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EFFECTS OF WATERSHED PERTURBATION ON STREAM POTASSIUM AND CALCIUM DYNAMICS^{1,2}

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Abstract. Three small streams located at Coweeta Hydrologic Laboratory, North Carolina, USA, on an old field watershed, a pine plantation watershed, and a hardwood forest watershed were investigated to determine effects of watershed perturbation on K and Ca dynamics in the stream ecosystems. Data collected included measurements of litterfall inputs, large particulate organic matter and benthic organism standing crops, large particulate organic matter and organism drift, and insect emergence. We used ⁸⁶Sr and ¹³⁴Cs to estimate detritivore ingestion and elimination rates of Ca and K, respectively.

We found that watershed perturbations had altered stream inputs and caused accompanying changes in the stream fauna. Our results indicated that the perturbed streams had less efficient physical processing of allochthonous inputs, but greater biological utilization of inputs. The streams exhibited high resilience to perturbation with complete recovery limited by the recovery rate of allochthonous inputs.

Key words: calcium; detritus; North Carolina; potassium; stream; stability.

INTRODUCTION

The defining feature of streams, unidirectional flow of water, has presented a challenge in formulating a theoretical perspective for stream studies (Margalef 1960, Hutchinson 1963). Some recent stream studies have, however, focused on functional aspects of running water ecosystems (Teal 1957; Nelson and Scott 1962; Minshall 1967; Tilly 1968; Hall 1972; Fisher and Likens 1972, 1973; Boling et al. 1974; Fisher 1977). Out of these studies has emerged a consistent picture of headwater streams (1st to 3rd order, Strahler 1957) as processors of organic matter synthesized in riparian ecosystems (Cummins 1974). Lindeman's (1942) study led to a traditional view of ecosystem energy flow encompassing primary producers, herbivores, carnivores, and decomposers. This view is evident in many early stream studies but the accumulation of evidence now indicates that the primary energy source to many headwater streams is leaves from the surrounding terrestrial environment (e.g., Cummins 1974, Hynes 1975). Considerable stream research over the past 15 or 20 yr has concerned processing and utilization of this allochthonous energy.

Control of the rate at which organic energy is incorporated into ecosystems is different in headwater streams than in most other ecosystems. In autotrophic ecosystems where organic energy is internally generated, production is often controlled by rates of internal

nutrient regeneration. Such ecosystems have been referred to as "circular causal systems" (Hutchinson 1948, Patten 1973). In a typically heterotrophic, headwater stream, no such feedback control over organic energy input exists. There is no feedback control over litterfall inputs, and stream ecosystems do not have the same homeostatic capabilities possessed by circular causal systems. Control of biological function in headwater streams is external to the stream ecosystem, in the surrounding watershed. The influence of the terrestrial ecosystem on a stream can be seen in a variety of other ways including plant growth nutrient concentrations, the hydrologic regime, available light energy, and water temperature. Hynes (1975) concluded, "in every respect the valley rules the stream."

Considering a stream at a single point, it is evident that material cycling is negligible. Cycling is prevented by unidirectional water movement. Turbulence and upstream movements of adult insects (e.g., Muller 1954, Roos 1957), benthic invertebrates (e.g., Ball et al. 1963, Minckley 1964, Elliott 1971), and fish (Hall 1972) contribute little to upstream material movement. Biotic and abiotic materials must be continually resupplied from upstream or from the watershed. Food received by an organism from upstream is utilized and passed on with very low probability it will again pass that point in the stream in contemporary time.

If, however, one considers the dynamics within a stream reach, significant recycling becomes apparent. Much of the energy ingested by detritivores is egested and again becomes part of the detritus pool. This detritus is available to other detritivores further downstream. Thus, the downstream movement of organic matter occurs in a "rolling motion" as has been described for nutrients on a larger scale (Leopold 1941). Because of the spatial aspect involved in this cycling,

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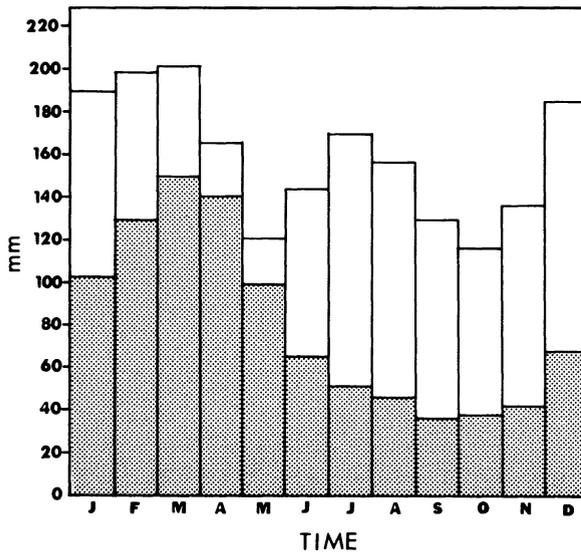


FIG. 1. Average precipitation (clear area) and discharge (shaded area) for the hardwood forest watershed (WS 18), based on 38 yr of precipitation data and 33 yr of stream flow records. Data from Coweeta Hydrologic Laboratory, North Carolina, USA, and Johnson and Swank (1973).

it might better be termed "spiralling" (Webster 1975, Wallace et al. 1977). Internal regulation of the stream ecosystem can be mediated by characteristics of the stream which shorten or tighten spiralling such as stream bed retention of particulate organic matter and insect filtering of fine particulate organic matter (Wallace et al. 1977).

Ecosystem stability is the ability of an ecosystem to (1) withstand and (2) recover from perturbation. These 2 properties have been designated as resistance and resilience, respectively (Webster et al. 1975). Streams are usually regarded as highly resilient ecosystems, a view based largely on the observation that if material such as a pollutant, is discharged into a stream, it is immediately carried away from the area of discharge (Cairns and Dickson 1977). Webster (1975) related ecosystem resilience to rapid turnover of ecosystem components. In streams, rapid turnover is produced by the continual flushing action of flowing water. Additionally, organisms found in headwater streams typically exhibit rapid turnover (Patrick 1970). The annual input of allochthonous detritus also contributes to stream resilience by replacing perturbation-removed biomass (Fisher and Likens 1973).

Webster et al. (1975) suggested that resistance and resilience are inversely related, that is, ecosystems with high resistance to perturbation typically exhibit low resilience and *vice versa*. In contrast to the high resilience exhibited by stream ecosystems, low resistance to perturbation is apparent. Margalef (1963) suggested that maintenance of ecosystem organization was dependent on biomass. This idea formed the basis for suggesting that the ability of an ecosystem to resist

perturbation is related to standing crop (O'Neill et al. 1975, Webster 1975). Streams have a low standing crop biomass relative to other ecosystem types (cf., Whittaker 1975:224) though recent studies have shown that some headwater streams may have relatively high standing crops in the form of dead logs (J. Sedell, *personal communication*). Perturbations involving additions to or removals from streams, such as organic pollutant discharge or flood scouring, have dramatic influences on the streams. However, these effects are rapidly ameliorated by resiliency mechanisms.

The stability of stream ecosystems can be attributed to their resilience. In any specific stream, resilience is regulated by external and internal control mechanisms as described above. Following perturbation, biomass and nutrients are replaced by watershed inputs, and pollutants are removed by waterflow. Internal function is regained by retention mechanisms and rapid recolonization and regrowth by stream fauna.

Potassium and calcium dynamics in stream ecosystems.—Potassium is essential to all organisms except possibly some blue-green algae. It is the major cation of cytoplasm and is important in a number of cellular functions including enzyme activation and control of protein conformation (Bowen 1966, Phipps 1976). In animals, overall control of K levels is maintained by a balance of intake and elimination. Potassium is rapidly assimilated from the gastrointestinal tract (Davis 1963). In aquatic insects, regulation of K in the haemolymph is highly efficient, being primarily controlled by gut uptake and adsorption by the malpighian tubules and rectum (Shaw and Stobbart 1963). Potassium is relatively abundant and has never been suggested as a limiting nutrient for plant growth in natural waters (Hynes 1970), though in highly productive lakes and ponds, epilimnetic K concentrations may be reduced by algal uptake (Barrett 1957, Wetzel 1975).

Calcium is essential to all organisms (Bowen 1966). The many insoluble Ca compounds provide structure in both plants and animals. In addition to forming structural material of both endoskeleton and exoskeleton, Ca is important in a number of physiological functions (Clark 1958, Hsiao 1963, Wasserman and Taylor 1969). In contrast to K, the gastrointestinal epithelium is relatively impermeable to Ca and there is evidence of active transport of Ca based on *in vivo* and *in vitro* studies of mammalian intestinal tissue (Wasserman and Taylor 1969). In insects, excess Ca is excreted as a salt, most commonly suspended calcium carbonate granules (Clark 1958, Wigglesworth 1965). Calcium concentrations in lakes and streams are highly variable and dependent primarily on the substrate rock type. Early limnological studies of Wisconsin lakes demonstrated that Ca can affect plant and animal distributions and limit lake productivity (Hsiao 1963). Subsequently, the distribution of most freshwater organisms has been related to Ca concentrations (Wetzel 1975).

The objective of this study was to examine stream ecosystem response to perturbation of the watershed terrestrial vegetation. On 1 watershed, the hardwood vegetation was removed, replaced with grass, and subsequently allowed to undergo natural succession. On another watershed, the hardwood vegetation was replaced with white pine. We have compared the streams on these 2 watersheds with the stream on an unperturbed, hardwood forest watershed. These comparisons are based on the dynamics of K and Ca in the streams.

DESCRIPTION OF STUDY SITE

Coweeta Hydrologic Laboratory, North Carolina, is located in the Nantahala Mountains in the Blue Ridge Province of the Southern Appalachians. Average annual precipitation at Coweeta ranges from 170 cm at lower elevations to 250 cm on upper slopes. Precipitation is fairly evenly distributed through the year with an average of at least 75 mm falling each month (Fig. 1) and <2% of the total occurring as snow (Dils 1957). As a result, stream flow does not show great fluctuations typical of streams in other areas.

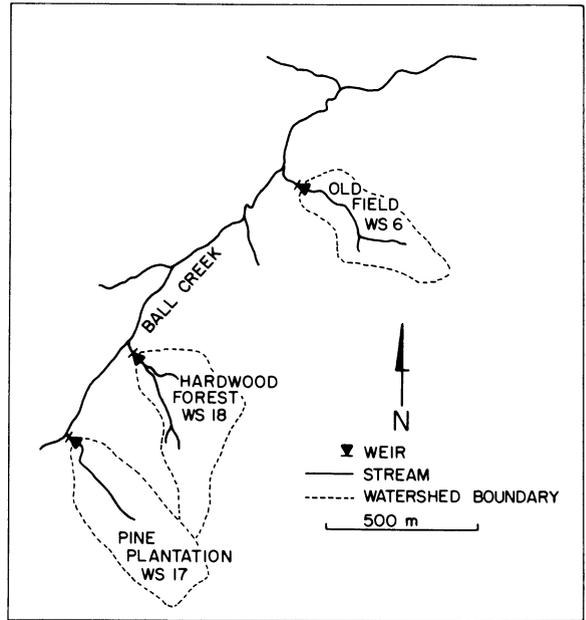


FIG. 2. Location of study streams, Coweeta Hydrologic Laboratory, Franklin, North Carolina, USA.

