

To the Graduate Council:

I am submitting herewith a thesis written by Robert Philip Larkin entitled "Deciduous Forest Litter Decomposition at Two Sulfur Input Rates." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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DECIDUOUS FOREST LITTER DECOMPOSITION
AT TWO SULFUR INPUT RATES

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ABSTRACT

Two similar forested watersheds in East Tennessee were studied to determine the effects of atmospheric sulfur inputs on litter decomposition. Cross Creek watershed, located near a large coal-fired power plant, has received greater sulfur inputs than the more remote Camp Branch watershed. Decomposition was estimated through the measurement of forest floor respiration, litter microflora populations, litter and soil microarthropod populations, and litter nutrient status. A laboratory study was also conducted in which microcosms taken from the forest floor were exposed to different levels of sulfur inputs and their respiration rate measured over time.

Average forest floor respiration rates were very similar, $4.84 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ or $1766 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Camp Branch and $4.90 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ or $1789 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Cross Creek. Fractional loss rates provided estimates of annual decay rates (k) of .35 and .39 for Camp Branch and Cross Creek, respectively. Litter decomposition was estimated to contribute 31.5% of the total CO_2 output at Camp Branch and 35% at Cross Creek, while root respiration accounts for about 60-65%.

High sulfur inputs were found to reduce respiration rates in soil and litter microcosms over a period of time. Initial sulfur additions at all levels produced a slight stimulation of respiration, but low to moderate inputs produced no lasting effects. There was no difference between microcosms taken from the two watersheds regarding physical characteristics, respiration rates, or response to sulfur treatments.

Bacterial and fungal populations were about equal in size at both watersheds, with bacteria averaging 100×10^6 per gram litter and fungi 23×10^6 per gram litter. Total numbers of arthropods were consistently greater (averaging 34% greater) at Camp Branch. Acarina populations averaged 59% higher at Camp Branch, but Collembola populations were about equal at the two watersheds.

Nutrient element mobility in the litter and soil was similar at both watersheds and followed the order $K > Mg > Ca > S > N > P$. Litterfall nutrient concentrations were slightly higher for all elements at Cross Creek, resulting in greater litter concentrations of calcium and magnesium. Litter concentrations of sulfur and nitrogen, however, were significantly greater at Camp Branch, indicating differences in the loss rates and cycling processes of these elements between the watersheds. There was no difference between the loss rates or litter concentrations of phosphorus, potassium, and sodium at the two watersheds.

Overall, decomposition was similar at the two watersheds. Present levels of sulfur inputs did not appear to have a major effect on decomposition rate, although sulfur inputs did appear to influence some mineralization and cycling processes and possibly lowered arthropod populations. Sulfur inputs when at high enough levels over a sufficient period of time can have an inhibitory effect on decomposition, but at lower levels, the influence of sulfur inputs on decomposition appear to be minimal.

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CHAPTER I

INTRODUCTION AND OBJECTIVES

Increased levels of anthropogenic sulfur emissions in recent years have resulted in the exposure of many previously unaffected ecosystems to substantial atmospheric inputs. High atmospheric concentrations of sulfur dioxide are known to cause injury to plants and animals (Guderian, 1977; Kellogg et al., 1972; Knabe, 1970; Mudd, 1975; Nriagu, 1978). Even at lower concentrations, SO_2 is eventually deposited or converted to H_2SO_4 , sulfate ions, and sulfate salts, and deposited in the ecosystem as precipitation and particulate matter. The effects of these inputs on important components of terrestrial ecosystems are not well known.

Forest ecosystems are characterized by an ability to cycle and accumulate nutrients efficiently, enabling them to become dominant and stable throughout the world (Witkamp and Ausmus, 1976). Nutrient cycling and energy flow in such systems is controlled largely by decomposition and mineralization processes. Decomposition is the rate-controlling step in mineral-nutrient turnover, and it ultimately determines the rates at which most other ecological processes proceed, thus shaping the structure and dynamics of the ecosystem (Witkamp and Ausmus, 1976; Witkamp, 1971b). It is important, then, to look at decomposition in regard to man-induced changes or stresses placed on the system, for its disruption (even acceleration) may have far-reaching effects throughout the ecosystem.

The rate at which decomposition occurs is governed primarily by the same factors that influence soil fauna and microbial activity, with

temperature, moisture, and chemical composition of the litter being the most important (Alexander, 1977; Witkamp, 1963, 1966a, 1971b). Decomposition has been shown to be adversely affected by additions of some environmental pollutants, including heavy metals and acid precipitation (Abrahamsen et al., 1977; Ruhling and Tyler, 1973; Tamm et al., 1977; Williams et al., 1977). Increased soil and litter acidity from acid rain inputs have been shown to inhibit decomposition rates and increase cation leaching (Abrahamsen, 1980; Alexander, 1980; Hagvar and Abrahamsen, 1980; Hovland et al., 1980). Many terrestrial ecosystems, however, are not readily susceptible to changes in soil acidity from acid rain. Some soils have sufficient buffering capacities or are already very acid, so that present levels of acid rain have little effect on soil pH, but they may be affected by the sulfur compounds themselves in ways not related to pH changes (Cole and Johnson, 1977; Frink and Voigt, 1977; Voigt, 1980; Wiklander, 1980). Relatively small environmental changes may disrupt or alter microbial and soil animal populations and change the characteristics of their metabolic turnover. Since decomposition processes rely on microbial and invertebrate activity, decomposition may be especially vulnerable to perturbation.

In the work reported here, the possible long term effects and changes in decomposition were studied by comparing decomposition at two watershed study sites. One site, located near a coal-fired power plant, has received anthropogenic sulfur inputs for almost 30 years. The other site is in a more remote area farther removed from sulfur and other pollutant sources and was used to represent background conditions.

Several important aspects of decomposition were monitored on each watershed. A laboratory study was also conducted in which microcosms taken from the forest floor of the two watersheds were exposed to controlled levels of sulfur inputs (as SO_2 and SO_4^{2-}) and their respiration rate measured over time. The value to using intact soil microcosms for the analysis of effects of environmental contaminants has been demonstrated by Ausmus and O'Neill (1978) among others.

The major objective of the study reported here was to compare litter decomposition rates at two deciduous forest sites which have received different levels of sulfur input. More specific objectives include determination of activity levels and populations of forest floor microflora and faunal organisms; the physical-chemical degradation and nutrient status of the litter; and the effects of simulated sulfur inputs on the decomposition of forest litter as determined by microcosm simulations.

CHAPTER II

EXPERIMENTAL AREA

Location and Physical Characteristics

Two research sites were used for this study--the Camp Branch Watershed located in Bledsoe County in eastern Tennessee (35°38'N; 85°18'W), and the Cross Creek Watershed located in Marion County (35°4'N; 85°51'W). These two sites were chosen for study after a number of potential locations were evaluated in terms of forest type, soil type, availability for long-term study, and level of atmospheric sulfur input (Kelly, 1979). The Cross Creek site is located 19 km northwest of a 1958-megawatt coal-fired power plant, while the Camp Branch site is located 80 km northeast of the Cross Creek site and 76 km southwest of a 1600-megawatt plant in an area removed from the direct impact of any major point source.

Climate of the area is temperate and continental. The winters are moderate with short cold periods and the summers are mild to hot. Annual rainfall for the Camp Branch watershed averages 145 cm compared to 155 cm at Cross Creek. Monthly temperature means at Camp Branch average slightly lower than at Cross Creek (Kelly, 1979).

Topographically, the watersheds have an undulating surface submaturely dissected by young valleys. The dominant soils are typically well-drained, highly leached, acidic (pH 4.6-4.8), shallow, and relatively infertile (CEC 6.8-10.7) (Kelly, 1980).

Both watersheds are vegetated with second growth oak forests of equivalent age and basal area. Various species of oak combine to

provide approximately 70% of the basal area at both locations. Quercus coccinea, Q. stellata, Q. alba, and Q. velutina are the dominants.

Additional information on stand characteristics along with climatic and edaphic information can be found in Ramseur and Kelly (1981) and Kelly (1979).

Sulfur Inputs

Total atmospheric sulfur inputs (as precipitation, dry particulate matter, and gaseous SO_2) amount to $27.1 \text{ kg S} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at Cross Creek and $21.8 \text{ kg S} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at Camp Branch (Table 1). Inputs to the forest floor (throughfall, stemflow, and litterfall) total $28.5 \text{ kg S} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at Cross Creek and $22.5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at Camp Branch (Table 1). Of the individual component inputs, gaseous SO_2 and stemflow are significantly higher at Cross Creek (Kelly, 1981, 1982a).

The total sulfur pool at Cross Creek is $2709 \text{ kg} \cdot \text{ha}^{-1}$ as opposed to $1928 \text{ kg} \cdot \text{ha}^{-1}$ at Camp Branch (Kelly, 1980). Total sulfur content of the mineral soil accounts for 97% of the total sulfur at both sites.

Differences between the sulfur inputs at the two watersheds are thought to have been much larger in the past, when less efficient emission controls resulted in higher local sulfur inputs at Cross Creek (Kelly, 1982a), as well as a less widespread distribution and therefore lower sulfur input at remote areas like Camp Branch. This is demonstrated by the large difference in the total sulfur pools and mineral soil sulfur accumulation at the watersheds. The 40% larger sulfur pool at Cross Creek presumably resulted from years of higher levels of sulfur inputs than are presently indicated.

Table 1. Annual sulfur input to the forest canopy and forest floor at Camp Branch and Cross Creek.*

Component	Location	
	Camp Branch	Cross Creek
<u>Forest Canopy</u>	<u>kg·ha⁻¹</u>	
Rainfall	9.3	9.4
Dry Particulate	2.0	2.4
<u>Gaseous</u>	<u>10.5</u>	<u>15.3</u>
Total	21.8	27.1
<u>Forest Floor</u>		
Throughfall	15.3	16.5
Stemflow	2.6	4.8
<u>Litterfall</u>	<u>4.6</u>	<u>7.2</u>
Total	22.5	28.5

* From Kelly, 1982a.

The effects of the many years of differential sulfur inputs will still be present on the watersheds even if current inputs do not represent the maximum difference in sulfur that was once deposited. Differences in sulfur loading may affect organisms and processes directly or indirectly and may influence current inputs through sulfur uptake by plants and deposition in throughfall, stemflow, and litterfall.

CHAPTER III

MATERIALS AND METHODS

Sampling Sites and Plots

Two locations within each watershed were selected and prepared as sampling sites. Two separate sites per watershed were used in order to estimate variation within watersheds as well as between watersheds. At each of these sites four plots (10 m X 10 m) were established for sampling. Plots were randomly located within an area of about one half hectare, had a slope of 0-5°, were primarily east or west facing, and had vegetation types as described for the overall watersheds. For most measurements three samples per plot were used. Sampling procedures and methods are summarized in Figure 1.

Decomposition Rate--Microbial Activity

Carbon dioxide evolution was measured as a general indicator of decomposition and microbial activity via an inverted box technique (Witkamp, 1966a, b) using soda-lime to absorb the CO₂ (Monteith et al., 1964; Minderman and Vulto, 1973a). The use of granular soda-lime as the CO₂-absorbing agent is a simple and efficient method of monitoring respiration and is especially suited for field comparisons (Howard, 1966; Minderman and Vulto, 1973a; Monteith et al., 1964). On each plot, three spots were randomly chosen to become permanent CO₂ sampling stations. The section of forest floor at each spot was marked and used for all CO₂ evolution determinations. A plastic box (20 cm X 32 cm X 12 cm deep) was placed over the section of forest floor, and an open

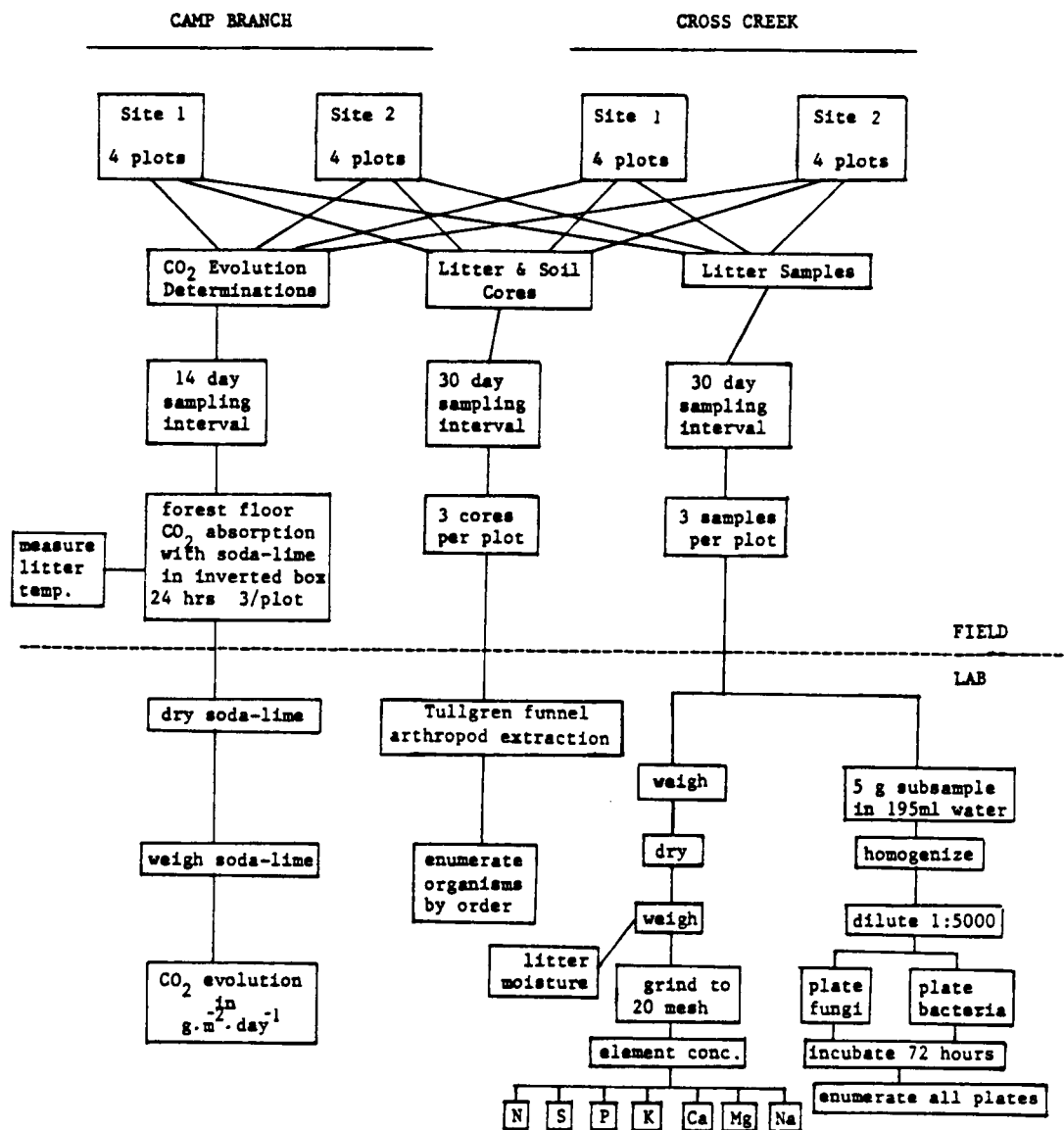


Figure 1. Block diagram summary of methods and procedures.

petri dish containing 30 grams of granulated soda-lime that had been oven-dried for 24 hours at 80°C and weighed to 0.001g placed inside. The inverted box was sealed by cutting the litter layer around its edges, pressing the box into the soil, and placing a weight on top to insure a tight seal. After 24 hours, the soda-lime was removed, transferred to a small sealed plastic container to prevent additional CO₂ absorption, returned to the lab, oven-dried for 24 hours at 80°C, and weighed. The amount of CO₂ absorbed was calculated directly as the increase in weight of the soda-lime sample, and expressed as grams CO₂ per square meter per day ($\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$).

