AN ABSTRACT OF THE THESIS OF

Michael John Phillips for the degree of Master of Science

in Soil Science presented on December 4, 1975

Title: COMPARATIVE RATES OF CO_2 PRODUCTION FROM THE FOREST FLOOR IN THE DOUGLAS-FIR ECOSYSTEM

Abstract approved: Redacted for Privacy

Chester T. Youngberg

To obtain data on the decomposition of the forest floor, a battery operated electrolytic respirometer was developed making it possible to measure CO_2 evolution from field moist forest floor samples in situ independent of root respiration. Banks of four respirometers powered by two 12-volt batteries were installed in three old growth Douglas-fir-hemlock stands, two clearcuts, and one clearcut that had been broadcast burned. All sites were located on or immediately adjacent to the H.J. Andrews Experimental Forest located in the western Cascades near Blue River, Oregon.

Seasonal and yearly totals of mineralized carbon were similar for the three habitat types. First year totals for the Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa association (RS 2), the Tsuga heterophylla/Castanopsis chrysophylla association (RS 6) and the Tsuga heterophylla/Polystichum munitum-Oxalis oregana association (RS 7) were 77.36, 75.67, and 78.86 mg C/g

litter. Spring and fall mineralization accounted for approximately 62% of this total on all three reference stands. The lowest rates occurred during the winter months. Carbon mineralization rates for the second fall of the study were similar to those of the first year. However, carbon mineralization during the second winter of the study increased unexpectedly by 88%, 123% and 142% for reference stands 2, 6 and 7, respectively. Presumably, this was due to warmer temperatures during the second winter.

Clearcutting enhanced the rate of carbon mineralization, the magnitude of the effect being greater on the older clearcut. On the 4-year-old clearcuts (plots 29 and 36), yearly totals averaged 102.97 mg C/g litter. On the 3-year-old clearcut (RS 33), total carbon mineralization was 89.49 mg C/g litter. Part of the variation was probably related to elevational effects on temperature, RS 33 being located 330 meters higher than the other clearcut. But it is also possible that the greater reestablishment of vegetation on the older clearcut could have contributed a higher proportion of fresh litter to the residual forest floor.

Clearcutting followed by broadcast burning decreased the rate of carbon mineralization. Plots were established on the site one month following a light burn. The yearly totals for carbon mineralization averaged 64.62 mg C/g litter, or 59% less than on the older

clearcut (29 and 36). Nitrogen levels remained relatively high, and there appeared to be an increase in the lignin fraction of the litter.

Decomposition was significantly correlated with litter moisture content or litter temperature on a seasonal basis. In general, litter moisture content was the dominant factor during the summer and fall months. Litter temperature was the dominant factor in the winter and spring months when statistically significant correlations could be obtained. Inadequate means of estimating litter temperature under snowpack may be the reason for fewer significant correlations during these periods.

Comparative Rates of CO_2 Production from the Forest Floor in the Douglas-fir Ecosystem

by

Michael John Phillips

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed December 1975

Commencement June 1976

APPROVED:

Redacted for Privacy

Professor of Forest Soils
in charge of major

Redacted for Privacy

Head of Department of Soil Science

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 4, 1975

Typed by Mary Jo Stratton for Michael John Phillips

ACKNOWLEDGEMENT

I thank my major advisor, Dr. Chester T. Youngberg, for his guidance and encouragement during my master's program. I thank Dr. Lowell Young for serving as my second major professor and Dr. William Ferrell for serving as my minor professor.

I thank Dr. Kermit Cromack and Dr. Robert Fogel for their collaboration in mutual areas of interest originating from this study.

I am grateful to Dr. Richard H. Waring and the Oregon segment of the Western Coniferous Forest Biome for their funding and cooperation accorded me during this study. Thanks are expressed to Al Brown and Gary Lumberg for their many hours of patient assistance in helping to prepare the computer program for my study. I thank Susan Phillips and Mrs. F. Glenn at the Forest Sciences Laboratory at Oregon State University for their help in the analysis of my samples.

I thank Dr. C.M. Gilmour and his colleagues in the Department of Bacteriology and Biochemistry at the University of Idaho for their assistance with the laboratory decomposition studies.

Thanks are extended to Dave McNabb and Susan Warner for their contributions to certain aspects of this study and the pleasure of their company during my own laboratory investigations.

Special thanks are extended to Marjory Meconis for her continuous encouragement and assistance throughout this investigation. I

am greateful to Linda Serbus for her help in the final preparation of this thesis.

Support for this project came from a National Science Foundation grant to the Coniferous Forest Biome, Ecosystem Analysis Studies, U.S. /International Biological Program.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF APPENDIX TABLES

LIST OF FIGURES

COMPARATIVE RATES OF CO_2 PRODUCTION FROM THE FOREST FLOOR IN THE DOUGLAS-FIR ECOSYSTEM

INTRODUCTION

Decomposition of forest litter is a multi-variable process involving complex interactions among physical, chemical and biological factors. The evolution of CO_2 is generally considered the best single index for quantifying this interrelationship. The ability to accurately measure CO_2 production would contribute substantially to furthering knowledge in the areas of carbon and energy flows and nutrient cycling processes in the ecosystem.

The biodegradation of forest litter is a function of all heterotrophs (Alexander, 1961). As much as 90% of the litter decomposition can be attributed to microbial activity (Macfadyn, 1963; Odum, 1971 from a review by Cromack, 1973). Microorganisms obtain energy for growth by degrading organic matter through secretion of extracellular enzymes.

Temperature and moisture are the major abiotic factors governing decomposition. These factors exert a quantitative effect on decomposition by influencing the types and numbers of microorganisms and the activity of these organisms. Temperature affects the rate at which the litter is decomposed. Respiration rates increase logarithmically with the rate doubling for each $10^{\circ}C$ increase in

temperature (Wiant, 1967b). Moisture generally limits decomposition when it is either low enough to depress decomposer activity or high enough to prevent air movement and cause a deficiency of O_2. In areas where moisture is rarely limiting, temperature is the dominant factor determining decomposition rates (Edwards, 1975). Studies dealing with the effects of drying and rewetting on decomposition rates (Birch, 1958; Sorensen, 1974) indicate that moisture as well as temperature becomes a dominant factor in areas subject to wet and dry seasons.

Potential decomposition is related to the quality of the substrate. Many investigators have used various chemical components of the litter layer to predict the rate and extent of decomposition (Hu et al., 1972; Cromack, 1973; Platt, 1973). Initial decomposition is rapid due to the presence of soluble labile carbon. Platt (1973) considered the determination of the levels of persulfate oxidizable carbon present in the litter fraction to be a rapid and accurate method for predicting the initial rates of decomposition. Cromack (1973) considered initial lignin content to be an excellent indicator of the potential decomposability of the organic matter over time.

Objectives

There were three main objectives in this study. One was to quantify seasonal and yearly totals of CO_2 production under field

conditions from the forest floor of three old growth forest communities. The second objective was to measure the effect of clearcutting and clearcutting followed by broadcast burning on CO_2 production. The third major objective was to determine which of the measured abiotic factors (temperature and moisture) were significantly influencing carbon mineralization rates on a seasonal basis. All study sites were located on or immediately adjacent to the H. J. Andrews Experimental Forest located near Blue River, Oregon.

REVIEW OF LITERATURE

Carbon is the most vital single element in nature and serves as the foundation for cell structure. Plant and microorganisms contain from 40 to 50% carbon on a dry weight basis. The ultimate source of this carbon is carbon dioxide derived from the earth's atmosphere. But CO_2 constitutes only 0.03% of the earth's atmosphere and must be continually recycled in order to maintain adequate levels of an element that would otherwise become unavailable for use.

This carbon cycle involves the movement of carbon from the inorganic to the organic form and then back to the inorganic state. Carbon dioxide is absorbed and incorporated into plant and microbial tissue. Eventually, most of the carbon is returned to the atmosphere through two processes: (1) by microbial and plant respiration, and (2) by the biological oxidation of organic matter to CO_2 via heterotrophic microorganisms. Carbon mineralization has been studied in detail, and the results of previous investigations will be discussed in the following review.

The Forest Floor

Accumulations of organic matter on the soil surface are a characteristic feature of forest soils, and the composite forest floor has been subdivided into several layers (Hoover and Lunt, 1952).

(1) Litter layer (L): the surface layer of the forest floor consisting of freshly fallen leaves, needles, twigs, stems, bark and fruits.

(2) Fermentation layer (F): a layer of partially decomposed litter still recognizable as to origin.

(3) Humus layer (H): a layer consisting of well decomposed organic matter unrecognizable as to origin.

The quantity of organic matter accumulated at a given site is governed by the additions of litter and the subsequent decomposition of that litter. These two processes constitute the major pathway by which nutrients are recycled in terrestrial ecosystems. Litter biomass is highly variable; its production based on the predominate influence of climate is summarized by Bray and Gorham (1964). Arctic-Alpine forests, Cool and Warm Temperate forests, and Equatorial forests produce an average of 1, 3.5, 5.5, and 11 metric tons of litter per hectare per year respectively.

Annual litter production is a composite of several components, the most important of which is leaf litter. Based on worldwide data, leaf litter averages 69-73% of total litter production, but varies between and within climatic regions (Bray and Gorham, 1964). Abee and Lavender (1972) found average annual litterfall production in the western Cascades to be approximately 1 1/2 times that reported by

Bray and Gorham (1964) for Cool Temperature regions. Leaf litter contributed only 53% to the total litterfall.

Decomposition is the antithesis of litter production. When litter reaches the forest floor, it undergoes alteration through physical, chemical and biological processes, and eventually the litter is transformed into humus. Hoover and Lunt (1952) developed a key for the classification of forest humus types based on the morphology and distribution of the H layer. Three general types were recognized:

(1) Mull: There is no H layer; the A1 horizon is an intimate mixture of organic matter and mineral soil, with a gradual transition between the A1 and the horizon beneath. The F layer may or may not be present.

(2) Mor: There is an H layer present and practically no mixing of the organic matter with the mineral soil. The transition from the surface organic matter to the mineral soil is abrupt.

(3) Duff mull: F and H layers are present with an underlying A1 horizon essentially similar to that of a true mull. There is a gradual transition from the H layer to the A1 and mineral soil beneath. This type possesses some of the characteristics of both mulls and mors.

Mull humus is generally associated with hardwoods and some conifers while mor humus is usually found under coniferous species. While both humus types show wide variation in their morphology,

different humus types maintain certain physical and chemical properties over wide geographical areas (Mader, 1953). The mor type is more acidic than mull and is also characterized by a higher content of total nitrogen and a lower content of ash.

Divergent opinions have existed as to the major factors responsible for the development of humus types. Romell and Heiberg (1935) felt that the type of humus formed was determined by the kind of microorganism involved in decomposition, with fungi being predominant in mor. This concept assumes that the type of humus formed is independent of the rate and amount of decomposition and is determined solely by the kinds of microorganisms involved. Broadfoot and Pierre (1939) felt that the formation of humus could be partially explained on the basis of the chemical composition of the litter components. Utilizing a wide variety of tree species, decomposition was correlated with a number of independent variables. During the first two months, total nitrogen and content of water soluble organic matter exerted the greatest influence on decomposition. Thereafter, the amount of excess base determined the extent of decomposition.

Nitrate formation was found to occur in deciduous leaf litter mixtures but was virtually absent in coniferous needle mixtures (Ivarson and Sowden, 1959). The authors felt that the higher decomposition rate of deciduous litter was in part due to the greater content of total nitrogen. Mor types were also thought to provide less

favorable conditions for nitrification because of increased acidity and toxic concentrations of terpenes, resins and tannins. When antifungal antibiotics were applied to the coniferous litter mixture, bacterial populations increased, but decomposition rates remained at low levels. This suggests that the type of litter is more important in determining decomposition rates than the kinds of microorganisms that are present.

The type of humus formed is an indicator of the time required for carbonaceous material to be mineralized. Formation of mull humus is associated with a more rapid rate of decomposition and a smaller accumulation of organic matter on the forest floor (Metz, 1954; Ovington, 1954; Kendrick, 1959; Bocock et al., 1960; Gilbert and Bocock, 1960; Witkamp and Van Der Drift, 1961; Bocock, 1964). Ovington (1954) reported forest floor weights under conifers to be 3 to 4 times those developed under hardwoods. Under Scot's pine in England, it takes about 10 years for fresh needles to be transformed to humus, with the needles spending 6 months in the L layer, 2 years in the F1 layer and approximately 7 years in the F2 layer (Kendrick, 1959). This suggests the formation of mor humus.

Differential rates of decomposition of the same leaf species exemplify the influence of different humus types. Bocock et al. (1964) measured dry weight losses of oak and ash leaf litters on moder (similar to duff mull) and mull humus types. Oak leaves disappeared

very slowly on both sites while the highest rates of dry matter loss in ash litter occurred on the mull site. For the first 3 months, dry matter losses were about the same on both sites due to higher content of water soluble compounds. Afterwards, rapid losses were observed on the mull site. This was attributed to the greater activity of large litter feeding invertebrates, particularly the earthworm.

The assertion that macrofaunal activity exerts a major influence on litter removal and breakdown on mull sites was borne out by chemical analysis (Gilbert and Bocock, 1960). Utilizing ash litter in nylon hair nets on a mull site, dry weight changes during the first month were influenced predominantly by the content of water soluble material. Thereafter, the carbon to nitrogen ratio varied little, suggesting that nitrogen and dry weight losses were about the same. This indicates that the litter was removed indiscriminately and loss was not due to selective removal of specific chemical component. Bocock (1964) reported that dry weight losses of ash litter were approximately the same on mull and moder sites when the litter on the mull site was protected from the large litter feeding invertebrates by use of fine mesh bags.

Witkamp and Van Der Drift (1961) compared litter production and breakdown of various species on mull and mor forest humus types. The amount of litter falling to the forest floor varied little between sites. However, evolution of CO_2 was consistently higher in

the mull than in the mor as was the activity of the large litter feeding organisms. By measuring the loss in dry weight of litter from the previous year, the authors found that only 20% remained on the mull site while 70% remained on the mor site.

Breakdown of organic debris and the formation of humus is influenced not only by leaf species, but also by factors of climate and soil (Kendrick, 1959). Wilde et al. (1937) felt that classification of organic remains of upland forests in the Lake States was useless unless account was taken of the characteristics of the underlying mineral soil, reaction and ground water level. Jenny et al. (1949, 1950) compared accumulation of organic matter in tropical and temperate soils. Tropical sites produce 800-3,000 pounds per acre per year. To test decomposition rates, weight losses were measured on the different sites. Nitrogen fixation and decomposition of litter are highest in the humid tropical and subtropical climates (Jenny et al., 1949). However, the decomposition of humus in tropical soils is much slower which allows for greater accumulations of organic matter in the mineral soil. In contrast, soil organic matter accumulations in the soils of the Sierras is inhibited by low rates of nitrogen gains due to unfavorable weather conditions. With low levels of litter production and slow rates of decomposition, a large portion of organic matter rests on the mineral soils with little incorporation (Jenny, 1950).

Schulze (1967) did a comparative study of organic matter accumulation and soil respiration rates for various vegetation types in Costa Rica. The vegetation types included a savanna, a tropical deciduous dry forest, and a young secondary growth vegetation. Lowest respiration rates were in the savanna and the dry deciduous forest (300 to 400 mg CO_2/m^2/hour), and the highest rates were in the secondary growth (2,000 mg CO_2/m^2/hour). Due to the warmer temperature, sufficiency of moisture, and the presence of little or no undecomposed litter on the forest floor of the gallery forest, the author concluded that decomposing soil organisms are limited by the amount of litter falling to the forest floor. In the continuously warm and tropically wet areas, soil respiration rates were estimated to be 5 times greater than the mean temperate European rates.

Physical Factors Affecting Decomposition

Accumulation and breakdown of forest litter is affected by a combination of interdependent factors and processes which include respiration, organism activity, leaching, temperature, moisture, comminution losses, physical removal and additions of materials, litter quality and its physical state, and time (Heal and French, 1974). Temperature and moisture comprise the major abiotic factors governing decomposition, but the magnitude of the effect will vary within forest ecosystems and between different ecosystems (Edwards, 1975).

These factors exert a quantitative effect on decomposition by influencing the types and numbers of organisms and the activity of these organisms in the decomposition process (Witkamp and Van Der Drift, 1961).

The influence of temperature on decomposition is well documented. Under normal field temperatures (20°-40°C) in temperate areas, soil respiration rates increase logarithmically with the rate doubling for each 10°C increase (Q_{10}=2) in temperature (Wiant, 1967b). Witkamp (1969) felt that carbon mineralization rates, based on CO_2 evolution from the forest floor at a given temperature and daily cycle of temperature, were unreliable unless the proper Q_{10} was available.

Working in a mixed deciduous forest in Tennessee, Edwards (1975) reported a significant correlation between litter temperature and total forest floor CO_2 evolution rates. Ninety-four percent of the variability in total CO_2 evolution was accounted for by this relationship. Reiners (1968) found CO_2 evolution to parallel soil temperatures. Working with various ecosystems, CO_2 evolution rates in spring and early summer were greatest in the swamp, followed by fen and oak stands. This ranking paralleled soil temperatures. Working with coniferous forests in Finland, Mikola (1960) reported litter decomposition rates to be 40% higher in southern compared to northern forests. The rate of decomposition increased proportionally to the mean summer temperature. Platt (1973), using litter collected from

the H. J. Andrews Experimental Forest in the western Cascades, found CO_2 evolution to be 38% higher at 26°C than at 14°C. Oxygen consumption was 40% higher over the same temperature range. This close agreement indicates that respiration and synthesis rates of microorganisms are similar.

Temperature affects the rate at which the chemical constituents of litter are decomposed. Waksman and Gerretsen (1931), working with oat straw maintained at a constant moisture content of 80%, showed that certain chemical components (e.g. hemicellulose, cellulose, lignin) disappeared more rapidly at higher temperatures. After 48 days at 37°C, 50% of the hemicelluloses and 74% of the cellulose had decomposed. For lignins, 50 to 60% had disappeared in 9 months. But at 7°C, little or no decomposition of these compounds occurred.

A number of studies have demonstrated the influence of seasonal and daily fluctuations in temperature on decomposition of forest litter (Douglas and Tedrow, 1959; Witkamp and Van Der Drift, 1961; Witkamp, 1966b; Ellis, 1969; Garrett and Cox, 1973; Heal and French, 1974; Jager and Bruins, 1975; Rosswall, 1974; Edwards, 1975). Edwards (1975) found a significant relationship ($P < 0.001$) between mean daily litter temperature and mean daily total forest floor CO_2 evolution rates. In temperate regions, changes in respiration rates in the winter are controlled primarily by temperature (Ellis, 1969). Seasonal changes in temperature and moisture are reflected in the

populations and activity of microorganisms. Increasing temperature and moisture lead to increased populations and activities of microorganisms and a resultant increase in CO_2 production (Witkamp and Van Der Drift, 1961). Comparison of several studies in tundra ecosystems (Heal and French, 1974) suggested little relationship between dry weight loss of litter and broad seasonal patterns. Short term climatic factors such as drought are more important than general seasonal trends. CO_2 evolution is also affected by daily fluctuations in temperature, a direct consequence of the temperature dependent metabolism of microorganisms (Witkamp, 1969). The author found maximum CO_2 production to occur in midafternoon and minimum production to occur before dawn.

The assumption that increased temperature will result in accelerated rates of decomposition is not valid for every species of litter. Daubenmire and Prusso (1963) found that leaf litter of Abies lasiocarpa [(Hook.) Nutt.] and Pseudotsuga menziesii [(Mirb.) Franco] decomposed more rapidly at 10°C than at 25°C. Apparently, the higher fungi that developed at the lower temperature were able to utilize the substrate more effectively than the organisms dominant at the higher temperature. The authors concluded that the ranking of the litter species according to their decomposability should be done at the optimum temperature for the individual species.

Decomposition rates are inversely proportional to moisture tension and directly proportional to moisture content below saturated conditions (Bartholomew and Norman, 1946). Moisture limits decomposition rates when it is either low enough to depress litter organism activity or high enough to reduce air movement and cause a deficiency of O_2. In general, respiration rates of soil microflora are greatest at 60 to 80% of the water-holding capacity (WHC) of the soil (Alexander, 1961). Platt (1973) observed that CO_2 production in one week at 18% WHC of the litter was 60% of the CO_2 production at 68% WHC. At 98% WHC, CO_2 evolution was 59% of the production at 68% WHC. The threshold moisture content (TMC) for active decomposition varies between species. For pine needles, the TMC is 15 to 17% (Bartholomew and Norman, 1946). Above the threshold moisture content, decomposition rates do not increase linearly with increased moisture contents. Bartholomew and Norman (1946) found that increasing moisture content from 60 to 150% produced a 50% increase in CO_2 evolution. A further increase to 250% resulted in only another 10 to 15% increase in CO_2 production.

At times, the influence of moisture may be more real than apparent. In some areas moisture is usually not limiting (Edwards, 1975) or else its effect is obscured because of the predominating influence of temperature (Douglas and Tedrow, 1959; Witkamp, 1966a; Reiners, 1968; Garrett and Cox, 1973). In Missouri, highest

moisture content occurs in early spring and winter, but the greater availability of moisture is offset by low temperature (Garrett and Cox, 1973). Douglas and Tedrow (1959), working with different arctic soils, found moisture content to be a more important factor at higher temperatures. As temperatures dropped, the differences in moisture content had less effect on decomposition than at higher temperatures. Heal and French (1974) reported that dry weight losses increased approximately 20% per 1000 ^{o}days above 0 ^{o}C at optimum moisture conditions (400% of dry weight).

Perhaps the influence of moisture can best be viewed from the results of experiments dealing with the effects of drying and wetting on production of CO_2. Drying and rewetting causes an increase in carbon mineralization rates. Sorenson (1974), working with labeled cellulose incubated in various soils, reported that after 284 days, drying and rewetting increased cellulose decomposition by 121% over the controls that were kept continually moist. However, when the incubation period was extended to 510 days, only 33% more labeled carbon had evolved from cellulose subjected to the drying and rewetting treatment than in the controls kept continually moist. So the effect of drying-rewetting treatment is decreased over time. Birch (1958) concluded that the decline was due to a decrease in microbial activity and not to substrate exhaustion.

Drying humus material results in chemical, physical and biological changes. Stevenson (1957) reported that drying caused a release of amino acids from humic material. The surface area of organic colloids is increased allowing for greater exposure to microbial attack (Birch, 1958). Drying also decreases the number of viable organisms present (Stevenson, 1957). Upon rewetting, organic material goes into solution and the magnitude of decomposition depends on the percentage of carbon in the soil (Birch, 1959) and on the amount of easily decomposable, water-soluble substances (Jager and Bruins, 1975). During the early stages after remoistening, there is a rapid increase in the metabolic activity of microorganisms characterized by high oxygen uptake, maximum enzyme activity, CO_2 and ammonia production (Birch, 1958).

Drying-rewetting cycles under field conditions have ecological implications. Reiners (1968) reported that peaks in CO_2 production during the summer occurred after rainfall. Birch (1958) suggested that sites characterized by drying-rewetting cycles would have greater cumulative carbon mineralization rates than sites subjected to periods of prolonged drying or wetting. He also suggested that areas with low rainfall, above a certain minimum, would have greater carbon mineralization rates due to the greater frequency of drying-rewetting cycles. Several authors have also found these cycles to increase nitrogen mineralization rates (Birch, 1958; Birch, 1959;

Jager and Bruins, 1975). Birch (1958) reported that each cycle resulted in an increase of 20 ppm nitrate nitrogen.

Chemical Factors Affecting Decomposition

Van Cleve (1974) recognizes two types of substrate quality. Primary substrate quality is the "physical, chemical and biological properties of the soil and its associated organic matter layers or the potential of the soil to decompose introduced organic matter." The primary type will influence the rate of decomposition. Secondary substrate quality is defined as the "physical and chemical properties or potential decomposability of organic matter periodically introduced upon or within the soil profile." This section of the review will be concerned with the chemical properties of litter and its effects on both the quantitative and qualitative aspects of decomposition.

Plant material that reaches the forest floor consists of a heterogeneous mixture of chemical substances. Alexander (1961) classified these into several broad categories.

(1) cellulose 15-60%
(2) hemicellulose 10-30%
(3) lignin 5-30%
(4) water-soluble fraction 5-30%
(e.g., simple sugar, amino acids, aliphatic acids)
(5) ether and alcohol-soluble fraction . .
(6) proteins . . . . . .
(7) ash 1-13%

These various chemical constituents supply microorganisms with energy for growth and carbon for the formation of new cell material. The differential rate at which each of these compounds is degraded leads to a change in the relative proportions of each over time (Starkey, 1924; Alexander, 1961; Minderman, 1968; Van Cleve, 1974).

Carbon to nitrogen ratios are useful indicators of the rates of decomposition. Narrower C:N ratios reflect higher amounts of readily metabolized substances and, therefore, greater rates of decomposition (Pinck et al., 1950; Alexander, 1961; Van Cleve, 1974). Sowden and Ivarson (1962) reported C:N ratios to be lower in hardwood litter soil mixtures than in coniferous mixtures. In an investigation by Jorgenson and Wells (1973), 84% of the variability in respiration in the mineral soil of pine stands was explained by C, N and Ca content. The C:N ratio accounted for 60% of the variation. Pinck et al. (1950) reported that significant loss of gaseous forms of nitrogen occurred when C:N ratios were 3 to 15. No significant loss occurred when C:N ratios were 18 and above. Coile (1937) found little correlation between C:N ratios and decomposition. For white oak, the high silica, tannin and lignin contents and low calcium contents offset the advantage of a low C:N ratio.