TABLE 1. Summary of physical characteristics of 3 watersheds and streams at Coweeta Hydrologic Laboratory, North Carolina, USA

	Watershed 6	Watershed 17	Watershed 18
Vegetation type	Old field	White pine	Hardwood
Watershed area* (ha)	8.86	13.48	12.46
Elevation, minimum* (m)	699	742	721
Elevation, maximum* (m)	905	1021	1006
Slope*	54	57	52
Total channel length (m)	450	210	564
Average channel width† (cm)	61.5	122.6	124.0
Average middle channel depth† (mm)	20.8	27.3	24.3
Total channel area (m ²)	276.8	379.9	699.2
Channel area/watershed area (%)	.31	.28	.56
Drainage density (m ha ⁻¹)	50.8	23.0	45.3
Channel gradient (m m ⁻¹)	.243	.249	.200
Average annual discharge (1 s ⁻¹)‡			
Water year 1973	3.69	5.03	6.19
Water year 1974	3.38	4.22	5.62
30-yr average	3.77
Maximum discharge (1 s ⁻¹)‡			
Water year 1973	79.9	84.7	105.6
Water year 1974	55.7	55.3	71.6
Maximum discharge (1 s ⁻¹)‡			
Water year 1973	0.8	0.7	0.8
Water year 1974	1.0	0.6	0.8
Average annual elemental concentrations (mg l ⁻¹)§			
NO ₃ -N	0.672	0.127	0.003
NH ₄ -N	0.005	0.004	0.004
PO ₄ -P	0.002	0.002	0.002
Cl	1.296	0.503	0.538
SO ₄	0.359	0.336	0.298
K	0.602	0.458	0.461
Na	1.102	0.784	0.883
Ca	1.074	0.518	0.626
Mg	0.649	0.227	0.296

* Data from Johnson and Swank (1973).
 † Based on measurements made at 5-m intervals.
 ‡ Data from Coweeta Hydrologic Laboratory.
 § Data from Swank and Douglass (1975).

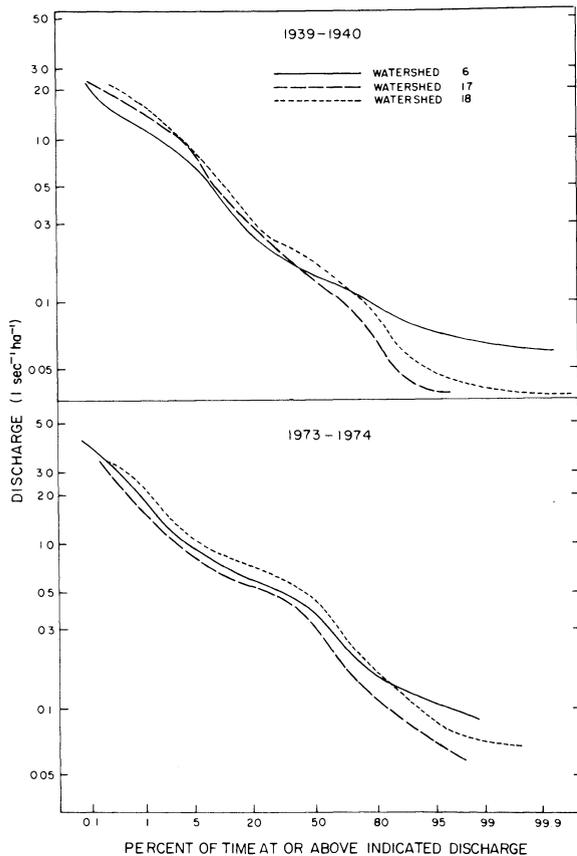


FIG. 3. Flow frequency diagrams for the 3 streams before (water years 1939 and 1940) and after (water years 1973 and 1974) perturbations. Data from Coweeta Hydrologic Laboratory, North Carolina, USA.

Our study was conducted on 3 watersheds with differing vegetation: a hardwood forest (Watershed 18), a white pine plantation (Watershed 17), and an old field (Watershed 6). The 3 watersheds are located within 2.59 km² and are all on NW facing slopes (Fig. 2). Physical characteristics of the watersheds and their streams are summarized in Table 1.

With exception of the chestnut blight, the hardwood forest watershed has remained undisturbed since at least 1924 (Johnson and Swank 1973). Prior to 1924, there was some selective logging. Dominant overstory vegetation includes chestnut oak (*Quercus prinus*), red maple (*Acer rubrum*), scarlet oak (*Quercus coccinea*), northern red oak (*Quercus rubra*), tulip poplar (*Liriodendron tulipifera*), pignut hickory (*Carya glabra*), and black oak (*Quercus velutina*), listed in order of contribution to basal area. Prominent understory species are rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and dogwood (*Cornus florida*) (Day and Monk 1974). Rhododendron is especially dense in many places along the stream.

The pine plantation watershed was cleared of all shrub and forest vegetation in 1942. Annual sprout

growth was cut back almost every year between 1942 and 1955. White pine was planted in 1956. Hardwood sprouts were cut or treated with herbicide as necessary to prevent competition with the pine (Johnson and Swank 1973).

The old field watershed has a long history of manipulations, beginning in 1942 when the riparian vegetation was cut. This was allowed to regrow until 1958 when all marketable timber was removed and the cover converted to Kentucky-31 fescue grass. From 1959 to 1965, various fertilizers were applied to the watershed (detailed in Johnson and Swank 1973) including dolomitic limestone. In May 1966, and for 2 subsequent yr, the grass cover was killed with herbicides (details described in Douglass et al. 1969). Since spring 1968, the watershed has been allowed to revert to successional vegetation. In 1968 and 1969 the vegetation consisted primarily of horseweed (*Erigeron canadensis*), fireweed (*Erechtites hierachifolia*), and grass species. By 1970, woody shrubs contributed up to 50% of the aboveground vegetation (Johnson and Swank 1973). During the period 1972–1974 blackberry (*Rubus* sp.) and black locust (*Robinia pseudoacacia*) were the predominant woody species.

Though the 3 streams and watersheds have some morphological differences (Table 1), their hydrologic properties are very similar (Fig. 3). The flow frequency diagrams (Fig. 3) indicate the quantity and variability of flow (Leopold et al. 1964). The relative shallowness of the slopes indicates the flow stability of these streams. The flow distribution is not log normal as would be indicated by a straight line, because of high frequencies of relatively high and low flows. This is apparently caused by high winter base flows and low summer base flows.

The flow frequency diagrams (Fig. 3) further show that the hydrologic properties of the streams on watersheds 6 and 17 have not been substantially changed by perturbations to these watersheds. Though water years 1939 and 1940 differed considerably from water years 1973 and 1974, the relationships of the flow frequency diagrams are similar. During both periods, there was somewhat less discharge per unit area from WS 17 than from WS 18. Careful analysis has shown the conversion to pine on WS 17 reduced flow (Swank and Douglass 1974), though it is not evident from these diagrams. The WS 18 and WS 17 graphs are nearly parallel, indicating similar flow variability. Discharge from WS 6 was very similar to the other watersheds, however the lesser slope of the graph indicates less flow variability, that is, WS 6 appears to exhibit greater flow stability, especially at low flows. Because this was true both before and after perturbation, it must be due to morphometric differences between WS 6 and WS 17 and 18. There is evidence of a greater ground-water reservoir on WS 6 than on the other watersheds (W. T. Swank, Coweeta Hydrologic Laboratory, *personal communication*).

Streams on the 3 watersheds are very small, 1st- and 2nd-order streams (Fig. 2). The substrate is sand and rocks ≤ 25 cm diameter. The gradient is steep in places and gentle in others with infrequent small pools. Exposed rocks are often covered with moss. In summer, the streams are heavily shaded, except for stretches in the old field watershed, and during fall and winter they are choked with leaves. Primary production in these streams is very low. In studies made on 2 similar Coweeta streams, no measurable chlorophyll was found during any season on artificial substrates incubated for 8 wk. Moss primary production is unknown but presumed low. Limitation of primary production appears to result from a combination of low light and nutrient levels (Table 1). To demonstrate the intense shading over the streams, on a clear day in August we made a series of solar radiation measurements with an Isco Model SR Spectroradiometer. At the point of measurement in the hardwood forest, only 0.17% of visible insolation reached the stream surface. Light penetration through the pine canopy was 1.51%. Three measurements made on the old field were 0.38, 2.69, and 26.26%, reflecting the patchiness of the old field vegetation.

METHODS AND MATERIALS

Abiotic parameters.—Forest Service personnel at Coweeta Hydrologic Laboratory continuously measured stream flow with a sharp-crested, V-notch blade set in a concrete weir at the base of each watershed. Weekly samples for chemical analysis were collected in the stream directly above each weir pond. Cation concentrations from both precipitation and stream water were analyzed with a Bausch and Lomb Model AC2-20 atomic absorption spectrophotometer. More data can be found in Johnson and Swank (1973) and Swank and Douglass (1975).

Water temperatures in the old field and the hardwood forest streams were measured by Forest Service personnel from July 1971 through April 1973 with Bendix Model 1443 soil thermographs. The sensing elements were located above the weir ponds in free flowing water in the shade. Point measurements showed that water temperatures in the pine plantation and hardwood forest streams were very similar (Woodall 1971) and continuous measurements were not made in the pine plantation stream.

Litterfall inputs.—We collected litterfall (not including branches >5 mm diameter) in 15×300 cm V-shaped aluminum troughs. Four troughs were located above each of the 3 streams. Troughs were cleaned at least biweekly from August 1972 through January 1974. The biomass of collected litter was determined after drying at 60°C for 24 h. Subsamples were ground in a Wiley mill and analyzed for K and Ca by spark emission spectrophotometry.

Standing crops of large particulate organic matter and benthic fauna.—Standing crop samples were col-

lected by R. Woodall, Georgia Power Company, Atlanta, Georgia, in 1968–1969 (Woodall 1971, 1972; Woodall and Wallace 1972, 1975). In addition to using Woodall's (1971, 1972; Woodall and Wallace 1972, 1975) data, we collected benthic fauna samples from the old field stream and detritus samples from all 3 streams.

During 1968–1969, Woodall collected 4 stratified random samples monthly from each stream using a 900 cm^2 Surber sampler with a mesh opening of 0.3 mm. The sampler was placed in the center of the stream channel and the substrate within disturbed by hand to a depth of ≈ 10 cm. Samples were transferred to a plastic bag, stored in crushed ice, and processed in the laboratory within 24 h. Organisms and large particulate organic matter (LPOM, > 0.3 mm) were sorted by hand from a white enamel pan. Dry weights of LPOM were obtained after drying at 105°C for 24 h. Nonquantitative samples were made for gut analysis and mineral analysis of organisms. Samples for mineral analysis were dried at 75°C overnight, weighed, acid digested and analyzed on a Bausch and Lomb Model AC2-20 atomic absorption spectrophotometer (Woodall 1972, Woodall and Wallace 1975).