Carbon dioxide collections were made at the same places on each plot every two weeks and continued for a full year. Sampling periods of 24 hours were used to allow for daily cycles of respiration corresponding to temperature cycles (Witkamp, 1969; Witkamp and Frank, 1969). Litter temperature was measured at the beginning and end of each sampling period with a mercury thermometer. Air temperature was also monitored continuously (Kelly, 1979). Litter moisture was determined for litter samples taken from each plot at the beginning and end of each sampling period and expressed as percent dry weight. Litter samples, three per plot, were collected by removing all litter from a 16 X 27 cm section of the forest floor. These were also used to derive fractional loss rates (Olson, 1963) for an improved estimate of decomposition rates.

Microbial Populations

Microbial populations were monitored using standard serial dilution plate counts. From each of the monthly litter samples of the

combined O_1 and O_2 horizons, a 5.0 gram (wet weight) sub-sample was taken, placed in 195 ml of sterile water, and mixed in a tissue homogenizer at 800 rpm for 10-15 seconds. A 0.1 ml aliquot of a 1:5,000 dilution of this mixture was then spread-plated on nutrient agar for bacterial determinations and on peptone-dextrose agar with rose bengal and streptomycin added (Martin, 1950) for fungal determinations. The plates were counted after incubation for 72 hours at 24°C. Total numbers of bacteria and fungal colonies were expressed per gram dry weight of litter.

Arthropod Populations

Arthropod populations were estimated by use of a Tullgren funnel extraction procedure (Tullgren, 1918). Three soil cores (5cm diameter X 15cm deep) were collected from each plot monthly. Each soil core (containing litter and mineral soil) was placed on a screen over a steepsided funnel and left for 3-4 days under the constant heat provided by a 40 watt light bulb. The organisms driven from the soil and litter fell into a glass vial containing a 70% alcohol - 5% glycerin solution and were preserved until they could be counted. The contents of each vial were examined under a binocular dissecting microscope, and the organisms present enumerated by order in numbers per square meter.

Nutrient Status

Litter samples collected for moisture determinations were also analyzed monthly for elemental composition. Samples were oven-dried for 48 hours and ground to pass through a 20 mesh sieve and analyzed

for: total nitrogen, total sulfur, phosphorus, potassium, calcium, magnesium, and sodium content. Total sulfur was determined by the LECO induction furnace method. Total nitrogen was determined colorimetrically following Kjeldahl digestion (AOAC, 1971). Other elements were determined by atomic absorption spectrophotometry (Kahn, 1971).

Laboratory Microcosm Study

Six microcosms were collected from each of three plots at each sampling site (36 microcosms/watershed--72 total). Each microcosm consisted of a section of the forest floor (16 cm X 27 cm X 5 cm deep) extracted intact by means of an extraction tool and placed in a plastic container (20 cm X 32 cm X 12 cm) (Chaney et al., 1978). Microcosms were weighed (field weight) immediately upon return to the laboratory. They were then placed on a growth bench maintained at 25°C and allowed to equilibrate for one month. Each week the microcosms were weighed and water added to replenish their moisture content. Since the litter and soil was abnormally dry at the time of sampling, an additional 100ml of water over their weight at the time of collection (representing a moisture increase of about 10%) was added to each microcosm and the moisture content maintained at this level. Adjusted field weights for the microcosms from Camp Branch averaged $1462.2 \pm 33.0\text{g}$ while Cross Creek microcosms averaged $1393.3 \pm 30.7\text{g}$. At the conclusion of the study, all microcosms were separated into litter and mineral soil components, and their dry weights and moisture contents determined.

After the equilibration period each set of microcosms began receiving a series of sulfur amendments in the form of SO_2 and a

liquid sulfate solution. The six treatments were as follows:

- 1) Control--No additional sulfur
- 2) Low Sulfur--0.05 ppm SO_2 , $0.1 \text{ g SO}_4^{2-} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$
- 3) Moderate Sulfur--0.15 ppm SO_2 , $0.2 \text{ g SO}_4^{2-} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$
- 4) High Sulfur--0.45 ppm SO_2 , $0.4 \text{ g SO}_4^{2-} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$
- 5) SO_2 Only--0.45 ppm SO_2 , No sulfates
- 6) Sulfate Only--No SO_2 , $0.4 \text{ g SO}_4^{2-} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$

Each SO_2 treatment consisted of a 24 hour constant exposure level within a fumigation chamber. A total of six fumigations of each treatment level were administered over a three month period at approximately two-week intervals. For each exposure sulfur dioxide levels were monitored continuously with a calibrated SO_2 analyzer.

Sulfate additions were in the form of K_2SO_4 added to a standardized rain solution (pH 5.5). The rain solution consisted of distilled water with trace quantities of various cations and anions in the approximate concentrations that occur in uncontaminated rain water (Ca^{+2} , $0.77 \text{ mg} \cdot \text{l}^{-1}$; Mg^{+2} , $0.10 \text{ mg} \cdot \text{l}^{-1}$; Na^+ , $0.08 \text{ mg} \cdot \text{l}^{-1}$; K^+ , $0.09 \text{ mg} \cdot \text{l}^{-1}$; NH_4^+ , $0.22 \text{ mg} \cdot \text{l}^{-1}$; NO_3^- , $0.74 \text{ mg} \cdot \text{l}^{-1}$; SO_4^{2-} , $0.68 \text{ mg} \cdot \text{l}^{-1}$; Cl^- , $0.99 \text{ mg} \cdot \text{l}^{-1}$). Each microcosm received 100 ml of the standardized rain solution once each week. Additional distilled water was added when necessary to maintain the moisture content of the microcosms at their initial levels. Separate solutions of standardized rain with the appropriate dose of K_2SO_4 for each sulfate treatment level were used, so that each microcosm (regardless of treatment) received only 100 ml of rain solution.

The treatment doses used over the 12-week period were slightly lower than the Camp Branch sulfur inputs (about $17 \text{ kg} \cdot \text{ha}^{-1}$), slightly

higher than the Cross Creek inputs (about $36 \text{ kg} \cdot \text{ha}^{-1}$), and about three times the Cross Creek input levels.

Respiration was measured for each microcosm before treatments began, and immediately following fumigation treatments. Fumigations were administered at approximately 2-week intervals, but varied somewhat due to time, space, and facility conflicts. Soda-lime was used to absorb CO_2 as in the field. The microcosms were sealed for the respiration measurements by clamping a square of masonite over the top of each microcosm. Respiration was measured over a 24 hour period, temperature was maintained at 25°C and humidity was maintained at approximately 70%. An additional 100 ml of water was added to each microcosm immediately prior to the respiration measurements to insure moisture was not limiting.

Statistical Analysis

The experimental layout used in the field study was a three-level nested design with three samples per plot/site/watershed for the measurement of CO_2 evolution, microbial populations, arthropod populations, and chemical composition of the litter. The microcosm study was conducted as a randomized complete block, with microcosm location as the block. All analyses were accomplished using standard SAS programs and procedures (SAS Institute, 1979). Means were separated by use of Duncan's New Multiple Range Test (Steel and Torrie, 1960), and all tests of significance were made at $p=.05$.

CHAPTER IV

RESULTS AND DISCUSSION

I. RESPIRATION AND DECOMPOSITION RATE

Field

Forest floor respiration (CO_2 evolution) is widely accepted as a general estimate of decomposition rate and microbial activity. Carbon dioxide evolution measurements have been shown to be highly correlated to other measures of decomposition, including loss of weight of litter, microbial populations, and microbial activity (Ausmus and Witkamp, 1974; Witkamp, 1964, 1966a, b, 1971a). Carbon dioxide evolution can also be used to estimate metabolic and mineral turnover (Witkamp, 1971b).

Mean biweekly estimates of CO_2 evolution rates for each watershed are shown in Figure 2 in relation to air temperature and litter moisture contents. The mean daily CO_2 evolution rate was approximately equal for both watersheds, averaging $4.84 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ at Camp Branch and $4.90 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ at Cross Creek. This output amounts to yearly totals of $1766 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Camp Branch and $1766 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Camp Branch and $1789 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Cross Creek.

General trends of the CO_2 evolution rates correspond closely with temperature and litter moisture at both watersheds. In general, forest floor respiration increased with temperature, but was often lower than would be expected due to low litter moisture levels. Normally, temperature has the greatest influence on respiration, and litter moisture affects respiration only under especially wet or dry

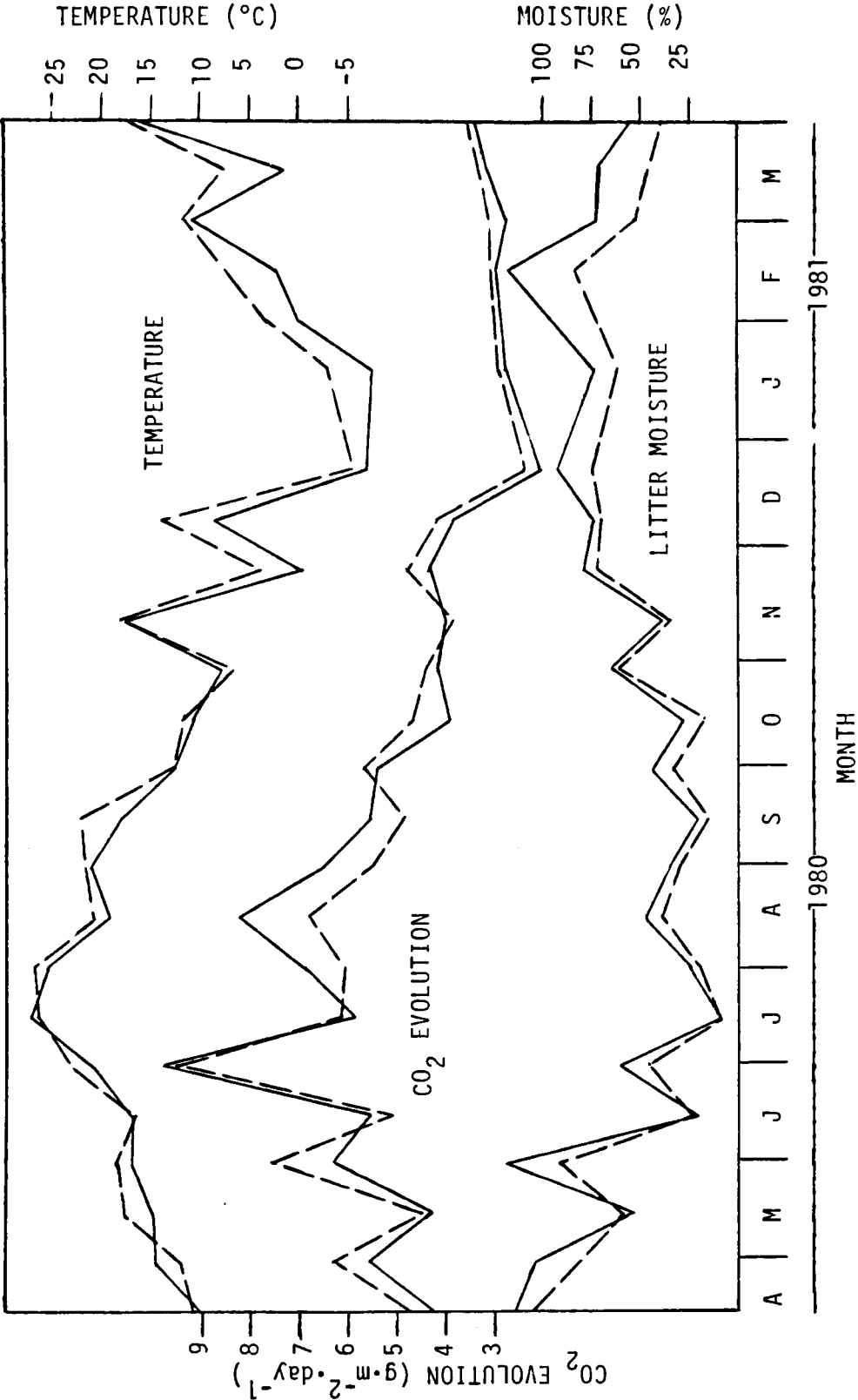


Figure 2. Mean forest floor CO₂ evolution rates in relation to mean air temperature and litter moisture at Camp Branch (——) and Cross Creek (-----).

conditions (Alexander, 1977; Edwards, 1975; Witkamp, 1964, 1971b). Litter moisture, however, played a critical role at these watersheds throughout the term of this study due to the unusually low levels of precipitation, particularly during the summer. Edwards (1975) observed lowered respiration rates when litter moisture content fell below about 85% of litter dry weight. Since litter moisture content of the watersheds was rarely above this level, the dry conditions tended to inhibit respiration rates through much of the year.

