the forest floor as detritus and becomes available to saprozoic food chains (Whittaker, 1970; Crossley, 1970). Organisms in this latter pathway process the majority of the materials released by primary producers. Complexes of fungi, bacteria, and animals interact and utilize nutrients in these dead materials and aid in releasing nutrients (Kurcheva, 1960; Edwards and Heath, 1963; Crossley and Witkamp, 1964; and Witkamp, 1971). These nutrients may become available for uptake again by plants, transferred from the ecosystem via runoff, or retained in deep soils. The rates of release of these materials and the pathways they follow in the microfloral—

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faunal complex may largely determine whether the entire watershed system conserves its nutrients or loses them.

Coweeta Hydrologic Station in North Carolina offers a variety of natural and manipulated watersheds. Watershed 18 is a mature deciduous hardwood forest and serves as a reference forest; burning and cutting have been restricted since 1924, and before that time logging was minimal. Adjacent watershed 17 serves as an experimental system because as a mature hardwood forest it was logged in 1942; in 1956 it was planted with white pine seedlings. Subsequent cutbacks of hardwood shoots have ensured that watershed 17 is essentially a young white pine plantation. Particulars of these catchments (Johnson and Swank, 1973) indicate that both watersheds are similar in slope, exposure, size, elevation, etc., but they differ, of course, in botanical composition.

Researchers at Coweeta have undertaken the determination of the movement of mineral elements—calcium and potassium—through the soil-litter fauna, using standing crops of elements, turnover rates from radioisotope measurements, and systems-analysis techniques. Gist (1972) synthesized data from the mature hardwood watershed with digital computer methods applied to a 10-compartment model. Cornaby (1975) concentrated on similar dynamics of the forest floor of the white pine watershed, using analog computer methods on a 6-compartment model. These studies were made to (1) determine numerical densities, biomasses, and standing crops of mineral elements in the soil-litter fauna; (2) measure the flow of calcium and potassium through their food webs; (3) detect the importance of the various animal groups in maintaining this flow; and (4) establish the importance of food-chain movement relative to the annual litter input of mineral elements to the forest floor. This paper compares the principal findings of these two studies.

MATERIALS AND METHODS

Field investigations were conducted at Coweeta Hydrological Station in North Carolina in fall and winter 1970 and in summer 1971 for the hardwood watershed and in fall and winter 1971 and in spring, summer, and fall 1972 for the pine system. Precipitation and temperature profiles were similar for the 2-year period. The watersheds used are described by Johnson and Swank (1973).

Forest-floor invertebrates were separated from litter on the two forest floors by pitfall trapping, Berlese extraction, and hand-retrieval techniques. Organisms were enumerated, weighed (dry-weight biomass), and prepared for whole-body analyses of chemical composition for calcium and potassium. Particulars of the sampling programs and chemical analyses are given by Cornaby (1973) and Gist and Crossley (1975). In addition, Gist (1972) and Gist and Crossley (1974) performed tracer studies, some of the results of which Cornaby (1975) used in estimating flows between populations. Exact values from radioisotope studies, as well as extensive literature reviews on feeding habits of some 20 taxa of

forest-floor invertebrates, are given by Gist (1972), Gist and Crossley (1975), and Cornaby (1975). Cromack's (1972) work on litter budgets in the two forests provided data for inputs to the forest-floor community.

RESULTS AND DISCUSSION

The conceptual models used for analysis of the role of the litter fauna in the hardwood and pine watersheds are shown in Fig. 1. Litter input of calcium and potassium goes directly to compartment X_1 (litter) where transfers may occur to any of several processors or to soil directly. Movement from animals occurs as egestion, death, and losses to predator compartments (populations). Numerous recycling pathways, including those from soil humus and/or soil microflora, to litter animals are factored into the models because connectivities represent the net balance of inputs and outputs for a given compartment. Gist (1972) annualized his summer models for both calcium and potassium dynamics. Cornaby's model (1975) was constructed to estimate only annual patterns.