During 1972–73, we collected 3 old field stream benthos samples per month. These samples were preserved with 10% formalin before sorting. After organisms had been removed, LPOM was elutriated from the samples and oven dried. We also collected 3 LPOM samples per month from the hardwood forest and pine plantation streams using the Surber sampler. These samples were oven dried at 60°C for 24 h immediately on return to the laboratory. All LPOM samples were subsequently washed to remove sand and gravel, and redried before weighing. Chemical analyses were made by spark emission spectrophotometry.

Drift of organisms and large particulate organic matter.—We measured drift of organisms and large particulate detritus by placing a 0.33-m wide drift net with a mesh opening of 0.7 mm in the stream at a point just above the weir pond. Sandbags directed total stream flow through the net. At the end of 24-h measurement periods, material collected in the net was emptied into a plastic bag and formalin added. In the laboratory, samples were treated in the same manner as materials collected with the Surber sampler. Organisms were sorted, identified, and counted and LPOM was dried, weighed, and analyzed. Sixteen 24-h samples were taken from the old-field stream, 17 from the pine plantation stream and 18 from the hardwood forest stream. An additional 8, 2, and 3 samples, respectively, were taken from each stream and analyzed for organism drift only.

Emergence of benthic insects.—We measured insect emergence with emergence traps modified from the design of Mundie (1971). Each pyramid-shaped trap had a 0.25-m^2 base with screen-covered sides (1.2 mm mesh opening). Insects were collected at the top

TABLE 2. Dissolved and sediment losses of potassium and calcium. Data from Coweeta Hydrologic Laboratory, North Carolina, USA and Monk (1975). Dissolved outputs are for water year 1973. Sediment data are from 1971 and 1972. Measurements are expressed per unit area of watershed

Watershed	Dissolved losses (kg ha ⁻¹)		Sediment losses (g ha ⁻¹)	
	K	Ca	K	Ca
Old field	7.4	13.9	8.7	161.1
Pine plantation	4.9	6.3	2.7	70.9
Hardwood forest	6.9	10.0	1.8	57.1

in an inverted 0.47-litre jar with a reservoir containing a solution of 10% formalin, glycerine, and detergent.

We placed 3 emergence traps in each stream, 1 near the weir, 1 near the head of the stream, and 1 in between. Traps were placed on exposed stones or stream bottoms so they were as close to the water as possible without blocking stream flow. Traps were operated continuously from July 1972 through August 1973, during which time we made collections at approximately biweekly intervals. In the laboratory, insects were counted and identified. To convert numbers data to biomass, K, and Ca, we collected adult insects from a black light. These insects were dried, weighed, wet ashed, and chemically analyzed by atomic absorption spectrophotometry.

Tracer determination of invertebrate elimination rates.—Behavior of radioisotopes in organisms and ecosystems is unique to specific isotopes. However, it is the assumption of radiotracer studies that chemically similar isotopes behave similarly and that measurements of radioisotopes reflect analogous behavior of nonradioactive isotopes.

In this study we tagged insects with ¹³⁴Cs and ⁸⁵Sr and used observed assimilation and elimination rates as estimates of K and Ca rates. Because of physical and chemical similarities between Cs and K, their physiological functions are grossly analogous (Davis 1963). Their similarity in metabolic processes has been recognized since studies by Ringer (1882), though there is no evidence that Cs and K follow the same metabolic pathways (Kornberg 1961). Discrimination between Cs and K has been shown in both plants and animals (McNeill and Trojan 1960, Bryan and Ward 1962, Davis 1963). However, because the radioisotopes of K are not very useful tracers (Phipps 1976), radiocesium has been widely used as a K analog.

Strontium is the closest chemical relative of Ca and its levels in organisms seem to be related to Ca levels (Comar and Wasserman 1964). Studies of Sr/Ca ratios have shown that differences are largely related to Sr/Ca ratios in the external medium or food supply (Nelson 1963, Ophel and Judd 1969) though discrimination has been demonstrated in a variety of organisms (e.g., Ophel and Fraser 1970). In general, Sr appears to be

a quite acceptable tracer of Ca dynamics. Kornberg (1961) indicated that Sr and Ca follow very similar metabolic pathways. Schurr and Stamper (1962) related fluctuation of ⁸⁵Sr body burden of crayfish to normal accumulation, fixation, redistribution, and loss of Ca during the molting cycle.

Both radiostrontium and radiocesium dynamics in insects and insect food chains have been extensively studied (Crossley and Pryor 1960; Crossley and Howden 1961; Crossley and Schnell 1961; Crossley 1963, 1966, 1967; Reichle and Crossley 1965, 1967; Reichle 1967; Crossley and Reichle 1969; Van Hook and Crossley 1969; Wilhm 1970). These radioisotopes have been previously used as a basis for K and Ca models (Gist 1972, Crossley and Gist 1973).

Our methods were essentially modifications of those involving terrestrial insects. Work was concentrated on 4 detritivore species (food habits discussed below): nymphs of *Peltoperla maria* (Plecoptera) and *Stenonema* sp. (Ephemeroptera), larvae of *Tipula* sp. (Diptera), and crayfish (*Cambarus bartoni*). Birch (*Betula lutea*) leaves which had been collected at Coweeta and air dried were soaked in isotope solution ($\approx 25 \mu\text{Ci ml}^{-1}$) for 24 h. They were then rinsed with tap water and air dried. Based on counts of small portions of these leaves at the time of feeding, the activity was $\approx 0.01 \mu\text{Ci mg}^{-1}$ for ¹³⁴Cs and $1 \mu\text{Ci mg}^{-1}$ for ⁸⁵Sr. Before feeding, leaves were soaked overnight in stream water. Animals used in the experiments were collected from Coweeta streams at least 1 day prior to beginning an experiment and placed in a plastic pan of stream water with aeration. At the beginning of an experiment, small pieces of tagged leaves were added to the pan. After 2 h, labeled animals were removed, counted, and isolated in plastic cups with running water. To test the possibility that animals could adsorb radioactive material which leached from the tagged leaves, we placed a screen down the middle of the feeding pan. Animals were placed on both sides of the screen and tagged leaves on 1 side. Over a 2 h period, none of the animals on the no-food side accumulated radioactivity significantly above background. A constant flow of fresh stream water was maintained through the plastic cups in which experimental animals were kept to assure proper oxygenation of the water and to prevent reingestion of egested materials. Temperatures in the cups were maintained as close as possible to 20°C; however, because water was taken directly from a nearby stream there was a 2°C to 4°C daily fluctuation.

Prior to counting, animals were placed in a small minnow net and rinsed with stream water. They were then placed in a 15 × 125 mm test tube containing 5 ml of stream water and counted in a Packard Auto Gamma Spectrometer Series 410A with a 5.08 × 5.08 cm sodium-iodide thallium-activated crystal enclosed in a lead shield (counting efficiencies: 12–13% for ¹³⁴Cs, 10% for ⁸⁵Sr; counting time = 1 min). Animals

TABLE 3. Litterfall into the 3 study streams

	Biomass (g m ⁻²)			K concentrations (mg g ⁻¹)			Ca concentrations (mg g ⁻¹)		
	Old field	Pine plantation	Hardwood forest	Old field	Pine plantation	Hardwood forest	Old field	Pine plantation	Hardwood forest
Winter	46.4	21.9	13.9	1.79	2.32	1.29	15.05	12.35	10.24
Spring	17.8	47.9	33.8	2.04	1.76	1.83	10.76	6.34	9.78
Summer	60.1	52.2	34.7	5.82	4.05	4.63	13.90	12.25	9.15
Fall	161.5	196.8	270.8	6.43	1.65	4.38	17.22	8.86	13.26
Total	285.8	318.8	353.2	5.28	2.10	4.48	15.77	9.28	12.42

were counted approximately every 2 h during the 1st day and 3× per day thereafter. Counting continued until the animal no longer contained sufficient radiotracer for a significant count or until sufficient data were obtained to estimate elimination rates.

RESULTS

Abiotic parameters.—Stream flows for the 3 streams are summarized in Table 1. From stream discharge records and stream water K and Ca concentrations, total export of dissolved K and Ca during water year 1973 was calculated (Table 2). Comparison with precipitation inputs indicated that all 3 watersheds had net losses of both elements, with little differences from analyses made by Johnson and Swank (1973) for water years 1970 and 1971. The major difference among the 3 watersheds was the greater Ca loss from the old field, likely due to limestone fertilization in 1959. (Hydrologic and chemistry data and analysis from W. T. Swank and J. E. Douglass, Coweeta Hydrologic Laboratory, *personal communication*.)

Sediment losses from the 3 watersheds were calculated from quarterly measurements and analysis of weir pond sediments (Table 2). Measurements were taken by Forest Service and University of Georgia personnel and reported by Monk (1975). Sediment losses were greatest from the old field, reflecting the least vegetational protection of the soil. When compared with dissolved nutrient outputs, losses of K and Ca as sediments were very small. Calcium sediment loss was ≈1% of dissolved loss and sediment loss of K was ≈0.1% of dissolved loss.

Mean annual temperatures for 1972 were 12.1°C and 10.8°C in the old field and hardwood forest streams, respectively. Highest recorded temperatures over 21 mo of record were 20°C in the old field stream in July 1972, and 17.2°C in the hardwood forest stream during August 1971 and July 1972. Lowest temperatures, 1.1°C and 2.8°C, occurred in the old field and hardwood forest streams, respectively, during January 1973. In general, temperature fluctuated more in the old field stream with maximum temperatures being higher and minimum temperatures lower than the hardwood forest stream. A maximum daily fluctuation of 6.7°C was measured in the old field stream. The great-

est daily fluctuation recorded in the hardwood forest stream was 3.3°C.

Litterfall inputs.—Litterfall rate was greatest during autumn on all 3 watersheds (Fig. 4). Autumn inputs were greatest in the hardwood forest, where 77% of annual litterfall biomass entered the stream during the 3 fall mo (Table 3). The comparable figures for the pine plantation and old field were 62 and 56%, respectively. In both forest ecosystems, a small pulse also occurred during April and May, corresponding to leafing out and flower production. Total litterfall for the hardwood forest and pine plantation was very similar to measurements made by Cromack (1972, Cromack and Monk 1975) for the same watersheds (362 and 321 g m⁻² respectively). Peak elemental concentrations of litter occurred in fall in the old field with minimums in spring. In the pine plantation peak concentrations were in summer and winter. We found the highest elemental concentrations of hardwood litter in fall. Annual average concentrations of both K and Ca were highest in the old field and lowest in the pine plantation. Cromack (1972) found K and Ca concentrations of 1.67 and 5.98 mg g⁻¹ in pine needle litter and 4.7 and 12.3 mg g⁻¹ in hardwood leaf litter. The higher elemental concentrations we found in the pine plantation litter (2.10 and 9.28 mg g⁻¹) were probably due to hardwood species invading the pine plantation along the stream where the pine canopy opened.