Oxygen supply, pH, available minerals and composition of the substrate influence decay processes. Nykvist (1959b) found that decomposition during anaerobic leaching was reduced to one half that

obtained during aerobic leaching. This agreed favorably with the results reported by Reddy and Patrick (1975).

The acidity of plant materials governs the type of microorganisms present in any ecosystem. A direct relationship exists between pH and bacterial populations during different stages of decomposition. In one study (Marten and Pohlman, 1942), bacterial numbers increased rapidly in several hardwood and conifer species as the pH rose during the first week of decomposition. The rise in pH depends on the air supply and the content of water-soluble substances (Nykvist, 1959a). Over a period of 42 days, the pH of the litter extract of Fraxinus excelsior increased from 5.6 to 9.1 under aerobic conditions. No appreciable change in pH occurred under anaerobic conditions. Sjors (1959) also reported an increase in the pH in 11 of 12 deciduous litter species. Gustafson (1943) found dry weight losses in pine and oaks to be greatest when both species were mixed than when separated. Apparently the acid reaction of the pine needles neutralized the high calcium content in the oak. Conditions were then favorable for the proliferation of both fungal and bacterial species, and the two together could decompose more material than either alone.

In order to understand the decomposition process for any site, it is important to know the behavior of the separate chemical constituents of the litter over time. Each component in pure form should follow an exponential decay curve while whole litter will be

represented by a number of different curves, each representing a different chemical constituent (Minderman, 1968). Over time, decomposition results in an increase of the more resistant compounds and a reduction in the overall availability of carbon as an energy source (Jorgenson and Wells, 1973).

The water-soluble components of litter are the least resistant to attack, and hence, are the first constituent to be metabolized by microorganisms (Marten and Pohlman, 1942; Alexander, 1961). Marten (1942) reported that the water-soluble portion of the organic matter was utilized most vigorously during the early stages of decomposition, regardless of the type of flora involved. Broadfoot and Pierre (1939), working with a variety of litter species, obtained a coefficient of correlation of 0.619 between water-soluble organic matter and decomposition during the first two months. Thereafter, the coefficient of correlation dropped to 0.334. A similar trend was reported for nitrogen. Hayes (1965) observed dry weight losses of up to 20% in coniferous needles over a 2 to 4 month period. Platt (1973) investigated carbon turnover rates in green and brown needles of Pinus ponderosa (Dougl. ex Loud.) and in forest floor litter samples from the H.J. Andrews Experimental Forest. In 9 months, only 20% of the carbon had been mineralized in the litter from the H.J. Andrews Experimental Forest. But after 8 weeks, 34% and 21% total carbon from the green and brown needles respectively, had been mineralized.

The author attributed this to the greater percentage of readily oxidizable carbon present in the green and brown needles.

Both Platt (1973) and Hu et al. (1972) considered the levels of readily oxidizable carbon to be a valid indicator of CO_2 evolution. Platt (1973) related 78% of the variation in respiration rates over a 6-day period to the persulfate oxidizable levels in the litter. Hu et al. (1972) reported that determination of soluble carbon was a valid measure of the state of decomposition and humification. The authors observed that levels of soluble carbon less than 12 mg/g of material indicated well decomposed and humified (H-layer) material; 12-20 mg/g of material indicated moderately decomposed and humified (F-layer) material; and greater than 20 mg/g of material indicated relatively undecomposed (L-layer) material.

As the easily soluble energy sources are metabolized, the more resistant constituents (lignin, cellulose, hemicellulose and protein) accumulate (Pinck et al., 1950; Alexander, 1961). Cellulose and hemicellulose are more resistant to decomposition than water-soluble substances, but nevertheless, they are metabolized in a relatively short time (Waksman and Gerretsen, 1931). These authors reported that during 48 days of decomposition at temperatures between 18°C and 37°C, 50% of the hemicelluloses and 74% of the cellulose had disappeared. Sowden and Ivarson (1962) observed that after 3 years under field conditions, 75% of the cellulose in coniferous litter and

83% of the cellulose in deciduous litter had decomposed. This compares favorably with results reported by Minderman (1968). He observed a 55% loss of cellulose in one year in an oak forest floor, and the loss had increased to 80% after 2 to 3 years. Golley (1960) reported 90% decomposition of cellulose strips on broomsedge sites within 4 months.

The lignin component of litter is highly resistant to enzymatic degradation by microorganisms (Alexander, 1961). It is slowly metabolized and hinders the breakdown of other materials by interlinkage with hemicellulose and cellulose. In pure culture, the percentage of cellulose decomposed is inversely proportional to the lignin content (Alexander, 1961). Marten and Pohlman (1942) investigating the decomposition of the chemical components of hardwood and coniferous litter species, found that in all but red maple, decomposition of cellulose was approximately twice that of lignin. During the first 8 weeks, there was an apparent synthesis of lignin before decomposition began. Waksman and Gerretsen (1931) reported a doubling of the lignin content in oat straw after 105 days of decomposition. After 273 days, the residual humus formed had a small concentration of cellulose and hemicellulose while 75% was made up of modified lignins, proteins and ash. The change in components over time results in an increase in higher carbon containing compounds as cellulose (42-44% C) decreases and lignin (62-64% C) increases (Lunt, 1931).

The influence of lignin is such that several investigators considered it to be the best indicator of the potential decomposability of organic matter over time (Cromack, 1973; Van Cleve, 1974). Data from a number of tundra sites tended to show that slower rates of decomposition were associated with a higher initial percentage of lignin in the organic matter (Van Cleve, 1974). Cromack (1973) reported a better correlation between leaf decomposition rates and lignin content ($r = 0.953$, $p < 0.001$) than between percentage leaf decomposition and C:N ratio ($r = 0.892$, $p < 0.05$). He also found a significant relationship between percentage lignin content and leaf sclerophyll indices ($r = 0.84$, $p < 0.001$) and with leaf C:N ratios ($r = 0.725$, $p < 0.001$).

Certain plant substances have an inhibitory effect on microbial activity and carbon mineralization. Tannins and other free polyphenolic compounds may influence the palatability of freshly fallen litter if present in large enough quantities (Bocock, 1964). Handley (1961) reported that stabilized leaf proteins in mesophyll tissues are resistant to enzymatic degradation by microorganisms. He considered this to be a plausible reason for the formation of mor humus types. Mull types may be more favorable to nitrification due to the lack of terpenes, tannins, and resins formed in mor types under conifers (Ivarson and Sowden, 1959). Benoit and Starkey (1968) noted the inhibitory effect of tannins on degradation of cellulose and

hemicellulose, decomposition being reduced by 74% and 84% respectively. Lewis and Starkey (1968) suggested that the effect was due to the complexing of microbial enzymes involved in the initial hydrolysis of the compounds. Minyard and Driver (1972), working with Douglas-fir needles, hypothesized that during the initial stages of decomposition, fungi are required to break down the waxes on the surface of the needles before the cellular component can be acted upon.

Biological Role in Decomposition: Effect of Microorganisms

Soil organic matter is colonized by a wide variety of heterotrophic microorganisms. They obtain energy for growth by degrading various components of organic matter through secretion of extracellular enzymes. As much as 90% of litter decomposition can be attributed to microorganism activity (Macfadyn, 1963; Odum, 1971 from review by Cromack, 1973). The efficiency with which microorganisms convert substrate carbon into cellular material, however, varies greatly among microbial groups. Fungi assimilate 30 to 40% of the carbon mineralized to form new mycelium while aerobic bacteria utilize only 5 to 10% of the carbon for new cell formation (Waksman, 1929).

The composition of the microbial population in the forest floor and soil varies in response to changes in environmental parameters. Wicklow and Whittingham (1974) envisioned this distribution as a continuum. Utilizing ordination techniques, each horizon was found to consist of a characteristic microflora. Population densities were highest in the L and F layers, and the majority of the species were sporulating types. Numbers decreased in the underlying horizons due to the decrease of readily available nutrients. These authors concluded that the interaction of vegetation and edaphic factors caused a majority of species in each population to occur in only one or two sites.

Equilibrium between the major groups of organisms and among species will depend to a great extent upon nutritional requirements and antagonistic effects. Lockhead and Chase (1943) noted certain trends between nutritional requirements of bacteria and morphological types. Sporeforming rods and Gram-negative non-sporeforming rods had simpler nutritional requirements while pleomorphic forms had more complex needs.

Goodfellow (1968) reported pleomorphic forms of bacteria to be metabolically inactive in a pine forest soil. Macauley and Thrower (1966) suggested that changes in fungal populations as decomposition progresses was a result of succession and not to differences in the initial litter fungi. Species of Coelomycetes and Moniliales were the

major initial colonizers of the litters of Eucalyptus regnans, but these were succeeded by species of Mucorales and Penicillium in the advanced stages of decay. The final microflora of the decomposing litter resembled that found in the A horizon.

The size and diversity of the microfungal population were reflected in the composition of the higher vegetation (Wicklow and Wittingham, 1974). In a comparative study between alder and conifer stands, a greater diversity of fungal species was found under alder which also had the greater number of codominant species (Wicklow et al., 1974). Of the 92 species of fungi identified, 55 occurred under the alder stand and 45 occurred under the conifer stand.

Witkamp (1963) reported that hardwood leaves were more favorable for the development of bacterial species due to higher nitrogen and calcium contents. Messenger (1975), working with northern hardwood and conifer forests, determined that higher concentrations of basic cations, lower C:N ratios and lower aluminum concentrations in the soils and humus layers of northern hardwood forests favor denser populations of microorganisms and hence, greater decomposition rates. Marten and Pohlman (1942) found a direct relationship between pH and bacterial numbers. Bacterial numbers increased with increasing pH as long as there was a sufficient amount of water-soluble material. Wright and Bollen (1961) found that an inverse relationship existed between the numbers of

bacteria and actinomycetes and the number of molds. McGill et al. (1975), using additions of ^{14}C-labeled acetate and ^{15}N-labeled ammonium sulfate, noted that fungal populations predominated during the first few days of decomposition, and that bacterial numbers increased only when the fungal populations declined. In another study (Witkamp, 1966a), bacterial colonies were found to be 155 times more numerous for the entire year than fungal colonies. This relationship applied to both conifer and hardwood stands.

Evidence exists that the type of litter is more important than the type of microorganisms in determining the level of decomposition. Ivarson and Sowden (1959) applied antifungal and antibacterial antibiotics separately to mixtures of coniferous litter and observed little effect on the decomposition rate. This same effect was also noted by Kowal (1969). However, Cromack (1973) reported that naphthalene-treated litter had a considerably higher lignin content after a year of decomposition than did the control. The author hypothesized that the naphthalene treatment interrupted fungal succession and prevented adequate development of Basidiomycetes. These organisms are primary lignin decomposers and occur in the later stages of fungal succession (Alexander, 1961).

One important aspect of microbial populations is their role in nutrient cycling processes. Stark (1972) studied the ability of litter fungi to concentrate biologically important elements and to hold them

against heavy leaching. In both North and South American forests, fruiting bodies of fungi were found to contain high levels of Fe, K, P and Zn relative to local leaves. Rhizomorph tissue contained high levels of Ca, Cu, Fe, Na, P and Zn relative to local leaves. Loss by leaching amounted to less than 1% for both live and dead tissue. It is also thought that these fungi have the ability to pass on these elements to other fungi.

Biological Role in Decomposition: Effect of Macroorganisms

Soil animals influence decomposition processes through interaction with litter and microorganisms. Smaller macroorganisms, such as nematodes, partially control microbial populations by feeding directly upon bacteria (Alexander, 1961). Tribe (1960) studied the decomposition of cellulose film and found that it was initially colonized by fungi, followed closely by bacteria. Nematodes then invaded the fungi and bacteria, and later stages of decomposition were characterized by physical disintegration by larger fauna such as mites, collembolans and enchytraeid worms.

The activity of macroorganisms contributes significantly to nutrient transfers in forest ecosystems. Elements in animal excreta are easily leached from the soil (Stark, 1972). A number of the larger litter feeding invertebrates will conserve nutrients. Gist and Crossley

(1975) reported a direct relationship between the sclerotinization of the soil animal and the calcium content. Snails (Pulmonata) and millipeds (Diplopoda) are calcium dependent and tend to hold the elements from being leached.

Of primary importance is the comminution of litter by the larger litter feeding invertebrates. Metz (1954) noted the importance of earthworms and millipedes in incorporating organic matter into the mineral horizons. Bocock (1964) studied 25 litter species and found that the majority were degraded more rapidly on mull humus sites than on the moder sites. He attributed this to a larger population of litter feeding invertebrates, especially the earthworm. When ash litter was protected from attack by the larger invertebrates, breakdown rates were approximately the same on both sites. When ash litter was not protected, large soil invertebrates removed 40% of the litter from the mesh bags on the mull sites compared to 10% on the moder sites over a 5 month period. Similar results were reported by Bocock and Gilbert (1957) and Witkamp and Van Der Drift (1961).

Cromack (1973) reported significant reductions in litter decomposition rates from treatment with naphthalene, which reduced the soil fauna population. First year litter breakdown rates were decreased an average of 10.5% and the reduction in the total mixed deciduous floor litter decomposition amounted to 6.3%.

Indicators of Decomposition Rates

A number of techniques are used to measure decomposition rates. Among these are (1) measurement of O_2 uptake and/or CO_2 evolution, (2) determination of the decrease in organic matter either chemically or by weight loss and (3) measurement of the weight loss of a particular constituent such as cellulose or lignin (Alexander, 1961).

Rates of CO_2 evolution are generally considered to be the most reliable index of microbial activity. Corbet (1934) suggested that when the microbial population is exhibiting exponential growth, CO_2 evolution is proportional to the number of microorganisms. During the phase of decrease, many of the organisms are not viable and, therefore, CO_2 production is not proportional to the numbers of microorganisms present. Kowal (1969) reported that under laboratory conditions, dry weight losses and CO_2 evolution were directly comparable. Platt (1973) determined that oxygen uptake and CO_2 evolution were similar over a range of temperature. Beck and Gilmour (1974) stated that electrolytic field respirometers were useful in providing information for determining carbon turnover rates.

Using CO_2 evolution to measure decomposer activity has been criticized. Production of CO_2 may not reflect metabolic activity if incomplete oxidation occurs or if there is a loss of CO_2 in drainage

water (Witkamp, 1969). Edwards and Sollins (1973), working in a Liriodendron tulipifera L. forest, reported that CO_2 evolution showed little agreement when different techniques were used. When litter moisture was 162% and litter temperature was 20°C, CO_2 production as measured by an infrared gas analyzer was 63% higher than obtained by using the CO_2 train method or static method. Wiant (1967a) stated that methods of determining soil respiration which measure CO_2 as it diffuses out of the soil give more reliable estimates than techniques which require the air to be drawn through or passed over the soil.

Total carbon dioxide production is reflected in the metabolic activity of microorganisms and in the respiration from live roots. To accurately determine carbon budgets and turnover rates, it is necessary to separate the two. Edwards (1975) found that litter respiration accounted for only 21% of the annual total CO_2 production.

Dry weight losses from litter bags of different sizes have been used by a number of investigators to measure turnover rates. Bocock (1964) found that the mesh size of the bag influenced the amount of material that could be removed and was, therefore, a measure of the activity of the larger litter feeding invertebrates. Witkamp (1966a) reported that CO_2 evolution from bagged oak leaves was significantly correlated with respiration rates from unconfined litter. In an earlier study, Witkamp and Olson (1963) reported that decomposition rates of confined and unconfined litter were dissimilar. This

could result from a change in the natural environment that occurs in the various sized bags (Van Cleve, 1971).

Turnover rates of the different components of litter can be determined by measuring the decomposition of the constituents in pure form. The substance in pure form may only be attacked initially by one or two microbial species while litter has an established microflora that will actively attack the leaf species (Rosswall, 1974). However, the pure substances will be rapidly metabolized once the microbial population is well established.

METHODS AND MATERIALS

Study Area

These investigations were undertaken within and adjacent to the H. J. Andrews Experimental Forest which is located approximately 73 km east of Eugene, Oregon. The forest communities that are present on the H. J. Andrews have been divided into two zones based on temperature (elevation) (Dyrness et al., 1974). The Tsuga heterophylla zone occurs between 300-1050 m in elevation, and the Abies amabilis zone is located between 1050-1500 m. Within a particular zone, moisture availability determines the distribution of the individual forest communities.

All study sites in this investigation were located within the Tsuga heterophylla zone. The dominant tree species is Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] which, on or near the H. J. Andrews Experimental Forest, commonly occurs in 450-year-old stands (old growth) and in 125-year-old stands (second growth). Wildfires within the area have been the primary cause for the development of second growth Douglas-fir stands. Other common coniferous species include western hemlock [Tsuga heterophylla (Raf.) Sarg.], western redcedar (Thuja plicata Donn) and Pacific yew (Taxus brevifolia Nutt.). Hardwood trees are less common but include such

species as bigleaf maple (Acer macrophyllum Pursh), red alder (Alnus rubra Bong.) and golden chinkapin [Castanopsis chrysophylla (Dougl.) A. DC.].

Climatic conditions are similar to those found throughout the western portions of the Pacific Northwest. The winters are typically mild and wet, and the summers are warm and dry. Mean annual precipitation varies from 230 cm at the lower elevations to 250 cm at the higher elevations, with an increasing proportion of the precipitation being in the form of snow at the higher elevations. The mean January temperature is 2.3°C and the mean July temperature is 20.6°C (Rothacher et al., 1967).

Soils on the H.J. Andrews Experimental Forest vary from shallow and stony to deep soils with well developed profiles. Most of these have developed from andesites, basalts, tuffs and breccias (Rothacher et al., 1967). Soils developed from tuff and breccia are generally found at the low to medium elevations (Dyrness et al., 1974). These include Reddish Brown and Yellowish Brown Lateritic soils (Haplumbrepts and Dystrochrepts) found in residuum and colluvium material with textures ranging from silt loams to silty clay loams. At the moderate to high elevations are soils derived from andesite and basalt. Many have weak profile development (Inceptisols) and textures ranging from sandy loams to silt loams. Alluvial

soils do not occupy an extensive area and are located on terraces adjacent to major streams.

Description of Study Sites

In August of 1973, plots were established in three forest communities to study litter decomposition in the Coniferous Biome. These communities were described by Dyrness et al. (1974), and each has been designated as a reference stand (RS). During May and June of 1974, several other sites were selected for study. These consisted of two clearcuts and one clearcut that had been broadcast burned. Each of the study sites will be discussed in some detail.

The Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa (Tshe/Rhma/Bene: RS 2) association is typical of the climatic climax at low to middle elevations and frequently occurs on intermediate mesic sites. Reference stand 2 is located on moderate slopes of 20% at an elevation ranging from 480-500 m. Slope aspect is 285 degrees. The soils have developed in colluvium and alluvium material from reddish tuffs and breccias into deep, well drained, brown to dark brown loams over silt loams. The forest floor consists of an 011 (4-3 cm) and an 012 (3-0 cm) layer. The A1 horizon contains 4.7% organic matter (Brown and Parsons, 1973).

Overstory vegetation consists of old growth Douglas-fir and western hemlock. Because of the dense overstory, the understory is

generally sparse. The tall shrub layer averages 15.6% cover. Pacific rhododendron (Rhododendron macrophyllum G. Don) is typically the dominant species in this layer, normally averaging 12% in this association; it averages only 4.3% on RS 2. The low shrub layer averages 14.5% cover, consisting primarily of Oregongrape (Berberis nervosa Pursh) which averages 12% cover. Herbs and mosses occupy 23.9% and 53.5% cover, respectively.

The Tsuga heterophylla/Castanopsis chrysophylla (Tshe/Cash; RS 6) association is typically found on relatively dry, exposed sites. Reference stand 6 is located on slopes varying from 55% to 80% at an elevation ranging from 590-635 m. Slope aspect varies from 170 to 190 degrees. The soils developed in alluvium and colluvium material from reddish tuff and breccia, and andesite. They are deep, well drained, dark yellowish brown to dark brown gravelly loams. The forest floor consists of an 011 (5-4 cm) layer and an 012 (4-0 cm) layer. The A1 horizon contains 4.3% organic matter (Brown and Parsons, 1973).

The overstory is composed of Douglas-fir and western hemlock, with Douglas-fir being the dominant species. However, reproduction in the understory is abundant for both species. Due to the low tree canopy cover, the understory has an abundant shrub layer. The tall shrub layer averages 92.3% cover. It is composed primarily of Pacific rhododendron and golden chinkapin which average 46% and

31.7% cover, respectively. The low shrub layer (29.5% cover) is dominated by salal (Gaultheria shallon Pursh). Because of the density of the shrub layer, herb and moss cover is minimal, averaging 14.3% and 4.9%, respectively.

The Tsuga heterophylla/Polystichum munitum-Oxalis oregana (Tshe/Pomu-Oxor: RS 7) association is found on the moistest and most productive sites in the Tsuga heterophylla zone. Reference stand 7 is located at elevations ranging from 450-470 m. Slope aspects are to the northwest and range from 350 to 360 degrees. Slope gradients vary between 50% and 60%. The soils are derived from parent material similar to that on RS 6. The soils are deep, well drained, dark brown gravelly loams over brown to dark brown clay loams. The forest floor consists of an 011 (4-3 cm) layer and an 012 (3-0 cm) layer. The A1 horizon contains 5.4% organic matter (Brown and Parsons, 1973).

The overstory is dominated by old growth Douglas-fir and western hemlock in stands of medium density. Western redcedar is also an important species in this association and shares climax status with western hemlock. Both the tall and the low shrub layers are less important and account for only 14.3% and 3.3% cover, respectively. Some of the common species making up the shrub layer are vine maple (Acer circinatum Pursh), red huckleberry (Vaccinium parvifolium Smith) and Oregongrape. The herb layer assumes a dominant role in

the understory, averaging 41.1% cover. Oregon oxalis (Oxalis oregana Nutt. ex T. &G.), swordfern [Polystichum munitum (Kaulf.) Presl] and twinflower (Linnaea borealis L.) comprise the largest part of this layer, and the average cover for each is 24.4%, 6.7%, and 6.1%, respectively.

In May and June of 1974, several sites were chosen to investigate the effects that clearcutting and broadcast burning have on carbon mineralization rates. Two criteria were used to select these sites. Of prime importance was the accessibility during winter months. The clearcut sites chosen were also to have been harvested within the past 4 years from the initiation of the study. The reasoning behind this criterion was that at least a portion of the residual forest floor would still be present, and the crown closure by invading species would not have developed. This would allow maximum expression of the effects of temperature and moisture on litter decomposition on exposed surfaces.

One of the clearcut areas (RS 33) was harvested in the fall of 1971. The forest community on the site was classified as a Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa (Tshe/Rhma/Bene) association (William Emmingham, personal communication). The slash was piled after harvesting. Slope gradients range from 0% to 5% and the elevation is approximately 800 m. The residual forest floor is sparse over much of the area. However, litter has

collected in areas protected from the wind, such as adjacent to logs. Several pioneer species, such as blackberry (Rubus sp.), rhododendron, huckleberry, vine maple and horsetail (Equisetum sp.), have invaded the site, but their total contribution to the litter layer is relatively small.

Two plots were established on a clearcut site located along Lookout Creek at an elevation of 470 m. Slope gradients range from 0% to 15%. The site was harvested in the fall of 1970. The vegetation consisted of old growth Douglas-fir and western hemlock. Western redcedar was also an important species in the stand. The understory consisted primarily of Pacific rhododendron and vine maple. The forest floor is relatively sparse and most of the litter has collected in areas that are sheltered from the wind. Regeneration includes such species as blackberry, raspberry (Rubus sp.), vine maple, Pacific rhododendron, western hemlock and salal.

On a site adjacent to the H.J. Andrews Experimental Forest, two plots were established on opposite sides of a 15.5 hectare clearcut that had been broadcast burned. The trees were felled in the spring of 1973, removed in the fall of 1973, and the slash burned in April of 1974. Slope gradients vary from 10% to 80%, and the elevations range from 500 to 620 m on southeastern aspects. The vegetation was dominated by old growth Douglas-fir (90% cover) and western hemlock (10% cover). The understory consisted primarily of vine

maple and Pacific rhododendron. Sparse regeneration is mostly fireweed (Epilobium angustifolium L.). A relatively thick 1 to 5 cm residual forest floor remains.