Differences between the two models are such that all the data from one watershed cannot be used for simulations on the model for the other watershed. For instance, the hardwood watershed model contains a finer compartmentaliza- tion of the fauna but does not provide for animal remains. And the study of the white pine watershed included some taxa not measured on the hardwood watershed. Nevertheless, comparisons of results are possible at two levels. Standing crops and faunal compositions can be compared since they are independent of the structures of the models. Also, gross comparisons of some of the internal dynamics and total outputs of the models are fruitful.

There were large differences in numerical densities, faunal composition, and standing-crop biomasses between faunas of the two watersheds. Annual average densities of litter invertebrates averaged 65,060 individuals per square meter on the hardwood watershed and exceeded by a factor of about 2 the density of 35,830 individuals per square meter on the white pine watershed (Table 1). Cryptostigmata and Collembola combined accounted for approximately 90% of both these annual densities, but the relative contributions of these two groups differed on the two watersheds. Diplopoda were conspicuously more abundant on the hardwood watershed. Average biomass on the white pine watershed was 1.30 g/m^2, compared with 3.81 g/m^2 on the hardwood watershed (Table 1). Biomass of nearly every faunal group was smaller on the pine watershed, exceptions being Collembola and such macroinvertebrates as Gastropoda and Aranea. The Collembola, in particular, may be the dominant group of fauna in the white pine watershed, where they maintained high biomasses (500 mg/m^2).

Figure 2 shows the relative inputs of calcium and potassium to the two forest floors and indicates the degree of resource partitioning by the respective soil-litter faunas. The percentage of the annual litterfall inputs which actually entered the food chains was comparatively small. On the hardwood watershed

TABLE 1

MEAN ANNUAL DENSITIES AND BIOMASSES OF LITTER FAUNA FROM
DECIDUOUS HARDWOOD AND HARDWOOD-CONVERTED-TO-WHITE PINE
FORESTS (Limits for 95% confidence intervals are provided in
parentheses after the mean)

Taxa	Deciduous hardwood	Hardwood converted to white pine
	Densities, individuals/m^2 *	
Cryptostigmata	55,630 (47,050; 64,410)	19,440 (18,570; 20,310)
Mesostigmata	1,500 (130; 2,870)	2,050 (1,760; 2,340)
Aranea (small)	400 (270; 530)	290 (250; 340)
Collembola	7,520 (6,230; 8,810)	13,220 (12,620; 13,820)
Other microarthropods	†	830 (710; 950)‡
Diplopoda	5	1
Other macroinvertebrates	2§	7¶
Totals	65,060 (56,270; 73,850)**	35,830 (33,050; 38,610)**
	Estimated biomass, mg (dry weight tissue)/m^2††	
Cryptostigmata	1,660	190
Mesostigmata	90	40
Aranea (small)	220	140
Collembola	280	500
Other microarthropods	†	40‡
Diplopoda	1,290	40
Other macroinvertebrates	270§	350¶
Totals	3,810	1,300

*Sample sizes for microarthropods were 36 and 210 0.01 per square meter for Berlesed samples of litter for hardwood and white pine forests, respectively; sample sizes for macroinvertebrates were 25 and 116 per square meter for hand-sorted samples of litter for hardwood and white pine forests, respectively. Densities are based on direct counts.

†Samples not tabulated for these two taxa (see footnote ‡).

‡Prostigmata and Pseudoscorpionida.

§Gastropoda, Aranea (large), Carabidae, and Orthoptera.

¶Gastropoda, Chilopoda, Aranea (large), Opiliones, Phalangida, Isopoda, Tettigoniidae, Carabidae, Staphylinidae, Formicidae, and Oligochaeta.

**Computation of limits for 95% confidence intervals were based on first four taxa; inclusion of last three groups would not have appreciably changed the confidence values.