Standing crops of large particulate organic matter.—Large particulate organic matter (LPOM) standing crops during 1972–73 are summarized in Table 4. Corresponding to litter input, LPOM standing crop was highest in the hardwood forest stream and lowest in the old field stream, though differences between the old field stream and the pine plantation stream were slight. A paired *t* test of seasonal data showed no significant ($\alpha = .05$) difference between LPOM standing crop in the old field and pine plantation streams nor between the hardwood forest and pine plantation streams. The hardwood forest and old field streams were significantly different.

In all 3 streams, fall biomass was greatest, followed by decrease during winter and an increase during spring. The spring increase was followed by another decrease during summer. The spring increase occurred

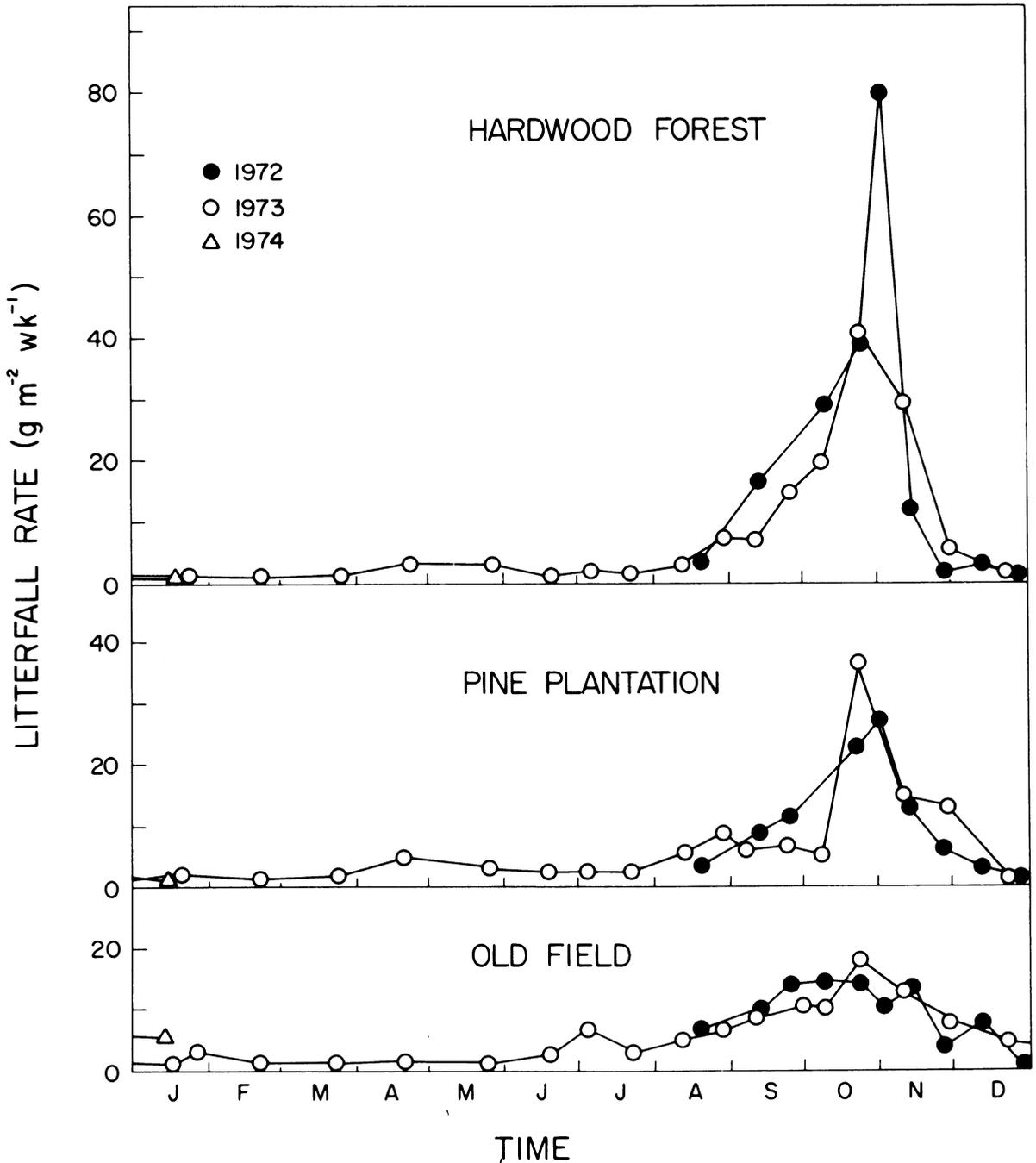


FIG. 4. Litterfall rates into the 3 study streams.

in all 3 streams, however, it was only significant ($\alpha = .05$) in the old field. These spring increases may in part be due to lateral movement of leaf litter into the streams. Webster (1977), in a study of a 2nd-order stream on another hardwood forest watershed at Coweeta, found that blow-in of leaf litter was $1.6\times$ as great as leaf fall and, though peaking in fall, continued through the winter and into spring.

Large particulate matter stored deep in the stream

sediments was not measured in this study. Recent studies have shown that significant amounts of large particulate organic matter may be deposited and stored deep (>10 cm) in the streambed and on the floodplain and subsequently removed during major storms (recurrence interval >1 yr). This may lead to significant errors in annual organic matter budgets (J. Sedell and K. Cummins, *personal communication*).

Patterns of element concentrations in LPOM (Table

TABLE 4. Standing crops of large particulate organic matter

	Biomass (g m ⁻²)			K concentrations (mg g ⁻¹)			Ca concentrations (mg g ⁻¹)		
	Old field	Pine plantation	Hardwood forest	Old field	Pine plantation	Hardwood forest	Old field	Pine plantation	Hardwood forest
Winter	44	70	125	0.27	0.75	<0.10 ¹	9.64	9.03	13.85
Spring	93	98	130	0.33	0.16	<0.10 ¹	6.97	7.94	10.25
Summer	71	107	111	0.38	0.73	0.34	11.06	12.36	12.31
Fall	181	148	294	0.71	0.37	<0.10 ¹	12.06	8.64	14.34
Annual mean	97	106	165	0.52	0.48	0.14	10.41	9.46	13.10

¹ K concentrations for this period were below the detection limits (100 $\mu\text{g}\cdot\text{g}^{-1}$).

4) were almost identical to patterns of litterfall element concentrations (Table 3). Peak concentrations of both elements occurred in the old field stream in fall. In the pine plantation stream, the peaks were in summer and winter. In the hardwood forest stream, the peak K concentration occurred in summer and the peak Ca concentration in fall.

Potassium concentrations in LPOM were substantially <K concentrations in leaf litter, but Ca concentrations were in some cases > in leaf litter. In terrestrial litter bag studies Attiwill (1968) and Gosz et al. (1973) found significant K decreases in the 1st few mo and slower losses thereafter. In both studies there was little Ca loss even after a year. For K, Cromack (1972, Cromack and Monk 1975) reported exponential loss rates of 1.7 yr⁻¹ and 1.8 yr⁻¹ from litter bags of pine needles and mixed hardwood litter, respectively. He found no significant Ca loss from pine bags and Ca loss rate from mixed hardwood bags was .34 yr⁻¹. Two studies have compared element losses in terrestrial and aquatic sites. Witkamp and Frank (1969) found exponential loss rates of ¹³⁴Cs from oak leaves of 3.5 yr⁻¹ in a forest, 8.3 yr⁻¹ in a pond, and 16.6 yr⁻¹ in a stream. In all 3 sites, ¹³⁴Cs losses were more rapid than weight losses. Thomas (1970) found that calcium loss rates were essentially identical to weight loss rates during leaf decomposition in a stream and the surrounding forest.

On an annual basis, LPOM standing crops in terms of biomass and Ca were higher in the hardwood forest stream than the other streams (Table 4). However, K standing crops were lowest in the hardwood forest stream. Standing crops of biomass, Ca and K in the pine plantation and old field stream were very similar.¹ The only significant ($\alpha = .05$) differences found by a paired *t* test were: LPOM biomass and Ca were greater in the hardwood forest than in the old field stream and K standing crop was higher in the pine plantation than in the hardwood forest stream.

Standing crops of benthic fauna.—The insect fauna of the 3 streams was dominated by *Peltoperla maria* (Plecoptera: Peltoperlidae), *Stenonema* spp. (Ephemeroptera: Heptageniidae), and tipulids (Diptera: Tipulidae), including *Tipula abdominalis*, *T. ignobilis*, *Eriocera longicornis*, *E. spinosa*, and *E. fultonensis*

(Woodall and Wallace 1972). These 3 groups of benthic insects are all detritivores.

Peltoperla maria, like other stoneflies of the suborder Filopalpia, is a shredder (Cummins 1973). Woodall (1972) found nothing but detritus in the foreguts of 10 specimens. Wallace et al. (1970) found that *P. maria* fed readily on deciduous leaves, preferring some leaf species over others. From gut analysis, Elwood and Cushman (1975) also designated *P. maria* as a shredder. *Peltoperla maria* accounted for 11, 30, and 31% of the average annual insect biomass in the old field, pine plantation, and hardwood forest streams, respectively.

Various species of *Stenonema* apparently feed from the surfaces of submerged material, which depending on the stream, may be deposits of fine organic particles, diatoms or other algae growing on the surfaces, or possible heterotrophic microbes on the surfaces of large organic particles. Trama (1957) studied energy transmutation by *Stenonema pulchellum* fed cultured algal cells. Minckley (1963) found primarily detritus in the digestive tracts of *Stenonema*. Coffman et al. (1971) determined that 2 species of *Stenonema* fed primarily on algae in a small Pennsylvania stream. Cummins et al. (1973) showed that, with only whole leaves available as food, growth of *Stenonema fuscum* depended on presence of invertebrate shredders. Shapas and Hilsenhoff (1976) determined the foregut contents of 6 species of *Stenonema* to be principally detritus. Studying insects collected at Coweeta, Woodall (1972) found only detritus and fungal hyphae in the guts of *Stenonema* spp. In the heavily shaded streams at Coweeta, where instream primary production is very low, *Stenonema* apparently depends entirely on terrestrial leaf detritus as its food source. The biomass of *Stenonema* was 5, 9, and 9% of the average annual insect biomass in the 3 streams.

Minckley (1963) found primarily algae and higher plant material in the guts of *Tipula nobilis*?, however, tipulids are generally recognized as shredder detritivores (Cummins 1973). Vannote (1969) classified *T. abdominalis* as a shredder and studied the energy budget of *T. abdominalis* fed on deciduous leaves. Cummins et al. (1973) found that *T. abdominalis* and *T. caloptera* grew and survived well on a diet of decid-

TABLE 5. Average annual standing crops of insect detritivores and crayfish. All values are mg m⁻²

	Insect detritivores	Crayfish
Old field	848	3909
Pine plantation	890	2915
Hardwood forest	1337	1607

uous leaves. Gut contents of *Tipula* collected at Coweeta were mostly detritus (Woodall 1972). The largest percentage of material in *Eriocera* gut contents was detritus, but Woodall (1972) also found insect fragments and algae. Tipulids accounted for a large percentage of the benthic insect biomass in the old field stream (56%) and an only somewhat smaller biomass in the pine plantation and hardwood forest streams (17 and 26%).