Litter Decomposition Methods

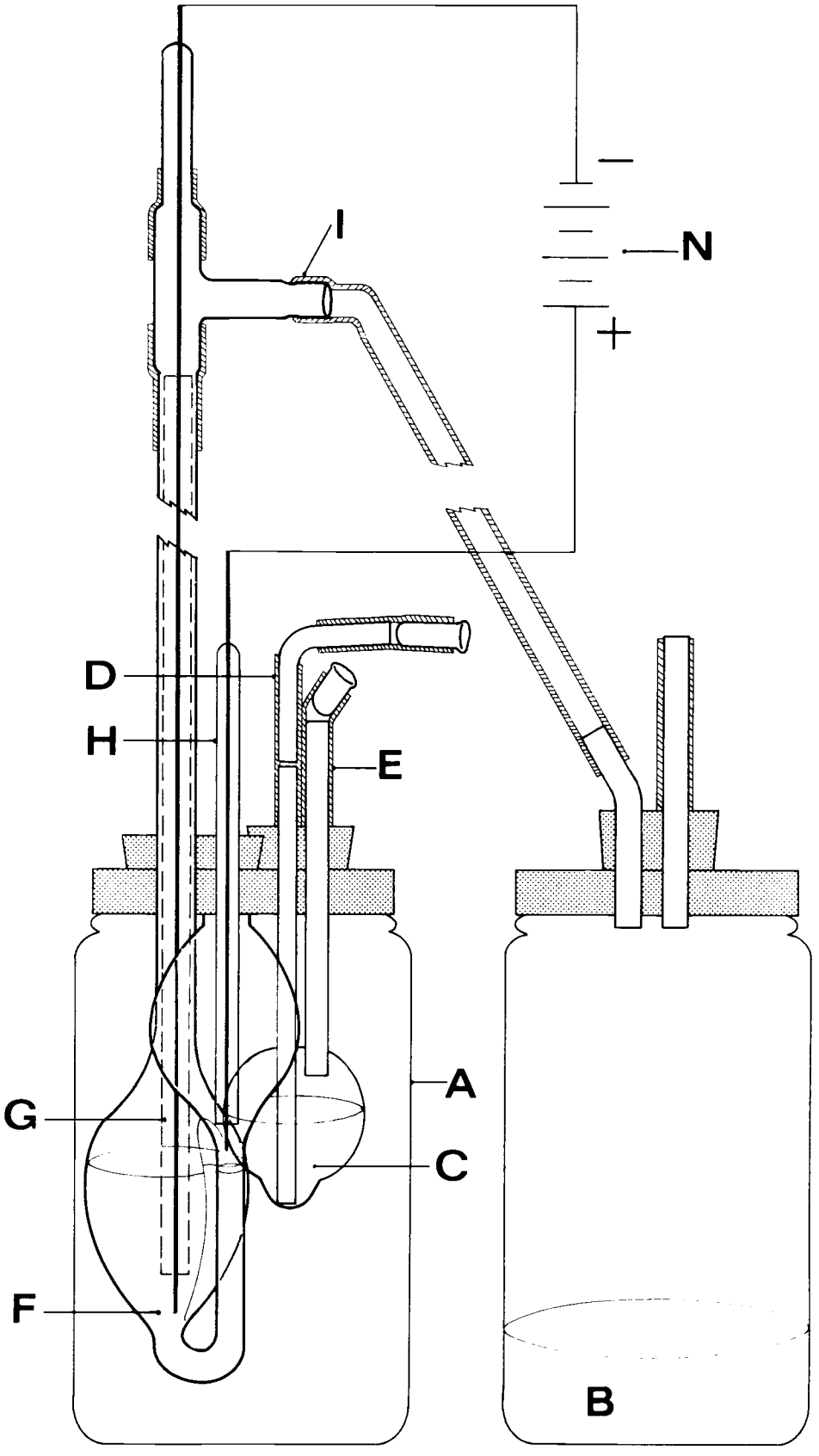
Field Respirometer

An electrolytic respirometer was designed to measure carbon dioxide production from the forest floor in situ independent of root respiration (Figure 1). A bank of four respirometers powered by two 12-volt batteries (N) was placed on each site. The field respirometer utilized two 945-ml wide-mouth screw-capped bottles. When a litter sample was put in bottle A, a 15 ml solution of 5N NaOH was placed in the alkali well (C) to absorb the CO_2 as it evolved from the sample. Tube (D) allowed the alkali to be removed during sampling and tube (E) allowed replacement of the alkali.

The electrolytic cell (F) was composed of an electrolyte (8% anhydrous $NaSO_4$) solution and two platinum electrodes. Hydrogen gas escaped at the cathode (G) while oxygen was produced at the anode (H). As decomposers on and in the litter sample consumed oxygen, the partial pressure dropped in bottle (A). This caused the electrolyte from reservoir (F) to rise and contact the anode, thus turning on the current and generating oxygen until equilibrium was reached with

Figure 1. Electrolytic respirometer.

A. respirometer bottle
B. barometric and temperature compensation bottle
C. alkali well
D. tube to remove alkali
E. tube for replacement of alkali
F. electrolyte
G. platinum cathode
H. platinum anode
I. connecting inlet
N. power source--two 12-volt batteries


I
N
D
H
E
A
G
C
F
B

atmospheric pressure. Temperature and barometric compensation were provided by bottle (B) through the connecting inlet (I) (Beck and Gilmour, 1974).

Litter Sampling

Four electrolytic respirometers were placed randomly on each study site in close priximity to one another. Respirometers on reference stands 2, 6, 7 and 33 were located close to litter bag decomposition studies being conducted by Cromack and Fogel. Field moist litter core samples were placed in the field respirometers at approximately 2 to 3 week intervals, at which time the alkali was also removed and replaced. The retrieved litter samples were put in small plastic bags until they could be returned to the laboratory for moisture and dry weight determinations. The alkali solution was removed by utilizing a vacuum pump attached to a test tube in which the sample was stored until it could be brought back to the laboratory for analysis. Two respirometers serving as blanks were also utilized to determine the absorption of atmospheric CO_2.

Litter samples were chosen randomly. A 945-ml bottle was placed on the forest floor and a core matching bottle circumference was cut with a knife through the 01 and 02 layers. A several centimeters thick litter core sample, consisting of non-woody material and small twigs and cones, was placed at the bottom of the respirometer chamber.

Temperature was monitored on reference stands 2, 6, 7 and 33. Grant miniature temperature recorders, Model D, were used on reference stands 2, 6 and 33. Temperatures were polled hourly and recorded on 30-day strip charts. A dual recording thermometer (Parthow Industrial thermometer, Model RFHTT) was used on reference stand 7, and was similar in design except that it utilized a 31-day strip chart. All recorders were placed in central shelters. One of the probes was placed under an insulated A-frame shield at 1 m above ground in order to measure air temperature. Probes were also placed in the litter layer and in the soil at a 5 cm depth.

Litter temperatures were not available for use except on reference stand 2. However, a regression equation was developed relating daily mean air temperature to litter temperature on reference stand 2.[1]

Litter temp. = 0.98937 + 0.86320 (air temp.)

This equation was also applied to reference stands 6 and 7. It was felt that this would be a more accurate measure of litter temperature than using air temperature. The equation does not predict litter temperature under snow.

Surface temperatures obtained from reference stand 33 were used to estimate surface temperatures on both clearcuts and the

---

[1]Special thanks is extended to Robert Fogel for supplying the regression equation for litter temperature.

clearcut that had been broadcast burned. Since all of these study sites were about 330 m below reference stand 33, an increase of 2°C was added to the temperature values obtained to compensate for the elevation.

Shelters were designed for the respirometers located on the clearcuts and burns.[2] It was felt that direct exposure of the bottles to sunlight on exposed surfaces would create artificially high temperatures within the respirometers. The shelters consisted of two inverted 12-inch aluminum pie pans nailed to two wooden dowel rods with approximately 3 inches between the pans. Holes cut in the center of both pans were wide enough for the shelter to facilitate easy placement over the respirometers. Both pans were covered with Scotch Brand (850) reflective pressure sensitive adhesive tape. Reflection of incoming radiation minimized possible "greenhouse effects" in the respirometer chambers. Periodic checks in the field showed that temperatures in the respirometers were within a 1.0° to 2.5°C of the litter temperature.

Determination of CO_2

Decomposer liberated CO_2, sorbed in the 5N NaOH and transported from the field to the lab in test tubes, was determined by

---

[2]Special thanks is extended to David McNabb for his help in designing the respirometer shelter.

titration with HCl using a Corning model 7 pH meter. Excess alkali was neutralized by addition of 2N HCl to pH 9.5 then with dilute 0.0833N HCl to pH 8.3. Further titration with 0.0833N HCl from pH 8.3 to pH 4.6 represents the amount of HCO_3^- present. Total mg of C resulting from litter decomposition equals (mls) (N) (eq. wt. of C). Total CO_2 evolved can then be determined by the following formula.

$$T\ CO_2 = (\text{meq acid}) \frac{(\text{Form. wt. } CO_2)}{(\text{Form. wt. C})}$$

Litter Processing

Each litter sample was weighed, oven dried at 63°C for 24 hours and then reweighed to determine sample dry weight and moisture content on a wet weight basis. The samples were then stored for further chemical analysis.

Analysis of Litter

Four samples per season from each study site were selected for determination of non-cell wall material (protein, fat, soluble carbohydrate, hemicellulose, pectin, tannin), cellulose, acid-insoluble lignin and ash. Analysis for the non-cell wall material followed procedures outlined by Van Soest (1963, 1966) utilizing the acid-detergent fiber method. Samples of litter were washed with acid-detergent to

remove non-cell wall material, followed by digestion with 72% H_2SO_4 to remove the cellulose. The remainder of the sample was acid-insoluble lignin and the ash left in the lignin fraction. Determination of ash was by combustion in a muffle furnace.[3]

Total nitrogen was determined by the micro-Kjeldahl technique outlined by Jackson (1958). Litter samples were ground to 40 mesh and a 0.45 to 0.55 gram sample was digested using H_2SO_4 and $CuSO_4$-Se catalyst. The resulting NH_3^+ was displaced by NaOH and distilled into the H_3BO_3 solution for titration with 0.069N HCl.

Samples were analyzed for total carbon by use of an induction furnace and the dry combustion method outlined by Allison, Bollen, and Moodie (1965).

The percentage of soil in the litter on each study site was determined by combustion of a 1 gram sample of litter at 600°C for 5.5 hours. Following combustion, the residue was washed alternately with a hot and cold solution of 2N HCl and filtered through Whatman No. 42 filter paper. The paper was then dried and weighed, and the change in weight of the filter paper was determined to be the percentage of soil in the sample.

---

[3]Appreciation is expressed to Dr. Kermit Cromack and Susan Phillips for their work in determining the carbon, lignin, and cellulose fractions in the litter.

Laboratory Decomposition Studies

Carbon dioxide evolution and O_2 uptake were monitored for 32 days by using electrolytic respirometers.[4] Litter samples were collected from all study sites. These samples were ground to 40 mesh, wetted to 60% water holding capacity and incubated at a constant temperature of 28°C. Carbon dioxide evolution was determined by standard titrometric procedures using 0.0833N HCl and O_2 uptake was monitored by measuring the production of H^+.

---

[4]Special thanks is expressed to Dr. C. Gilmour and Dave Tisson from the University of Idaho for the laboratory analysis of decomposition.

RESULTS AND DISCUSSION

Introduction

It is generally recognized that the measurement of CO_2 evolution from decomposing forest litter is the single most reliable index of microbial activity and carbon turnover rates (Witkamp, 1966a, 1969; Ellis, 1969). The ability to accurately measure CO_2 production under field conditions will provide the necessary information for studies dealing with carbon budgets and nutrient cycling processes.

In selecting a procedure for determining carbon turnover rates, the objectives of the study and the relative strengths and weaknesses of the method must be considered. For example, litter bag studies are good indicators of decomposition rates, but altering the mesh size will influence the relative contribution of microorganisms and macroorganisms with respect to decomposition (Witkamp, 1966a). Van Cleve (1971) also suggested that placing litter in bags could alter the natural environment. Studies that utilize litter constituents, such as cellulose and lignin, in pure form may underestimate decomposition rates because these substances will initially be attacked by a limited number of microorganisms (Rosswall, 1974).

Respiration rates can be measured by methods employing the passage of CO_2 free air over the surface of the litter and capturing

the evolved CO_2 in an alkali solution (Edwards and Sollins, 1973; Edwards, 1975). Use of this method results in a minimum of disturbance to the litter layer. However, air flow rate may influence the absorption of CO_2 in the alkali (Edwards and Sollins, 1973). The contribution of root respiration to measured CO_2 values must also be estimated.

Use of the electrolytic field respirometer has two distinct advantages: (1) inputs from root respiration are eliminated, and (2) the system can be operated continuously over an indefinite period of time. The method, however, has several limitations. There is disturbance to the litter layer when the core sample is placed in the respirometer bottle. Leaching of the litter and the stimulatory influence of morning dew are also eliminated. Possibly the greatest disadvantage of this system occurs because the fluctuations in field moisture between sampling periods are not reflected by the static moisture conditions that are maintained in the respirometer. An assumption is made that this effect will predominate only at the beginning and end of the wet season and that the discrepancies will balance out over time.

Carbon Mineralization Rates in Three Forest Communities

The decomposition process is a complex multi-variable system

involving the interaction of a wide variety of biotic and abiotic environmental factors. Due to the difficulty in measuring most of these parameters, temperature and moisture are commonly employed, as these variables are considered to be the major abiotic factors operating in the Western Cascades.

The interval totals of carbon mineralization for the three reference stands as a function of litter temperature and moisture content are shown in Figures 2 through 7. From the experimental data obtained in this experiment, temperature and litter moisture content are inadequate for determining the variability in CO_2 production on an annual basis.

Litter moisture content exerts the most pronounced influence on litter decomposition, and this effect is apparent during the fall months. Edwards (1975) found temperature to be the single most important variable in determining decomposition rates, but his study was undertaken in an area where moisture is rarely limiting or excessive. In the fall, peaks in CO_2 production closely follow peaks in moisture content. This pattern has been noted in a number of studies dealing with the effect of drying-rewetting on carbon mineralization rates (Birch, 1958; Sorensen, 1974).

The present study was initiated in August of 1973 following a 3-month dry period. During the dry period and prior to the onset of fall rains, substances that contain a high proportion of labile carbon

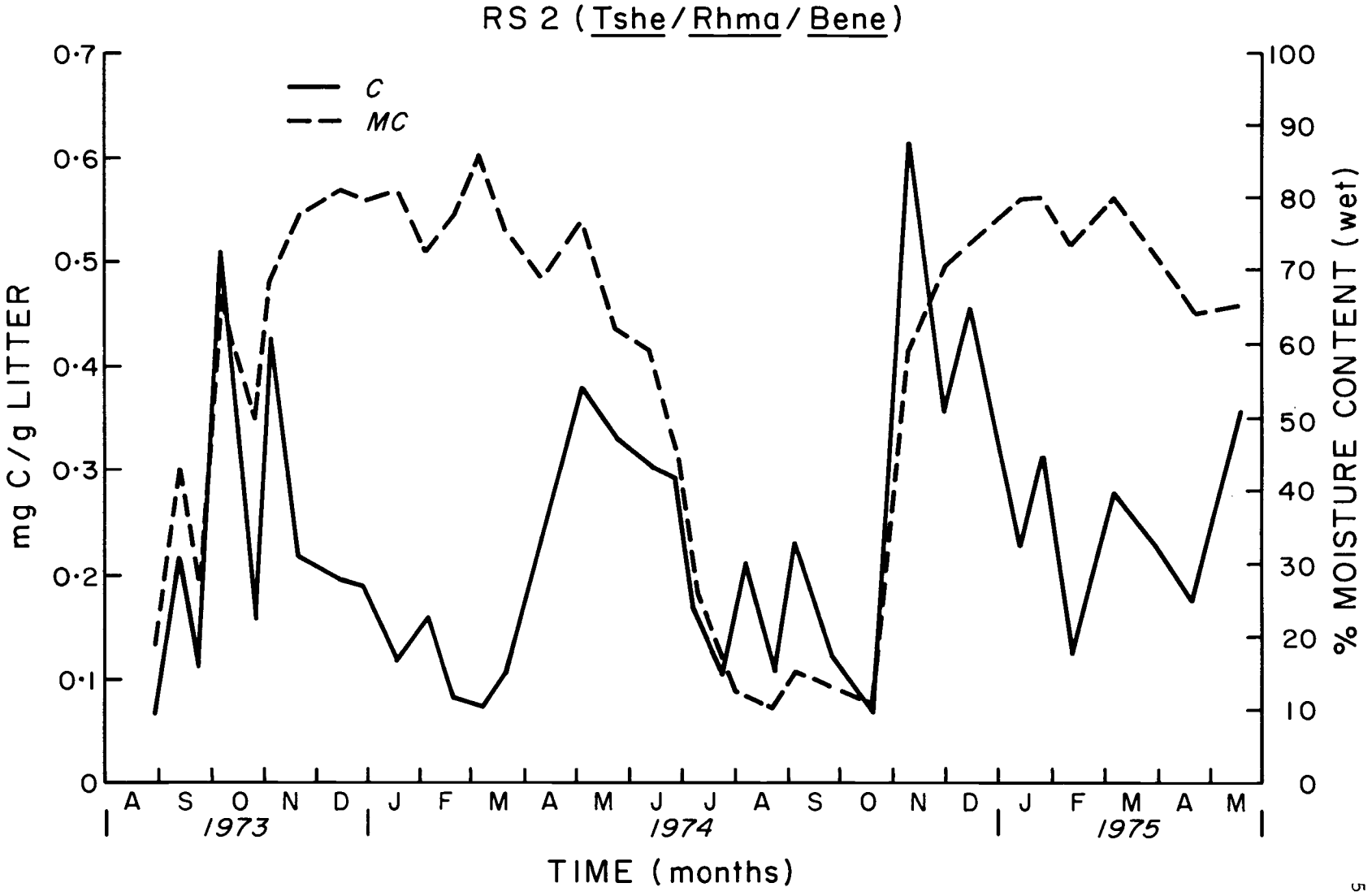


Figure 2. Carbon mineralization and litter moisture content as a function of time.

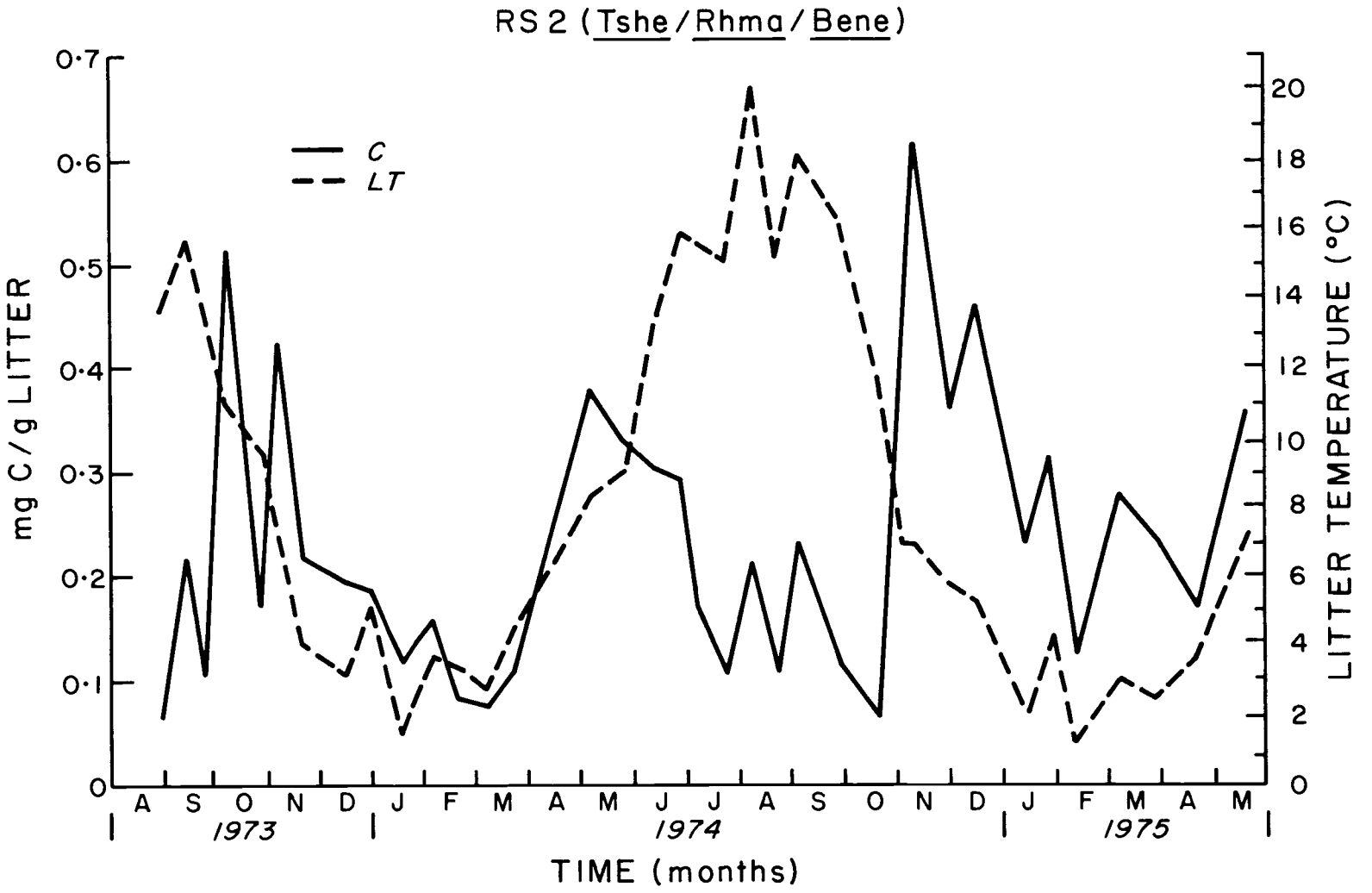


Figure 3. Carbon mineralization and litter temperature as a function of time.

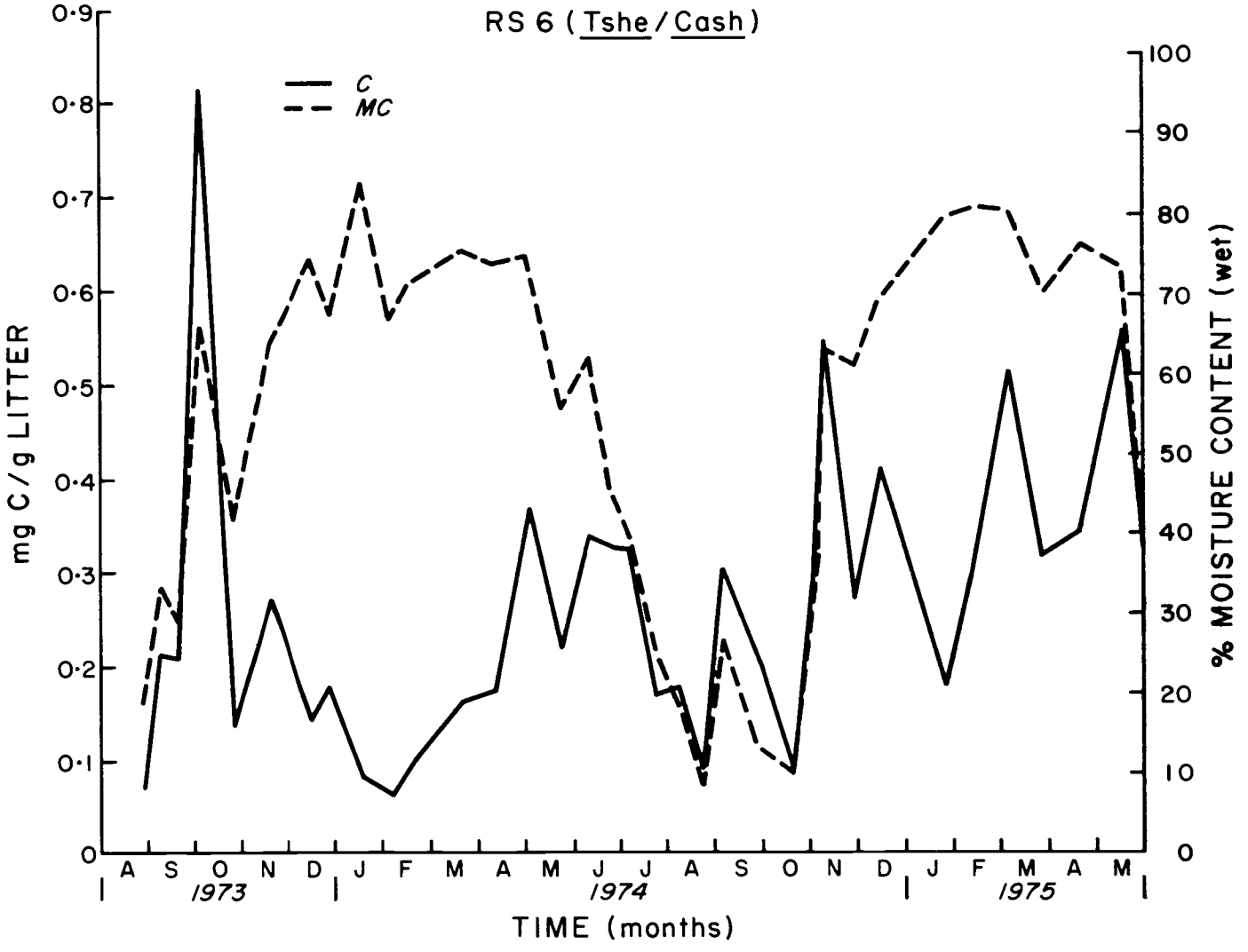


Figure 4. Carbon mineralization and litter moisture content as a function of time.