††Biomass values are based on average weights per individual (based on direct weighings of many individuals) multiplied by direct counts.
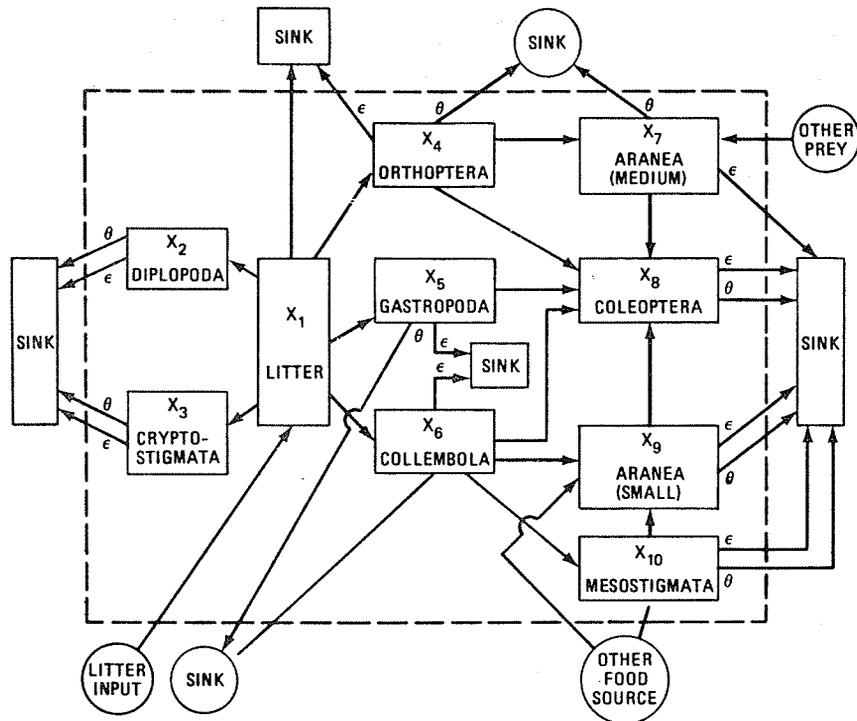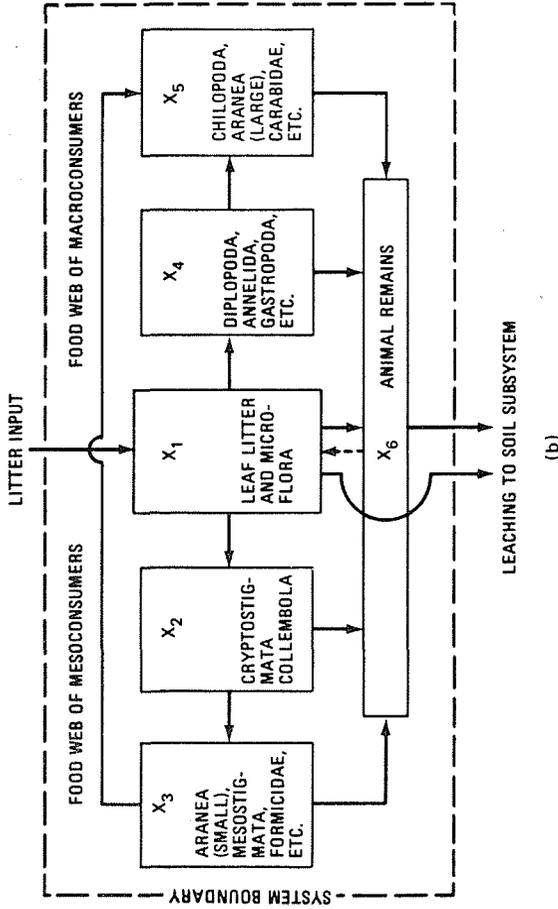
(a)