On an annual basis, these 3 groups of insects, *Peltoperla maria*, *Stenonema*, and tipulids, accounted for 73, 56 and 67% of the total insect biomass of the old field, pine plantation, and hardwood forest streams, respectively. Excluding predaceous insects (primarily odonates, setipalpi stoneflies, and rhyacophilid caddisflies), these dominant insects comprised 84, 71, and 76% of the primary consumer insect biomass.

Among the Trichoptera, net spinning caddisflies comprised 11, 13, and 9% of the average annual insect biomass in the old field, pine plantation, and hardwood forest streams, respectively. Species included *Diplectrona modesta*, *Parapsyche cardis*, *Dolophiodes* sp., *Chimarra* sp., and *Wormaldia* sp. Though the diets of these insects, especially *Parapsyche cardis* in the final instar, include other insects (e.g., Wallace et al. 1977), all except *P. cardis* are primarily detritivores when the complete life cycle is considered.

TABLE 6. Dry weight (mg) and potassium and calcium concentrations (μg g⁻¹) of dominant stream detritivores. Data on crayfish and immature insects from Woodall (1972)

Taxonomic group	Immatures			Adults		
	Dry weight	K	Ca	Dry weight	K	Ca
<i>Cambarus</i>						
small (<2 cm)				57.7	1 900	100 300
medium (2-5 cm)				265.9	1 900	100 300
large (>5 cm)				2049.0	1 900	100 300
Tipulidae						
<i>Eriocera</i>	2.19	7100	3800			
<i>Tipula</i>	43.82	7300	4300	43.83	9 000	8 500
small tipulids				0.54	10 500	3 200
medium tipulids				5.18	9 200	1 200
Chironomidae	0.15	2100	7900	0.07	12 600	2 800
<i>Stenonema</i>	4.29	1900	3800	2.84	11 400	1 200
<i>Peltoperla</i>	2.88	1800	3500	4.10	12 400	4 100
Hydropsychidae				2.57	8 400	2 800
<i>Diplectrona</i>	1.33	2700	3500			
<i>Parapsyche</i>	4.33	1900	3200			

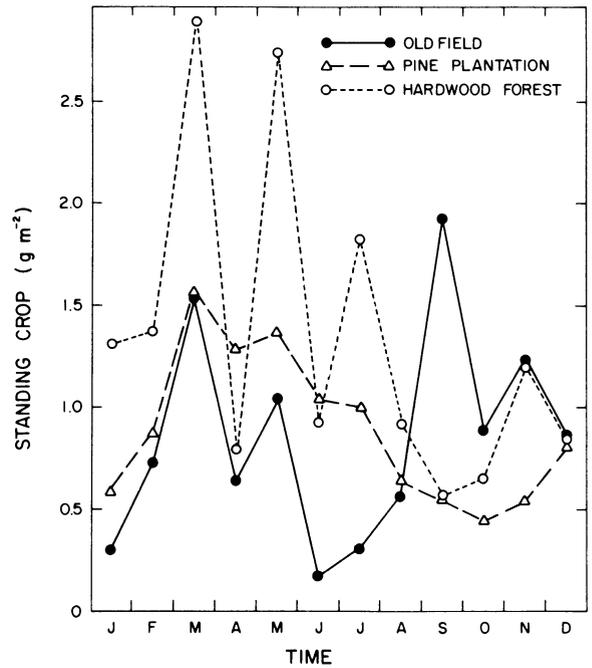


FIG. 5. Standing crops of benthic detritivore biomass in the 3 study streams.

There were a number of other regularly occurring insects found at Coweeta which Woodall (1972) or others have determined to be principally detritus feeders. These included the mayflies *Ephemera* spp., *Baetis* sp., and *Paraleptophlebia* sp. Two other Filopalpia stoneflies were found, *Nemoura* sp. and *Leuctra* sp. Detritus feeding Trichoptera other than the net spinners included *Fattigia pele*, *Pycnopsyche* spp., and *Lepidostoma* sp. Diptera other than tipulids found in the 3 Coweeta streams included simuliids, dixids, cer-

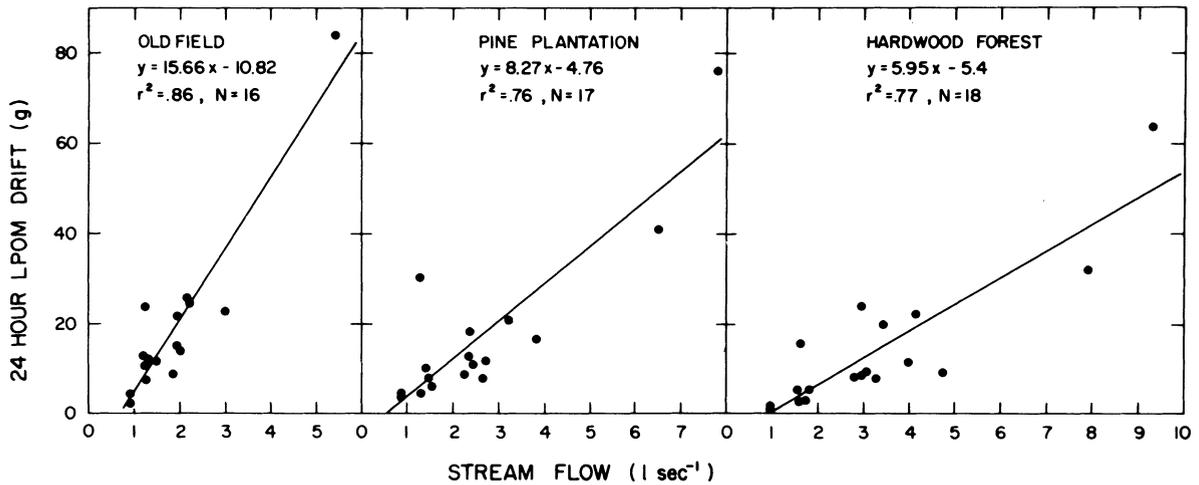


FIG. 6. The relationship of large particulate organic matter (LPOM) drift to stream flow in the 3 study streams.

atopogonids, and chironomids. Of the chironomids collected, only *Conchapelopia* sp. was in the Tanyptodinae. Members of this subfamily are generally considered to be predators (Woodall and Wallace, 1972, Cummins 1973), but the other species of chironomids are probable detritivores. All these groups together along with other, less abundant, taxa, accounted for <15% of the detritivore biomass in any of the streams. However, because of rapid turnover, the chironomids especially may have a greater production than we have attributed to them.

Hynes (1970) described an idealized seasonal cycle of insect biomass in an unpolluted stream: minimum biomass occurs during summer when emergence and egg laying take place, followed by increase to an early spring peak. Detritivore biomass in the 3 study streams generally followed this trend (Fig. 5). In the hardwood forest and pine plantation streams, peak biomass occurred in early spring and minimum biomass was found in fall. In the old field stream, a biomass peak occurred in early spring, then a minimum in summer, and a second peak in fall. The September peak was due to the large number of tipulids present at that time.

The average standing biomass of insect detritivores was significantly ($\alpha = .05$) greater in the hardwood forest stream than in the other 2 streams (Table 5). The old field and pine plantation streams were not significantly different.

The crayfish (*Cambarus bartoni*) was also a significant detritivore. Average standing crop biomass was the reverse of insect biomass being greatest in the old field stream and least in the hardwood forest stream (Table 5). In all 3 streams, crayfish biomass was > detritivore insect biomass, however, because of much slower turnover, their large biomass does not reflect their impact on the stream ecosystems.

Dry weights and K and Ca concentrations determined for the more abundant detritivores are shown in Table 6.

Large particulate organic matter drift.—Fisher and Likens (1973) found that concentrations of coarse particulate organic matter were proportional to discharge. Similarly, Hall (1972) reported that the log of leaf mass discharge was linearly proportional to water stage. However, we found a significant ($\alpha = .05$) linear relationship between LPOM drift and discharge on all 3 streams (Fig. 6). In comparing these relationships by analysis of covariance, the regression slopes were similar for the hardwood forest and pine plantation streams. However, the slope was significantly greater for the old field stream. That is, a unit increase in stream flow in the old field stream produced a greater increase in LPOM discharge than in the other 2 streams.

We used the regression equations of LPOM drift as a function of stream discharge to estimate total output of particulate detritus. Monthly values were found from mean monthly discharge. Annual drift of LPOM was greatest from the old field stream and least from the hardwood forest stream (Table 7). It is difficult to evaluate the significance of these differences, noting especially that the sampling periods represented <5% of the annual cycle. However, these data are sup-

TABLE 7. Drift of large particulate organic matter (LPOM), insect detritivores, and crayfish from the study streams. All values in $\text{mg m}^{-2} \text{yr}^{-1}$

	LPOM	Insect detritivores	Crayfish
Old field	62 500	243.8	405
Pine plantation	35 300	52.6	158
Hardwood forest	17 100	50.5	57

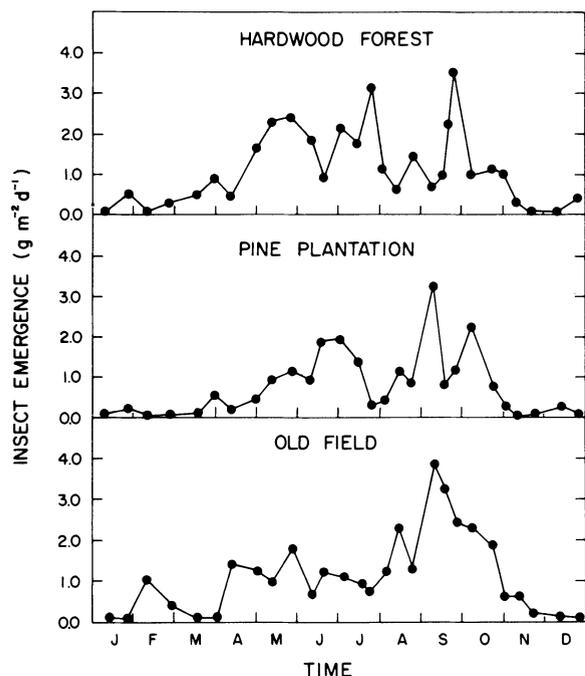


FIG. 7. Detritivore insect emergence from the 3 study streams.

ported by strong correlation with annual inorganic particulate discharge (Table 2).

Organism drift.—In a correlation analysis between insect detritivore drift and stream flow, we found no significant relationship for the pine plantation and hardwood forest streams ($r^2 = .02$ and $.19$, respectively). However, for the old field stream, there was a statistically significant relationship ($r^2 = .63$, $N = 25$). There was no significant relationship between drift and standing crop for any of the streams.

In calculating annual drift for the hardwood forest and pine plantation streams, a simple mean value was used because there was no apparent relationship to stream flow. For the old field stream, a linear regression equation was used to calculate drift from mean monthly stream flows. Annual insect detritivore drift was considerably greater from the old field stream than from the other 2 streams (Table 7). Tipulids, *Stenonema*, *Peltopera*, and hydropsychids together comprised 55, 86, and 93% of the insect detritivore drift from the old field, pine plantation, and hardwood forest streams, respectively.