Peak CO_2 evolution rates at both watersheds were reached on June 26, while moisture levels were still high, with $9.75 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ evolved at Camp Branch and $9.50 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ at Cross Creek. Litter moisture contents reached a low of about 9% dry weight at both watersheds on July 14, accompanied by large reductions in respiration rates. Respiration remained lower throughout the dry summer. Through the fall, respiration decreased with temperature even though moisture conditions were improving. A slight increase in respiration during November was presumably caused by the influx of organic matter in the form of litterfall, which caused a stimulation of microbial activity. Respiration was lowest through the cold winter months, reaching a minimum of $2.06 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ at Camp Branch and $2.38 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ at Cross Creek on December 20.

Annual CO_2 evolution rates at Camp Branch ($1766 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and Cross Creek ($1789 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) are within the range of values reported in the literature for similar forested ecosystems considering local differences in environmental conditions. Witkamp (1966b) reported a yearly CO_2 output of $1522 \text{ g} \cdot \text{m}^{-2}$ from a white oak stand in East

Tennessee. Anderson (1973b) reported values of $2306 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and $2107 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in a chestnut and beech-dominated forest, respectively, while Edwards (1975) reported rates of $3900 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ in a rich mesic forest.

Despite the nearly identical yearly averages, there were significant differences between the respiration rates at the two watersheds on several of the biweekly sampling dates. In the spring, on April 12 and May 24 Cross Creek had an average respiration rate significantly higher than Camp Branch. In the summer, however, the relationship reversed and on August 28 and September 15 Camp Branch had significantly higher respiration rates. In the fall, Cross Creek regained generally higher CO_2 evolution rates throughout the remainder of the year, producing significantly greater CO_2 outputs on October 11, October 24, and December 7.

This seasonal reversal in respiration rates cannot be explained by temperature or moisture differences on the watersheds. In general, litter moisture was lower at Cross Creek although the differences do not correspond with respiration differences. Average air and litter temperatures over the 24 hour collection periods were similar at both watersheds throughout the year, with Cross Creek averaging only slightly higher. The extreme drought conditions for much of the summer may have caused the respiration turnaround, but why these conditions caused lower respiration at Cross Creek is not really known. It may be due to some inherent difference in the microflora or to a complex interaction of environmental conditions.

If the lower respiration during the summer was due to the dry conditions of that year and does not represent a yearly cycle, then under more average conditions Cross Creek may have a higher yearly respiration rate. Even when the summer respiration rates are excluded, however, CO_2 evolution comparisons over the rest of the year demonstrated no significant differences between the watersheds. The slightly higher yearly respiration rate observed at Cross Creek is probably explained by the differences in temperature, litter accumulation, and other environmental conditions and does not represent any major differences in decomposition processes between the watersheds.

Respiration within each watershed was also quite variable, but CO_2 evolution from plots within each site as well as sites within watersheds were generally very similar. There were significant differences, however, observed between sites within watersheds on April 24 and August 13 (Figure 3). Presumably these differences were caused by local environmental conditions, although differences in temperature and moisture do not adequately explain the wide range of respiration rates on these dates.

The complex interdependent effects of temperature and moisture on CO_2 evolution rates, which may not always be immediately apparent, have been noted by many (Edwards, 1975; Howard and Howard, 1979; Kowalenko, 1978; Wildung et al., 1975). Particularly important is the observation that temperature generally has a greater effect at high moisture contents and moisture has a greater effect at high temperatures. Witkamp (1971b) observed that temperature and moisture together could account for as much as 88% of the variability in CO_2 evolution rates.

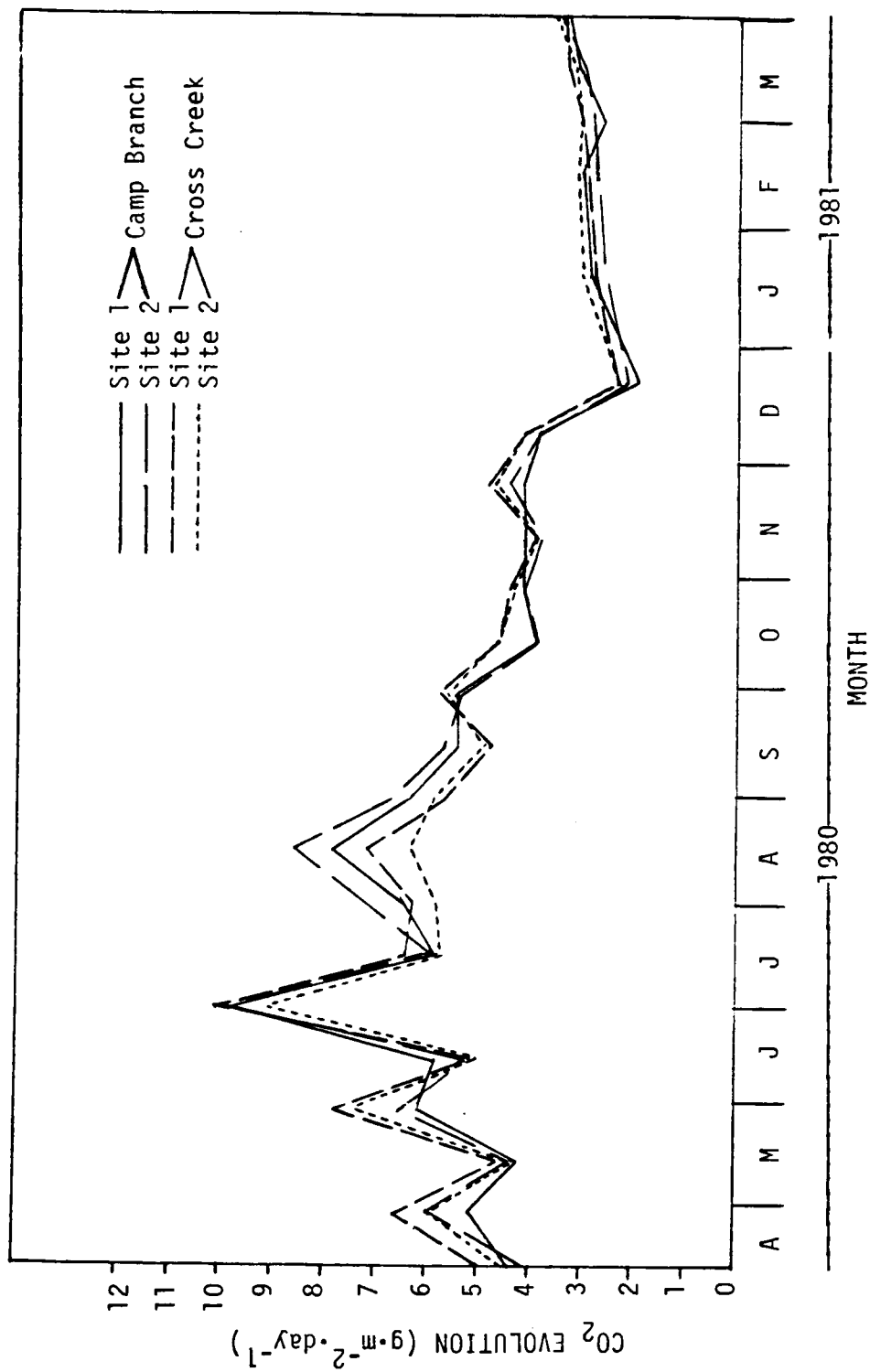


Figure 3. Mean forest floor CO₂ evolution rates by site at Camp Branch and Cross Creek.

Temperature and moisture, along with their interaction in a multiple correlation, accounted for 44% of the variability ($R^2 = .44$) in the respiration rates at the two watersheds. Addition of the fungal populations as another term increased R^2 to .48. The highest correlation coefficient with all terms significant ($R^2 = .52$) was achieved using temperature, temperature-moisture interaction, fungal populations, and collembola populations to account for the variability of CO_2 evolution rates.

Microcosms

Microcosm studies provided additional information on respiration and the effects of sulfur inputs in a more controlled setting. Initial respiration rates of the microcosms were variable, but with no significant differences due to the location the microcosms were collected from or the treatment group each was placed in. The average respiration of all microcosms at the start of the experiment was $4.08 \pm .68 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Overall, respiration rates remained at similar levels throughout the course of the study with only relatively small increases and decreases.

The location the microcosms were collected from did not affect respiration rate, nor did it affect or interact with treatment effects. There was no indication that microcosms from the different watersheds or sites within watersheds responded differently to the various treatments, for at no time throughout the study were there significant location effects (Table 2). Physical characteristics of the microcosms were also very similar. There were no significant differences between

Table 2. Mean microcosm respiration rates by site over the 12-week study period.

Location	Number of Weeks				
	Initial	2	5	8	12
After Initiation of Sulfur Treatment					
	$\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$				
Camp Branch--Site 1	3.93*	4.12	4.03	4.15	3.93
--Site 2	4.02	4.19	4.14	4.15	4.07
Cross Creek--Site 1	4.11	4.01	4.37	4.42	3.99
--Site 2	4.26	4.28	4.04	4.37	4.16

*No significant differences among sites at any time.

the microcosms from the different sites or watersheds for percent soil content, litter dry weight, total dry weight, or moisture content (Table 3).

The similarity between the physical attributes of the microcosms taken from different locations show the comparability of the two watersheds used in this study. The similar respiration rates suggest that there are no large inherent differences between the numbers and kinds of organisms present in the litter and soil of each watershed or between organism activity levels there. The microcosms from each watershed did not appear to respond differently to the various sulfur treatments, suggesting that the organisms are not necessarily adapted to the particular sulfur levels at each watershed and are not particularly susceptible to changes in these inputs.

Significant differences between treatments were found only after the second week (2 fumigations) and at the conclusion of the 12-week study period (Table 4). After two weeks, the first measure of respiration following the initiation of sulfur treatment showed the Low Sulfur (0.05 ppm SO_2 , $0.1 \text{ g SO}_4 \cdot \text{m}^{-2} \cdot \text{wk}^{-1}$), Moderate Sulfur (0.15 ppm SO_2 , $0.2 \text{ g SO}_4 \cdot \text{m}^{-2} \cdot \text{wk}^{-1}$), and High Sulfur (0.45 ppm SO_2 , $0.4 \text{ g SO}_4 \cdot \text{m}^{-2} \cdot \text{wk}^{-1}$) treatment respiration to increase. The respiration rates of the Control, Sulfate Only ($0.4 \text{ g SO}_4^{2-} \cdot \text{m}^{-2} \cdot \text{wk}^{-1}$), and SO_2 Only (0.45 ppm SO_2) treated microcosms, however, declined slightly. Respiration of the Low Sulfur treatment was significantly greater than the rates of the Moderate Sulfur, SO_2 Only, and Control microcosms (Table 4). The High Sulfur treatment respiration was also significantly greater than that of the Moderate Sulfur treatment microcosms.

Table 3. Mean microcosm total dry weight, litter dry weight, percent mineral soil content and percent moisture content.

Location	Total Dry Weight (g)	Litter Dry Weight (g)	Percent Mineral Soil(%)	Moisture Content (% dry wt)
Camp Branch:				
Site 1	1044.87*	81.01	91.70	47.40
Site 2	994.42	71.81	92.23	46.68
Mean	999.64	76.41	91.96	47.04
Cross Creek:				
Site 1	1008.18	78.27	92.07	40.19
Site 2	1007.30	82.26	91.59	38.00
Mean	1007.74	80.26	91.82	39.09

* No significant differences between sites or watersheds for any characteristic measured.

Table 4. Mean microcosm respiration rates and percent change in respiration rate by treatment over the 12-week study period.

Treatment # Description	Number of Weeks After Initiation of Sulfur Treatments					Mean	Percent Change
	Initial	2	5	8	12		
			$\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$				
1. Control	4.15a*	4.02a	4.20a	4.37a	4.28a	4.21a	6.27ab
2 Low Sulfur	3.87a	4.67c	4.52a	4.38a	4.22ab	4.32a	16.03a
3 Moderate Sulfur	3.61a	3.65a	4.20a	4.24a	4.09ab	3.96a	14.93a
4 High Sulfur	4.18a	4.42bc	3.76a	4.32a	3.68c	4.07a	-9.54b
5 SO ₂ Only	4.28a	3.89a	4.06a	4.24a	4.03ab	4.11a	-5.60b
6 Sulfate Only	4.39a	4.27bc	4.14a	4.09a	3.92bc	4.18a	-9.91b

* Rates within columns followed by the same letter are not significantly different at $p=.05$.

Subsequent measurements at approximately five weeks and eight weeks time after the initiation of sulfur treatments showed respiration rates to be fluctuating slightly with no significant differences between any treatments. By the eighth week, respiration appeared to level off and converge, for there was less variability both among and within treatment respiration rates.

The final measure of respiration, after 6 SO_2 fumigations and 12 weeks of sulfate treatment, showed a decline in all treatment respiration rates from the 8-week levels. The final results showed that the average respiration rate of the High Sulfur treated microcosms was significantly lower than that of the Control, Low Sulfur, Moderate Sulfur, and SO_2 Only treated microcosms (Table 4). The Sulfate Only treatment respiration was also significantly less than the Control respiration.

Thus, high sulfur inputs were found to reduce respiration over a period of time. After 12 weeks, the effects were just beginning to appear, but had this study been continued for a longer period, the relationship would be expected to continue and become even more apparent over time. The ranked order of the respiration rates at the conclusion of the study indicate the relative influences of the various sulfur inputs. The decreasing respiration rates are consistent with the hypothesis that high levels of sulfur inputs over a sufficient period of time may reduce respiration.