Fig. 1 Conceptual models of cryptozoan food webs on two forest floors. Populations are shown as compartments and feeding interactions as connectivities where the head of an arrow indicates the direction of calcium and potassium movement and the tail identifies the donor. (a) A 10-compartment model for a mature deciduous hardwood forest (Gist, 1972) where θ = nonpredatory mortality and ϵ = egestion. (b) A 6-compartment model for a nearby hardwood-converted-to-pine forest (Cornaby, 1975).
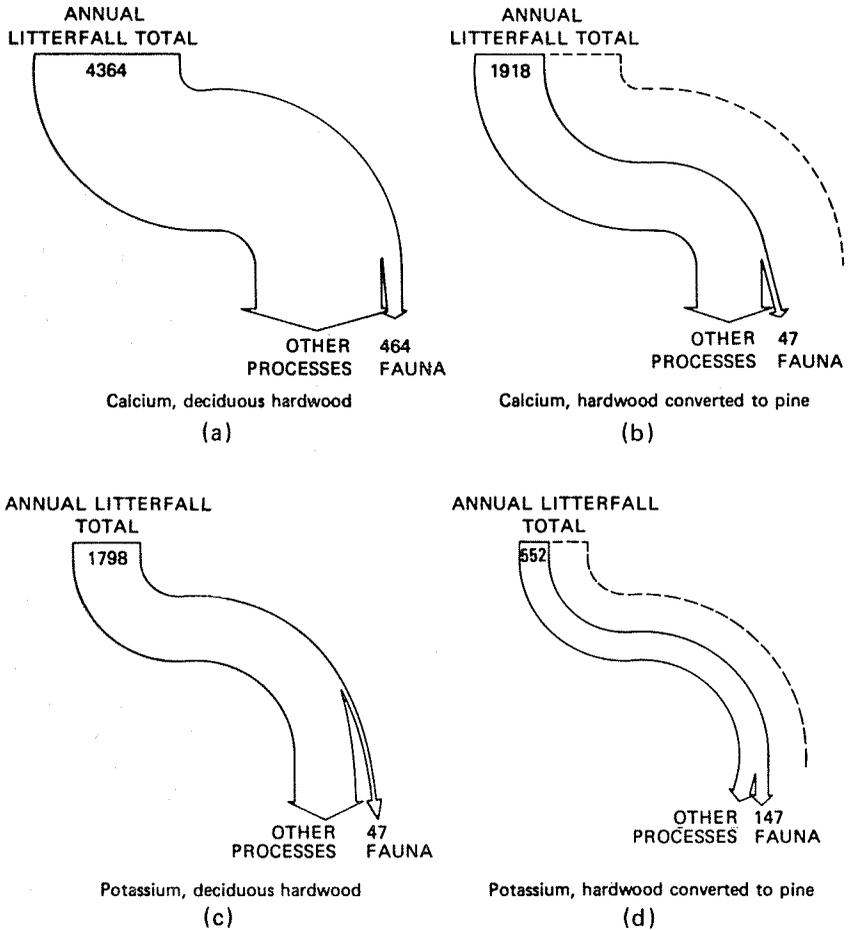
ANNUAL
LITTERFALL TOTAL

4364

OTHER   464
PROCESSES   FAUNA

Calcium, deciduous hardwood

(a)

ANNUAL
LITTERFALL TOTAL

1918

OTHER   47
PROCESSES   FAUNA

Calcium, hardwood converted to pine

(b)

ANNUAL LITTERFALL
TOTAL

1798

OTHER   47
PROCESSES   FAUNA

Potassium, deciduous hardwood

(c)

ANNUAL LITTERFALL
TOTAL

552

OTHER   147
PROCESSES   FAUNA

Potassium, hardwood converted to pine

(d)

Fig. 2 Flows of calcium and potassium in a mature, deciduous hardwood forest and nearby hardwood converted to white pine forest. Differences in litter input, standing crops of litter faunas, and turnover rates of these populations, as measured with radioisotopes and systems models (see Fig. 1), resulted in the observed resource partitioning. All values are expressed as milligrams of element per square meter per year. Dotted lines show probable inputs of calcium and potassium at the time of the present study if there had been no past modifications of the two forest ecosystems.

the models showed that about 11% of annual input of calcium was ingested by animals; the remaining 89% remained in the decomposing detritus—microflora complex or moved on to the mineral soil. For potassium about 3% of the annual litter input entered the detritus food web of the hardwood forest. In the white pine watershed, the soil-litter fauna processed about 2% of the calcium input and 28% of the potassium input from annual litterfall. Although small, these percentages indicate considerable modification of nutrient movement in the litterfall pathway following hardwood replacement with white pine.

Before 1942 both watersheds were mixed hardwood forests at similar stages in development. We assume that the structure and function of the forest-floor faunas were similar. Furthermore, it is expected that annual litterfall would have been similar in the two forests. The logging and planting of white pine on the experimental watershed have altered nutrient cycling (Johnson and Swank, 1973) as well as the soil-litter fauna, evidently leading to differences in nutrient utilization by the complexes of organisms in the food webs.