We found no significant correlations between crayfish drift and stream flow. Annual crayfish drift was calculated from a mean value of daily samples. Crayfish drift was greatest from the old field stream and least from the hardwood forest stream and, in all 3 streams, $>$ insect drift (Table 7).

Insect and crayfish drift losses were small fractions of standing crops. Annual insect detritivore drift rep-

TABLE 8. Emergence of adult detritivore insects from the 3 study streams

	Annual emergence (mg m^{-2})	Standing crop (%)
Old field	375.4	44
Pine plantation	254.7	29
Hardwood forest	389.7	29

resented 29, 6, and 4% of the average standing crop in the old field, pine plantation, and hardwood forest streams, respectively. Crayfish drift was 10, 5, and 4% of standing crops.

Emergence of benthic insects.—Most insect emergence occurred during late spring, summer, and early fall, though some emergence, primarily philopotamids, winter stoneflies, and chironomids, took place during the winter (Fig. 7).

Annual emergence was greatest from the hardwood forest stream and least from the pine plantation stream (Table 8). Emergence from the old field and hardwood forest streams were not significantly different ($\alpha = .05$), though emergence from each stream was significantly $>$ emergence from the pine plantation stream. Annual emergence represented 29% of the average standing crop on the hardwood forest and pine plantation streams, but 44% on the old field stream. This difference can be attributed to the bias of emergence samplers. In particular, a large number of philopotamids were caught in the emergence traps in the old field stream, whereas this group was not abundant in the benthic samples. In general, the emergence traps selected against larger insects. For example, we seldom found the stonefly, *Peltopera maria*, in emergence samples, though it was abundant in benthic samples, whereas the smaller and less abundant stoneflies, *Leuctra* and *Nemoura*, were common in emergence samples. Among Trichoptera, smaller psychomyiids and philopotamids were more commonly caught in emergence traps than larger and more abundant hydropsychids.

On an annual basis, *Peltopera maria*, *Stenonema*, tipulids, and hydropsychids represented 55, 61, and 59% of total emergence biomass from the old field, pine plantation, and hardwood forest streams, respectively. From analysis of K and Ca concentrations in adult insects, we found that K concentrations were considerably greater in adults than in immatures (Table 6).

Tracer determination of invertebrate elimination rates.—The 2-compartment elimination model developed by Reichle and Crossley (1965) was used in analysis of radiotracer elimination data. In this model, the radioisotope is represented as being in 2 components, body and gut, with independent elimination from each component:

TABLE 9. Isotope elimination rates (h⁻¹) and assimilation efficiencies (%) of stream organisms. *k_B* is body elimination rate; *T_B* is body half-time (*ln 2/k_B*); *k_G* is gut elimination rate; *T_G* is gut half-time (*ln 2/k_G*). Half-times in hours

Species	Isotope	Assimilation efficiency ± SE	Sample size	<i>k_B</i> ± SE	<i>T_B</i>	Sample size	<i>k_G</i> ± SE	<i>T_G</i>	Sample size
<i>Peltoperla maria</i>	¹³⁴ Cs	11.0 ± 4.2	9	0.026 ± 0.006	26.4	25	0.308 ± 0.050	2.2	27
	⁸⁵ Sr	28.1 ± 10.0	5	0.020 ± 0.002	35.2	18	0.153 ± 0.030	4.5	18
<i>Stenonema</i> sp.	¹³⁴ Cs	9.8 ± 1.5	4	0.011 ± 0.003	62.9	11	0.378 ± 0.089	1.8	11
	⁸⁵ Sr	11.9 ± 9.8	3	0.041 ± 0.006	16.7	5	0.458 ± 0.090	1.5	5
<i>Tipula</i> sp.	⁸⁵ Sr	27.3 ± 6.2	9	0.045 ± 0.006	15.4	9	0.491 ± 0.096	1.4	9
<i>Cambarus bartoni</i>	¹³⁴ Cs	33.2 ± 7.8	5	0.0012 ± 0.004	587.4	7	0.046 ± 0.012	15.0	7
	⁸⁵ Sr	83.3 ± 2.7	5	0.0010 ± 0.004	719.5	5	0.058 ± 0.034	12.0	5

$$\frac{dB(t)}{dt} = aI(t) - k_B B(t), \tag{1}$$

and

$$\frac{dG(t)}{dt} = (1 - a)I(t) - k_G G(t), \tag{2}$$

where *B(t)* is body content, *G(t)* is gut content, *a* is the assimilation fraction, *k_B* is body elimination rate, *k_G* is the gut elimination rate, and *I(t)* is the ingestion rate. Other models have been developed for invertebrate elimination, however, Webster and Crossley (1978) demonstrated that this model was satisfactory at the level of resolution of this study.

Time series data from each tracer experiment were fitted to a solution equation for Eqs. 1 and 2:

$$X(t) = aI_0 e^{-k_B(t-t_0)} + (1 - a)I_0 e^{-k_G(t-t_0)}, \quad t \geq t_0, \tag{3}$$

where *X(t)* is the sum of gut and body tracer content, *I₀* is the activity of radioisotope ingested during the acute feeding period or the total activity of the animal at the end of a chronic feeding, *t₀* is the time of the initial count, and other symbols are as above. After correction for background and physical decay, normalization, and logarithmic transformation, linear regression was used to find the slope (*k_B*) and intercept (*a*) of the long portion of the curve. This line was then "stripped" from the curve and linear regression used to find the slope (*k_G*) of the short component.

Results of the radioisotope elimination study are summarized in Table 9. For each species studied, we found 2-component elimination curves for both ¹³⁴Cs and ⁸⁵Sr. In some cases, assimilation efficiencies were not calculated because feeding occurred over a period >2 h (chronic feeding).

The crayfish, *Cambarus bartoni*, eliminated both isotopes much more slowly than any of the insects. Among the insects, *Tipula* sp., the largest insect studied, eliminated ⁸⁵Sr more rapidly from both body and gut than either *Peltoperla maria* or *Stenonema* sp. Elimination of ⁸⁵Sr by *Peltoperla* was considerably slower than by either *Tipula* or *Stenonema*. Gut elimination of ¹³⁴Cs was faster by *Stenonema* than by *Peltoperla* but body elimination was faster by *Peltoperla*.

Assimilation efficiencies were generally low with the exception of ⁸⁵Sr assimilation by crayfish which averaged 83.3% of ingested ⁸⁵Sr. In all cases assimilation of ⁸⁵Sr was > assimilation of ¹³⁴Cs.

Few measurements of radioisotope elimination by aquatic insects have been made. Kevern et al. (1964) found ¹³⁴Cs turnover rates for *Ephemera varia* and *Chironomus commatatus* which were somewhat slower (*k_B* = .08 d⁻¹ and .06 d⁻¹, respectively) than insect turnover rates found in this study. Schurr and Stamper (1962) found a ⁸⁵Sr elimination rate (*k_B*) for *Cambarus longulus* of .13 d⁻¹, faster than found for *C. bartoni* in this study. Turnover rates of ¹³⁴Cs and ⁸⁵Sr by terrestrial insects are generally slower than the rates we measured (Crossley and Pryor 1960, Crossley and Schnell 1961, Hubbell et al. 1965, Reichle and Crossley 1965, Crossley 1966, Reichle 1967, Williams and Reichle 1968, Kowal 1969, Van Hook and Crossley 1969, Moulder et al. 1970, Crossley et al. 1971, Van Hook 1971, and Gist 1972). With the exception of *Cambarus bartoni*, the rates of ¹³⁴Cs and ⁸⁵Sr assimilation by the aquatic detritivores were in the same range of assimilation of elements, biomass, or energy found in other aquatic and terrestrial detritivores, 10–30%. (Aquatic: Kevern et al. 1964, Cummins 1969, Vannote 1969, and McDiffett 1970. Terrestrial: Gere 1956, Bocock 1963, Hartenstein 1964, Hubbell et al. 1965, Reichle 1967, Crossley and Van Hook 1970, Crossley et al. 1971, and Van Hook 1971.)

From Table 6, it is evident that crayfish concentrate Ca and higher assimilation and slower turnover of ⁸⁵Sr relative to ¹³⁴Cs were expected. However, among the insects, Ca and K concentrations were similar. Because Ca concentrations were generally an order of magnitude > K concentrations in their food source (Table 4), we expected that ⁸⁵Sr would be assimilated less or turned over more rapidly (Table 9). One possible explanation may be that Ca in plant tissue is not available to insects because it is mainly in cell walls, whereas the ⁸⁵Sr used in these experiments was just a surface tagging. An alternative explanation is that significant amounts of K were absorbed directly from the water.

By assuming steady state, that is, growth rates are

TABLE 10. Consumptive indices of benthic organisms estimated from radiotracer elimination rates

Organism	Consumptive index (d ⁻¹)			B(ss)/ [B(ss) + G(ss)] ¹
	K	Ca	Biomass ²	
<i>Peltoperla maria</i>	3.37		43.6	59
<i>Stenonema</i> sp.	2.12	1.28	0.34	75
		4.97	1.43	60
<i>Tipula</i> sp.		3.18	1.04	80
<i>Cambarus bartoni</i>	0.081		1.10	95
		0.027	0.21	99

¹ Percent of element in body component at steady state.

² Consumptive index biomass = consumptive index element × concentration element in organism/concentration element in food.

negligible compared to elimination and egestion rates, ingestion rates necessary to support the turnover rates given in Table 9 can be calculated. The steady state solution to Eqs. 1 and 2 is:

$$X(ss) = \frac{a}{k_B} + \frac{1-a}{k_G} l(ss), \tag{4}$$

where (ss) indicates the steady state value. Rearranging Eq. 4 gives

$$\frac{l(ss)}{X(ss)} = \frac{k_B k_G}{ak_G + k_B - ak_B}, \tag{5}$$

where the ratio on the left, $l(ss)/X(ss)$, is Waldbauer's (1968) consumption index. Ingestion rates estimated by this method (Table 10) can be compared with rates found in other studies (Table 11). Estimates of biomass ingestion calculated from ⁸⁵Sr elimination are in the

range of values in Table 11, though generally faster. However, biomass ingestion rates calculated from ¹³⁴Cs elimination are much higher. The explanation of these very high values is the low K concentration of leaf material (139 mg g⁻¹) used to convert from K ingestion to biomass ingestion. Again, the difficulty may be direct absorption of K from the water, though this was not indicated by the partitioned pan feeding experiments.

Ratios of body elemental content to total elemental content (Table 10) were calculated from Eqs. 1 and 2 as:

$$\frac{B(ss)}{B(ss) + G(ss)} = \frac{(k_G - k_B)a}{(k_G - k_B)a + k_B}. \tag{6}$$

Values calculated from this equation are shown in Table 10. In a comparable study, Hubbel et al. (1965) estimated that 77% of ⁹⁰Sr was in the body component of isopods. Elwood et al. (1976) found that gut contents of *Tipula* spp. comprised 8.5% of K, 60.3% of Cs, and 78.6% of Ca body burden.