The overall mean respiration rates of the treatment groups showed no significant differences between any of the treatments. Low

Sulfur treated and Control microcosms had the highest overall respiration, while the High and Moderate Sulfur treated microcosms had the lowest.

To clarify the changes in respiration rate by treatment over time, differences between the initial respiration rate and the final respiration rate for each treatment group were expressed as a percent change (Table 4). Respiration rates for High Sulfur, Sulfate Only and SO_2 Only treated microcosms all decreased, whereas the respiration rates for the Control, Low Sulfur, and Moderate Sulfur treatments all increased over the course of the study. The percent change in respiration for the SO_2 Only, High Sulfur, and Sulfate Only treated microcosms, at -5.60, -9.54, and -9.91%, respectively, were significantly less than the percent change in respiration of the Low Sulfur and Moderate Sulfur treated microcosms (16.03 and 14.93% respectively).

Actual levels of CO_2 output measured in these microcosms are difficult to compare with CO_2 evolution results reported in the literature because of differences in techniques, methods, conditions, and type of microcosm used. The levels are consistent with the observed field values and are also comparable to the values reported by Ausmus and O'Neill (1978) using similar intact soil core microcosms.

The slight increase in respiration rates through the first eight weeks of the study may be due in part to the stimulation of microbial activity following removal from the field and placement in the laboratory environment. The increased aeration, optimum temperature and moisture levels, death and decay of roots, and reaction to disturbance often lead to a flush of microbial activity. Jensen (1974)

and Bond et al. (1976) report this period of increased respiration to last for one to four weeks, whereafter respiration rates level off. For this reason microcosms were allowed a one month equilibration period before respiration measurements or treatments were applied. The seemingly adequate equilibration period allowed, as well as the observation that the respiration of only some treatment groups increased while others decreased indicate that something else must have caused the increase observed. All microcosms were collected at approximately the same time and there were no differences between treatment groups, as they were made up of almost identical groupings of microcosms from the different locations, so the microcosms should have all reached equilibrium at approximately the same time.

Initial respiration increases were observed in the Low, Moderate, and High Sulfur treatment doses. The Control, Sulfate Only, and SO_2 Only microcosm respiration all decreased initially. Thus, it may be that the addition of sulfur initially enhanced respiration. If sulfur is deficient, microbial activity and decomposition will be inhibited, and addition of sulfur will stimulate respiration (Stewart et al., 1966a, b; Stotzky and Norman, 1961). Sain and Broadbent (1977) concluded, however, that sufficient sulfur for adequate plant growth was also sufficient for maximum rates of decomposition. The sulfur content of the soil and litter in the microcosms, then, would appear to be sufficient to meet the requirements for maximum decomposition. There is no evidence in the literature that further sulfur increases beyond these levels will increase decomposition, even temporarily. Even though the respiration of the Moderate Sulfur treated microcosms

were the lowest of all microcosms, they also showed a slight increase from the initial rate. However, the respiration of the Sulfate Only and SO_2 Only treated microcosms did not increase as might be expected, making it difficult to draw any definite conclusions in attributing the enhanced respiration to the addition of sulfur. If all microbial requirements have been met, the mechanism of a sulfur-induced stimulation is not known.

In a study of this length one would expect a gradual decrease in respiration as the amount of readily decomposable organic substrate is diminished and the actual number of organisms decrease over time, as was observed by Chaney et al., (1978). That this eventual decline did not begin to occur until the very end of the study indicates that the organic material present was sufficient to maintain the soil organism populations for an extended period of time. The temperature and moisture conditions were suitable for maintaining adequate soil organism activity for indefinite periods. Ausmus and O'Neill (1978) and Bond et al. (1976) observed respiration rates of soil and litter microcosms to remain at fairly constant levels over six to seven week study periods. The decrease in virtually all respiration rates observed between the 8th and 12th weeks represents the reduction of available organic substrate.

The finding that high sulfur inputs can decrease decomposition rates has not as yet received much documentation in the literature. It is known that increased acidity due to acid rain sulfur inputs can inhibit decomposition (Abrahamsen and Dollard, 1978; Hagvar and Abrahamsen, 1980; Hovland et al., 1980; Ishac and Hovland, 1976).

Tamm et al. (1977) also observed that additional sulfur as elemental sulfur or H_2SO_4 caused a distinct depression in the evolution of CO_2 even when pH was not affected. Microcosm pH was not measured for any changes caused by the sulfur additions, but the pH of the sulfate solution was very mild ($\sim\text{pH } 5.5$).

The mechanism for reduction in decomposition or microbial activity caused by sulfur inputs, other than acidity effects, is not known. No toxic effect of excess sulfur has been demonstrated on soil microorganisms, but it is conceivable that extreme levels could cause deleterious effects. It is also not necessarily inconsistent for low levels of sulfur inputs to stimulate respiration while large inputs depress respiration over time. It has been demonstrated that some substances, such as heavy metals, can stimulate microbial activity at low levels and inhibit microbial activity at high levels (Chaney et al., 1978; Bond et al., 1976; Loomis, 1971).

There were no significant differences between the Sulfate Only and SO_2 Only treatments. This suggests that there are no immediately obvious differences in the extent of individual contributions of gaseous and liquid sulfur components to the effects of sulfur inputs. A more in-depth long-term study would be necessary to adequately deal with this question. However, the trend indicates that sulfates may be more important, since the microcosms treated with Sulfate Only had a significantly lower respiration rate than the Control microcosms at the end of the study. Sulfate Only microcosms also showed the largest percent decline in respiration over the course of the study. However, at the low doses used, both gaseous and liquid inputs were generally necessary to produce significant effects.

The sulfur level which reduced respiration rates was substantially greater than that which is currently being deposited on either of the two watersheds. The amount of sulfates alone added to the microcosms over the 12-week period is more than what would be the total sulfur input over a whole year at Cross Creek, or about $36 \text{ kg S}\cdot\text{ha}^{-1}$. Sulfur levels approximately equal to and even greater than the current rate of inputs at the two watersheds did not produce any lasting effects. This is in agreement with the field observations, where no difference was observed between respiration rates at the two watersheds. However, it is impossible to tell what effects even these levels might produce in the long term. From the microcosm study, there are no indications that low to moderate sulfur inputs have any major short term effect on decomposition.

Contributions to Respiration

In addition to CO_2 evolved from the microflora and decomposer organisms, forest floor respiration rates also include CO_2 given off by the mineral soil and most notably, roots. Root respiration itself includes CO_2 given off by live roots, rhizosphere organisms--the microflora intimately associated with roots--and the decay of dead root material. Estimates of the contribution of soil and root respiration to total CO_2 output have been quite variable, ranging from insignificant (Feher, 1933) to over 75% (Edwards and Harris, 1977). Many different techniques have been employed in an effort to get better estimates but as yet there are no truly precise measures. Nearly all of these estimates have large errors or unrealistic assumptions. It

is nearly impossible to isolate the individual contributions of litter, roots, and soil without their disturbance. Thus, true estimates of their natural activity within the soil ecosystem are not possible. Measurement of root respiration directly was not attempted in this study. However, estimates of root respiration were approximated through extrapolations of previously established data.

Ramseur and Kelly (1981) found the fibrous root biomass in the upper 10 cm of the soil to be $1546 \text{ g}\cdot\text{m}^{-2}$ at Camp Branch and $1844 \text{ g}\cdot\text{m}^{-2}$ at Cross Creek. Unpublished data* from a more intensive study indicates lower biomass estimates ($850\text{--}880 \text{ g}\cdot\text{m}^{-2}$) where respiration samples were taken. The average of these estimates of root biomass along with estimates of root respiration per gram of root material based on respirometer measurements from the literature give a rough approximation of the CO_2 output of the roots and their associated microflora on each watershed. Considering the mean temperature at the watersheds and the size of the roots, an average estimate of root respiration is $0.10 \text{ mg CO}_2\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ (Edwards and Harris, 1977; Edwards and Sollins, 1973; Minderman and Vulto, 1973b). Over the entire year this indicates a value of $1060 \text{ g CO}_2\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ given off by roots at Camp Branch and $1160 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at Cross Creek. This amounts to 60% of the total CO_2 output from the forest floor at Camp Branch and 65% of the total at Cross Creek. These are rough estimates based on CO_2 evolution per gram of root and cannot be considered absolute. The true range of CO_2

* Preliminary data from root survey still in progress conducted by J. M. Kelly.

contribution by roots is most probably within the range of 50 to 70% of the total CO_2 output, as is most often reported in the literature (Minderman and Vulto, 1973b; Edwards and Harris, 1977; Edwards and Sollins, 1973; Wiant, 1967; Witkamp and Frank, 1969).

Although Cross Creek has greater root respiration due to its larger root biomass, the difference is less than 10%. This difference is also reflected in the generally higher forest floor respiration at Cross Creek, producing similar proportions to the total CO_2 evolution and suggesting similar contributions due to litter decomposition at the two watersheds.

Reichle et al. (1975) quantified the relative contributions of various decomposer groups to CO_2 evolution and estimated that 99.7% of the total CO_2 evolved by a decomposer community was contributed by microflora and only 0.3% by all soil invertebrates. Of the invertebrate respiration, arthropods contributed 49.4% (.1% of total), Annelida 7.3% (.02%), Nematoda 41.3% (.1%) and Pulmonata 2.0% (.005%). Thus, even though invertebrates may constitute most of the decomposer biomass, the microflora contribute practically all of the CO_2 evolved by decomposers. Anderson and Domsch (1973) estimated the relative contribution of fungi and bacteria to their combined CO_2 output and found that even though bacteria was 64 times more abundant in dilution plate counts, fungi contributed an average of 78% of the microflora CO_2 . The dominance of fungi was evident at the two watersheds in June when fungal populations and CO_2 evolution rates reached their peak levels for the year while bacterial populations decreased.

Litter Fractional Loss Rates

Annual decomposition rates were also estimated with litterfall and litter accumulation data using equations based on exponential decay models developed by Jenny et al. (1949), elaborated on by Olson (1963), and used by Cromack (1973), Reiners and Reiners (1970), and Witkamp and Olson (1963). In this model litter breakdown is expressed as a constant negative slope, $-k$, on a semi-log graph.

Decomposition of forest floor litter is expressed by the general case of litter accumulation with discrete annual litterfall (Olson, 1963). The fraction of the forest floor decomposed each year is given by:

$$k' = L/T \quad (1)$$

Where T represents the maximum value of forest floor standing crop, occurring in autumn just after the leaf fall, L represents the annual litterfall input, assumed to be a discrete addition during the fall, and k' represents the fraction of standing crop lost. The annual decay rate (k) of the forest floor, of which k' is a fraction, is calculated from k' as follows:

$$k = -\ln (1 - k') \quad (2)$$

Camp Branch litterfall averages $475.1 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, while Cross Creek litterfall averages $645.2 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Kelly, 1982b). Litter standing crop was estimated from the monthly litter samples collected at both watersheds. The maximum value of standing crop occurred after litterfall and was equal to $1590 \text{ g}\cdot\text{m}^{-2}$ of litter at Camp Branch and $1990 \text{ g}\cdot\text{m}^{-2}$ at Cross Creek. The difference between the standing crop of litter at the watersheds is due to the larger annual litter input

at Cross Creek and its resulting accumulation rather than to any large difference in decomposition rates. Entering these litter values into equations (1) and (2) yield annual decay rates (k) of .39 and .35 for Cross Creek and Camp Branch, respectively, which is equivalent to an annual weight loss of 32% at Cross Creek and 30% at Camp Branch.

Cromack (1973) reported a somewhat higher overall k value of .61 for a mixed hardwood forest in North Carolina as well as individual species loss rates of about .6 and .7 for chestnut oak and white oak, respectively. Others have also reported exponential loss rates in the range of .5 to .7 for similar forested areas (Crossley and Witkamp, 1964a; Witkamp, 1966a; Witkamp and Crossley, 1966; Witkamp and Olson, 1963). However, some have reported fractional loss rates similar to those found here, with k between .3 and .4 (Sollins et al., 1973; Thomas, 1970). Rates reported in the literature as percent weight loss of oak litter range from about 20 to 60% per year, with 30 to 40% being the most common range (Bocock and Gilbert, 1957; Bocock et al., 1960; Kelly, 1973; Shanks and Olson, 1961).

A slightly different estimate of litter decomposition can be arrived at by comparing the monthly forest floor litter weights over the year. Subtracting the smallest amount of litter before litterfall from its highest value after litterfall gives an estimate of the amount of litter broken down in one year (Witkamp and van der Drift, 1961). Litter standing crop just prior to litterfall was at its lowest in August ($1630 \text{ g}\cdot\text{m}^{-2}$ at Cross Creek and $1280 \text{ g}\cdot\text{m}^{-2}$ at Camp Branch) subtracted from the maximum standing crop ($1990 \text{ g}\cdot\text{m}^{-2}$ at Cross Creek and $1590 \text{ g}\cdot\text{m}^{-2}$ at Camp Branch) yields a net decrease of

360 $\text{g}\cdot\text{m}^{-2}$ litter material at Cross Creek and 310 $\text{g}\cdot\text{m}^{-2}$ at Camp Branch. This decrease corresponds to about 22% of the litter standing crop at Cross Creek and 24% at Camp Branch.

These estimates indicate a slightly slower decomposition rate than the exponential loss rates suggested, but these are based on losses over a period of less than a year since the lowest litter standing crop level occurred in August and the maximum levels occurred in November. So, actual yearly losses might be slightly higher.

The 360 and 310 $\text{g}\cdot\text{m}^{-2}$ of litter material broken down represents 176.4 and 151.9 $\text{g C}\cdot\text{m}^{-2}$, respectively, that would be given off as CO_2 from litter decomposition (assuming a litter carbon content of 49%). The yearly CO_2 output of the forest floor at the two watersheds expressed as grams of carbon amount to 481.6 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at Camp Branch and 487.9 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at Cross Creek. Thus, about 31.5% of the total CO_2 evolved at Camp Branch comes from litter decomposition, and about 35% at Cross Creek.