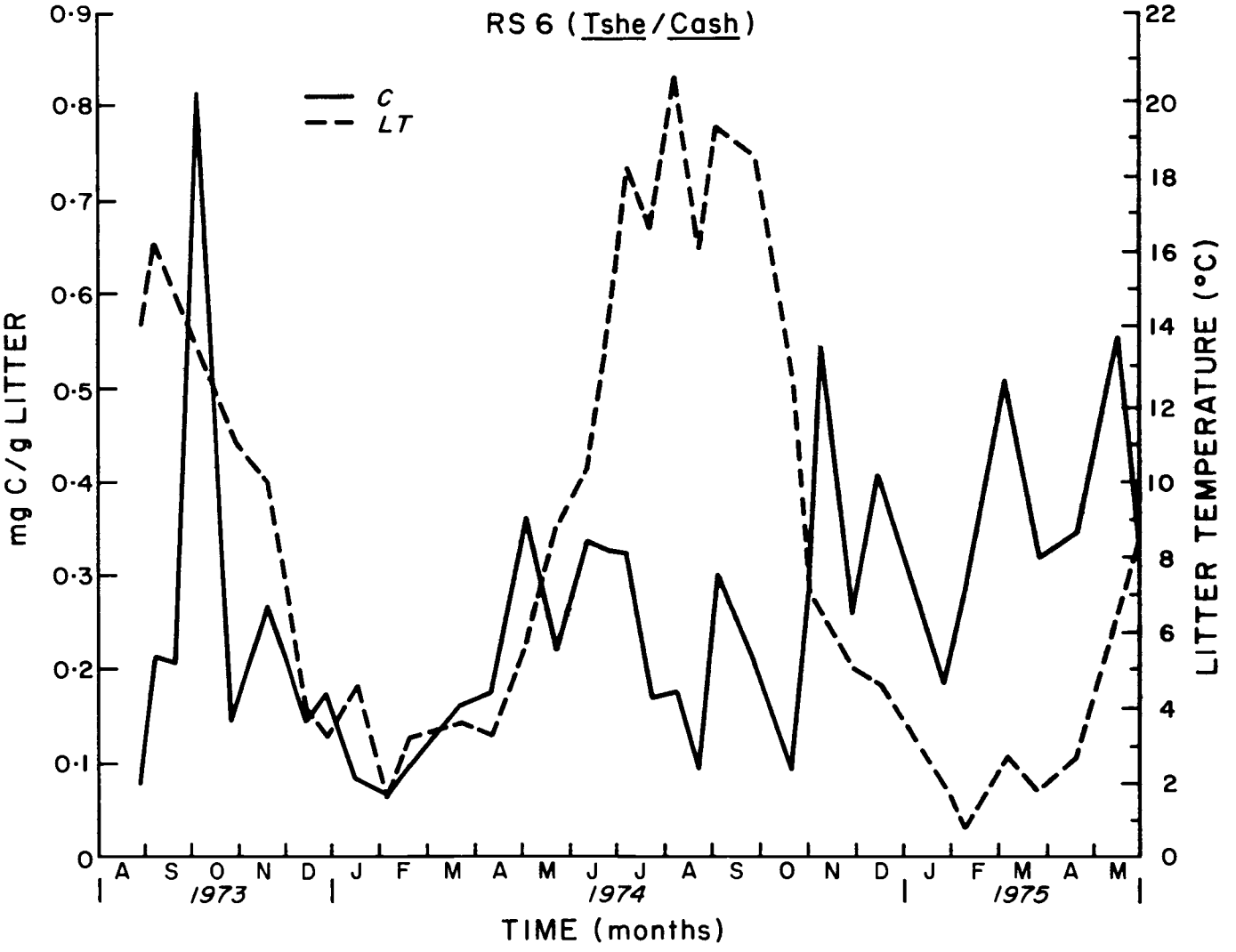


Figure 5. Carbon mineralization and litter temperature as a function of time.

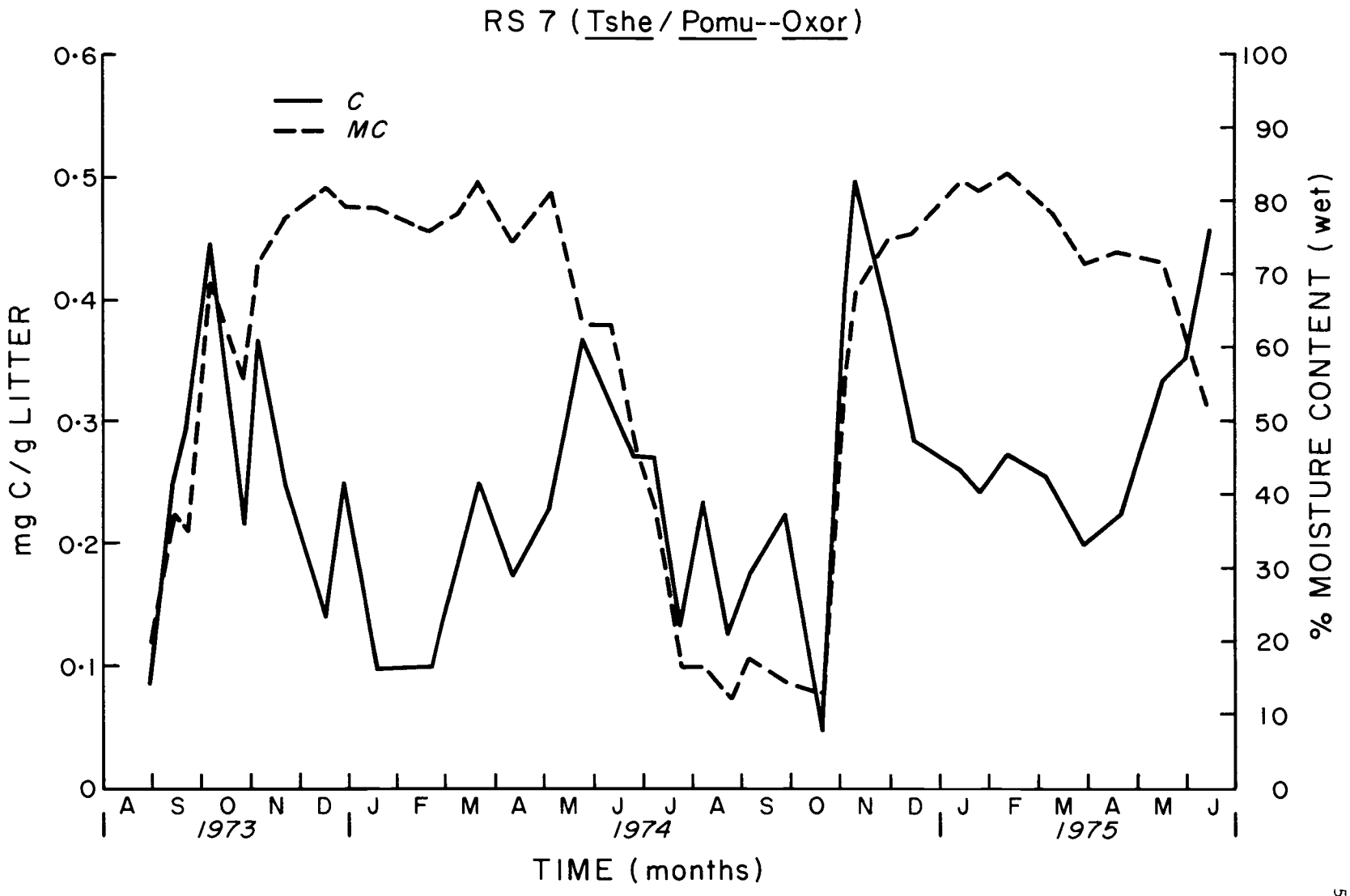


Figure 6. Carbon mineralization and litter moisture content as a function of time.

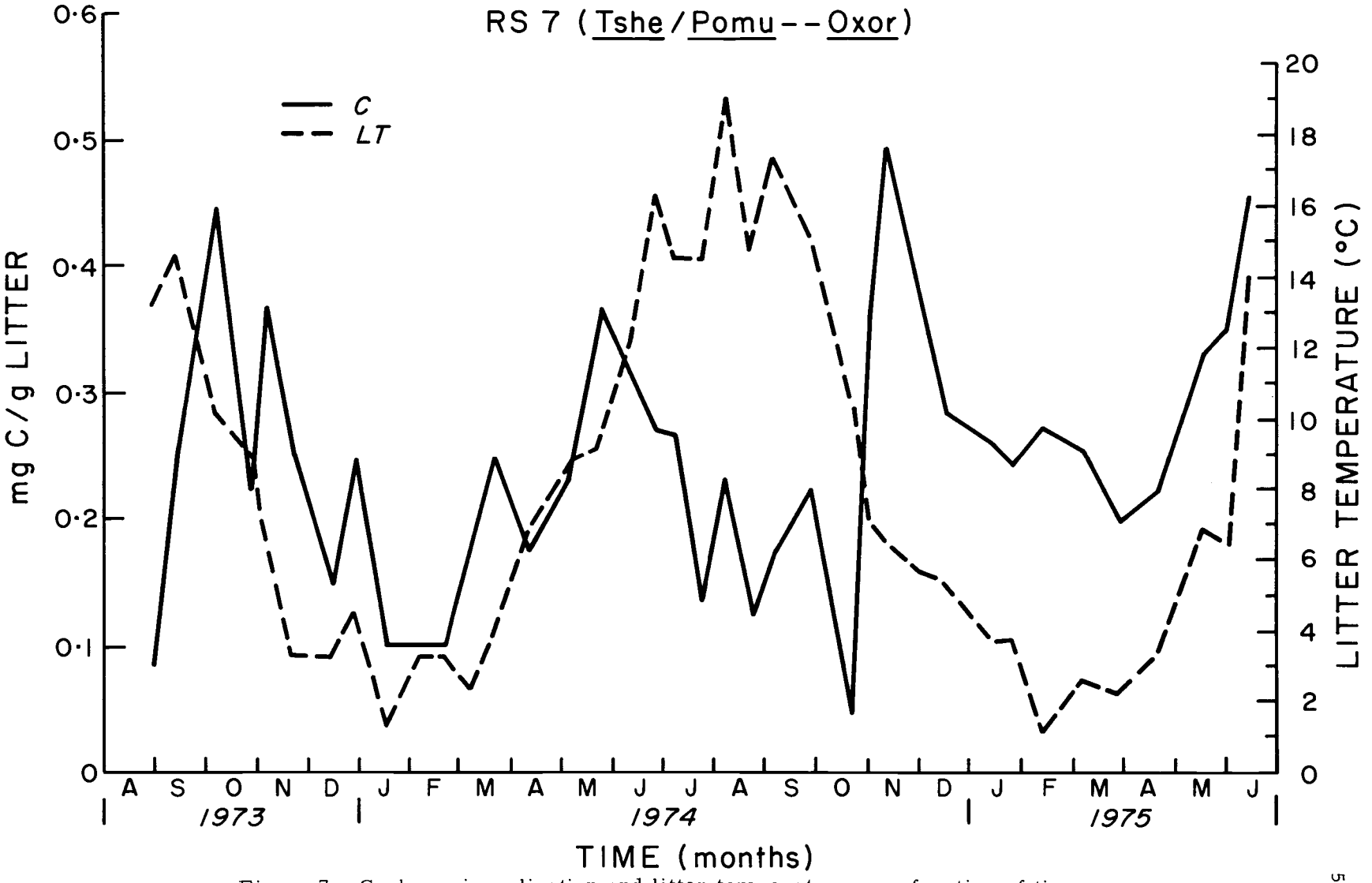


Figure 7. Carbon mineralization and litter temperature as a function of time.

and nitrogen would tend to accumulate because decomposer activity is low. Upon rewetting, CO_2 production would increase substantially because of the favorable moisture conditions and the presence of an adequate supply of readily decomposable substances. It is also possible that during the fall months, antibiotic activity is at a minimum (K. Cromack, personal communication). It is interesting to note that during the end of September, an exceptionally high concentration of pollen was observed on reference stand 6 (Figures 4 and 5) (K. Cromack, personal communication). This is an easily decomposable substrate and is the probable source of the high decomposition value that was obtained during early October.

A dissimilarity in litter moisture patterns exists between the fall of 1973 and 1974 (Figures 2, 4 and 6). Precipitation for the fall of 1973 began in early September in contrast to the fall of 1974 when substantial precipitation was delayed until late October. However, decomposition was significantly correlated with litter moisture content on the forest communities during both the fall of 1973 (RS 2: $r = 0.80$, $p < 0.05$, $n = 8$; RS 6: $r = 0.90$, $p < 0.02$, $n = 7$; RS 7: $r = 0.79$, $p < 0.05$, $n = 8$) and the fall of 1974 (RS 2: $r = 0.95$, $p < 0.05$, $n = 5$; RS 6: $r = 0.95$, $p < 0.05$, $n = 5$).[5] (Significant regression models are given in Appendix Table 4.)

---

[5] Mean decomposition values between each sampling period are used and are regressed against the weighted mean for litter moisture content and sample dry weight.

The effect of both litter temperature and litter moisture content on decomposition values appears to be significant only on reference stands 6 and 7 (RS 6: $r = 0.93$, $p < 0.05$, $n = 7$; RS 7: $r = 0.89$, $p < 0.05$, $n = 8$). When the fall months of both years are combined, decomposition is significantly correlated with moisture content (RS 2: $r = 0.84$, $p < 0.01$, $n = 13$; RS 6: $r = 0.72$, $p < 0.01$, $n = 12$; RS 7: $r = 0.80$, $p < 0.01$, $n = 13$).

On the three reference stands, a statistical relationship could not be determined between carbon mineralization and either litter temperature or litter moisture content for the winter of 1973 and spring of 1974. From Figures 3, 5 and 7, however, the obvious effect of temperature on carbon mineralization can be seen. The lack of any correlation with litter temperature could possibly result from using air temperature to estimate litter temperature during the winter. When snowpack is present, litter temperatures will be controlled by the snow temperature at the snow-litter interface in combination with temperature inputs from the soil. Also, air temperature fluctuations will be greater than those under snowpack.

During the following winter (1974), again correlations were not statistically significant between decomposition values and either estimated litter temperature or litter moisture content on reference stands 6 and 7. However, a highly significant correlation existed between carbon mineralization and litter temperature on reference stand 2 ($r = 0.97$, $p < 0.01$, $n = 5$).

Air temperature and precipitation patterns during the spring of 1975 were different from those of the previous spring. The spring months of 1975 were cooler, and consequently, snowpack remained longer on the higher study sites, e.g. on reference stand 6 to the end of April. Decomposition values on reference stand 7 were significantly correlated with litter temperature during this period ($r = 0.99$; $p < 0.01$, $n = 4$). Possible correlations could not be determined on reference stands 2 and 6 because bears severely disturbed the equipment with consequent loss of data, particularly on reference stand 2. Repeated breakage of the respirometers on reference stands 2 and 7 finally caused termination of the experiment on these sites in late spring of 1975.

In areas that experience drought conditions over the summer months, moisture content is considered to be the limiting factor governing the rate of decomposition (Alexander, 1961). During the summer of 1974, litter moisture content remained above 30% on all sites until the beginning of July. A significant correlation was found between decomposition and litter moisture content on reference stands 6 and 7 (RS 6: $r = 0.93$, $p < 0.02$, $n = 6$; RS 7: $r = 0.84$, $p < 0.10$, $n = 6$). Litter temperature together with moisture content produced a significant correlation on reference stand 7 ($r = 0.96$, $p < 0.05$, $n = 6$). The correlation with litter temperature and litter moisture content was not significant on reference stand 2.

Summary

Results from the current study indicate that in areas subject to wet and dry seasons, neither litter temperature nor litter moisture content, as measured by techniques used in this study, could adequately explain the variation in litter decomposition rates on an annual basis. Significant correlations are obtained with these variables on a seasonal basis.

Moisture content appears to be the dominant factor in explaining the variability in decomposition rates, particularly during the fall and summer months. To a large extent this was attributed to the influence of drying-rewetting cycles. Litter temperature is probably more of a determining factor in winter than is apparent from the analysis. The use of air temperature to estimate litter temperature during the winter months is most likely inadequate when snow is present on the study sites.

Comparative Rates of CO_2 Evolution among Reference Stands

Seasonal totals of carbon evolved for the three habitat types are given in Table 1. A number of interesting points are indicated by the data. During the first year of the study, maximum carbon mineralization rates occurred during the spring and fall months on each of the habitat types. This is the time when litter temperature and moisture

Table 1. Carbon mineralization (mg C/g litter) from the forest floor (01 + 02) of old growth forest communities.

Date	Reference stand		
	2	6	7
8/16/73 - 11/30/73	24.67	25.05	26.62
12/ 1/73 - 2/28/74	12.53	9.97	12.09
3/ 1/74 - 5/31/74	24.94	22.29	23.15
6/ 1/74 - 8/15/74	15.22	18.36	17.00
Yearly totals	77.36	75.67	78.86
8/16/74 - 11/30/74	26.33	25.18	25.80
12/ 1/74 - 2/28/75	23.60	24.15	26.97
3/ 1/75 - 5/17/75	20.34		
3/ 1/75 - 5/30/75		37.53	
3/ 1/75 - 6/13/75			30.32

content would be most favorable for decomposer activity. Lowest seasonal totals during the first year occurred in the winter months when litter temperatures were lowest. Carbon mineralization over the summer of the first year of the study was higher than might be expected. However, a moderate amount of precipitation occurred through June and early July.

An interesting feature of the data is the similarity in decomposition values between the reference stands, both seasonally and yearly. The differences in understory vegetation, elevation and moisture regimes (wet, intermediate, and dry) of the sites are not reflected in the amount of C being mineralized on the sites. Spring and fall accounted for 64%, 63%, and 63% of the total yearly decomposition on reference stands 2, 6, and 7, respectively. Winter decomposition

rates were 16%, 13% and 15% of the total for reference stands 2, 6, and 7, respectively, while summer rates were 20%, 22%, and 24%, respectively (see Appendix Table 1).

Cumulative carbon mineralization for the fall of 1974 was similar to that during the previous year for the three reference stands. Peaks in carbon production occurred when litter moisture either leveled off or increased (Figures 2, 4, and 6). Previous studies (Birch, 1958; Sorensen, 1974) have demonstrated the effect of drying-rewetting on stimulating CO_2 production. From experimental results obtained in the present study, it appears that possibly decreasing the rate of drying after an extended dry period may have a short term stimulatory effect on decomposition.

Increases in decomposition rates during the second winter of the study (Table 1) were also noted on the three reference stands. The increases for reference stands 2, 6 and 7 were 88%, 123% and 142%, respectively. These higher rates highlight the importance of temperature in controlling carbon turnover rates. Daytime air temperatures during the second winter were significantly higher, especially in January, than the air temperatures from the previous winter. This is not reflected in Figures 2, 4, and 6 because the weighted mean of both day and night temperatures was used.

Decomposition rates during the spring of 1975 were similar to those obtained from the previous spring on reference stands 2 and 7.

On reference stand 6, however, there was a 71% increase in decomposition over the previous year. This is an interesting result in view of the fact that air temperatures were higher in the spring of 1974. The increase might be due to the influence of snow cover on decomposition rates. Snowpack remained on reference stand 6 for a longer period of time in the spring of 1975. Some studies have indicated that turnover rates under conditions of low temperature or snowpack are relatively rapid (Witkamp and Van Der Drift, 1961). However, Witkamp and Van Der Drift (1961) considered the breakdown to be due to leaching and the activities of the litter feeding invertebrates. Garrett and Cox (1973) also noted that CO_2 evolution rates were greater on the higher slopes in winter. This can be compared to the conditions that existed on reference stand 6 during the first 6 to 7 weeks of the spring of 1975.

Average annual litter fall for the three reference stands was estimated to be 549 g/m^2 (K. Cromack, personal communication). Using this value, cumulative CO_2 evolution for the first year of the study would be 155 g/m^2. This is considerably lower than the values reported by Garrett and Cox (1973). In their investigation, they assumed the forest floor to be under steady state conditions. So carbon turnover would equal equivalent carbon additions. The measured value the authors reported was 731 g CO_2 $/m^2/yr$ for non-woody litter. From the carbon mineralization rates measured in this study,

and using the average percentage of carbon listed in Table 2 for the various study sites, it would take approximately 6.0, 5.7, and 5.2 years for complete carbon turnover on reference stands 2, 6, and 7, respectively.

Table 2. Carbon (%), nitrogen (%) and C:N ratios of forest floors for forest communities, cleacuts, and burns.

Site	C	N	C:N
Tshe/Rhma/Bene	46.04	1.06	43.43
Tshe/Cash	43.38	0.96	45.19
Tshe/Pomu-Oxor	41.03	1.05	39.08
Clearcut (RS 33)	45.34	1.26	35.99
Clearcut (29)	44.92	1.28	34.60
Clearcut (36)	43.70	1.18	37.03
Burn (17)	46.91	1.15	40.79
Burn (25)	46.04	1.10	41.85

This compares favorably with estimations of turnover rates determined by the ratio

$$\frac{\text{forest floor weight (non-woody litter)}}{\text{annual litter production (non-woody litter)}} .$$

Annual non-woody litter additions for the three reference stands average 5.5 metric tons per hectare (K. Cromack, personal communication). Information on forest floor weights was obtained from C. T. Youngberg (personal communication): RS 2 = 55, 120 kg/ha, RS 6 = 51, 840 kg/ha, RS 7 = 48, 688 kg/ha. Assuming 60% non-woody litter, the turnover time for carbon by this method would be 6.0, 5.7, and 5.3 years for reference stands 2, 6, and 7, respectively. Platt

(1973) calculated the half life of decomposing litter from the H. J. Andrews Experimental Forest to be approximately 2 years under laboratory conditions.

Comparative Rates of Carbon Mineralization among Clearcuts

Interval totals of carbon mineralization for the clearcuts (29, 36 and RS 33) as a function of litter moisture content and litter temperature are illustrated by Figures 8 through 13 (see Appendix Table 2). Regression equations (see Appendix Table 4) were determined for periods of time when natural breaks in trends between litter temperature and moisture occurred.

The experimental results show that on an annual basis, neither litter temperature nor litter moisture content alone or in combination were adequate for explaining the variation in carbon mineralization. Significant relationships were found only on a seasonal basis. Between May 24, 1974 and October 20, 1974, carbon mineralization was significantly correlated with litter moisture content on 29 and RS 33 (29: $r = 0.92$, $p < 0.01$, $n = 9$; RS 33: $r = 0.74$, $p < 0.05$, $n = 8$). The correlation for 36 was not significant. A better correlation was obtained on 36 and RS 33 by regressing against both litter moisture content and litter temperature (36: $r = 0.83$, $p < 0.05$, $n = 9$; RS 33: $r = 0.85$, $p < 0.05$, $n = 8$).

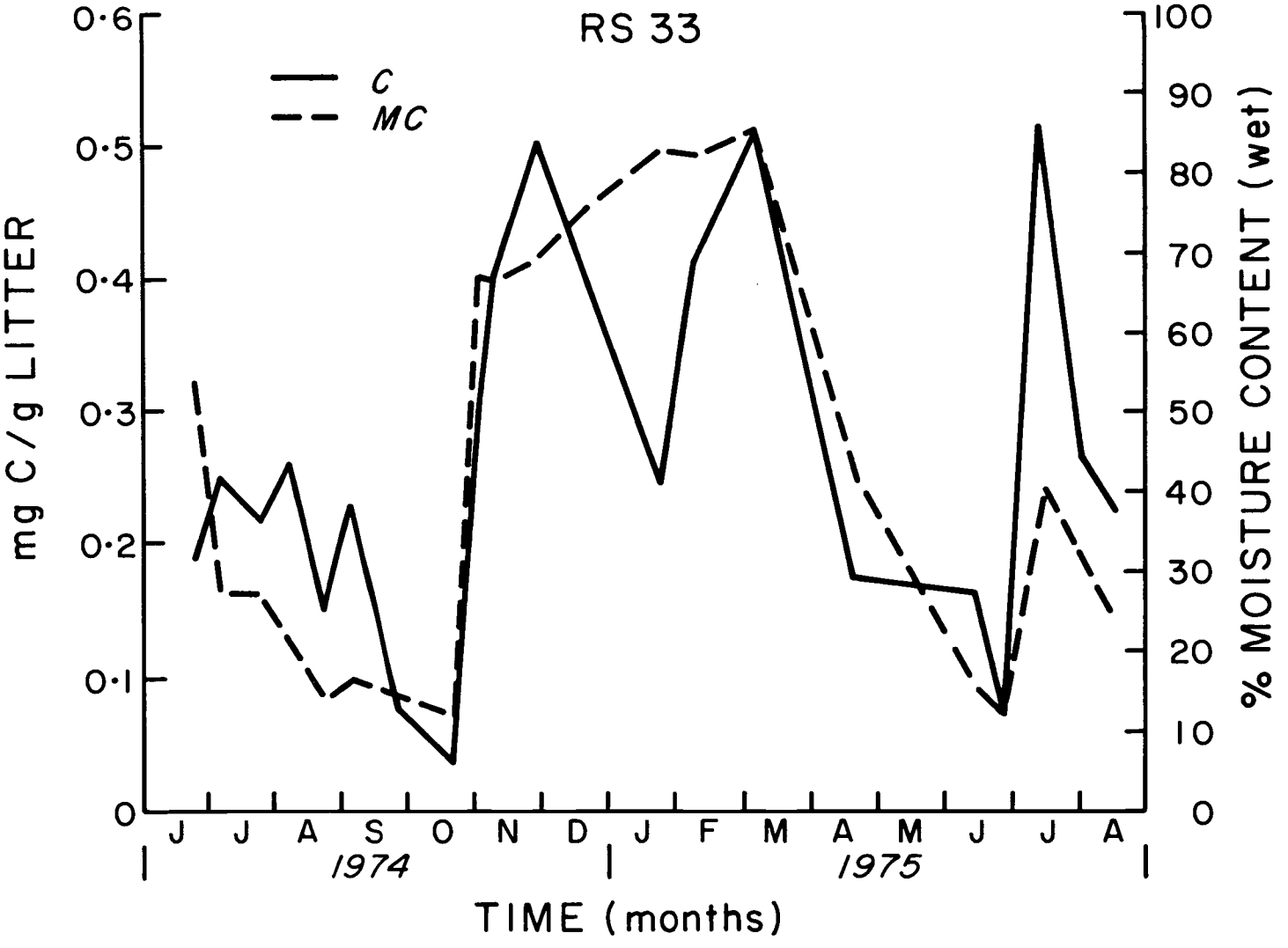


Figure 8. Carbon mineralization and litter moisture content on the younger clearcut as a function of time.