DISCUSSION

Results of the field studies and experimental radioisotope study were used to calculate K and Ca dynamics for the 3 streams (Fig. 8). Standing crop values were calculated from Tables 4 and 5, organism and LPOM drift from Table 7, insect emergence from Table 8, and litterfall from Table 3. Elimination rates were calculated from rates in Table 9 as:

$$\text{Egestion} = \left(1 - \frac{B_i(ss)}{B_i(ss) + G_i(ss)}\right) k_B 2^{\frac{T-20}{10}} x_i(ss) \tag{7}$$

and

$$\text{Excretion} = \frac{B_i(ss)}{B_i(ss) + G_i(ss)} k_B 2^{\frac{T-20}{10}} x_i(ss), \tag{8}$$

TABLE 11. Consumptive indices of aquatic organisms

Organism	Food	Temperature (°C)	Consumptive index (d ⁻¹)	Reference
<i>Banksiola crotchi</i>	algae	18	1.41	Winterbourn 1971
<i>Neophylax concinnus</i>	algae and detritus	4-5	1.20 ¹	Sedell 1971
<i>Stenonema pulchellum</i>	algae	20	0.19 ¹	Trama 1957
<i>Peltoperla maria</i>	detritus	15	0.08 ²	Wallace et al. 1970
<i>Pteronarcys scotti</i>	detritus	10-15	0.062 ¹	McDiffett 1970
<i>Pycnopsyche guttifera</i>	detritus	5	0.332	Cummins et al. 1973
<i>Pycnopsyche gentilis</i>	detritus	...	0.02-1.00	Mackay and Kalff 1973
<i>Pycnopsyche luculenta</i>	detritus	...	0.02-0.81	Mackay and Kalff 1973
<i>Stenonema</i> spp.	detritus	5	0.04-0.23	Cummins et al. 1973
<i>Tipula</i> spp.	detritus	5	0.16-0.19	Cummins et al. 1973
<i>Tipula abdominalis</i>	detritus	...	0.041 ¹	Vannote 1969
<i>Acroncuria californica</i>	predator	18	0.03 ³	Heiman and Knight 1975
Chironomidae	predator	20	1.52-2.71	Luferov 1961 ⁴
Odonata	predator	...	0.3	Benke 1972
<i>Banksiola crotchi</i>	predator	18	1.66	Winterbourn 1971

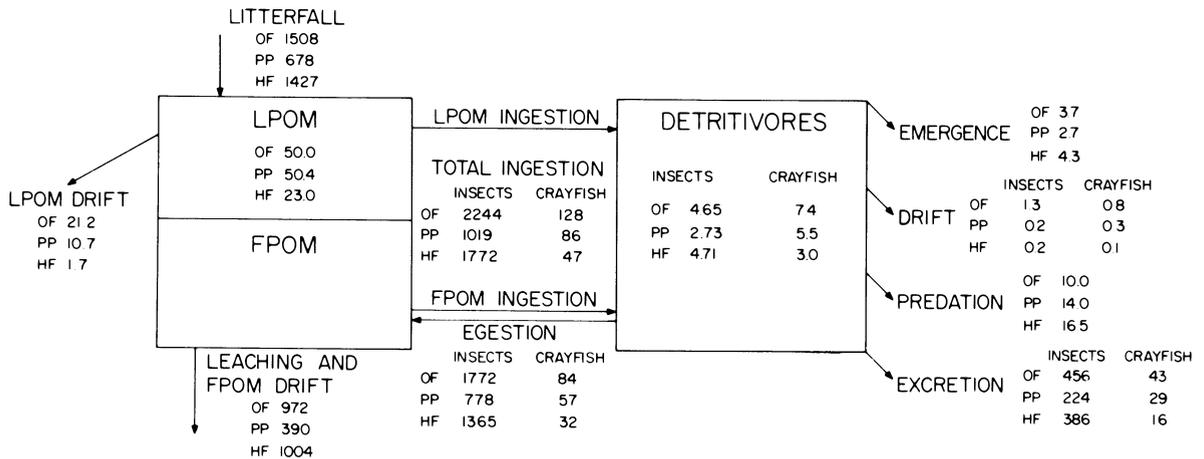
¹ Index calculated by Cummins et al. (1973).

² Mean value.

³ Assuming equivalent caloric values for *Acroncuria* and prey species.

⁴ As cited in Monakov (1972).

POTASSIUM



CALCIUM

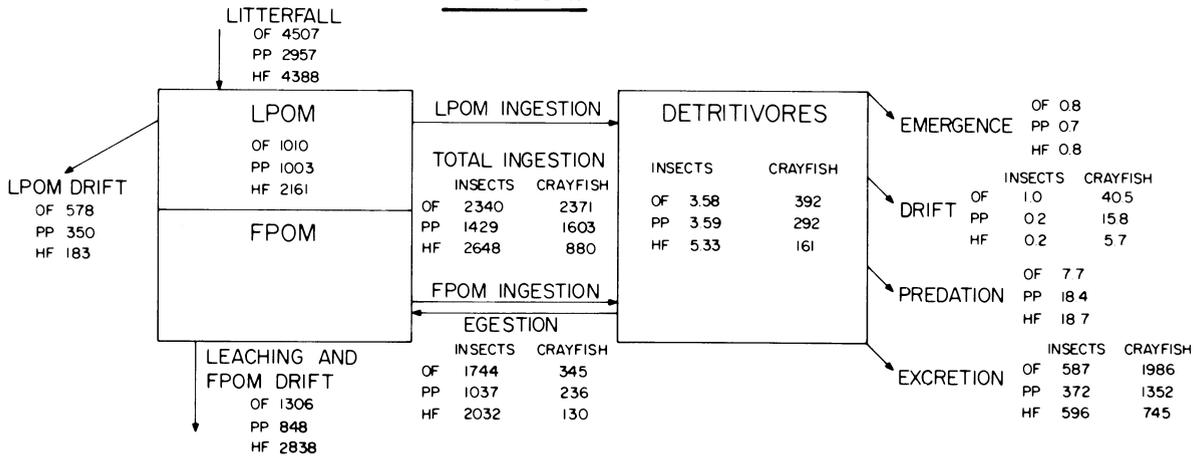


FIG. 8. Potassium and calcium dynamics in the old field (OF), pine plantation (PP), and hardwood forest (HF) watershed streams. Standing crops are mg m^{-2} ; flows are $\text{mg m}^{-2} \text{ yr}^{-1}$.

where T is the mean annual stream temperature and other symbols are as above. In Eqs. 7 and 8, the temperature term converts rates from experimental temperatures (20°C) to stream temperatures according to a Q_{10} of 2 (Reichle and Crossley 1965, Crossley 1966, Hasanen et al. 1967). For insect detritivores, elimination rates were calculated as means of *Peltoperla maria*, *Stenonema*, and *Tipula* rates, weighted according to their abundance.

Insect predation was calculated from measured insect predator standing crops (Woodall 1971, 1972; Webster 1975) and published ingestion rates (Lawton 1971, Winterbourn 1971, Heiman and Knight 1975). Salamander predation was similarly calculated from standing crops and published ingestion rates (Fitzpatrick 1973a, 1973b). Additionally, Woodall's (1972) analyses of salamander gut contents were used to derive the benthic insect fraction of salamander ingestion.

Detritivore ingestion was calculated to balance detritivore losses: emergence, drift, predation, excretion, and egestion. Leaching and FPOM losses, which were not measured, were estimated to balance litterfall inputs. For each element in each stream, we assumed that inputs (litterfall) and losses (emergence, organism drift, predation, excretion, particulate drift, and leaching) were equal for an annual cycle. This assumption is certainly only an approximation because bed storage of particulates and subsequent loss during extreme floods takes place over longer than annual periods (J. Sedell and K. Cummins, *personal communication*).

No allowance was made for detritivore uptake of dissolved ions. We assumed excretion of K and Ca occurs as dissolved ions, subsequently unavailable to the detritivores. Egested material, however, is recycled back into the particulate organic matter pool, available for subsequent uptake by filter and deposit feeding detritivores. The K data discussed below

TABLE 12. Parameters of potassium and calcium dynamics derived from Fig. 8. Parameters are explained further in the text. LPOM = large particulate organic matter

Parameter	Potassium			Calcium		
	Old field	Pine plantation	Hardwood forest	Old field	Pine plantation	Hardwood forest
LPOM turnover rate (yr^{-1})	36.5	13.3	62.0	4.5	2.9	2.0
LPOM processing efficiency (%)	98.6	98.4	99.9	87.2	88.2	95.8
Ingestion of crayfish (% of total ingestion)	5	8	3	50	53	25
Litterfall ingestion efficiency (%)	157.3	164.7	127.5	104.6	102.5	80.4
Detritivore production (mg element m^{-2})	15.8	17.1	21.0	49.9	35.1	25.4
Insect detritivore production (mg element m^{-2})	15.0	16.8	20.9	9.5	19.3	19.7
Crayfish production (mg element m^{-2})	0.8	0.3	0.1	40.5	15.8	5.7
Production efficiency (%)	1.0	2.6	1.5	1.1	1.2	0.6
Insect turnover (yr^{-1})	3.2	6.2	4.4	2.6	5.4	3.7
Crayfish turnover (yr^{-1})	0.11	0.05	0.03	0.10	0.05	0.04
Assimilation/litterfall (%)	34.2	40.3	29.7	58.2	59.6	31.1
Recycled (%)	78.3	75.5	76.7	44.3	42.0	61.3
FPOM and solution/litterfall (%)	64.4	58.1	70.3	29.0	28.7	64.7

should be evaluated in light of possible uptake of dissolved ions.

Input of K and Ca as litterfall were greatest in the old field stream and least in the pine plantation stream (Fig. 8). This contrasts with biomass inputs, which were greatest in the hardwood forest and least in the old field stream (Table 3), because of the high elemental concentrations of old field litter and low elemental concentrations of pine litter. Standing crops of large particulate organic matter K were very low because of the high degree of leaching of this element, especially from the hardwood forest litter. Calcium standing crops in LPOM were much higher, suggesting that this element was not leached. Calcium concentrations in LPOM were similar to litterfall concentrations throughout the year (Tables 3 and 4).

Turnover of LPOM, litterfall over LPOM standing crop, was much faster for K than Ca because of rapid K leaching, especially from hardwood litter (Table 12). Turnover of LPOM calculated from the Ca budgets should, as discussed above, approximate weight loss. From the Ca data, LPOM turnover was fastest in the old field stream and slowest in the hardwood forest stream. The LPOM turnover rates in Table 12 would be somewhat greater if lateral movement inputs were included and less if corrections were made for deep storage of detritus. In litterbag studies in a second-order stream on another forested Coweeta watershed, turnover rates of 0.9 to 7.2 yr^{-1} were found for various species (J. B. Waide, *personal communication*). Incorporating these rates into a model which predicted LPOM standing crop from species specific leaffall inputs, an average turnover rate of $\approx 1.5 \text{ yr}^{-1}$ was found.