The greater amount of litter decomposed at Cross Creek each year is presumedly attributable to the slightly higher temperature and moisture conditions there, as well as the higher annual litterfall inputs which provide more readily decomposable substrate material for the microorganisms to act on. The difference, however, is small and does not appear to represent any inherent differences in the decomposition processes between the watersheds.

From these estimates, litter respiration appears to account for about 30-35% of the total forest floor respiration while roots appear to contribute about 60-65%, leaving a small fraction that is

attributable to other processes in the mineral soil (including CO_2 derived from root leachates and exudates, additional root decay, and other soil microorganism respiration not associated with litter decomposition).

II. MICROFLORA

The mean annual density for litter bacteria at Camp Branch was 95.7×10^6 organisms per gram dry weight of litter, while the Cross Creek annual mean was 100.7×10^6 per gram (Table 5). These estimates are within the range of bacterial populations commonly reported in the literature for deciduous litter (Holm and Jensen, 1972; Kelly, 1973; Witkamp, 1963, 1964, 1966a). There was no significant difference between the annual mean bacteria populations of the two watersheds. There was also no significant difference between the mean monthly bacteria populations at the two watersheds within any individual month of the year. Monthly bacterial counts at Camp Branch ranged from a low of 23.4×10^6 per gram litter in February to the high of 235×10^6 in November. At Cross Creek the high was in August, reaching 232×10^6 per gram while the low was 28.8×10^6 in February.

The mean annual fungi count for Camp Branch was 24.1×10^6 viable propagules per gram dry weight of litter, with 22.8×10^6 per gram at Cross Creek (Table 5). These population estimates are within the range of fungal populations reported in the literature, but they are higher than what is often observed, particularly in relation to the bacteria population (Alexander, 1977; Kelly, 1973, Witkamp, 1963, 1964, 1966a). This may be due to the highly acid litter and soil at both

Table 5. Mean monthly bacterial and fungal colony counts ($\times 10^6$) per gram dry weight of litter at Camp Branch and Cross Creek.

Date	Location					
	Camp Branch			Cross Creek		
	Site 1	Site 2	Mean	Site 1	Site 2	Mean
<u>Fungi</u>						
April 1980	3.6	9.8	6.6	3.9	9.9	7.0
May	11.8	17.8	14.9	24.7	13.8	19.2
June	71.7	99.5	85.6	74.9	99.8	87.9
July	29.8	32.3	31.1	19.9	24.9	22.4
August	31.8	36.2	34.0	36.3	27.4	31.9
September	5.7	9.0	7.3	7.5	11.1	9.3
October	36.4	20.7	28.2	28.8	11.9	20.0
November	24.5	11.9	18.2	24.2	29.3	26.7
December	10.5	8.6	9.5	9.2	12.4	10.8
Jan. 1981	3.9	7.7	5.8	14.3	11.8	13.1
February	6.0	9.1	7.6	6.7	5.2	5.9
March	<u>23.4</u>	<u>23.6</u>	<u>23.5</u>	<u>9.0</u>	<u>19.0</u>	<u>14.0</u>
Mean	22.9	25.2	24.7	21.8	23.9	22.8
<u>Bacteria</u>						
April 1980	27.0	36.7	31.6	88.2	172.8	128.6
May	142.0	121.6	131.3	144.5	127.8	137.1
June	82.4	73.7	78.1	56.2	92.2	74.9
July	210.7	91.4	151.1	100.3	87.1	93.7
August	144.4	169.0	157.2	173.5	285.6	232.0
September	51.5	44.1	47.8	26.6	33.4	30.3
October	97.5	79.1	87.9	119.1	63.2	86.7
November	284.7	183.3	235.3	216.2	155.6	185.9
December	49.6	64.3	57.2	64.1	65.8	65.0
Jan. 1981	30.7	63.2	46.8	51.9	50.9	51.4
February	22.4	24.4	23.4	32.6	25.0	20.8
March	<u>60.6</u>	<u>52.2</u>	<u>56.4</u>	<u>44.3</u>	<u>51.5</u>	<u>48.1</u>
Mean	106.6	85.0	95.7	96.9	104.4	100.7

watersheds (pH 4.6 - 4.8). Fungi are more tolerant of low pH than bacteria; so, low pH favors the growth of fungi over bacteria, allowing the fungi a much higher proportion of the total microflora than in more neutral soils (Alexander, 1977, 1980). The large fungal counts may also be due to the vast amounts of spores present in the litter which readily develop on dilution plates (Witkamp, 1971a, 1974).

There were no significant differences between the fungal population estimates at the two watersheds either on a mean annual basis or within any particular month. Mean monthly counts at Camp Branch ranged from the low of 5.8×10^6 per gram in January to the high of 85.6×10^6 in June. At Cross Creek monthly counts ranged from 5.9×10^6 in February to 87.9×10^6 in June.

Variation between sites within watersheds and among plots within sites was large, often larger than the differences between watersheds, but showed no significant differences. This variability was due primarily to the heterogeneous distribution of microorganisms and the sampling intensity employed.

Monthly fluctuations in microbial populations are caused mainly by temperature and moisture changes (Witkamp, 1963; Witkamp and van der Drift, 1961). Population peaks were found in the spring and fall when high temperatures and high moisture contents were conducive to microbial growth. Fall population increases are also caused by the input of new organic substrate in the litterfall (Minderman and Daniels, 1967). Similar seasonal fluctuations have been noted by Söderström (1979) and Witkamp (1960, 1963), among others (McBrayer et al., 1974; Rahno et al., 1978; Witkamp and van der Drift, 1961). Large populations

were also observed in August, when litter moisture was still quite low. This was probably due to the large numbers of spores produced by the larger spring and summer populations.

Population levels were very similar at both watersheds throughout the year, indicating that there were no local conditions that significantly affected the microorganisms. Differences in sulfur loading between the two watersheds appear to have no effect on the microflora population levels. It is not known whether there were any qualitative differences in the types of microorganisms on each watershed. Considering the similar vegetation, soils, and other environmental characteristics, the microflora taxonomy is probably also very similar.

III. MICROFAUNA

Microarthropods extracted from soil cores from both watersheds were dominated by the orders Acarina and Collembola. For this reason, only those two orders and the total arthropod populations were evaluated statistically for comparisons between the watersheds. Other orders frequently observed but in much lower numbers included Protura, Symphyla, Coleoptera, and Diptera. Orders only occasionally encountered in very low quantities included Hemiptera, Hymenoptera, Araneida, Pseudoscorpionida, Diplopoda, Chilopoda, Pauropoda, Isopoda, Lepidoptera, and Thysanoptera.

The mean annual arthropod population at Camp Branch was 46,200 organisms·m⁻² (Table 6) which was significantly greater than the Cross Creek average of 34,400 organisms·m⁻². Mean Acarina populations were

Table 6. Mean monthly Acarina, Collembola, and total arthropod populations ($\times 10^3$) per square meter at Camp Branch and Cross Creek.

Date	Location					
	Camp Branch			Cross Creek		
	Site 1	Site 2	Mean	Site 1	Site 2	Mean
<u>Acarina</u>						
April 1980	58.1	32.4	45.2	28.4	31.3	29.9
May	30.4	33.0	31.7	23.5	39.0	31.5
June	47.8	21.7	34.8	25.0	7.7	15.1
July	15.5	43.8	29.7	20.8	3.7	12.6
August	20.1	32.7	26.1	13.9	33.0	23.4
September	38.3	27.9	33.1	15.9	22.6	19.2
October	25.2	42.0	33.6	15.2	18.2	16.7
November	30.8	50.6	40.7	13.9	28.2	21.0
December	40.7	34.1	37.4	26.6	20.5	23.6
Jan. 1981	30.3	45.9	38.1	17.9	38.2	28.1
February	22.6	27.5	25.0	9.1	15.1	12.1
March	<u>24.6</u>	<u>17.1</u>	<u>21.0</u>	<u>14.7</u>	<u>12.7</u>	<u>13.7</u>
Mean	32.0	34.1	33.1	18.7	22.8	20.8
<u>Collembola</u>						
April 1980	10.6	10.6	10.6	10.4	19.1	14.7
May	11.8	11.8	11.8	20.0	16.1	17.6
June	18.0	3.9	11.0	20.6	.8	9.3
July	2.1	10.2	6.1	8.7	.1	4.6
August	7.2	8.4	6.1	8.4	11.8	9.5
September	6.4	9.0	7.7	3.1	16.2	9.7
October	8.4	11.2	9.8	10.4	10.3	10.4
November	7.5	12.0	9.8	7.2	7.1	7.2
December	4.7	10.9	9.2	7.0	12.3	8.8
January 1981	9.0	9.9	9.5	8.4	6.7	7.5
February	7.0	9.0	8.0	4.7	9.5	7.1
March	<u>6.5</u>	<u>13.8</u>	<u>10.0</u>	<u>8.9</u>	<u>7.6</u>	<u>8.3</u>
Mean	8.0	10.0	9.0	9.4	9.9	9.7

Table 6. (Continued)

Date	Location					
	Camp Branch			Cross Creek		
	Site 1	Site 2	Mean	Site 1	Site 2	Mean
<u>Total Arthropods</u>						
April 1980	75.7	47.7	61.7	44.6	56.3	50.4
May	47.7	46.6	47.1	48.9	60.6	54.8
June	71.8	26.8	49.3	51.7	9.8	27.7
July	18.5	57.4	37.9	32.1	4.1	18.7
August	26.2	51.8	35.7	23.0	51.8	37.4
September	47.2	44.1	45.7	20.6	43.7	32.1
October	37.9	52.9	47.9	29.9	33.5	31.7
November	46.2	66.1	56.1	26.6	39.3	33.0
December	54.0	47.2	50.6	38.5	35.9	37.2
January 1981	41.9	59.8	50.9	30.7	49.0	39.9
February	32.5	40.0	36.3	16.0	27.5	21.7
March	<u>35.0</u>	<u>33.2</u>	<u>34.2</u>	<u>26.8</u>	<u>22.4</u>	<u>24.7</u>
Mean	44.6	47.8	46.2	32.2	36.6	34.4

also significantly greater at Camp Branch, estimated at $33,100 \cdot \text{m}^{-2}$, compared with $20,800 \cdot \text{m}^{-2}$ at Cross Creek. Collembola populations were comparable at both watersheds, averaging $9,000 \cdot \text{m}^{-2}$ at Camp Branch and $9,700 \cdot \text{m}^{-2}$ at Cross Creek.

Mean annual populations at the two watersheds are within the range of values reported in the literature for similar forest types, but are lower than a number of recent estimates ($70,000 - 100,000$ organisms $\cdot \text{m}^{-2}$) using comparable methods (Edwards et al., 1969; Gist and Crossley, 1975; McBrayer and Reichle, 1971).

The lower population levels observed at these two watersheds could be due to a variety of reasons. Sampling procedures, extraction devices, and personal technique used probably account for most of the differences. Yet, there may indeed be a lower arthropod density in forests on the plateau, because of particular environmental conditions there. Soils of the area are shallow, highly leached, infertile, acid, and support poor quality second growth oak-hickory stands, and thus may have lower soil fauna numbers than more fertile, mesic sites. Soil fauna appear to be more affected by environmental conditions than by the types and species of forest vegetation present (Anderson, 1975).

Overall, arthropod populations were greatest in the spring and fall, with lowest populations occurring during the dry summer. Winter populations were moderate. Mean monthly arthropod populations at Camp Branch ranged from the low in March, 1981, of $34,200$ organisms $\cdot \text{m}^{-2}$ to the peak in April, 1980, of $61,700 \cdot \text{m}^{-2}$ (Table 6). The total populations at Cross Creek ranged from $18,700$ in July to $54,800 \cdot \text{m}^{-2}$ in May. Monthly total arthropod and Acarina population estimates at Camp Branch were consistently higher than the Cross Creek values.

Variation between sites within each watershed could not be estimated because throughout most of the study, sites within each watershed were not sampled on the same day, due to space limitations on the Tullgren extractor. So, temperature and moisture effects were confounded with the site differences. On the sampling dates when full sets of samples from all sites were collected, sites within each watershed, although variable, showed no significant differences. Variation among plots within sites was large, but generally showed no significant differences.

Month to month fluctuations in arthropod populations were not always adequately explained by changes in temperature and litter moisture. Gasdorf and Goodnight (1963) observed that other factors were necessary to explain seasonal variations. Seasonal trends of egg-laying, development of immature forms, and emergence of new adults have been shown to contribute to the arthropod population highs and lows (Gasdorf and Goodnight, 1963; Wallwork, 1959). Arthropods also have the ability to seek out microsites with higher moisture levels than the surrounding soil and litter, and thus are able to maintain fairly high populations even during severe dry spells (Gasdorf and Goodnight, 1963). This response contributes greatly to the aggregated distribution of soil arthropods (Usher, 1976). Additional fluctuations known to occur due to the vertical movement of arthropods through the soil and litter profiles for feeding, mating, and egg-laying (Gist and Crossley, 1975; Wallwork, 1959) were minimized by the use of soil cores that sampled the entire range of depths that most soil organisms frequent.

The seasonal fluctuations corresponded to those found by Gist and Crossley (1975) as well as McBrayer et al. (1974) in southern hardwood forests. They observed similar spring and fall population peaks and lowest densities in the summer. Gist and Crossley (1975) suggested the population increases were caused by a response to decreases in mesofaunal predator activities, as well as a response to increased microfloral activity commensurate with autumn leaf fall. The spring peak is brought on mainly by the warm temperatures, and is largest in early spring before the mesofaunal predator populations become very large.

The significant difference in total soil arthropods and Acarina observed between the two watersheds is presumably due to differences in local conditions and physical properties at the watersheds. Temperature and moisture differences are not large enough to be responsible for any major discrepancy between the watersheds. The difference may be a direct or indirect result of the higher sulfur input received at Cross Creek, but it is difficult to positively identify it as such.