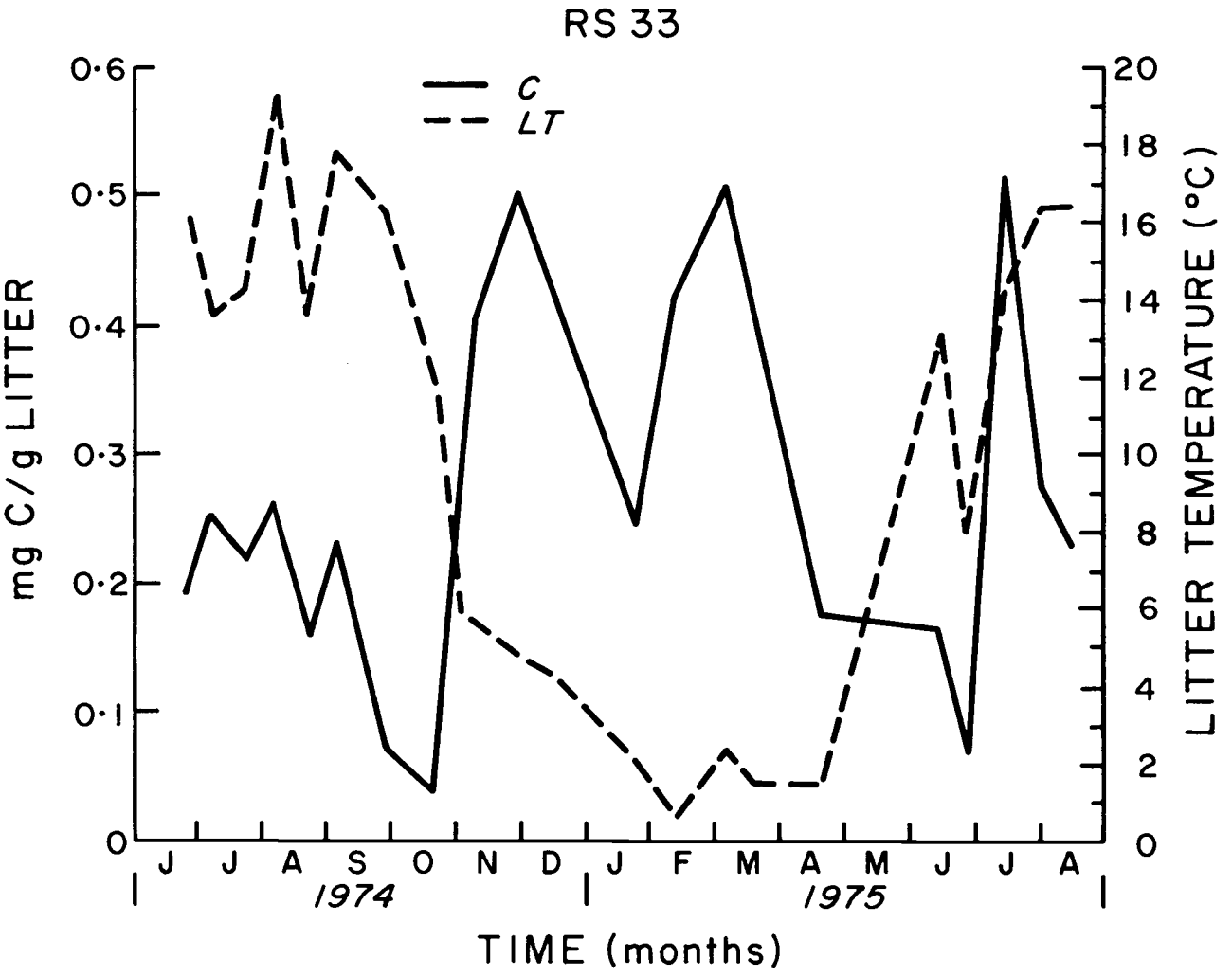


Figure 9. Carbon mineralization and litter temperature on the younger clearcut as a function of time.

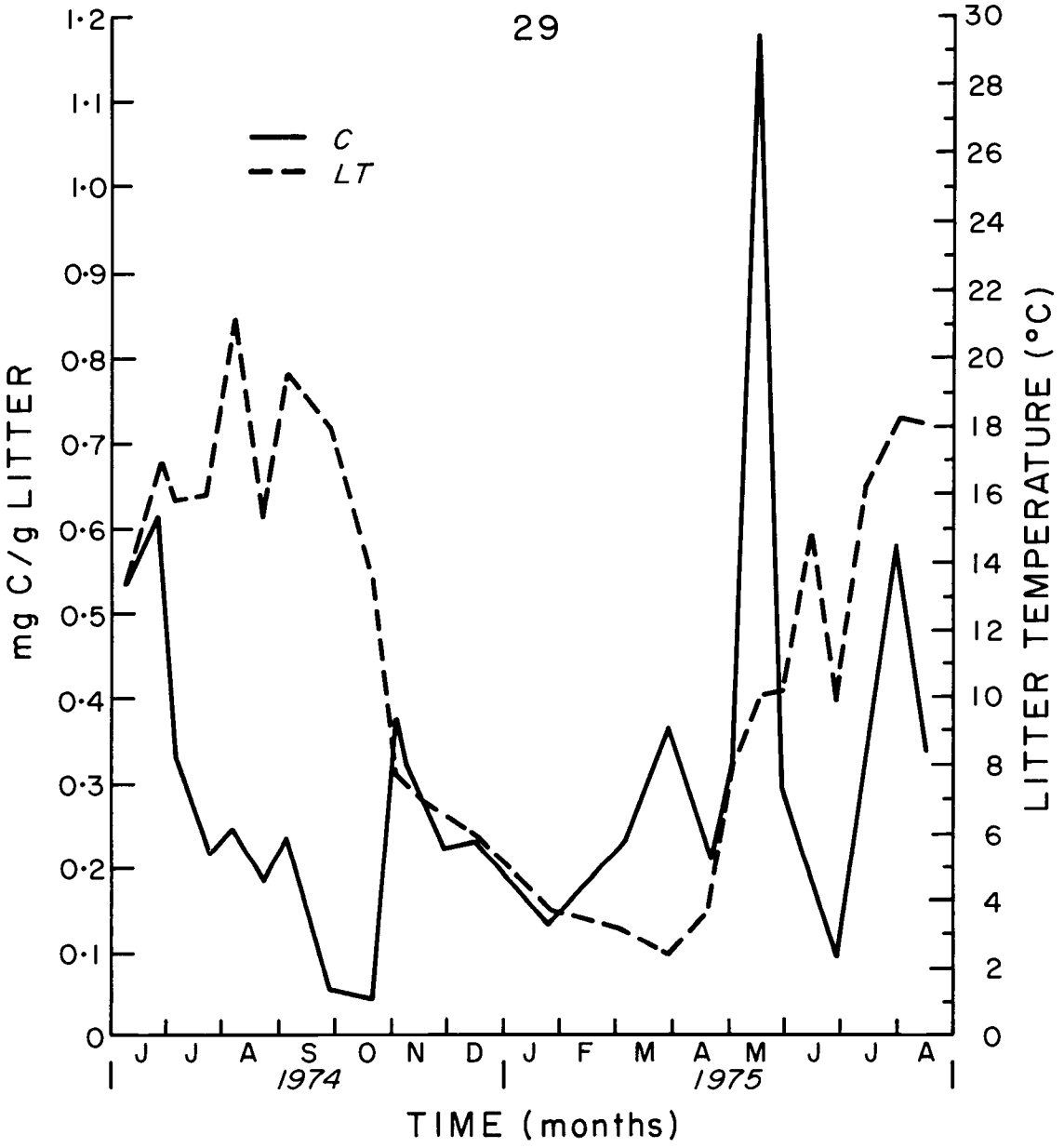


Figure 10. Carbon mineralization and litter moisture content on the older clearcut as a function of time.

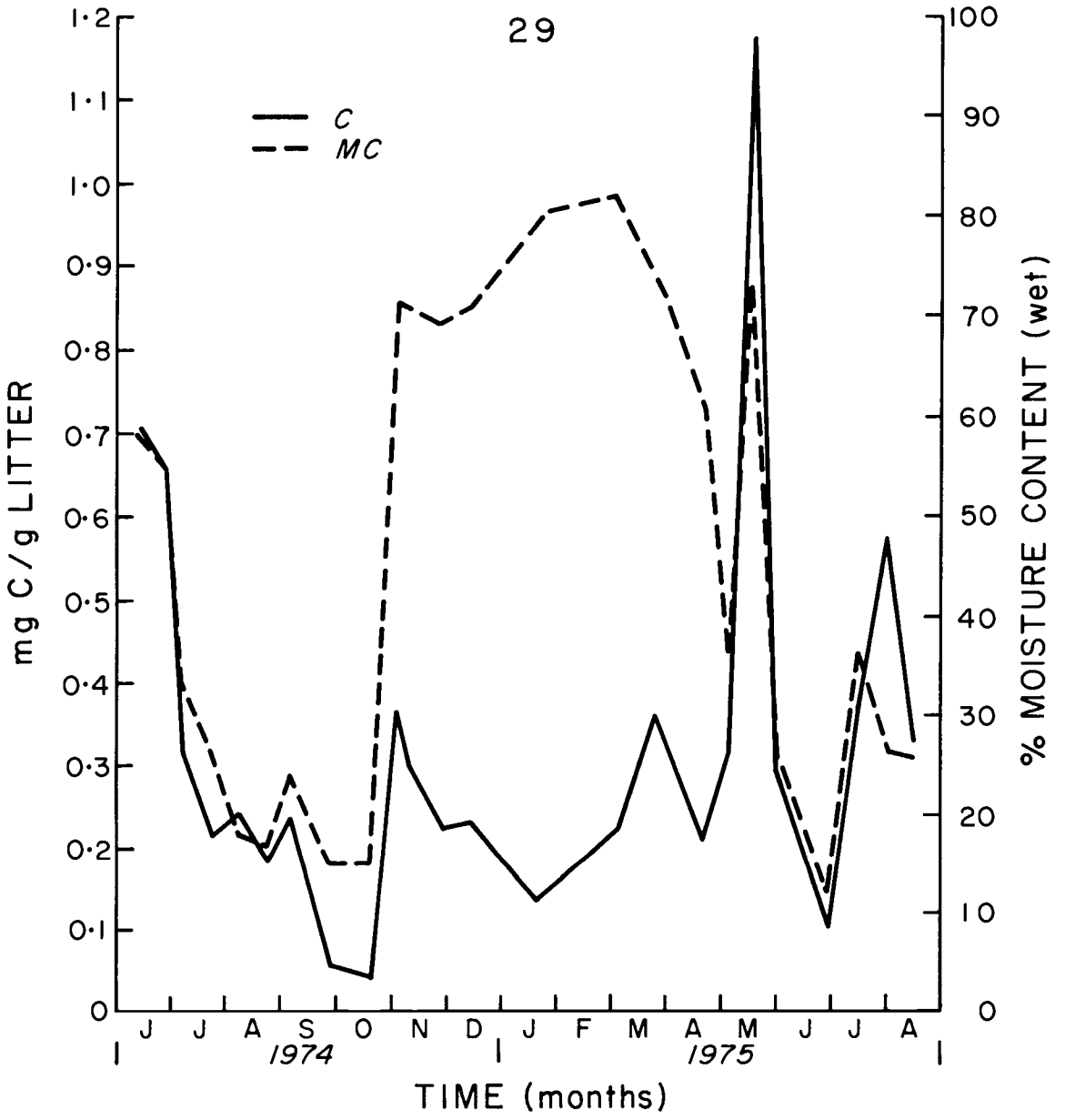


Figure 11. Carbon mineralization and litter temperature on the older clearcut as a function of time.

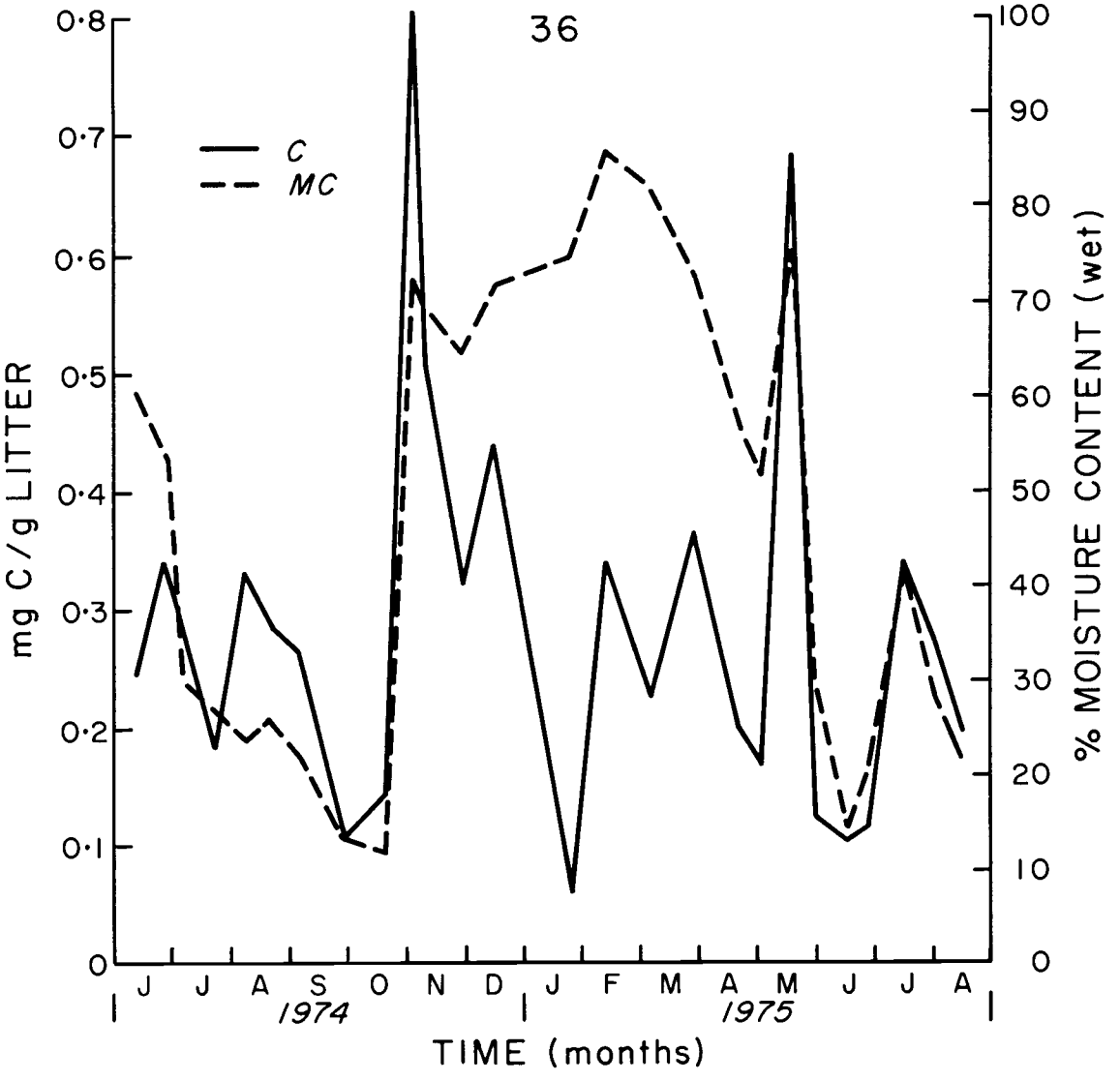


Figure 12. Carbon mineralization and litter moisture content on the older clearcut as a function of time.

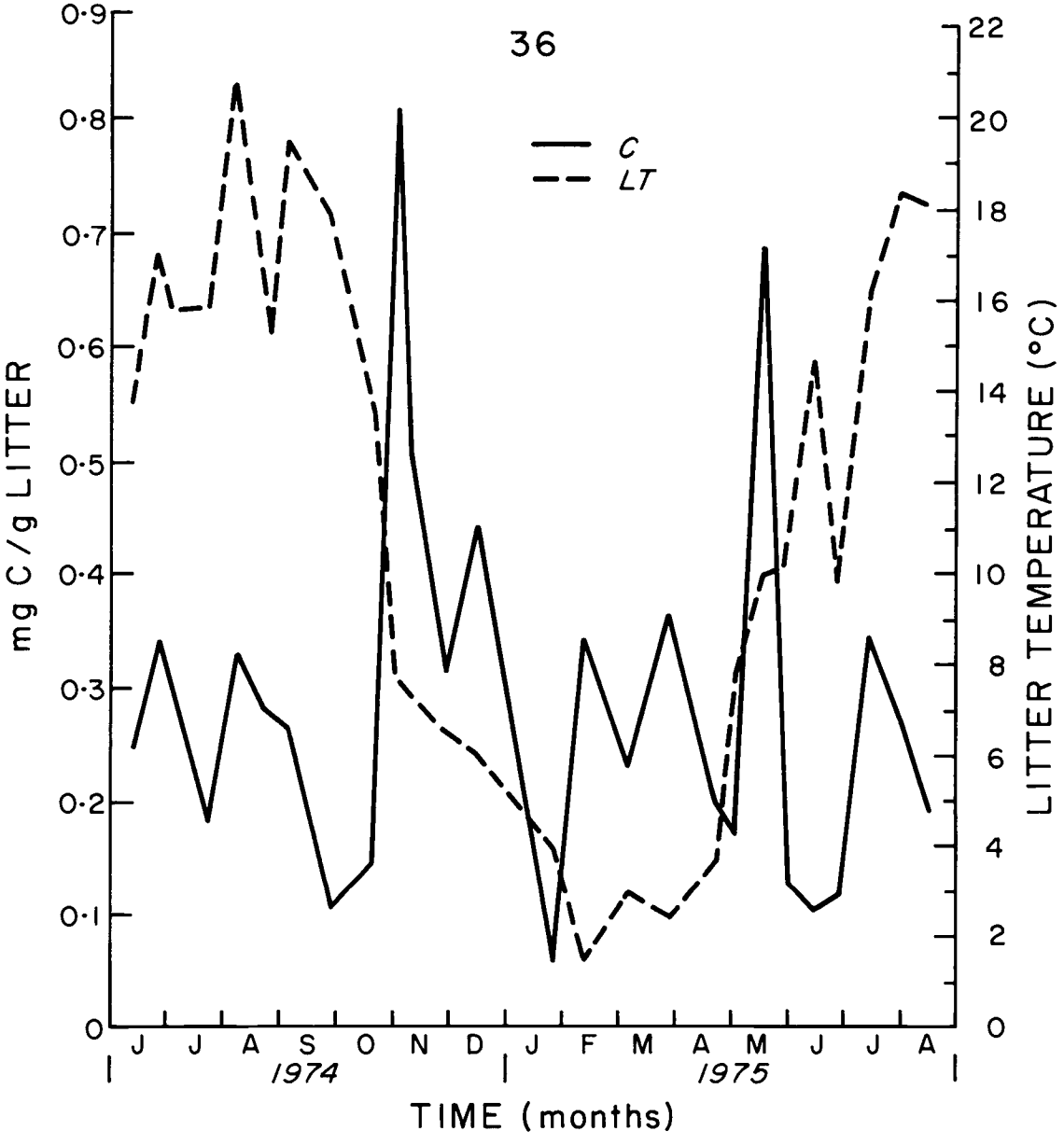


Figure 13. Carbon mineralization and litter temperature on the older clearcut as a function of time.

Table 3. Carbon mineralization (mg C/g litter) from the forest floor of three clearcut plots.

Date	Clearcut 29	Clearcut 36	Date	Clearcut RS 33
5/24/74- 8/31/74	34.58	27.11	6/12/74- 8/31/74	17.44
9/ 1/74-11/30/74	15.31	28.45	9/ 1/74-11/30/74	20.49
12/ 1/74- 2/28/75	16.80	19.08	12/ 1/74- 2/28/74	32.29
3/ 1/75- 5/23/75	37.47	27.14	3/ 1/74- 6/11/74	19.27
Yearly totals	104.16	101.78		89.49
5/24/75- 8/15/75	27.37	17.20	6/12/75- 8/15/75	18.52

Litter moisture conditions on the clearcuts were similar to those for the forest communities during this period of time. Precipitation was intermittent but more rain would reach the forest floor on the clearcuts because of decreased interception. Evaporation would be greater and normally the thin litter layer on the clearcut would dry out more rapidly. However, samples for the most part were taken from sheltered areas where the litter had collected. Shading thus reduced excessive evaporation.

Between October 21, 1974 and April 20, 1975, correlations between carbon mineralization and litter moisture content or litter temperature were not statistically significant. It is generally thought that low temperatures control carbon mineralization rates during the winter (Witkamp and Van Der Drift, 1961, Mikola, 1960; Reiners, 1968). The lack of correlation with litter temperature in the present study was probably due to the same reasons as stated earlier. During

the winter and early spring, snowpack covered the sites for a considerable part of this time.

Between April 21, 1975 and August 15, 1975 carbon mineralization was significantly correlated with litter moisture content on the three clearcuts (29: $r = 0.86$, $p < 0.02$, $n = 8$; 36: $r = 0.71$, $p < 0.05$, $n = 8$; RS 33: $r = 0.97$, $p < 0.02$, $n = 5$).

Seasonal totals for carbon mineralization of litter on the clearcuts are given in Table 3. Variability in seasonal totals between clearcuts (29 and 36) was considerable. The results were surprising because of the close proximity of the plots. The dissimilarity was probably due to the method of selecting the samples. Greatest accumulations of litter were located in scattered sheltered areas and core samples were obtained from these areas. The variability in litter quality of the samples between sampling periods would likely be considerable. However, the yearly totals for carbon mineralization were similar. Apparently, the random variability in litter quality averaged out over time.

The yearly totals for carbon mineralization on reference stand 33 was 15% lower than on the other clearcuts. Most likely, this is in part due to elevational effects on temperature, reference stand 33 being 330 meters higher. Another probable cause relates to the age of the clearcuts. The lower clearcut (plots 29 and 36) was harvested a year earlier than reference stand 33, and reestablishment of the site

by invading species had progressed to a greater extent. Thus the contribution of fresh litter to the residual forest floor was greater.

Yearly decomposition rates were considerably higher on clearcuts than on any of the reference stands. Accelerated decomposition is to be expected due to the higher temperatures in the litter layer. Nitrogen values were also greater and C:N ratios lower for litter on the clearcuts (Table 2). For reference stand 33, highest seasonal rates occurred during the winter. Stark (1972) reported that considerable decomposition by fungal species occurred under snow during the winter months, possibly due to stable litter temperatures in the litter layer.

These results have implications for nutrient cycling processes. When a forested area is harvested, an increase in surface moisture and temperature occurs which accelerates decomposition processes. At the same time a greater amount of water will move through the soil due to the decreased interception and evapotranspiration. Increased CO_2 production could result in increased bicarbonate (HCO_3^-) ion activity. As a mobile anion, bicarbonate could potentially move cations through the soil and out of the potential rooting zone, since roots would not be present to remove the cations out of solution. Cole et al. (1975) have shown that bicarbonate anion movement through the soil is highly dependent on the buffering capacity of the soil.

Comparative Rates of Carbon Mineralization on Clearcuts that Have Been Broadcast Burned

Figures 14 through 17 show the interval totals of carbon mineralization for the burned plots as a function of litter content and air temperature (see Appendix Table 3). No direct measurements of litter temperature on the burns were made. It was decided to use air temperature estimations because the presence of the blackened surface would subject the litter layer to more rapid fluctuations in temperature than those occurring on the mineral soil of a clearcut or the forest floor in an uncut stand.

Significant correlations between carbon mineralization and air temperature or litter moisture content were found. Regression equations (Appendix Table 4) were determined for the same time periods as those for the clearcuts. Litter moisture content was the factor determining turnover rates between May 24, 1974 and October 20, 1974 (17: $r = 0.97$, $p < 0.01$, $n = 9$; 25: $r = 0.87$, $p < 0.01$, $n = 9$). Between October 21, 1974 and April 20, 1975, air temperature was the dominant factor (17: $r = 0.91$, $p < 0.01$, $n = 7$; 25: $r = 0.78$, $p < 0.01$, $n = 9$). During the period between April 21, 1975 and August 15, 1975, a significant correlation with both litter moisture content and air temperature was evident for plot 17 ($r = 0.89$, $p < 0.05$, $n = 8$). No significant correlations were found for plot 25.