Litter fauna used only one-tenth as much calcium in the experimental watershed as in the control (Fig. 2). For potassium the amount of this element entering the fauna was about three times larger on the experimental watershed than on the control. These changes may be the result of shifts in faunal composition, possibly as a result of calcium limitation to some faunal or process groups.

Further differences between the role of fauna in the processing of nutrients on the two watersheds appeared when the rates of utilization were compared with standing crops of elements in the litter faunas. Only values for summer are shown; however, they reveal trends typical of other seasons and of the year. The standing crop of an element was determined by multiplying observed concentrations by biomasses. The standing crop of calcium in detritivores was 560 mg/m^2 in the hardwood watershed, compared with 54 mg/m^2 in the white pine watershed. This nine-tenths reduction corresponds closely with the nine-tenths reduction in the rate of calcium intake by the fauna which was estimated to be 464 mg m^{-2} year^{-1} for hardwood vs. 47 mg m^{-2} year^{-1} for the white pine. The calcium contained in the standing crop of litter was similar in the two watersheds: 10.7 g/m^2 for hardwood vs. 10.4 g/m^2 for hardwood converted to pine forests. Thus the utilization rate of calcium by the fauna was related to the standing crop of fauna and perhaps to annual input of litter [Fig. 2(a,b)] but evidently not to the standing crop of litter, at least not in any obvious manner.

For potassium the relationships between standing crops and inputs were not clear. Detritivores on the hardwood watershed had a standing crop of potassium which was about three times greater than that on the white pine watershed, where about 10 mg/m^2 and about 30 mg/m^2 were observed. Yet the smaller standing crop of litter animals on the white pine watershed processed three times more potassium than did the larger standing crop in the hardwood watershed [Fig. 2(c,d)]. The litter component of the forest floors contained similar amounts of potassium with 1.8 g/m^2 vs. 2.3 g/m^2 for hardwood and pine,

respectively. Whether this difference in potassium turnover is a property of the composition of the soil-litter fauna in the white pine watershed or is due to some difference in potassium retention within the litter—detritus system (or both) remains to be resolved. Since Collembola were the dominant litter animals in terms of biomass (Table 1), studies of potassium metabolism by Collembola may reveal further insight into the behavior of this element in this forest-floor system.

These studies evaluated the role of the litter-soil fauna in cycling of calcium and potassium in litter—detritus systems. Comparisons of the results lead to further questions about the context in which soil-litter fauna should be considered. Each of us has expressed the opinion that soil fauna process only a small fraction of the input of mineral element into the forest floor (Crossley, 1970; Gist, 1972; Cornaby, 1975). Yet, the present results show that this is not necessarily so. Fauna processed about 28% of the annual litter input of potassium in the white pine watershed and 11% of the annual calcium input in the hardwood watershed. These are not entirely trivial numbers, when it is considered that about half the calcium input of white pine litter remains immobilized after a year. Further, both models apparently underestimate calcium input into fauna. Each model required that the annual input of calcium was about equal to the summer standing crop of detritivores. Calcium turnover for soil fauna is not well measured, but an amount three to four times that suggested by models could be reasonable (Kowal and Crossley, 1971).

It is not clear whether the food chains should be referenced to annual input of litter (as was done here) or to total annual input including throughfall. In the latter case the percentages of mineral elements passing through food chains would be reduced by factors ranging from 1.2 (calcium in the hardwood watershed) to 6 (potassium in the white pine watershed). It is also unclear what fraction of the entire litter—detritus elemental pool may be available to the soil fauna. It would be desirable to reference the feeding of soil fauna to the microflora as a food base, but our knowledge of elemental concentrations and turnovers in soil microflora is limited such that it seems impossible to do so at present (Cromack, Todd, and Monk, 1975).

Comparisons of the results of the two studies provide estimates and some explanations for the amounts of calcium and potassium being processed by the food webs of the leaf-litter faunas. The significance of these partitionings will be best understood as the results of ongoing studies on producers, consumers, and abiotic factors at Coweeta and elsewhere are synthesized from an ecosystem perspective.

ACKNOWLEDGMENTS

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