Acidity of the litter and soil can have a definite influence on the numbers and kinds of soil organisms. Organisms in acid soil tend to be very acid-tolerant, and even prefer acid soils (Abrahamsen et al., 1980; Bååth et al., 1980). Significant increases in *Collembola* (particularly the dominant species) with increasing soil acidity have been observed, whereas mite populations generally have not shown significant changes with acidity, although the oribatid mites have increased in dominance in some studies (Abrahamsen et al., 1980; Bååth et al., 1980; Hagvar and Abrahamsen, 1977; Hagvar and Amundsen,

1981; Hagvar and Kjøndahl, 1981). Acidity effects appear to operate on the species level, for within each group of organisms studied there have been some species that increase and others that decrease with increasing acidity (Hagvar and Abrahamsen, 1980). Species which dominate a particular soil are dependent on the soil pH since the dominance structure and sometimes total numbers will be altered with changes in pH. A possible correlation between soil pH and reproduction success in several species is the most likely cause of the acidity effects (Hagvar and Abrahamsen, 1980; Overrein et al., 1980). Acidity, however, cannot explain the differences in arthropod populations seen at the two watersheds, because soil pH is highly acid at both.

Considering the overall environmental similarities of the two watersheds, it is very possible that the discrepancy in soil arthropod numbers is in some way related to the differences in sulfur inputs. It is not known whether the lower numbers could be a direct effect of increased quantities of sulfur compounds, whether it may be a related effect caused by some other factor, or whether it is totally unrelated to sulfur inputs and a result of some other attribute or process acting on the watersheds. Lowered arthropod numbers would not account for the lowered respiration rates observed in the High Sulfur treated microcosms because arthropods contribute only a minute fraction to CO_2 evolution (Reichle et al., 1975), and so could not be the mechanism by which sulfur inhibits respiration.

The effect of the lower numbers of arthropods at Cross Creek is difficult to assess. The importance of soil arthropods in decomposition is well known, yet the measures of other aspects of decomposition

reveal no inhibition or disruption of decomposition in any way. This may indicate that the population levels monitored may be the normal levels in this ecosystem and not the result of any disturbance induced by anthropogenic changes. The microflora populations were not lower or less active because of a lack of preliminary fragmentation of the litter by the arthropods. It would appear that the ecosystem is adjusted to and operating efficiently with the current levels of arthropods. Unless the lower numbers of arthropods is a trend toward a continued decrease in numbers, there does not appear to be any major effects on decomposition processes at the watershed as a whole. Even if a decline of arthropods is in some way related to sulfur inputs, there are no immediately apparent differences in decomposition, and the surrounding communities have adjusted or compensated to the lower levels. However, if arthropod levels are lowered further with continued sulfur inputs serious effects on decomposition may be seen over a long period.

IV. LITTER NUTRIENT CONCENTRATIONS

The forest floor is a major reservoir of nutrients for the ecosystem and as such influences most of the functional processes throughout the ecosystem. The litter and humus layers play a crucial role in nutrient cycling. It is here that a portion of the nutrients returned in litterfall, throughfall, and stemflow are stored and made available to plants and animals. The rates at which the nutrients are mineralized or immobilized determines whether they will be available for plant uptake, remain tied up in organic complexes, or be leached away and possibly lost from the system.

Individual nutrient release rates are controlled by complex interactions of many factors, but among the most important are the nutrient requirements of the microbial heterotroph community and the existence of critical Carbon to element ratios (e.g. C:N, C:S, C:P) as well as element to element ratios (e.g. N:S, N:P, S:P) (Gosz et al., 1973; Lousier and Parkinson, 1978). Initial concentrations of the litter inputs also may be important in determining whether an element is mineralized or immobilized, resulting in a high degree of feedback within the system, for nutrients that are in short supply are held more tightly than those that are in abundance (Gosz et al., 1973; Maclean and Wein, 1978).

Total concentrations of nitrogen, sulfur, phosphorus, calcium, potassium, magnesium, and sodium were measured monthly in litter samples collected from the forest floor of each watershed (Table 7). Overall, Camp Branch litter had significantly higher sulfur and nitrogen concentrations, while Cross Creek had significantly higher calcium and magnesium concentrations. Phosphorus, potassium, and sodium concentrations were approximately equal at both watersheds. Since Cross Creek has substantially more litter material accumulated than Camp Branch (approximately $1767 \text{ g}\cdot\text{m}^{-2}$ at Cross Creek to $1434 \text{ g}\cdot\text{m}^{-2}$ at Camp Branch), comparing nutrient concentrations alone does not give an accurate indication of the absolute amount of nutrients in the organic layers of the two watersheds (Table 8). In addition to observing the changes in nutrient concentrations within the forest floor, it is necessary to know the changes in nutrient status since litterfall in order to see the entire process of element loss and

Table 7. Litter nutrient concentrations at Camp Branch and Cross Creek.

Element	Location					
	Camp Branch			Cross Creek		
	Site 1	Site 2	Mean	Site 1	Site 2	Mean
	$\mu\text{g}\cdot\text{g}^{-1}$					
Total--N	10500	10600	10550a	9300	9100	9200b
Total--S	1150	1170	1160a	1050	1010	1030b
P	550	590	570a	590	590	590a
Ca	5300	5400	5350a	8200	8200	8200b
Mg	460	530	500a	600	540	570b
K	640	680	660a	660	660	660a
Na	50	60	60a	60	60	60a

* Watershed means within each row followed by the same letter are not significantly different ($p=.05$).

Table 8. Total element weight, litterfall concentration, and percent of litterfall concentration remaining in litter layers at Camp Branch and Cross Creek.

Element	<u>Element Weight</u>		<u>Litterfall Concentrations</u>		<u>Concentration Remaining</u>	
	Camp Branch	Cross Creek	Camp Branch	Cross Creek	Camp Branch	Cross Creek
	<u>—kg·ha⁻¹—</u>		<u>—μg·g⁻¹—</u>		<u>— % —</u>	
Total--N	151.3	162.2	8463	9578	124.7	95.8
Total--S	16.6	18.2	975	1131	118.7	91.1
P	8.2	10.5	425	608	134.6	97.8
Ca	77.1	144.8	8180	12513	65.7	65.5
Mg	7.2	10.0	1046	1167	47.6	48.6
K	9.5	11.6	3914	4857	16.9	13.6

* From Kelly, 1982b.

retention occurring within the litter layers. The percentage of initial litterfall concentration remaining in the litter layers was determined based on litterfall data from Kelly (1982b) and average litter concentrations (Table 8).

Sulfur

Monthly litter sulfur concentrations ranged from 840 to 1390 $\mu\text{g}\cdot\text{g}^{-1}$ at Camp Branch and 900 to 1280 $\mu\text{g}\cdot\text{g}^{-1}$ at Cross Creek (Figure 4). The mean annual litter sulfur concentration was 1160 $\mu\text{g}\cdot\text{g}^{-1}$ at Camp Branch and 1030 $\mu\text{g}\cdot\text{g}^{-1}$ at Cross Creek, which are within the range reported in the literature (Ausmus and Witkamp, 1974; Gosz et al., 1973, 1976; McBrayer et al., 1974; Rodin and Bazeliivitch, 1967). Sulfur concentrations were highest in May-June at both watersheds and decreased throughout the rest of the year, with the exception of a slight increase in October-November. Lowest sulfur concentrations were observed in late winter-early spring. The sharp increase in litter concentration in May-June was presumably due to the sulfur-rich spring inputs of litterfall, throughfall, and stemflow. The concentration of many elements, primarily nitrogen, sulfur, and phosphorus, are at their peak at the start of the growing season. The spring flush of vegetation and reproductive parts contain high concentrations of these nutrients, which are leached by throughfall and stemflow and deposited in litterfall (Grizzard et al., 1976; Likens et al., 1977; Reiners and Reiners, 1970).

Camp Branch litter sulfur concentration was significantly greater than the Cross Creek concentration through most of the year. This is in direct contrast to the greater sulfur inputs, including

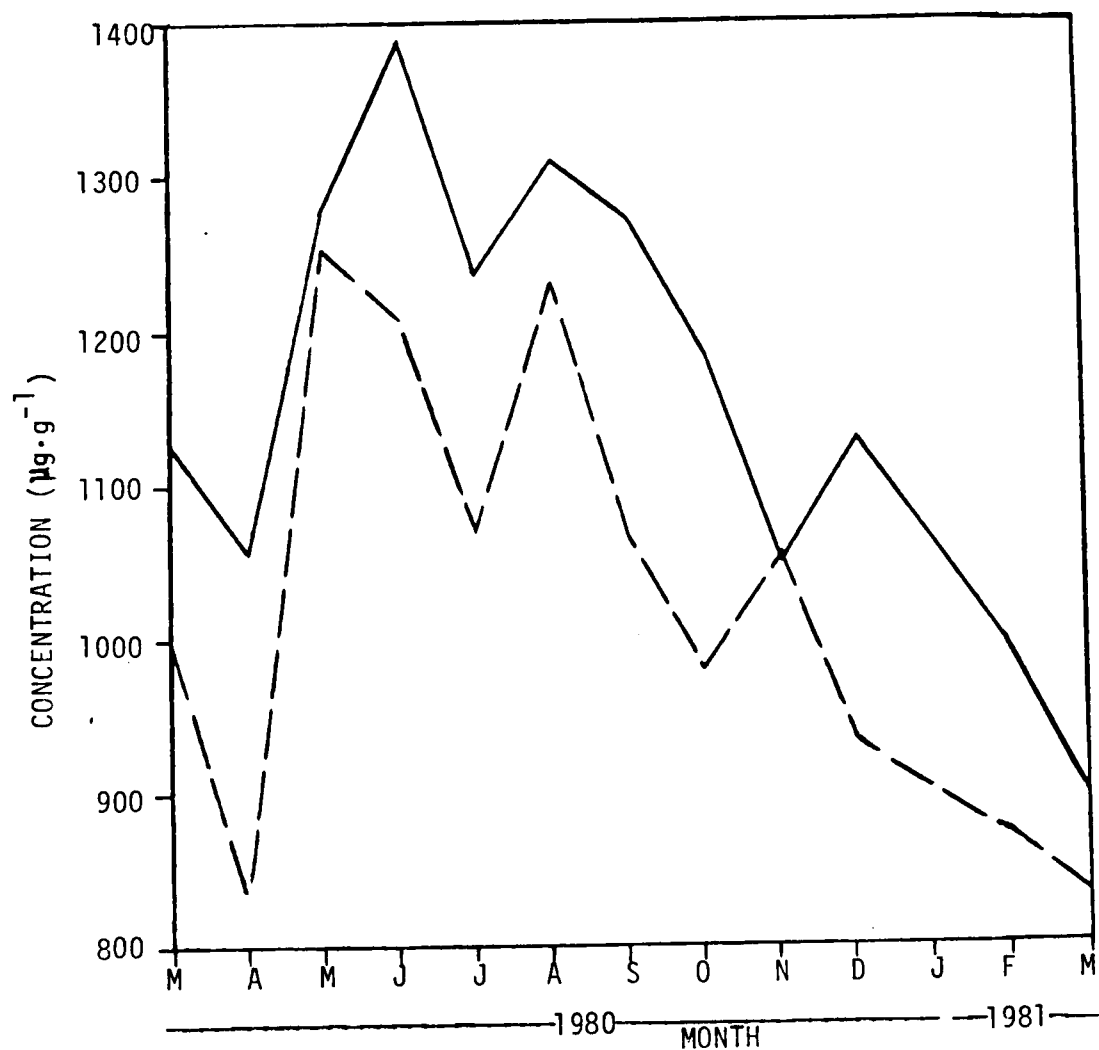


Figure 4. Mean monthly sulfur concentrations in litter at Camp Branch (————) and Cross Creek(—— ——— ———).

higher initial litterfall sulfur concentrations received by Cross Creek. However, even with lower litter sulfur concentrations, the total weight of sulfur in the litter at Cross Creek is greater than at Camp Branch ($1.82 \text{ g} \cdot \text{m}^{-2}$ to $1.66 \text{ g} \cdot \text{m}^{-2}$) due to the greater accumulation of litter at Cross Creek. In the early stages of decomposition, litter at Cross Creek evidently lost sulfur while Camp Branch litter retained and immobilized the sulfur from its inputs. The average sulfur concentration in litterfall was 975 and $1130 \mu\text{g} \cdot \text{g}^{-1}$ at Camp Branch or 119% of the litterfall input and $1030 \mu\text{g} \cdot \text{g}^{-1}$ or 91% of the litterfall input at Cross Creek (Table 8). The sulfur concentration increased at Camp Branch because the rate of loss of sulfur was slower (due to immobilization) than the overall weight loss of litter material, thus increasing the sulfur content per gram of litter material. The drop in concentration at Cross Creek indicates a loss rate greater than the overall weight loss or decomposition of the litter material, and is caused by leaching and/or mineralization.

Gosz et al. (1973) observed litter sulfur concentrations of some species to increase, whereas in species that had significantly higher sulfur concentrations initially, an overall decrease as well as a large initial leaching loss of sulfur was noted. The final sulfur concentration of litter from all the species were very similar. It was concluded that the sulfur content would continue to increase through immobilization or decrease through mineralization and leaching until the critical sulfur concentration was reached (Gosz et al., 1973).

A similar process appears to be occurring at the watersheds wherein sulfur was initially lost from the high sulfur content Cross Creek litter, while at Camp Branch because of the lower initial sulfur concentrations, sulfur was retained. This difference appeared to be important only in the early stages of decomposition because the sulfur concentration decreased similarly over the year at both watersheds. Also, it is not clear whether the lower sulfur concentrations observed in Cross Creek litter and the initial losses there represent a lower sulfur microbial requirement, whether the litter levels will begin to increase again, or whether it represents a long term change in nutrient cycling caused by the high sulfur input. The total mass of nutrient may also be important in establishing critical ratios and loss rates, thus better explaining the discrepancies between the sulfur contents of the two watersheds.