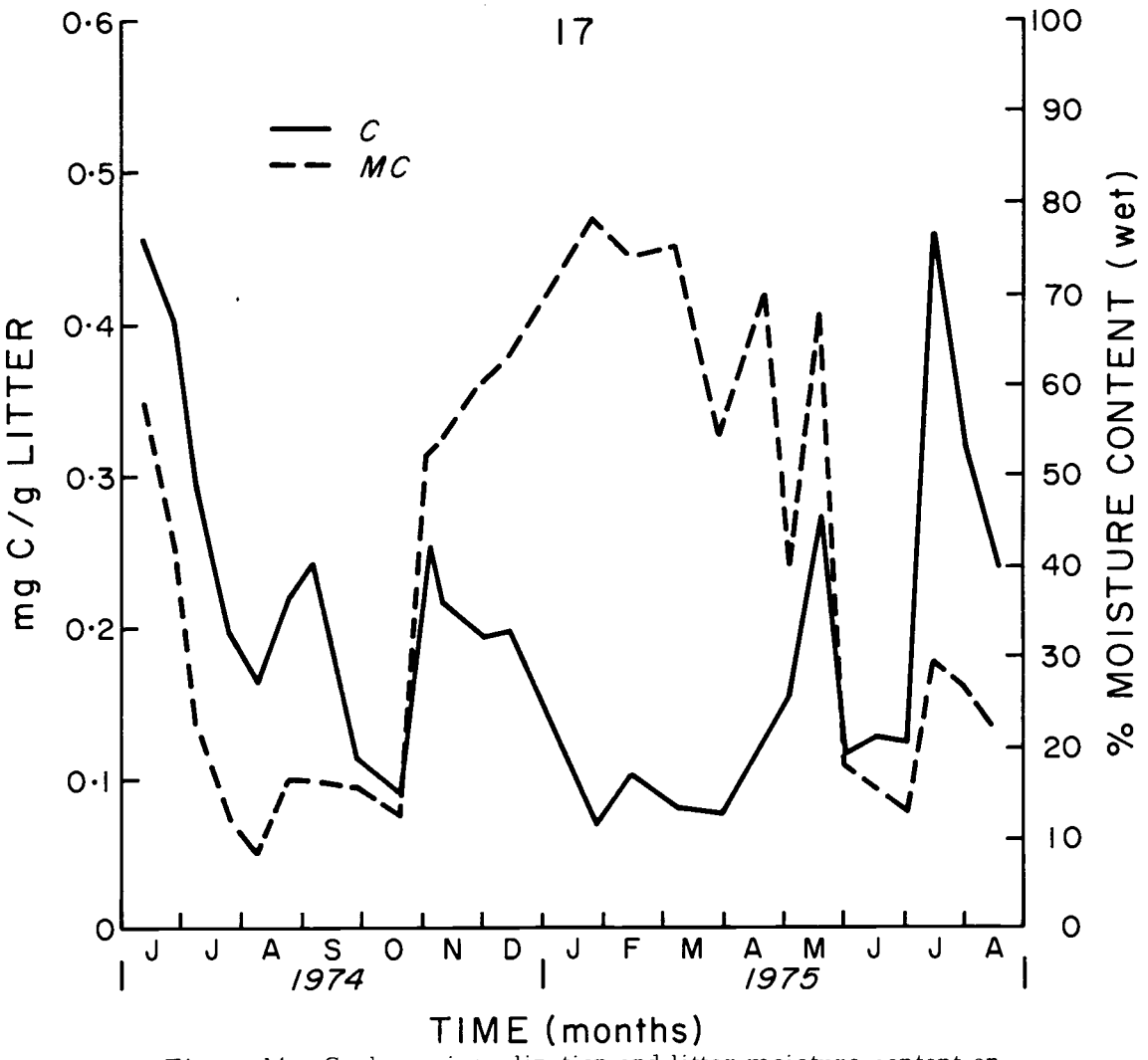


Figure 14. Carbon mineralization and litter moisture content on the broadcast burn as a function of time.

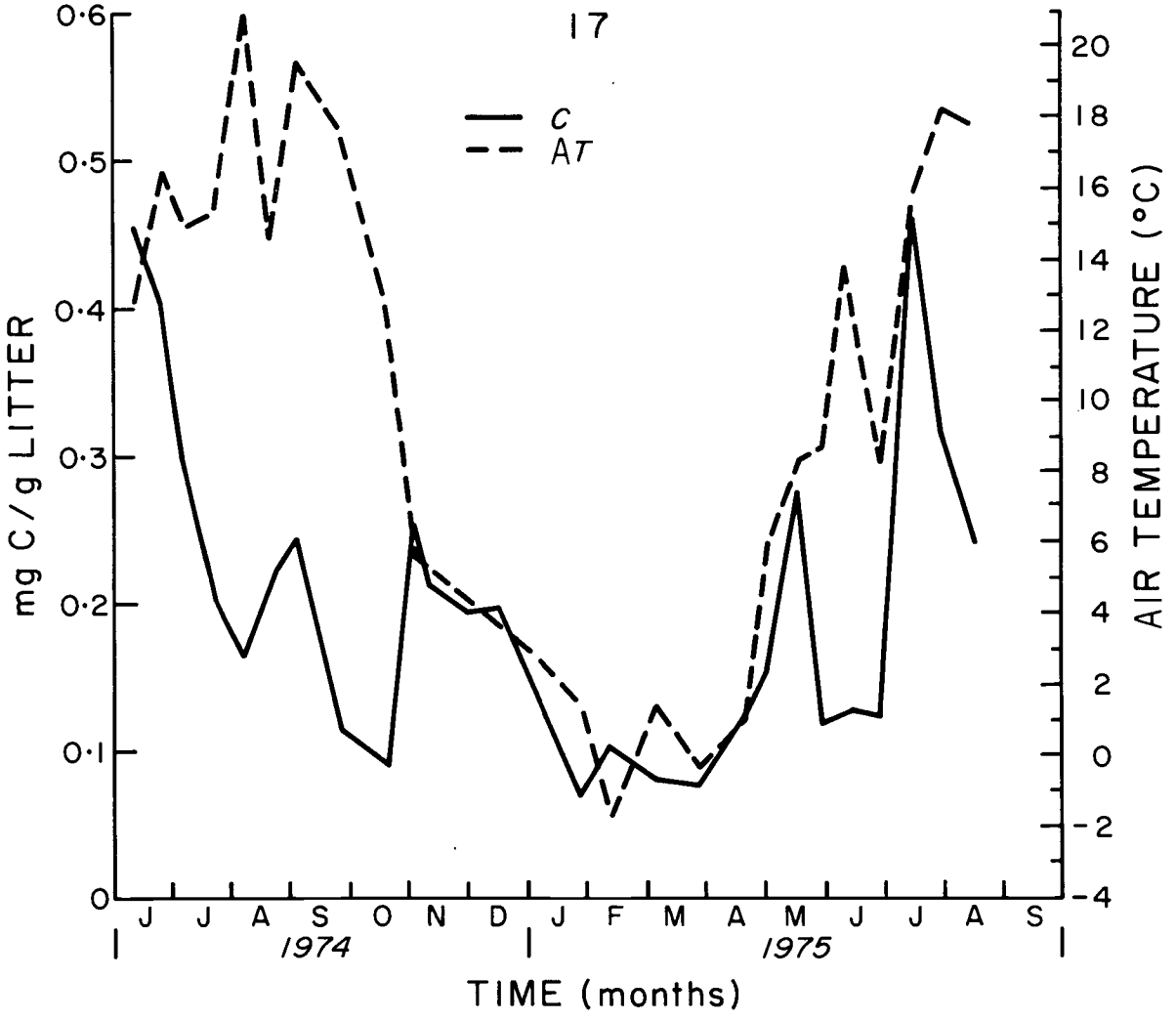


Figure 15. Carbon mineralization and air temperature on the broadcast burn as a function of time.

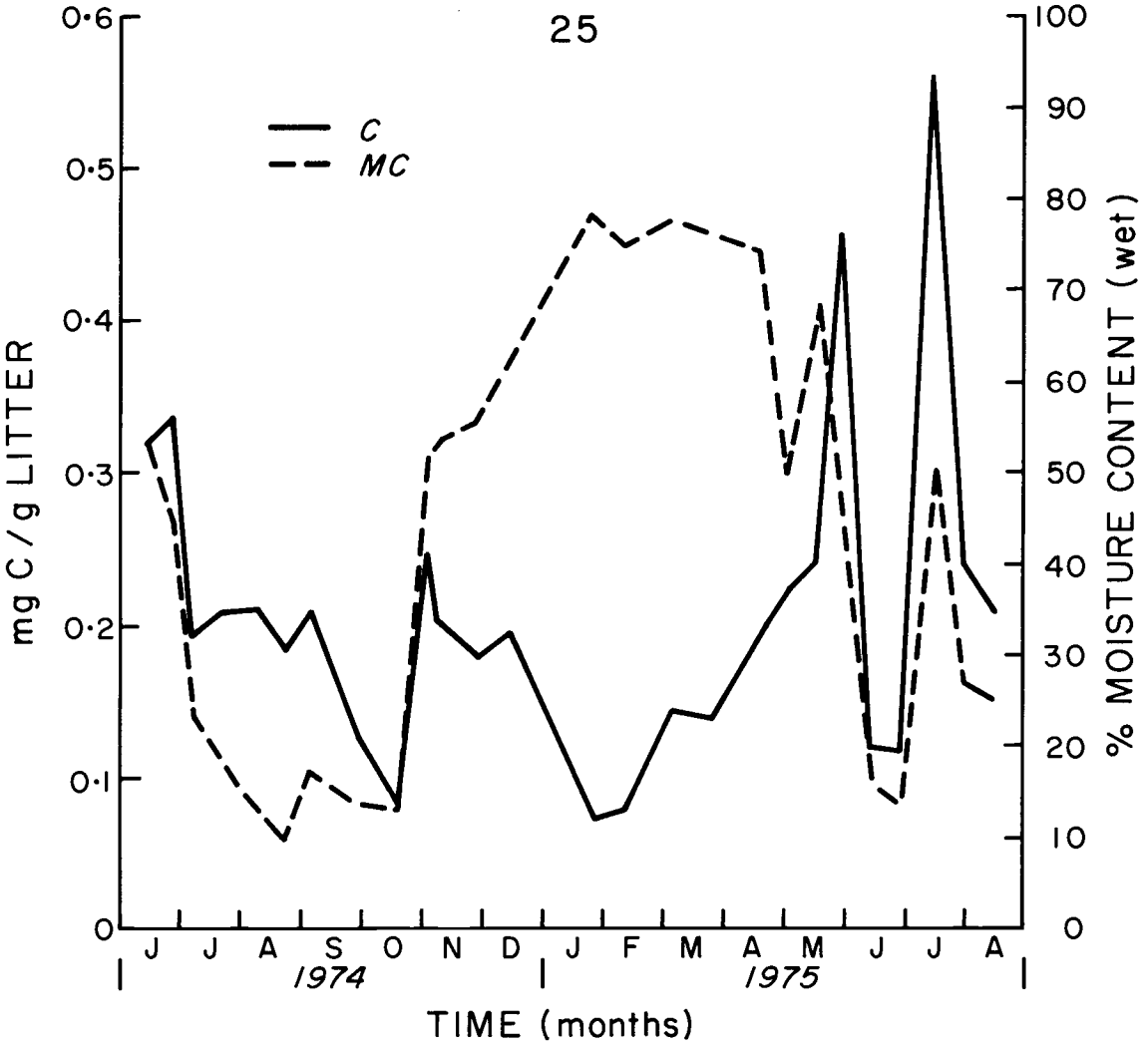


Figure 16. Carbon mineralization and litter moisture content on the broadcast burn as a function of time.

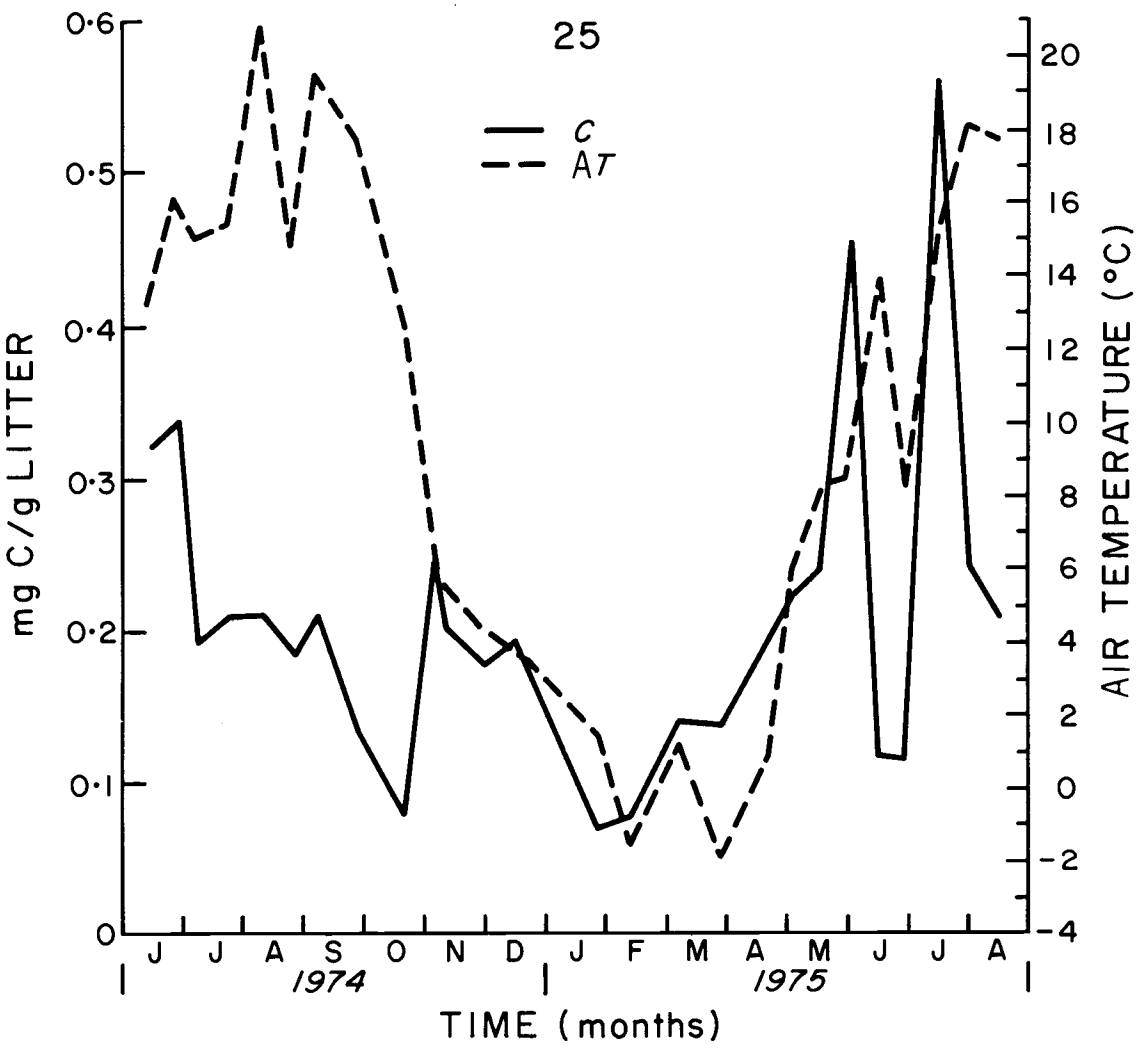


Figure 17. Carbon mineralization and air te erature on the broadcast burn as a function of time.

Table 4. Carbon mineralization (mg C/g litter) from the forest floor of a clearcut that has been broadcast burned.

Date	Burn	
	17	25
5/24/74 - 8/31/74	28.45	23.98
9/ 1/74 - 11/30/74	14.76	14.25
12/ 1/74 - 2/28/75	8.90	9.47
3/ 1/75 - 5/23/75	11.81	17.62
Yearly totals	63.92	65.32
5/24/75 - 8/15/75	20.81	23.35

Seasonal totals for the burn plots are given in Table 4. Highest mineralization rates were obtained during the summer period. P lots on the site were established one month after the area had been broadcast burned in April, 1974. The litter layer was relatively moist during the burn and spring rains continued for approximately a month and a half following the treatment. It is interesting to speculate on the initial rates of carbon mineralization following the burn. Oxidation of the litter layer during the burn would effect the release of cations which could be utilized by microorganisms. This would be reflected by higher pH values for the litter layer. No determination of litter pH values was made before the burn, but an average litter pH value of 5.88 (n = 12) was determined for the site 2 months following the burn (S.Warner, personal communication). This value is higher than pH values from similar unburned sites. Nitrogen values normally

decrease due to volatilization (Cole et al., 1975; Wells, 1971), but as shown in Table 2, nitrogen values remained high in the litter layer.

Decomposition rates were probably rapid following the burn. However, precipitation following the burn may have quickly leached the cations (in the form of soluble oxides) out of the litter layer. From Figures 14 and 16, decomposition rates are seen to continually decrease during the first few sampling periods. The decline closely followed the decrease in litter moisture content, but it is also possible that part of this decrease was due to the loss of cations through leaching.

Yearly totals of carbon mineralization were similar for both burn plots, with the highest rates occurring during the first few months following the burning treatment. When compared to the other study sites, carbon mineralization on the burns was 20% less than on the three forested communities, 39% less than on reference stand 33, and 59% less than on the clearcuts 29 and 36.

Loss of nitrogen was apparently not the reason for the decrease in carbon mineralization rates. It was then considered that the burning may have reduced the amount of labile carbon present in the litter layer. This would have increased the relative percentage of resistant substances, particularly lignin. Selected samples from each season on each of the study sites were analyzed for lignin, cellulose, non-cell wall material and ash, and the results are given in Table 5.

Table 5. Seasonal averages of non-cell wall material[1], lignin[1], cellulose[1], and ash for each study site.

Season	% NCW	% L	% Cellulose	% Ash	% NCW	% L	% Cellulose	% Ash
	RS 2				RS 6			
Fall	47.96	32.86	19.18	4.61	45.76	32.11	22.13	7.00
Winter	40.32	41.91	17.76	5.13	45.03	34.70	20.27	9.70
Spring	45.06	39.40	15.53	4.60	41.20	35.76	23.04	7.56
Summer	43.29	43.44	13.26	5.07	41.08	43.23	15.69	14.73
	RS 7				RS 33			
Fall	44.39	34.98	19.94	3.40	40.11	40.94	18.97	2.31
Winter	42.83	34.08	23.45	4.25	48.80	32.33	18.62	3.21
Spring	46.25	34.60	19.16	4.28	54.16	29.08	16.76	3.37
Summer	39.35	40.77	19.88	6.74	40.87	44.54	14.59	7.46
	29				36			
Fall	41.46	40.70	17.84	2.85	55.57	30.10	14.32	6.44
Winter	44.95	37.58	17.47	6.48	45.98	35.94	18.22	3.21
Spring	52.76	28.09	19.16	8.33	45.82	31.98	22.20	7.41
Summer	38.88	45.81	15.31	7.27	33.29	51.10	15.62	12.30
	17				25			
Fall	41.63	43.17	15.20	4.56	41.98	37.18	20.84	3.14
Winter	40.05	42.45	17.51	7.44	44.97	40.48	14.55	12.96
Spring	41.61	43.91	14.48	8.42	40.74	43.09	16.17	8.80
Summer	41.34	44.87	13.82	5.63	38.45	48.20	13.36	6.45

[1]Sample weight corrected for ash.

The average seasonal percentage of lignin on each of the sites is illustrated in Figure 18. Figure 19 shows the trends in lignin content between RS 2, 6 and 7. No attempt was made to statistically analyze the data. The analysis was done only to show the general trends between sites. Under normal conditions, the lignin content in the litter layer is generally lowest in the fall, but the relative proportion increases over time as the easily decomposable substances are utilized during mineralization. As can be seen from Figure 18, the lignin content on the burns was consistently higher than on the other sites. It is assumed that this is due to the loss of labile carbon species during the burning treatment. However, the charcoal present in the litter samples from the burns contributes to the increase in resistant substances and would not be removed in the 72% H_2SO_4 hydrolysis treatment. So the higher percentage on the burn would be a combination of both acid-insoluble lignin and charcoal.

Analysis for Carbon and Nitrogen

From the experimental results obtained in this study, no apparent relationship between carbon mineralization and nitrogen content or C:N ratios could be determined. Seasonal averages of total nitrogen and C:N ratios are given in Table 2. Nitrogen contents were highest and C:N ratios lowest on the clearcuts.

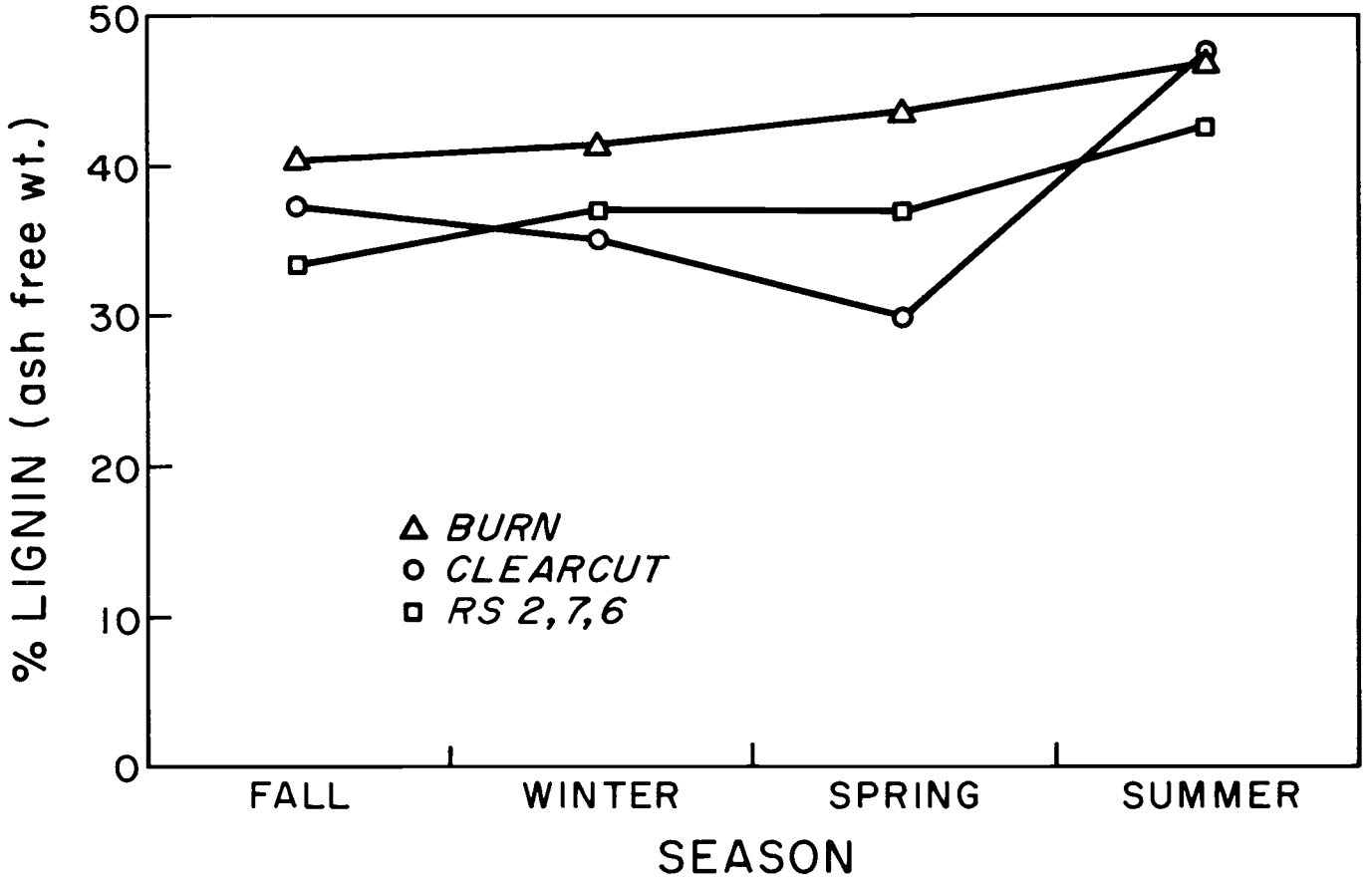


Figure 18. Comparative mean percent lignin content of the forest floor from the forest communities, clearcuts and burns on a seasonal basis.