Drift of K and Ca as LPOM was greatest from the old field stream and least from the hardwood forest

stream. Expressed as a percentage of litterfall input and subtracted from 100% to reflect percent processed, the LPOM processing efficiency (Webster 1977) was very high for both elements in all 3 streams (Table 12). That is, a large fraction of litterfall input was processed by combined chemical, mechanical, invertebrate, and microbial action to FPOM and dissolved material by the time it left the streams. Processing efficiencies of LPOM were greater for K than Ca, reflecting the solubility of K. For both elements, LPOM processing efficiencies were greatest in the hardwood forest stream.

The ingestion data further point to dissolved K uptake by the insect detritivores. The percent of total ingestion attributable to crayfish is much greater for Ca than for K (Table 12). If there were no dissolved uptake, these percentages would be identical for the 2 elements in each stream. The lower percent K ingestion by crayfish can probably be attributed to dissolved K uptake by the insects, as suggested by the high estimates of consumptive indices from ^{134}Cs elimination (Table 10).

Litterfall ingestion efficiencies were calculated as total detritivore ingestion over litterfall input (Table 12). As shown by these figures, total detritivore ingestion exceeded litterfall in all cases except Ca in the hardwood forest stream. Litterfall ingestion efficiencies $> 100\%$ indicated by K probably resulted from dissolved ion uptake. However, high Ca litterfall ingestion efficiencies appear to indicate reingestion of egested materials. For comparisons of ingestion at 1 trophic level to input at the previous level (I_n/I_{n-1}), efficiencies of 20% or less are usual (Kozlovsky 1968). However, in saprovores food chains, where consumer activities do not alter the rate of resource supply, higher food base utilization is possible (Wiegert and

Owen 1971). In the Coweeta stream ecosystems, high ingestion efficiencies probably result from filter feeder and deposit feeder ingestion of primarily shredder feces. Short and Maslin (1977) showed clearly that collectors utilize shredder feces. Because food that a stream detritivore ingests and subsequently egests is normally transported downstream prior to reingestion by another detritivore, the process is not cyclic but is better described as spiralling (Webster 1975, Wallace et al. 1977).

In terms of K, insect detritivore standing crops were similar in the old field and hardwood forest streams and lower in the pine plantation stream (Fig. 8). Crayfish standing crops were highest in the old field stream and lowest in the hardwood forest stream. Crayfish standing crop as K exceeded insect detritivores in the old field and pine plantation streams but not in the hardwood forest streams. Because of the slow turnover of K by crayfish (Table 9), uptake of K, whether ingestion or dissolved uptake, represented only a small portion of total K uptake by detritivores (Table 12). Because of a fairly low detritivore assimilation efficiency, most K was egested. Most of the remainder was lost as excretion with a small fraction being lost to emergent adults, drift, and predation.

Insect detritivore standing crops of Ca were greatest in the hardwood forest stream and similar in the other 2 streams (Fig. 8), reflecting biomass standing crops. Crayfish standing crops as Ca were highest in the old field stream and lowest in the hardwood forest stream. Due to the very high Ca concentrations of crayfish, Ca standing crops as crayfish greatly exceeded insect standing crops. Even with very slow Ca turnover (Table 9), estimated crayfish ingestion of Ca was about as great as insect ingestion because of the high crayfish standing crops. Crayfish ingestion represented 50% of total Ca ingestion in the old field stream, 53% in the pine plantation stream, but only 25% in the hardwood forest stream (Table 12). Because of their highly efficient assimilation of Ca, much of the detritivore Ca excretion was due to crayfish. Egestion of particulate Ca back to the particulate organic matter pool was mainly by insects.

Detritivore production was calculated as the sum of insect emergence, organism drift, and predation (Table 12). Insect production was greatest in the hardwood forest stream and least in the old field stream in terms of both elements. Crayfish contributed very little to production as K, however, because of high Ca concentration in drifting crayfish, their contribution to production as Ca was substantial. Because of the contribution from crayfish drift, total detritivore production as Ca was greatest in the old field stream and least in the hardwood forest stream. The production efficiency, the ratio of detritivore production to litterfall input, was very low for all 3 streams and for both elements (Table 12). For both K and Ca, the production efficiency was highest in the pine plantation

stream, reflecting primarily the large number of predators and high predation in this stream, and low litterfall input.

Insect turnover ratios, annual production over mean annual standing crop, ranged from 2.6 to 6.2 (Table 12). These turnover ratios are very similar to estimates made for other streams (Waters 1966, 1969; Hynes and Coleman 1968; Hamilton 1969; Fisher and Likens 1973; Waters and Crawford 1973; Cushman et al. 1975; Resh 1977). Turnover ratios estimated from the K budgets were somewhat higher than the Ca budget estimates because of the relatively higher K concentrations of emerging adult insects (Table 6). Turnover ratios were greatest in the pine plantation stream and least in the old field stream. The main contributing factor to high insect turnover in the pine plantation stream was predation.

Crayfish turnover ratios were much < insect turnover ratios, as might be predicted from the element turnover rates (Table 9). Turnover ratios for the 2 elements were identical (within rounding error) because they were calculated from the same biomass data. Crayfish turnover ratios were greatest in the old field stream and least in the hardwood forest stream. This is entirely attributable to crayfish drift because this was the only crayfish production parameter measured. Inclusion of other factors of crayfish production, such as predation by raccoons and loss of shed exoskeletons, would lead to higher crayfish production and turnover estimates.

More than either ingestion or production, the actual utilization of nutrients by the detritivores is best expressed by assimilation. Assimilated material is what is actually utilized, either in anabolic (production) or catabolic (maintenance) processes. Percent litterfall assimilation was calculated as detritivore production plus excretion as a percent of litterfall input (Table 12). For both elements, assimilation was greatest in the pine plantation stream and least in the hardwood forest stream. Thus, it appears that the detritivores were making less efficient use of available resources in the unperturbed stream in the hardwood forest than in the 2 perturbed streams. This conclusion becomes clearer as other aspects of Fig. 8 are considered.

The percent recycled was calculated as egestion over ingestion (Table 12). The percent of ingested K recycled was similar for all 3 streams. The recycling of Ca was lower because of the very high Ca assimilation of crayfish. The greater recycling of Ca in the hardwood forest stream can be attributed to the lower abundance of crayfish in this stream. This can also be interpreted as lesser utilization by the hardwood forest stream detritivores.

Input of litterfall not lost from the streams as LPOM, production, or excretion we assumed was lost as leachate and FPOM (Table 12). This loss was relatively high for K, and may have been even higher because much of the excretion loss may have come

TABLE 13. Comparison of various potassium and calcium losses. All values in g/yr

	Potassium			Calcium		
	Old field	Pine plantation	Hardwood forest	Old field	Pine plantation	Hardwood forest
Dissolved	65 260	66 680	86 410	122 830	84 950	121 820
Sediment	77.4	36.9	22.7	1 427	956	712
Large particulate organic matter	5.87	4.06	1.19	160	133	128
Fine particulate organic matter	361 ¹	235 ¹	1 984 ¹
Organism drift ²	0.63	0.30	0.35	13.5	7.3	5.7
Insect emergence ²	1.05	1.22	3.26	0.23	0.40	0.77

¹ These figures are based on the assumption of no calcium leaching from organic material.

² These figures include drift and emergence of predators.

from dissolved K uptake, as previously discussed. Based on the similar Ca concentrations of LPOM and litterfall (Tables 3 and 4), there appears to be little leaching of Ca. Therefore, the estimates of Ca leaching and FPOM losses are mainly FPOM. Assuming no Ca leaching, FPOM losses relative to inputs were very similar for the old field and pine plantation streams but much larger for the hardwood forest stream (Table 12). This further exemplifies the lower detritivore utilization of available resources in the hardwood forest stream. However, this conclusion and the other conclusions summarized below must be evaluated according to the accuracy of measurements made in this study and with realization of the factors such as lateral movement and deep storage, which were not measured.

CONCLUSIONS

Perturbations to Watersheds 6 and 17, the old field and pine plantation watersheds, caused changes in the stream ecosystems of these watersheds. These changes were reflected in the K and Ca dynamics of the stream. Because of the indicated probability of dissolved K uptake, we have based our conclusions primarily on our determinations of Ca dynamics. The major changes correlated with watershed perturbation were:

1. Higher litterfall inputs in the old field stream despite a lower litterfall rate because of high elemental concentrations of the old field vegetation.
2. Lower litterfall inputs in the pine plantation stream because of lower elemental concentrations and a lower litterfall rate.
3. More rapid turnover of LPOM if leaching is not considered.
4. Greater inorganic sediment loss.
5. Greater LPOM drift, indicating lower LPOM processing efficiency.
6. Increased production and standing crop of crayfish.
7. Decreased benthic insect production and standing crop.
8. Increased utilization of litterfall inputs, as indicated by detritivore ingestion, assimilation, and production.

9. Less spiralling of Ca.

Taken together, these observed changes suggest that there was less efficient physical processing of inputs in the perturbed streams. Organic and inorganic particulate materials were passed through the streams more rapidly with less processing of the organic matter.

Biologically, there were shifts in the detritivore communities to greater importance of crayfish with lesser importance of the benthic insects. We do not know what caused this shift, though it is correlated with higher nutrient levels (Table 1). This shift illustrates the tendency for generalists to dominate perturbed ecosystems, whereas specialists dominate unperturbed ecosystems (Odum 1969). Another important consideration involves timing of inputs. As indicated in Fig. 4, watershed perturbations caused a less pronounced autumnal litterfall peak. Therefore, the litterfall available to benthic insects with life cycles adapted to autumnal inputs was a smaller fraction of total annual litterfall. Crayfish, because they are not univoltine, may be better adapted to the more uniform litterfall input.

Associated with the community change was an increase in biological utilization of litterfall inputs. A factor not considered in this study was the biological decomposability of the litterfall inputs. Leaf species such as black locust and blackberry decompose rapidly, whereas oaks and rhododendron are very slow to decompose (Petersen and Cummins 1974, J. B. Waide and R. L. Todd, *personal communication*). This factor certainly contributed to greater biological processing in the old field stream and lesser biological processing in the hardwood forest stream.

One justification for including stream studies in watershed nutrient studies has been the effect of instream processes on watershed budgets. We conclude from this study that effects of the stream ecosystems at Coweeta on whole watershed K and Ca budgets are very small. If there were no instream biological, chemical, or mechanical processing of litterfall inputs to dissolved K and Ca, the change in the net dissolved element losses from the watersheds would be <4%. Losses of K and Ca from the streams and watersheds

due to insect emergence and invertebrate drift were small in comparison to abiotic losses (Table 13). The major element losses for all 3 watersheds were dissolved ions. Sediment losses were next largest, except for the hardwood forest where organic particulate loss of Ca was > sediment loss.

Finally, we observed that the streams in the old field and pine plantation watersheds are functionally little different from the unperturbed stream. Though we do not know the magnitude of the stream perturbation, nor the resistance of the streams to the perturbations as reflected by functional changes during and immediately following perturbation, it is evident that any changes were followed by rapid recovery. This high resilience of the stream ecosystems can be attributed to the rapid turnover of the components. Any current differences between the perturbed and unperturbed streams reflect primarily differences in quantity, quality, and timing of allochthonous inputs. In general, the great resilience of stream ecosystems based on their internal characteristics is limited by the external regulation.

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