Gosz et al. (1973) and MacLean and Wein (1978) agreed that the initial chemical concentration of the litter and the microorganism demand largely determined the rate and direction of nutrient flux with decomposition. Although the ultimate effects of the watershed differences regarding litter sulfur cannot be determined, it is apparent that the higher inputs of sulfur do have an effect on the flux and cycling of sulfur through the litter layers.

Nitrogen

Monthly litter nitrogen concentrations ranged from 9500 to 12200 $\mu\text{g}\cdot\text{g}^{-1}$ at Camp Branch and 8500 to 10300 $\mu\text{g}\cdot\text{g}^{-1}$ at Cross Creek (Figure 5). Mean annual values were 10550 and 9200 $\mu\text{g}\cdot\text{g}^{-1}$ at Camp Branch and Cross Creek, respectively, which are within the range of

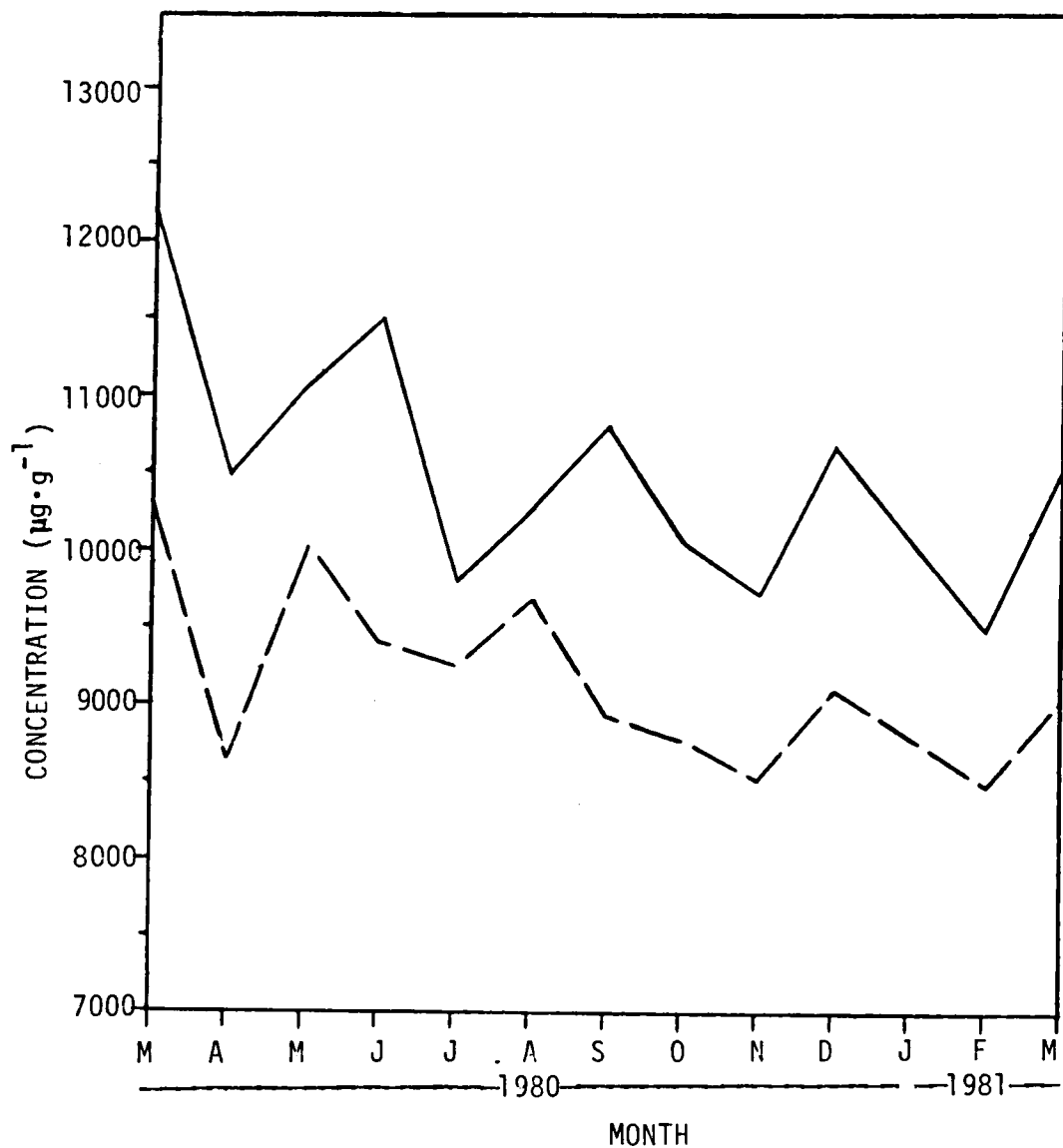


Figure 5. Mean monthly nitrogen concentrations in litter at Camp Branch (————) and Cross Creek(—— ———).

values (5,000 to 24,000 $\mu\text{g}\cdot\text{g}^{-1}$) reported in the literature (Cromack, 1973; Gosz et al., 1973, 1976; Lousier and Parkinson, 1978; MacLean and Wein, 1978; Reiners and Reiners, 1970). Nitrogen content was variable but in general decreased slightly throughout the year. This is in contrast to several studies where nitrogen concentration and sometimes even the absolute amounts of nitrogen increased with decomposition (Anderson, 1973a; Bocock, 1964; Gilbert and Bocock, 1960; Gosz et al., 1973, 1976). Other investigators, however, have reported equal or decreasing nitrogen concentrations with increasing decomposition (Ausmus and Witkamp, 1974; Kelly, 1973; McBrayer et al., 1974; Reiners and Reiners, 1970). Even though the nitrogen concentration decreased over the year, there were indications that nitrogen had been immobilized and concentrated during the initial stages of decomposition at Camp Branch, because the litter concentrations were still higher than those found in the litterfall (Table 8).

As with sulfur, litter nitrogen concentrations were significantly greater at Camp Branch throughout the year even though litterfall nitrogen inputs were higher at Cross Creek. However, absolute nitrogen weight was very similar at both watersheds due to the larger accumulation of litter at Cross Creek. Litter nitrogen concentrations decreased from the higher litterfall input levels at Cross Creek, while Camp Branch litter nitrogen concentrations increased from its lower litterfall levels, similar to the process observed for sulfur loss and retention. It is presumed that critical element requirements along with the initial concentrations are controlling the immobilization and mineralization processes.

The somewhat ironic finding that the watershed receiving substantially higher nutrient inputs had significantly lower litter concentrations of sulfur and nitrogen may be important to overall nutrient cycling. It shows that the additional sulfur and nitrogen does not stay or accumulate in the litter and upper soil layers, but may leach away to be lost from the soil system or adsorbed in the lower soil horizons where it may be unavailable for plant or animal uptake.

Other Elements

Monthly litter concentrations of phosphorus, calcium, magnesium, potassium, and sodium (Figure 6) reveal comparable levels of phosphorus, potassium, and sodium between the watersheds, whereas calcium and magnesium concentrations demonstrated significant differences. Over the year at both watersheds, phosphorus concentrations were observed to decrease slightly from spring to winter, potassium and magnesium levels increased from spring or summer to winter following winter to spring declines, and calcium and sodium concentrations fluctuated widely but demonstrated no consistent trend to increase or decrease. Based on this, the release of calcium, sodium, and phosphorus appeared to be most closely associated with litter weight loss or overall decomposition, whereas potassium and magnesium were retained and lost at slower rates after initial leaching losses (Attiwill, 1968; Gosz et al., 1973, 1976; Lousier and Parkinson, 1978; MacLean and Wein, 1978).

Litter concentrations of potassium, magnesium, and calcium at both watersheds were lower than the average literature values (Cromack, 1973; Gosz et al., 1973, 1976; Lousier and Parkinson, 1978; MacLean and Wein, 1978; Yount, 1975). This is possibly a result of the highly acid,

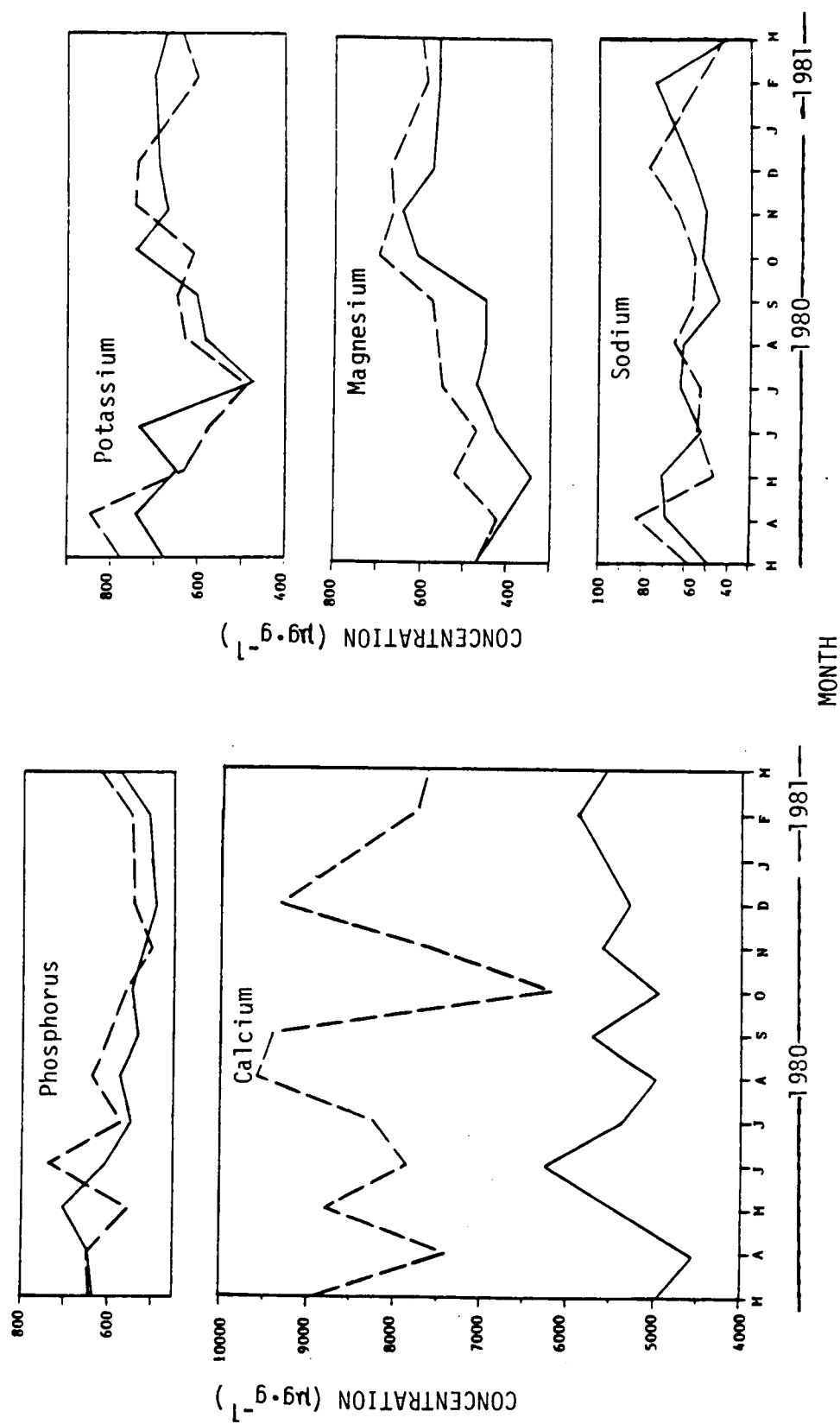


Figure 6. Mean monthly phosphorus, calcium, potassium, magnesium, and sodium concentrations in litter at Camp Branch (—) and Cross Creek (---).

low cation exchange capacity characteristics of the litter and soil at the watersheds. Increasing acidity of litter and soil has been shown to cause increased cation leaching in many cases (Cronan, 1978; Malmer, 1976; Norton, 1977; Overrein, 1972; Tamm, 1976). Since the availability of nutrients was not measured, however, fertility of the litter and soil cannot be determined.

Phosphorus, like sulfur and nitrogen, appeared to show a difference in the initial loss and retention pattern between the two watersheds. Cross Creek received higher phosphorus concentrations in the litterfall and initially lost some through leaching, whereas the lower concentrations of phosphorus in the Camp Branch litter were retained and accumulated initially until the concentrations at both watersheds were about equal (MacLean and Wein, 1978). After this initial difference the loss of phosphorus appeared to be associated with the loss of dry matter, as was also observed by Attiwill (1968) and Lousier and Parkinson (1978). Others, however, have observed phosphorus concentrations to increase with decomposition (Gosz et al., 1973, 1976; Toth et al., 1975; Yount, 1975).

Calcium concentrations showed the largest difference between the two watersheds of all the nutrients examined. This difference was primarily a result of the large difference in the litterfall concentrations (Table 8, p. 49). The net rate of loss from the initial litterfall concentrations was about the same at both watersheds, with about 65-66% of the litterfall concentrations remaining in the litter layers. These initial losses were primarily due to leaching, for after this rapid reduction calcium loss appeared to correspond with

decomposition of the litter material (Attiwill, 1968; Gosz et al., 1973, 1976; Thomas, 1970). The reason for the large difference in calcium concentrations and, to a lesser extent, magnesium concentrations remains unclear. It could possibly be the accumulated result of years of higher calcium and magnesium input at Cross Creek. It may also be related to sulfur input and mobility, because the less mobile sulfur complexes may tie up or slow down the movement of calcium and magnesium resulting in a relative increase in concentration. Over many years, small differences between the watersheds may have been exaggerated.

Potassium concentrations decreased to a minimum in July and then increased through the remainder of the year as was also observed by Gosz et al. (1973), Attiwill (1968), Lousier and Parkinson (1978), and MacLean and Wein (1978). The minimum potassium concentrations were very similar at both watersheds although initial levels were quite different, suggesting that the minimum concentrations represent critical levels or the levels corresponding to heterotroph requirements (Gosz et al., 1973). Potassium was by far the most mobile element, with litter retaining only 17% and 13.5% of the litterfall input concentrations at Camp Branch and Cross Creek, respectively.