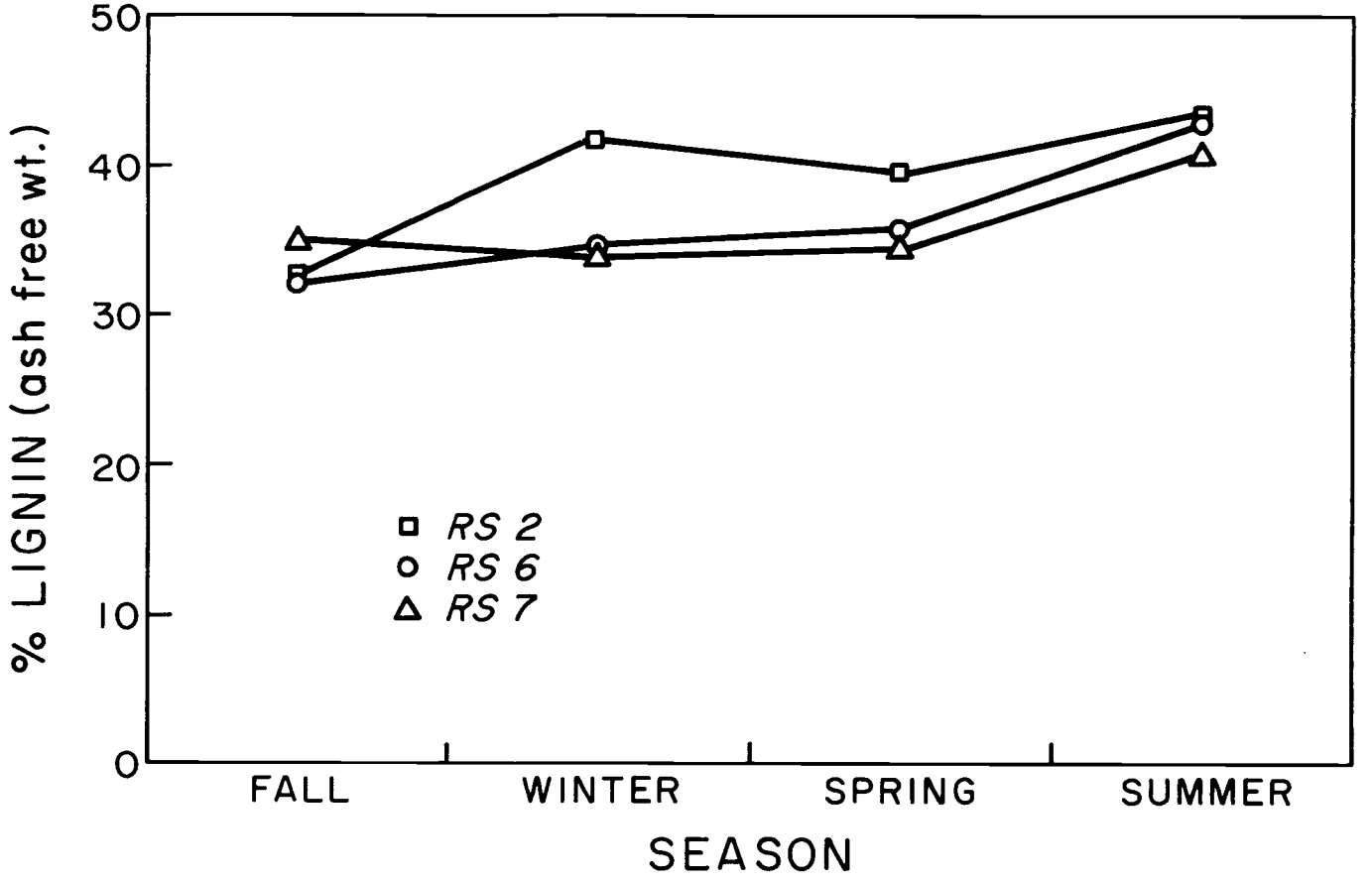


Figure 19. Comparative mean percent lignin content of the forest floor among forest communities on a seasonal basis.

Laboratory Determination of Carbon Mineralization Rates

Decomposition rates were determined under laboratory conditions for litter collected during the summer of 1975 from each of the study sites. Carbon dioxide production was measured for a 32-day period, and daily totals are given in Table 6. Graphical analysis of the data is illustrated by Figures 20, 21 and 22. Initially, there was a rapid rise in CO_2 production for all litter samples due to the exposure of easily decomposable substances by the grinding process. A decline in CO_2 production occurred after 2 to 3 days, and by the end of the week, decomposition had reached a steady state level characterized by a slow oxidation rate.

Decomposition values between the burns and clearcut plots 29 and 36 were similar (Table 6). The value obtained for reference stand 33 was approximately 11% higher (Table 6). Dissimilar rates of CO_2 production were obtained for reference stands 2, 6 and 7. Total production on reference stand 6 was 13% and 62% higher than on reference stands 2 and 7, respectively. Part of the variability could be due to a difference in litter pH. Reference stand 6 had a higher proportion of deciduous leaf species in the litter mixture which would be reflected in a higher pH value. The average value for litter from reference stand 6 was pH 5.4 ($n = 22$). Average values for reference stands 2

Table 6. Carbon mineralization (mg CO_2/g litter) of selected litter samples from each of the study sites under laboratory conditions.

Day	RS 2	RS 6	R 7	RS 33	29 36 $\bar{\mu}$	17	25
1	1.52	2.21	1.34	1.51	1.70	1.88	1.70
2	1.26	1.77	1.32	1.36	1.17	1.07	1.14
3	0.79	1.04	0.76	0.81	0.63	0.79	0.83
4	0.78	1.06	0.63	0.77	0.68	0.89	0.93
5	0.72	0.88	0.53	0.81	0.70	0.71	0.77
6	0.60	0.78	0.51	0.79	0.70	0.67	0.72
7	0.60	0.69	0.43	0.76	0.61	0.54	0.62
11	0.56	0.71	0.42	1.00	0.76	0.60	0.68
13	0.60	0.67	0.38	1.11	0.77	0.67	0.68
15	0.62	0.59	0.35	0.70	0.79	0.67	0.68
17	0.69	0.64	0.29	0.95	0.75	-	0.67
19	0.64	0.49	0.22	0.74	0.57	0.36	0.49
21	0.64	0.45	0.22	0.63	0.54	0.38	0.47
23	0.67	0.52	0.26	0.69	0.61	0.48	0.49
27	0.55	0.51	0.24	0.45	0.55	0.43	0.45
32	0.51	0.29	0.29	0.31	0.45	0.47	0.47
Total	11.75	13.30	8.19	13.39	11.98	11.28	11.79

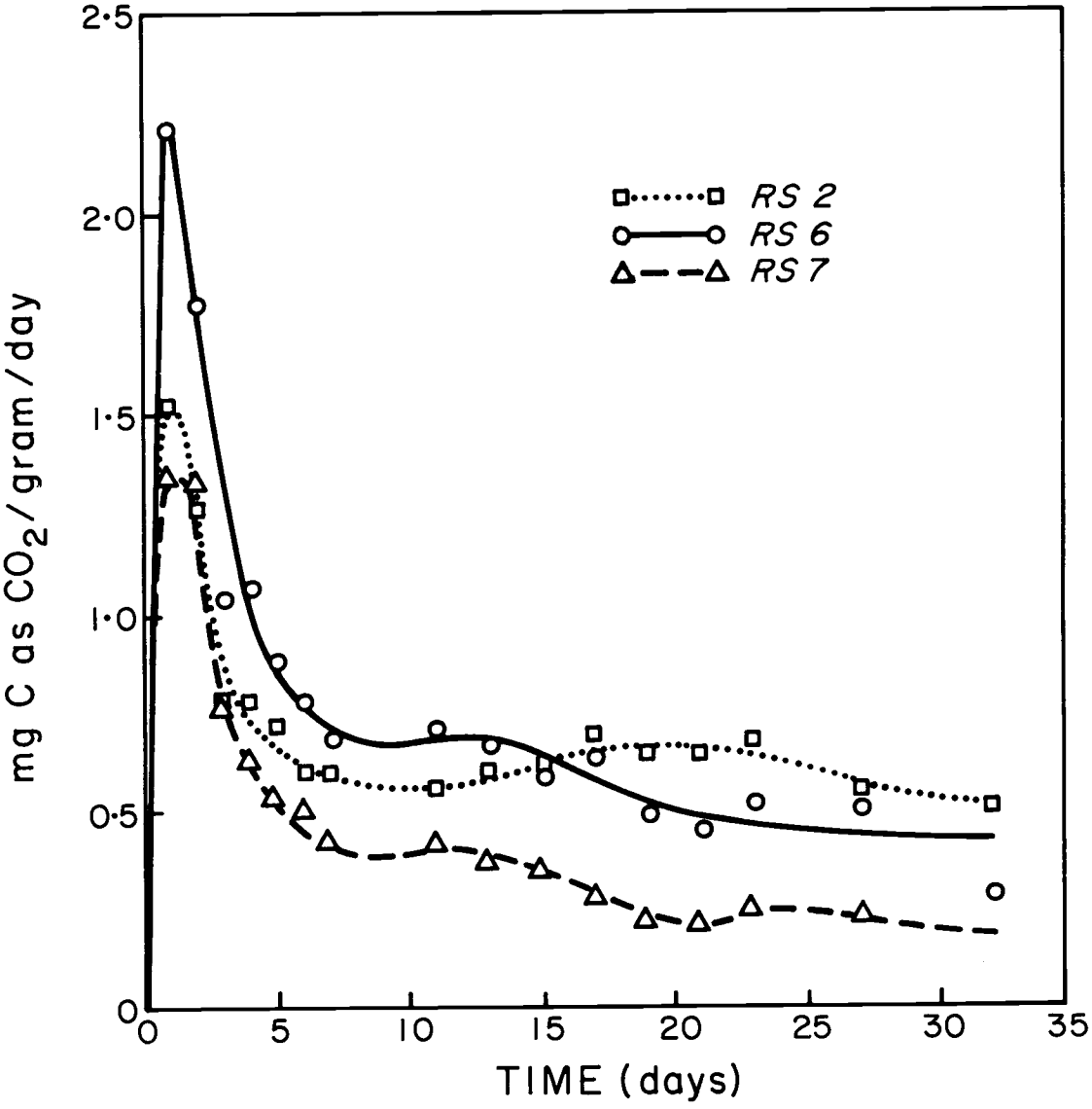


Figure 20. Carbon dioxide evolution from litter from burn plots under laboratory conditions.

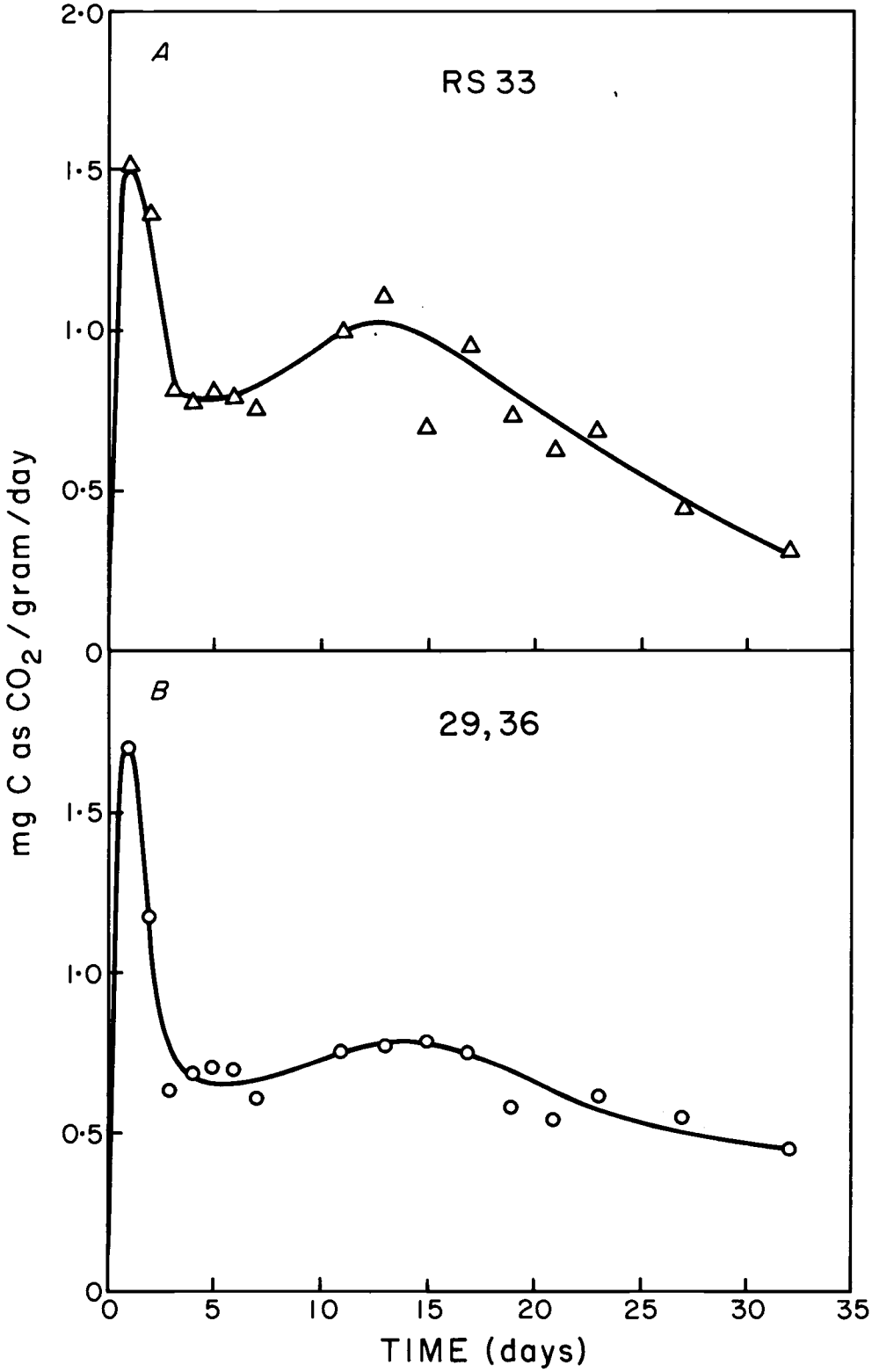


Figure 21. Carbon dioxide evolution from litter from clearcut plots under laboratory conditions.

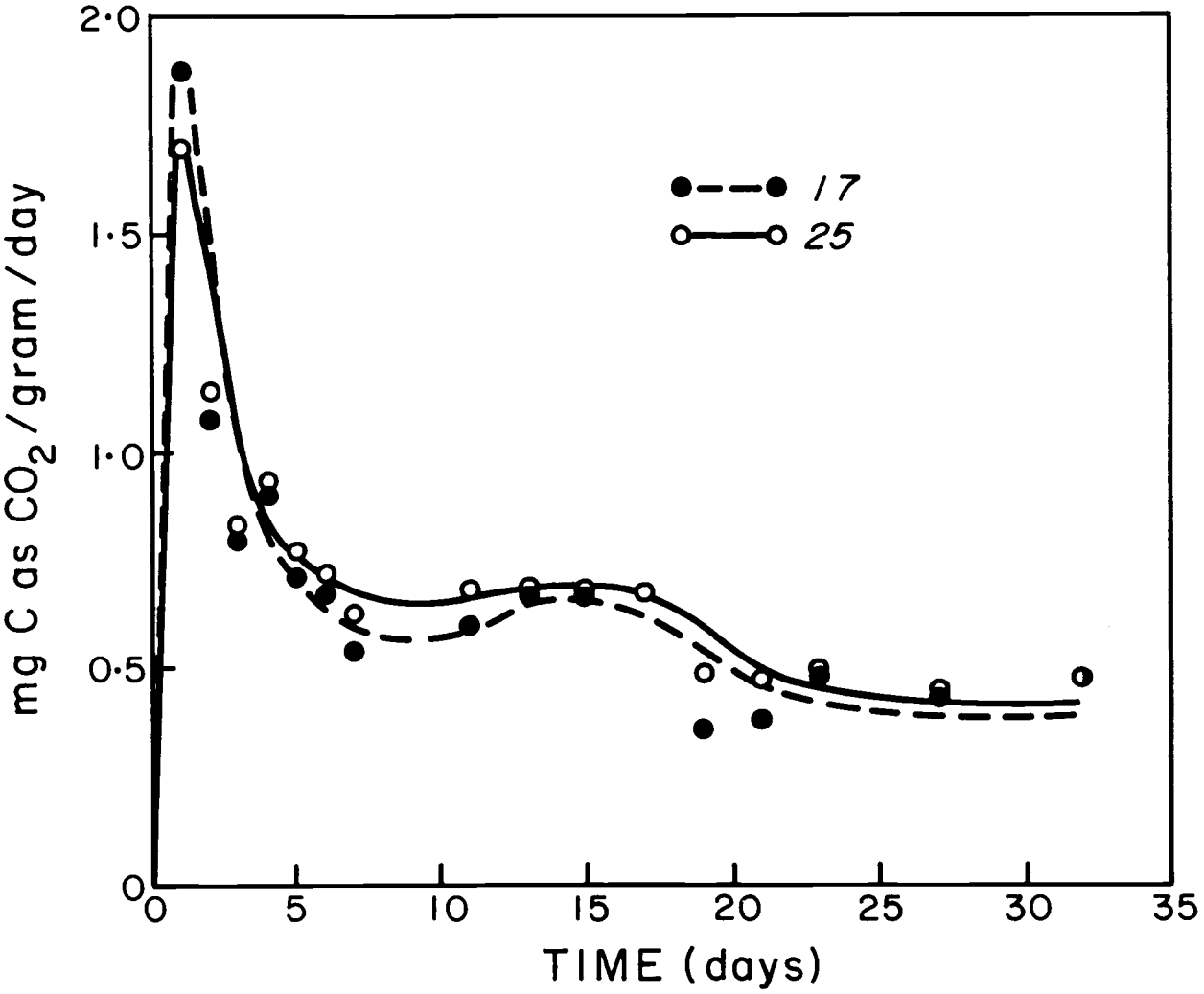


Figure 22. Carbon dioxide evolution from litter from forest communities under laboratory conditions.

(n = 17) and 7 (n = 26) were pH 4.81 and pH 4.77, respectively (S. Warner, personal communication).

The final decomposition values (steady state level) obtained under laboratory conditions for the three reference stands were lower than the carbon mineralization rates from the field studies. The greater production of CO_2 under field conditions could have resulted from the litter being subjected to alternate drying and rewetting patterns.

SUMMARY

(1) Carbon mineralization of litter from the forest floor of three old growth forest communities, measured as CO_2 liberated in field site glass electrolytic respirometers, was similar, both seasonally and yearly; maximum production of CO_2 occurred during the fall and spring months when temperature and moisture were most favorable for decomposer activity.

(2) Peaks in CO_2 production on all sites closely followed increases in moisture content, particularly during the early fall months.

(3) Clearcutting increased the rate of carbon mineralization, the magnitude of the increase in part being related to the age of the clearcut.

(4) Broadcast burning following a clearcut reduced the rate of carbon mineralization of residual litter. It was thought to be due in part to a relative increase in resistant substances, particularly lignin and charcoal.

(5) Carbon mineralization under snow was high compared to uncovered sites, possibly due to stabilized litter temperatures which might stimulate the growth of fungal populations.

(6) Litter temperature and litter moisture content as estimated by present study techniques did not yield correlations useful for

predicting carbon mineralization rates on an annual basis in areas subjected to wet and dry seasons. Significant correlations between these two factors and litter decomposition as measured by CO_2 evolution were found only for data for certain seasons.

(7) Litter moisture content was the dominant abiotic factor operating during the fall and summer months. Litter temperature appeared to dominate during the winter months although correlations were not statistically significant for all sites, possibly due to the inaccuracy of estimating litter temperature under snowpack.

(8) Decomposition of litter was greater in field site respirometers than in constant temperature, constant moisture laboratory incubations, possibly due to the stimulating effect of drying-rewetting on CO_2 production under field conditions.

LITERATURE CITED

Abee, Albert and Denis Lavender. 1972. Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands. In J.F. Franklin, L.J. Dempster and R.H. Waring (eds.). Proceedings--Research on coniferous forest ecosystems--A symposium, p. 133-143. USDA Forest Service, Portland, Or.

Alexander, M. 1961. Introduction to soil microbiology. John Wiley and Sons, Inc., New York. x + 472 p.

Allison, L.E., W.B. Bollen and C.D. Moodie. 1965. Total carbon, p. 1346-1366. In C.A. Black, D.D. Evans, J.L. White, L.E. Ensminger and F.E. Clark (eds.). Methods of soil analysis, Part 2. American Society of Agronomy, Inc. xlii + 801 p.

Bartholomew, W.V. and A.G. Norman. 1946. The threshold moisture content for active decomposition of some mature plant materials. Soil Sci. Soc. Amer. Proc. 7:270-279.

Beck, S.M. and C.M. Gilmour. 1974. Progress report: Land disposal of cattle feedlot waste. Univ. of Idaho, Moscow. 12 p.

Benoit, R.E. and R.L. Starkey. 1968. Enzyme inactivation as a factor in the inhibition of decomposition of organic matter by tannins. Soil Sci. 105:203-208.

Birch, H.F. 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil 10:9-31.

_____. 1959. Further observations on humus decomposition and nitrification. Plant and Soil 11:262-286.

Bocock, K.L. and O.J.W. Gilbert. 1957. The disappearance of leaf litter under different woodland conditions. Plant and Soil 9:179-185.

Bocock, K.L., O. Gilbert, C.K. Capstick, D.C. Twinn, J.S. Waid and M.J. Woodman. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. I. Losses in dry weight of oak and ash leaf litter. J. Soil Sci. 11:1-9.

Bocock, K.L. 1964. Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecology 52:273-284.

Bray, Roger J. and Eville Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101-157.

Broadfoot, W.M. and W.H. Pierre. 1939. Relation of rate of decomposition of tree leaves to their acid-base balance and other chemical properties. Soil Sci. 48:329-348.

Brown, R.B. and R.B. Parsons. 1973. Soils of the reference stands--Oregon IBP. Internal report 128. Coniferous Forest Biome. Ecosystem analysis studies. 76 p.

Coile, T.S. 1937. Composition of the leaf litter of forest trees. Soil Sci. 43:349-355.

Cole, D.W., W.J.B. Crane and C.C. Grier. 1975. The effect of forest management practices on water chemistry in a second-growth Douglas-fir ecosystem, p. 195-207. In B. Bernier and C.H. Winget (eds.)., Forest soils and forest land management. Les Presses de L'universite Laval, Quebec. x + 675 p.

Corbet, Steven A. 1934. Studies on tropical soil microbiology. I. The evolution of carbon dioxide from the soil and the bacterial growth curve. Soil Sci. 37:109-115.

Cromack, K., Jr. 1973. Litter production and decomposition in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina. PhD. thesis. Univ. of Georga, Athens, Ga. 160 p.

Daubenmire, R. and Don C. Prusso. 1963. Studies of the decomposition rates of tree litter. Ecology 44:589-592.

Douglas, L.A. and J.C.F. Tedrow. 1959. Organic matter decomposition rates in arctic soils. Soil Sci. 6:305-312.

Dyrness, C.T., J.F. Franklin and W.H. Moir. 1974. A preliminary classification of forest communities in the central portion of the Western Cascades in Oregon. Bulletin No. 4, Coniferous Forest Biome. Ecosystem analysis studies. 123 p.

Edwards, N.T. and P. Sollins. 1973. Continuous measurement of carbon dioxide evolution from partitioned forest floor components. Ecology 52:406-412.

Edwards, N.T. 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Amer. Proc. 39:361-365.

Ellis, R.C. 1969. The respiration of the soil beneath some Eucalyptus forest stands as related to the productivity of the stands. Aust. J. Soil Res. 7:349-357.

Garrett, H.E. and G.S. Cox. 1973. Carbon dioxide evolution from the forest floor of an oak-hickory forest. Soil Sci. Soc. Amer. Proc. 37:641-644.

Gilbert, O. and K.L. Bocock. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. II. Changes in the nitrogen content of oak and ash leaf litter. J. Soil Sci. 11:10-19.

Gist, C.S. and D.A. Crossley, Jr. 1975. The litter arthropod community in a southern Appalachian hardwood forest: numbers, biomass and mineral element content. American Midland Naturalist 93:107-122.

Golley, Frank B. 1960. An index to the rate of cellulose decomposition in the soil. Ecology 41:551-552.

Goodfellow, M. 1968. Properties and composition of the bacterial flora of a pine forest soil. J. Soil Sci. 19:154-167.

Gustafson, Felix G. 1943. Decomposition of the leaves of some forest trees under field conditions. Plant Physiology 18:704-707.

Handley, W.R.C. 1961. Further evidence for the importance of residual leaf protein complexes in litter decomposition and the supply of nitrogen for plant growth. Plant and Soil 13:37-73.

Hayes, A.J. 1965. Studies on the decomposition of coniferous leaf litter. I. Physical and chemical changes. J. Soil Sci. 16:121-140.

Heal, O.W. and D.D. French. 1974. Decomposition of organic matter in tundra. In A.J. Holding et al. (eds.). Soil organisms and decomposition in tundra, p. 279-309. Tundra Biome Steering Committee, Stockholm.

Hoover, M.D. and H.A. Lunt. 1952. A key for the classification of forest humus types. Soil Sci. Soc. Amer. Proc. 16:368-370.

Hu, Lily, C.T. Youngberg and C.M. Gilmour. 1972. Readily oxidizable carbon: An index of decomposition and humification of forest litter. Soil Sci. Soc. Amer. Proc. 36:959-961.

Ivarson, K.C. and F.J. Sowden. 1959. Decomposition of forest litters. I. Production of ammonia and nitrate nitrogen, changes in microbial population and rate of decomposition. Plant and Soil 11:237-248.

Jackson, M.L. 1958. Soil chemical analysis. Prentice Hall, Englewood Cliffs, N.J. 498 p.

Jager, G. and E.H. Bruins. 1975. Effect of repeated drying at different temperatures on soil organic matter decomposition and characteristics, and on the soil microflora. Soil Biol. Biochem. 7:153-159.