Magnesium concentrations reached their minimum levels in spring at both watersheds and then began increasing through the rest of the year, as did potassium. The minimum levels reached were different at each watershed, and the concentrations remained significantly greater at Cross Creek through much of the year. The lowest concentration levels represented only 36% and 33% of the average litterfall concentrations at Cross Creek and Camp Branch respectively, showing that

magnesium was mobile and much was lost initially due to leaching, but that the relative losses were about the same at both watersheds.

Summary of Elements

Nutrient element mobility was similar at the two watersheds, following the order $K > Mg > Ca > S > N > P$. This ranking generally corresponds with mobility series reported by several authors (Gosz et al., 1973; Lemee and Bichaut, 1975; Rapp, 1971; Toth et al., 1975), but differs slightly from others (Attiwill, 1968; Best and Monk, 1975; Lousier and Parkinson, 1978; MacLean and Wein, 1978).

Cross Creek litterfall contained higher concentrations of all nutrient elements, which resulted in differences in element loss rates and immobilization processes for nitrogen, sulfur, and phosphorus between the watersheds. For all three elements, Cross Creek initially lost moderate amounts through leaching and mineralization, whereas Camp Branch began accumulating these nutrients through immobilization. These differences resulted in Camp Branch retaining significantly higher concentrations of nitrogen and sulfur throughout the year. The importance of the initial litter element concentrations in influencing the rates and direction of decomposition was demonstrated. The difference appears to be caused by the higher atmospheric sulfur and nitrogen inputs at Cross Creek. It is not clear, however, whether the lower nitrogen and sulfur concentrations found in Cross Creek litter, despite its higher input levels, is an indication of a lower heterotroph requirement for the elements, a long term change in nutrient cycling processes, or a minor difference equalized by greater litter accumulation.

The loss rates of the cation nutrients were about the same at both watersheds, with calcium, magnesium, potassium, and sodium subjected to approximately the same degree of loss and retention despite greater litter concentrations of calcium and magnesium at Cross Creek. Reasons for this difference in litter concentrations remain unclear, but presumably developed from small differences in input and mobility exaggerated over many years.

V. INTERACTIONS AND RELATIONSHIPS BETWEEN DECOMPOSITION MEASURES

No one measure of decomposition can give an accurate portrayal of the complex decomposition processes operating in any ecosystem. The many different aspects of decomposition may be influenced and controlled by a wide variety of factors that are not the same for each component and therefore cannot be properly evaluated by one overall measure. Estimates such as decomposition rates are very helpful in evaluating and comparing decomposition with other systems, but by themselves give no indication of the size, structure, or mechanics of the microflora and fauna populations, or the actual rates of element cycling and mineral turnover. The various aspects of decomposition are closely interrelated, but in complex ways that are not always apparent. By measuring several different aspects of decomposition, a better understanding of the intricacies and interrelationships of the decomposition processes can be attained (Howard, 1972; Nannipieri et al., 1978).

Respiration measurements provided an indication of overall decomposition rate, while other aspects of decomposition measured provided information on a particular component of the overall process.

This served to expand and clarify the results of the respiration measurements and isolated important areas where differences in decomposition might occur.

Microbial population observations supported the respiration results, finding no differences between the watersheds. Arthropod populations, however, were an aspect of decomposition not adequately represented in respiration rates and significant differences between the watersheds were found. Litter nutrient concentrations also revealed significant differences between the watersheds regarding cycling processes of sulfur and nitrogen as well as differences in their litter concentrations.

Simple correlations between the various measures of decomposition (Table 9) point out some of their interactions and relationships. The controlling factor temperature was correlated to most of the decomposition measures, including respiration rate, fungal populations, and arthropod populations, but was not correlated with bacteria or collembola populations. Litter moisture was correlated only with fungal populations, but temperature-moisture interaction was significantly correlated to respiration, as well as fungi, Acarina, and total arthropod populations. Respiration rates were correlated with fungi, bacteria, and collembola populations. The multiple correlation accounting for the most variation in respiration rates included temperature, temperature-moisture interaction, fungal populations, and collembola populations as factors ($R^2 = .52$). It is apparent that other factors are involved in controlling respiration because only about 50% of its variability could be accounted for. The interaction of numerous

Table 9. Simple correlation coefficients between measures of decomposition and related factors.

	Moisture	CO ₂ Evolution	Fungi	Bacteria	Total Arthropods	Acarina	Collembola
Temperature	.088*	.399*	.054*	.000	.014*	.013*	.006
Moisture	---	.010	.009*	.005	.007	.008	.002
Temp.-Moisture	---	.173*	.021*	.001	.014	.010*	.009
CO ₂ Evolution		---	.110*	.009*	.006	.002	.011*
Fungi			---	.015*	.023*	.010	.043*
Bacteria				---	.008	.003	.007
Total Arthropods					---	.894*	.396*
Acarina						---	.146*
Collembola							---

* indicates correlation significant (p=.05).

environmental conditions are often important in influencing respiration rates (Kowalenko, 1978; Wilding et al., 1975).

Fungi and bacteria were correlated with each other, but showed differences in their correlation to other factors. Bacterial and fungal populations are known to show distinct differences in their response to certain moisture levels as well as having antagonistic effects on each other (Rahno et al., 1978; Shields et al., 1973). All groups of arthropod populations were correlated with each other demonstrating that many of the same factors influence all of the organisms to some degree.

The microflora and soil fauna are themselves very closely related with each other and governed by many of the same controlling factors. The distribution of soil invertebrates and microorganisms in different soil layers are often similar. Collembola as well as Oribatid mites feed mainly on fungi in the litter, even though litter is also ingested (Edwards et al., 1973). Collembola have been shown to have a large effect on the size and species makeup of fungal populations even with relatively low rates of selective grazing (Hanlon and Anderson, 1979; Parkinson and Visser, 1980). Collembola populations at the two watersheds were negatively correlated with fungal populations. Increases in Collembola numbers were generally made at the expense of the fungal populations. McBrayer et al. (1974) observed fungivores to comprise 50 to 62% of the total arthropod populations, and found them to be correlated with the standing crop of fungi.

Although correlations between litter nutrient concentration levels and the other measures of decomposition were not made, it is

known that they too are closely interrelated. Microbial populations have much influence and control, both quantitatively and qualitatively, over the nutrient status of the litter. Microorganisms determine the nutrient requirements and critical element to element ratios dictating the mineralization and immobilization processes. Some element release rates are controlled by dry matter loss or CO_2 evolution rates, as observed for phosphorus and calcium in this study, while others are controlled more by microbial mineralization and immobilization processes. Invertebrate populations may also be closely related to element release and especially important in the transfer of particular elements, such as phosphorus (McKerker et al., 1979). Individual changes in litter element concentrations suggest associations between nitrogen and sulfur flux, as well as between potassium and magnesium concentrations. These similarities are due to the similar chemistry, organism requirements, and overall reactions of these elements.

Direct comparisons between the various decomposition measures are not possible because they represent different aspects of decomposition. Even though the respiration rates and microbial population estimates indicated that there are no differences in decomposition between the watersheds, while arthropod populations and litter nutrient concentrations show that there are differences, there is no contradiction because they measure different things. It demonstrates the importance of monitoring several different aspects because changes in one component may or may not be reflected in other areas. If respiration rate alone would have been measured, the differences in arthropod populations and nutrient status would not have been discovered. Even

if these differences do not drastically alter the overall rate of decomposition, they may be important. The lower arthropod numbers at Cross Creek may indeed be closely related to the lower sulfur and nitrogen litter concentrations and changes in loss and retention observed there, but the relationship may be too complex to determine. Only through the observation of all of these aspects of decomposition can the complex process of decomposition even begin to be evaluated. Each component contributes to the overall functioning of decomposition, but is also interdependent on and interacts with several other components.

CHAPTER V

SUMMARY AND CONCLUSIONS

Litter decomposition was compared at two similar deciduous forested watersheds whose main difference lies in their distance from sources of anthropogenic sulfur and thus receive different levels of sulfur inputs. Decomposition was estimated at the two watersheds through the measurement of the following decomposition parameters over one year: (1) forest floor CO_2 evolution, (2) litter bacterial and fungal populations, (3) litter and soil microarthropod populations, and (4) litter nutrient element concentrations. With additional data from a laboratory experiment in which microcosms taken from the forest floor were exposed to different levels of sulfur inputs and their respiration rate measured over time, the role of sulfur inputs in influencing decomposition processes was investigated.

The controlled microcosm study was necessary to determine whether sulfur inputs have a direct effect on decomposition. The laboratory environment and regulated sulfur inputs excluded many of the numerous variables and factors operating in the field which made it difficult to attribute observed differences to sulfur inputs.

The average respiration rate of the forest floors at the watersheds were about equal, $4.84 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ or $1766 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Camp Branch and $4.90 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ or $1789 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at Cross Creek. There were, however, significant differences between the two watersheds at different times of the year. Cross Creek evolved generally greater amounts of CO_2 in the spring, fall, and winter, while Camp

Branch showed higher respiration rates during the summer. The seasonal difference was attributed to the interaction of summer drought and other environmental conditions. Overall, Cross Creek has slightly higher respiration, due to slightly higher temperature and moisture conditions, larger litterfall inputs, and greater root respiration. Root respiration on the two watersheds was estimated to account for about 60% of the annual CO_2 output at Camp Branch and about 65% at Cross Creek.

Fractional loss rates (k) for the watersheds were estimated at .35 for Camp Branch and .39 for Cross Creek based on litter accumulation and litterfall inputs. Litter decomposition contributed about 31.5% of the total forest floor CO_2 output at Camp Branch and 35% at Cross Creek.

There were no differences found between microcosms taken from the two different watersheds or from sites within each watershed regarding physical characteristics, respiration rates, or sulfur treatment response. Thus there were no inherent differences in organism activity or adaptation resulting from the differential sulfur input at the two watersheds.

High sulfur levels were found to reduce respiration rates in the microcosms, indicating that high sulfur levels can over a period of time reduce decomposition. Initial sulfur additions from low to high levels caused a temporary stimulation of respiration, but low to moderate sulfur inputs produced no lasting effects.

Microbial populations, both bacterial and fungal, were equivalent at both watersheds throughout the year, with no significant differences observed at any time. The bacteria populations averaged

95.7×10^6 per gram dry weight litter at Camp Branch and 100.7×10^6 per gram at Cross Creek. Fungi counts averaged 24.1×10^6 and 22.8×10^6 per gram at Camp Branch and Cross Creek respectively.

Total numbers of arthropods were consistently greater at Camp Branch watershed. The mean annual arthropod population at Camp Branch was 34% greater than the Cross Creek average, at 46,200 and 34,400 organisms $\cdot m^{-2}$ respectively. The biggest difference was accounted for by the Acarina or mites, with Camp Branch averaging a 59% greater mite population than Cross Creek (33,100 and 20,800 organisms $\cdot m^{-2}$ respectively). Collembola populations were not significantly different, with an average population of 9,000 organisms $\cdot m^{-2}$ at Camp Branch and 9,700 organisms $\cdot m^{-2}$ at Cross Creek.

Initial litterfall nutrient concentrations were higher at Cross Creek for all elements. Cross Creek litter calcium and magnesium concentrations were significantly greater than at Camp Branch. Litter sulfur and nitrogen concentrations, however, were significantly greater at Camp Branch. Concentrations of phosphorus, potassium, and sodium were approximately equal at both watersheds.

Nutrient element mobility was similar at both watersheds and followed the order $K > Mg > Ca > S > N \geq P$. The loss rates of the cation nutrient elements, potassium, magnesium, calcium, and sodium, were about the same at both watersheds, undergoing leaching losses initially following litterfall, and then potassium and magnesium was slowly accumulated, while calcium and sodium loss corresponded with litter weight loss. The loss rates for nitrogen, sulfur, and phosphorus, however, were quite different at each watershed. Initially after litterfall, Cross

Creek lost moderate amounts of all three elements through leaching and mineralization, whereas Camp Branch began accumulating these nutrients. These differences in initial cycling processes appeared to be stimulated by the differences in initial litterfall concentrations, which in turn reflect the differences in atmospheric element inputs. After the initial differences, loss rates became approximately equal at both watersheds, but Camp Branch retained significantly higher sulfur and nitrogen concentrations. Total litter nutrient mass, however, was greater at Cross Creek for all elements because of the greater litter accumulation at that watershed. Atmospheric inputs of sulfur and nitrogen did affect the cycling processes of those elements, but the ultimate effects of the changes remain unclear.

Overall, decomposition at the two watersheds was very similar, having comparable microbial populations, litter respiration rates, litter weight loss, and for many elements similar litter nutrient status. The microcosm experiment demonstrated that sulfur inputs can have an inhibitory effect on decomposition when at high enough levels. However, low to moderate levels, as are presently being deposited at the two watersheds, did not produce any lasting effects on decomposition. The only large difference between the watersheds were in the arthropod populations and initial element loss rates and litter concentrations of sulfur and nitrogen. Even these differences do not appear to have a recognizable effect on the overall decomposition or nutrient turnover rate of the two watersheds.

The importance of sulfur inputs on decomposition and mineralization processes has nonetheless been demonstrated, for large inputs

were shown to influence decomposition. Even at the levels observed at the watersheds, sulfur inputs influenced litter nutrient status and element loss rates, and possibly soil arthropod numbers, although no overall change in decomposition rate was observed. Overall decomposition rate and processes appear to be relatively stable and resistant to sulfur changes, while mineralization and nutrient cycling processes seem to be most readily affected by changes in sulfur inputs. This indicates that sulfur inputs (and possibly other atmospheric inputs) are factors which should be taken into consideration in areas of sizable anthropogenic input, for they may be of notable influence on decomposition. Further research is necessary to determine the precise role and mechanism of sulfur inputs in influencing decomposition rates. In any event, the changes brought about by the differences in sulfur inputs at these two watersheds appear to be minor and at present do not represent any major disturbance or unnatural stress to the overall decomposition and nutrient cycling processes operating there.

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