Jenny, Hans, S.P. Gessel and F.T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68:419-432.

Jenny, Hans. 1950. Causes of the high nitrogen and organic matter content of certain tropical forest soils. Soil Sci. 69:63-69.

Jorgensen, J.R. and C.G. Wells. 1971. Apparent nitrogen fixation in soil influenced by prescribed burning. Soil Sci. Soc. Amer. Proc. 35:806-810.

Kendrick, W.B. 1958. Micro-fungi in pine litter. Nature 181:432.

_____. 1959. The time factor in the decomposition of coniferous leaf litter. Can. J. Botany 37:907-912.

Kowal, Norman Edward. 1969. Effect of leaching on pine litter decomposition rate. Ecology 50:739-740.

Lewis, J.A. and R.L. Starkey. 1968. Vegetable tannins, their decomposition and effects on decomposition of organic compounds. Soil Sci. 106:241-247.

Lockhead, A.G. and F.E. Chase. 1943. Qualitative studies on soil microorganisms. V. Nutritional requirements of the predominant bacterial flora. Soil Sci. 55:185-195.

Lunt, Herbert A. 1931. The carbon-organic matter factor in forest soil humus. Soil Sci. 32:27-33.

Maccauley, B.J. and L.B. Thrower. 1966. Succession of fungi in leaf litter of Eucalyptus regans. Trans. Br. Mycol. Soc. 49:

Macfadyen, A. 1963. Animal ecology. Sir Isaac Pitman and Sons, London. xxiv + 344 p.

Mader, Donald L. 1953. Physical and chemical characteristics of the major types of forest humus found in the United States and Canada. Soil Sci. Soc. Amer. Proc. 17:155-158.

Marten, E.A. and G.C. Pohlman. 1942. Forest soil studies. II. Changes in microflora and chemical composition of decomposing tree leaves. Soil Sci. 54:67-77.

McGill, W.B., J.A. Shields and E.A. Paul. 1975. Relation between carbon and nitrogen turnover in soil organic fractions of microbial origin. Soil Biol. Biochem. 7:57-63.

Messenger, A.S. 1975. Climate, time and organisms in relation to podzol development in Michigan stands. I. Relationships between chemical element concentrations in mature tree foliage and upper humic horizons. Soil Sci. Soc. Amer. Proc. 39:698-702.

Metz, Louis J. 1954. Forest floor in the Piedmont region of South Carolina. Soil Sci. Soc. Amer. Proc. 18:335-338.

Mikola, Peitsa. 1960. Comparative experiment on decomposition rates of forest litter in southern and northern Finland. Oikos 11:161-166.

Minderman, G. 1968. Addition, decomposition and accumulation of organic matter in forests. J. Ecology 56:355-362.

Minyard, P.L. and C.H. Driver. 1972. Initial steps in decomposition of Douglas-fir needles under forest conditions, p. 216-263. In J.F. Franklin, L.J. Dempster and R.H. Waring (eds.). Proceedings--Research on coniferous forest ecosystems--A symposium. USDA Forest Service, Portland, Or.

Nykvist, N. 1959a. Leaching and decomposition of litter. I. Experiments on leaf litter of Fraxinus excelsior. Oikos 10:190-211.

_____. 1959b. Leaching and decomposition of litter. II. Experiments on needle litter of Pinus silvestris. Oikos 10:212-224.

Odum, E.P. 1971. Fundamentals of ecology. 3rd ed. W.B. Saunders Co., Philadelphia. xiv + 574 p.

Ovington, J.D. 1954. Studies of the development of woodland conditions under different trees. II. The forest floor. J. Ecology 42:71-80.

Pinck, L.A., F.E. Allison and M.S. Sherman. 1950. Maintenance of soil organic matter. II. Losses of carbon and nitrogen from young and mature plant materials during decomposition in soil. Soil Sci. 69:391-401.

Platt, R.L. 1973. Carbon mineralization of coniferous forest litter. M.S. thesis. Univ. of Idaho, Moscow. 84 p.

Reddy, K.R. and W.H. Patrick, Jr. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential and nitrogen loss in a flooded soil. Soil Biol. Biochem. 7:87-94.

Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecology 49:471-483.

Romell, L.G. and S.O. Heiberg. 1935. Ecological problems of the humus layer of the forest. N.Y. (Cornell) Agr. Exp. Sta. Mem. 170 p.

Rosswall, T. 1974. Cellulose decomposition on the tundra, p. 325-340. In A.J. Holding et al. (eds.). Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm.

Rothacher, J., C.T. Dyrness and R.L. Fredriksen. 1967. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. USDA For. Serv. Pacific Northwest Forest and Range Exp. Sta. Misc. Paper. 54 p.

Schulze, E.P. 1967. Soil respiration of tropical vegetation types. Ecology 48:652-653.

Sjors, H. 1959. Changes in pH of leaf litter during a field experiment. Oikos 10:225-231.

Sorensen, L.H. 1974. Rate of decomposition of organic matter in soil as influenced by repeated air drying-rewetting and repeated additions of organic material. Soil Biol. Biochem. 6:287-292.

Sowden, F.J. 1962. Decomposition of forest litters. III. Changes in the carbohydrate constituents. Plant and Soil 14:389-400.

Stark, N. 1972. Nutrient cycling pathways and litter fungi. Bio Science 22:355-360.

Starkey, R.L. 1924. Some observations on the decomposition of organic matter in soils. Soil Sci. 17:293-314.

Stevenson, I. 1957. Some observations on the microbial activity in remoistened air-dried soils. Plant and Soil 8:170-182.

Tribe, H.T. 1960. Aspects of decomposition of cellulose in Canadian soils. I. Observations with the microscope. Can. J. Microbiol. 6:309-316.

Van Cleve, K. 1974. Organic matter quality in relation to decomposition, p. 311-324. In A.J. Holding et al. (eds.). Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm.

Van Soest, P.J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. Journal of the A.O.A.C. 46:829-835.

_____. 1966. Nonnutritive residues: A system of analysis for the replacement of crude fiber. Journal of the A.O.A.C. 49:546-551.

Waksman, S.A. 1929. Chemical nature of soil organic matter, methods of analysis, and the role of microorganisms in its formation and decomposition. Trans. 2nd Comm. Intern. Soc. Soil Sci., Budapest, Part A.

Waksman, S.A. and F.C. Gerretsen. 1931. Influence of temperature and moisture upon the nature and extent of decomposition of plant residues by microorganisms. Ecology 12:33-60.

Wells, C.G. 1971. Effects of prescribed burning on soil chemical properties and nutrient availability, p. 86-97. USDA Forest Service. Prescribed burning symposium proceedings. Asheville, N.C. Southeastern For. Exp. Sta. 160 p.

Wiant, H.V., Jr. 1967a. Has the contribution of litter decay to forest "soil respiration" been overestimated? J. Forestry 65:408-409.

Wiant, H.V., Jr. 1967b. Influence of temperature on the rate of "soil respiration." J. Forestry 65:489-490.

_____. 1967c. Influence of moisture content on "soil respiration." J. Forestry 65:902-903.

Wicklow, M.C., W.B. Bollen and W.C. Denison. 1974. Comparison of soil microfungi in 40-year-old stands of pure alder, pure conifer and alder-conifer mixtures. Soil Biol. Biochem. 6:73-78.

Wicklow, M.C. and W.F. Whittingham. 1974. Soil microfungal changes among the profiles of disturbed conifer-hardwood forests. Ecology 55:3-16.

Wilde, S.A., S.F. Buran and H.M. Galloway. 1937. Nutrient content and base exchange properties of organic layers of forest soils in the Lake States region. Soil Sci. 44:231-238.

Witkamp, M. and J. Van Der Drift. 1961. Breakdown of forest litter in relation to environmental factors. Plant and Soil 15:295-311.

Witkamp, M. 1963. Microbial populations of leaf litter in relation to environmental conditions and decomposition. Ecology 44:370-377.

Witkamp, M. and J.S. Olson. 1963. Breakdown of confined and non-confined oak litter. Oikos 14:138-147.

Witkamp, M. 1966a. Decomposition of leaf litter in relation to environment, microflora and microbial respiration. Ecology 47:194-201.

_____. 1966b. Rates of carbon dioxide evolution from the forest floor. Ecology 47:492-494.

_____. 1969. Cycles of temperature and carbon dioxide evolution from litter and soil. Ecology 50:922-924.

Wright, Ernest and W.B. Bollen. 1961. Microflora of Douglas-fir forest soil. Ecology 42:825-828.

APPENDIX

Appendix Table 1. Interval mean decomposition values (mg C/g litter) and weighted mean of litter temperature and litter moisture content for the forest communities.

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
RS 2	73 228-73 242	18.03	13.7	0.07
	73 242-73 256	43.08	15.2	0.22
	73 256-73 265	28.40	13.4	0.11
	73 265-73 278	65.57	10.9	0.51
	73 278-73 299	49.84	9.5	0.17
	73 299-73 309	69.08	7.0	0.43
	73 309-73 324	77.71	3.9	0.22
	73 324-73 349	81.41	3.1	0.19
	73 349-73 362	79.71	5.1	0.19
	73 362-74 17	80.83	1.5	0.12
	74 17 -74 37	72.96	3.8	0.16
	74 37 -74 51	77.63	3.4	0.08
	74 51 -74 66	78.92	2.8	0.07
	74 66 -74 80	75.57	4.5	0.16
	74 80 -74 101	68.74	6.3	0.23
	74 101-74 124	77.36	8.3	0.23
	74 124-74 144	61.98	9.1	0.33
	74 144-74 164	58.83	13.5	0.30
	74 164-74 177	46.26	15.9	0.29
	74 177-74 188	28.14	15.6	0.17
	74 188-74 204	16.84	15.1	0.10
	74 204-74 219	11.96	20.1	0.21
	74 219-74 234	10.51	15.1	0.11
	74 234-74 248	15.57	18.1	0.23
	74 248-74 270	13.04	16.4	0.12
	74 270-74 293	13.05	17.9	0.11
	74 293-74 307	45.82	7.0	0.43
	74 307-74 314	58.92	6.9	0.61
	74 314-74 333	70.88	5.7	0.36
	74 333-74 349	74.67	5.2	0.46
	74 349-75 13	79.67	2.1	0.23
	75 13 -75 26	80.07	4.2	0.31
	75 26 -75 43	73.36	1.2	0.13
	75 43 -75 65	79.95	3.0	0.28
	75 65 -75 87	72.74	2.5	0.23
	75 87 -75 110	64.17	3.6	0.17
	75 110-75 137	65.12	7.2	0.36

(Continued on next page)

Appendix Table 1. (Continued)

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
RS 6	73 228-73 242	19.17	14.1	0.08
	73 242-73 256	32.93	16.2	0.21
	73 256-73 265	29.23	13.6	0.21
	73 265-73 278	66.20	11.0	0.81
	73 278-73 299	41.72	9.9	0.14
	73 299-73 324	64.01	4.0	0.27
	73 324-73 349	74.51	3.2	0.14
	73 349-73 362	67.27	4.6	0.18
	73 362-74 17	83.67	1.6	0.08
	74 17 -74 37	66.90	3.2	0.06
	74 37 -74 51	71.98	3.6	0.10
	74 51 -74 80	75.65	3.2	0.16
	74 80 -74 101	64.04	5.7	0.17
	74 101-74 124	74.61	8.9	0.37
	74 124-74 144	55.63	10.3	0.22
	74 144-74 162	62.11	14.6	0.34
	74 162-74 176	44.98	18.2	0.33
	74 176-74 188	39.14	16.5	0.32
	74 188-74 204	24.75	15.5	0.17
	74 204-74 220	17.90	20.8	0.18
	74 220-74 235	8.37	16.1	0.09
	74 235-74 248	26.21	19.3	0.34
	74 248-74 270	13.31	18.5	0.21
	74 270-74 293	9.93	13.3	0.09
	74 293-74 307	30.52	7.1	0.31
	74 307-74 314	63.09	6.4	0.55
	74 314-74 333	61.07	5.0	0.27
	74 333-74 349	69.98	4.6	0.41
	74 349-75 25	79.79	2.1	0.18
	75 25 -75 43	80.76	0.7	0.28
	75 43 -75 65	80.43	2.7	0.51
	75 65 -75 86	70.27	1.8	0.32
	75 86 -75 110	76.17	2.7	0.34
	75 110-75 137	73.22	6.4	0.56
	75 137-75 150	37.21	8.5	0.34

(Continued on next page)

Appendix Table 1. (Continued)

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
RS 7	73 228-73 242	20.65	13.1	0.07
	73 242-73 256	37.87	14.6	0.25
	73 256-73 265	34.99	12.3	0.31
	73 265-73 278	68.65	10.1	0.45
	73 278-73 299	54.61	8.8	0.22
	73 299-73 309	71.73	6.1	0.37
	73 309-73 324	77.15	3.2	0.26
	73 324-73 349	81.98	3.1	0.14
	73 349-73 362	78.89	4.5	0.25
	73 362-74 17	78.98	1.2	0.10
	74 17 -74 37	76.75	3.3	0.10
	74 37 -74 51	75.39	3.1	0.10
	75 51 -74 66	78.50	2.3	0.17
	74 66 -74 80	82.29	4.0	0.25
	74 80 -74 101	74.35	7.1	0.17
	74 101-74 124	80.77	8.7	0.23
	74 124-74 144	63.14	9.1	0.37
	74 144-74 162	63.20	12.3	0.31
	74 162-74 176	47.32	16.2	0.27
	74 176-74 188	37.78	14.5	0.27
	74 188-74 204	16.00	14.5	0.13
	74 204-74 219	16.07	19.1	0.23
	74 219-74 234	11.88	14.6	0.12
	74 234-74 248	17.80	17.4	0.17
	74 248-74 270	14.39	15.2	0.23
	74 270-74 293	12.58	10.6	0.05
	74 293-74 307	57.56	6.9	0.41
	74 307-74 314	68.24	6.5	0.50
	74 314-74 333	74.96	5.6	0.39
	74 333-74 349	75.93	5.4	0.29
	74 349-75 13	82.57	3.6	0.26
	75 13 -75 25	80.81	3.8	0.24
	75 25 -75 43	83.85	1.1	0.27
	75 43 -75 65	78.37	2.6	0.25
	75 65 -75 87	70.90	2.2	0.20
	75 87 -75 110	72.81	3.2	0.22
	75 110-75 136	75.38	6.8	0.33
	75 136-75 151	37.24	10.4	0.36
	75 151-75 164	51.92	14.0	0.45

Appendix Table 2. Interval mean decomposition values (mg C/g litter) and weighted mean of litter temperature and litter moisture content for clearcuts (29, 36 and RS 33).

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
29	74 144-74 163	58.81	13.8	0.55
	74 163-74 177	54.95	17.0	0.62
	74 177-74 187	33.54	15.8	0.33
	74 187-74 204	26.70	15.9	0.21
	74 204-74 219	18.50	21.1	0.25
	74 219-74 234	17.47	15.3	0.18
	74 234-74 248	24.22	19.5	0.24
	74 248-74 270	15.15	7.9	0.06
	74 270-74 293	15.10	13.6	0.04
	74 293-74 307	71.67	7.7	0.38
	74 307-74 314	70.70	7.3	0.30
	74 314-74 333	69.28	6.5	0.23
	74 333-74 349	71.13	6.0	0.23
	74 349-75 24	80.41	3.8	0.13
	75 24 -75 65	82.06	3.0	0.23
	75 65 -75 87	82.65	2.4	0.37
	75 87 -75 110	60.73	3.7	0.21
	75 110-75 122	37.01	7.8	0.32
	75 122-75 137	73.10	10.0	1.18
	75 137-75 151	26.28	10.2	0.29
	75 151-75 165	19.19	14.7	0.20
	75 165-75 178	12.66	9.8	0.09
	75 178-75 195	36.24	16.2	0.37
	75 195-75 211	26.38	18.3	0.58
	75 211-75 227	25.92	18.1	0.35
36	74 144-74 163	60.03	13.8	0.25
	74 163-74 177	53.16	17.0	0.34
	74 177-74 187	29.50	15.8	0.28
	74 187-74 204	29.01	15.9	0.18
	74 204-74 220	23.33	20.8	0.33
	74 220-74 234	25.89	15.3	0.28
	74 234-74 248	18.76	19.5	0.27
	74 248-74 270	13.05	17.9	0.11
	74 270-74 293	11.70	13.6	0.15
	74 293-74 307	72.46	7.7	0.81
	74 307-74 314	68.34	7.3	0.51
	74 314-74 333	64.49	6.5	0.32

(Continued on next page)

Appendix Table 2. (Continued)

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
36	74 333-74 349	71.82	6.0	0.44
(cont'd)	74 349-75 25	74.99	3.9	0.07
	75 25 -75 43	85.71	1.4	0.34
	75 43 -75 87	71.07	2.5	0.23
	75 87 -75 110	56.43	3.7	0.20
	75 110-75 122	51.54	7.8	0.17
	75 122-75 137	74.59	10.0	0.69
	75 137-75 151	28.95	10.2	0.13
	75 151-75 165	13.99	14.7	0.10
	75 165-75 178	20.69	9.8	0.12
	75 178-75 195	43.22	16.2	0.34
	75 195-75 211	28.41	18.3	0.27
	75 211-75 227	21.53	18.1	0.19
RS 33	74 162-74 176	31.87	16.1	0.19
	74 176-74 187	27.38	13.6	0.25
	74 187-74 204	27.18	14.2	0.22
	74 204-74 219	21.72	19.4	0.26
	74 219-74 234	14.93	13.6	0.15
	74 234-74 248	17.11	17.8	0.23
	74 248-74 270	14.76	16.2	0.07
	74 270-74 293	11.96	11.9	0.04
	74 293-74 307	68.26	5.9	0.29
	74 307-74 314	68.32	5.6	0.41
	74 314-74 333	68.37	4.7	0.50
	74 333-74 349	73.49	4.3	0.43
	74 349-75 24	82.58	2.1	0.24
	75 24 -75 43	82.08	0.6	0.42
	75 43 -75 65	84.61	2.4	0.51
	75 65 -75 110	43.12	1.4	0.17
	75 110-75 151	28.63	7.2	0.16
	75 151-75 165	14.14	13.0	0.16
	75 165-75 178	12.85	8.0	0.07
	75 178-75 195	41.43	14.4	0.52
	75 195-75 211	28.47	16.6	0.28
	75 211-75 227	24.24	16.4	0.23

Appendix Table 3. Interval mean decomposition values (mg C/g litter) and weighted mean of air temperature and litter moisture content for clearcuts that have been broadcast burned.

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
17	74 144-74 163	53.03	12.9	0.45
	74 163-74 177	41.38	16.5	0.40
	74 177-74 188	22.90	15.0	0.29
	74 188-74 204	11.50	15.4	0.20
	74 204-74 220	8.12	20.9	0.16
	74 220-74 235	16.91	14.8	0.22
	74 235-74 248	16.47	19.6	0.24
	74 248-74 270	13.64	17.6	0.13
	74 270-74 293	10.05	12.6	0.09
	74 293-74 307	15.69	5.7	0.26
	74 307-74 314	55.96	5.3	0.22
	74 314-74 333	60.23	4.4	0.19
	74 333-75 26	74.83	1.5	0.06
	75 26 -75 43	73.45	-1.7	0.10
	75 43 -75 65	84.61	1.4	0.51
	75 65 -75 86	53.83	-0.02	0.07
	75 86 -75 110	70.17	1.0	0.13
	75 110-75 122	40.13	5.9	0.16
	75 122-75 137	60.26	8.4	0.27
	75 137-75 151	18.65	8.7	0.12
	75 151-75 165	15.73	13.9	0.12
	75 165-75 179	12.16	8.2	0.12
	75 179-75 196	49.44	15.9	0.46
	75 196-75 211	26.44	18.3	0.32
	75 211-75 227	21.98	17.8	0.24
25	74 144-74 164	53.41	13.3	0.32
	74 164-74 177	44.30	16.1	0.34
	74 177-74 188	23.16	15.0	0.19
	74 188-74 204	17.64	15.4	0.21
	74 204-74 220	13.16	20.9	0.21
	74 220-74 235	9.59	14.8	0.18
	74 235-74 248	17.64	19.6	0.21
	74 248-74 270	13.64	17.6	0.13
	74 270-74 293	12.79	12.6	0.08
	74 293-74 307	51.23	5.7	0.25

(Continued on next page)

Appendix Table 3. (Continued)

Site	Julian date	% Moisture content (wet)	Litter temp. (°C)	Decomposition
25 (cont'd)	74 307-74 314	53.39	5.3	0.20
	74 314-74 333	55.42	4.4	0.18
	74 333-74 349	62.20	3.8	0.20
	74 349-75 26	78.55	1.4	0.07
	75 26 -75 43	74.83	-1.7	0.08
	75 43 -75 65	77.99	1.4	0.14
	75 65 -75 86	76.00	-0.2	0.14
	75 86 -75 110	74.01	1.0	0.20
	75 110-75 122	49.82	5.9	0.22
	75 122-75 137	69.09	8.4	0.24
	75 137-75 151	43.48	8.7	0.46
	75 151-75 165	15.73	13.9	0.12
	75 165-75 179	13.10	8.2	0.11
	75 179-75 196	49.44	15.9	0.56
	75 196-75 211	27.37	18.3	0.24
	75 211-75 227	25.43	17.8	0.21

Appendix Table 4. Significant regressions of carbon mineralization and litter temperature and litter moisture content as a function of time.

Site	Date	Regression model	No. of samples	Correlation coefficient (r)
RS 2	8/16/73-12/15/73	$Y = -1.8716\ E\text{-}02 + 6.8136\ E\text{-}02 \times (MC)$	8	0.800***
RS 2	9/6/74-11/29/74	$Y = 9.8801\ E\text{-}02 + 6.6549\ E\text{-}02 \times (MC)^3$	5	0.952***
RS 2	11/30/74-3/6/75	$Y - 5.2575\ E\text{-}02 + 7.3550\ E\text{-}02 \times (LT)^1$	5	0.969**
RS 2	8/16/73-12/15/73 +9/6/74-11/29/74	$Y = 3.7482\ E\text{-}02 + 6.4518\ E\text{-}02 \times (MC)$	13	0.836*
RS 6	8/16/73-12/15/73	$Y = -2.8651\ E\text{-}01 + 9.228\ E\text{-}01 \times (MC)$	7	0.904**
		$Y = -4.2173\ E\text{-}01 + 1.1390\ E\text{-}02 \times (LT) + 1.9839\ E\text{-}01 \times (MC)$		0.929***
RS 6	6/3/74-9/5/74	$Y = 6.9914\ E\text{-}02 + 8.3204\ E\text{-}02 \times (MC)$	6	0.931**
		$Y = -1.5763\ E\text{-}01 + 1.2819\ E\text{-}02 \times (LT) + 8.3644\ E\text{-}02 \times (MC)$		0.969***
RS 6	9/6/74-11/29/74	$Y = 1.4670\ E\text{-}01 + 4.5044\ E\text{-}02 \times (MC)$	5	0.947***
RS 7	8/16/73-12/15/73	$Y = 5.3173\ E\text{-}02 + 5.1822\ E\text{-}02 \times (MC)$	8	0.790***
		$Y = -1.1897\ E\text{-}01 + 1.2714\ E\text{-}02 \times (LT) + 6.6866\ E\text{-}02 \times (MC)$		0.890***

(Continued on next page)

Appendix Table 4. (Continued)

Site	Date	Regression model	No. of samples	Correlation coefficient (r)
RS 7	6/13/74-9/5/74	Y = 1.1573 E-01 + 4.7518 E-02 x (MC)	6	0.843****
		Y = -1.4912 E-01 + 1.6034 E-02 x (LT) + 5.2039 E-02 x (MC)		0.963***
RS 7	3/6/75-6/13-75	Y = 1.6198 E-01 + 2.1567 E-02 x (LT)	4	0.989***
RS 7	8/16/73-12/15/73	Y = 1.1011 E-01 + 4.3502 E-02 x (MC)	13	0.798*
	+9/6/74-11/29/74	Y = 2.4034 E-02 + 7.0404 E-03 x (LT) + 4.9568 E-02 x (MC)		0.816*
RS 7	3/7/74-6/11/74 +3/6/75-6/13/75	Y = 1.5933 E-01 + 1.6456 E-02 x (LT)	9	0.728****
RS 33	6/11/74-10/20/74	Y = 5.3143 E-02 + 8.8139 E-02 x (MC)	8	0.741****
		Y = -1.5745 E-01 + 1.4293 E-02 x (LT) + 8.2490 E-02 x (MC)		0.851****
RS 33	5/31/75-8/15-75	Y = -1.6707 E-01 + 2.7111 E-01 x (MC)	5	0.974**
29	5/24/74-10/20-74	Y = -1.5475 E-02 + 1.4952 E-01 x (MC)	9	0.924*
29	4/20/75-8/15/75	Y = -8.8189 E-02 + 2.3214 E-01 x (MC)	8	0.861**
		Y = -5.9173 E-01 + 3.1230 E-02 x (LT) + 2.7583 E-01 x (MC)		0.929**

(Continued on next page)

Appendix Table 4. (Continued)

Site	Date	Regression model	No. of samples	Correlation coefficient (r)
36	5/24/74-10/20/74	Y = -1.2824 E-01 + 1.6107 E-02 x (LT) + 5.4402 E-02 x (MC)	9	0.827****
36	4/20/75-8/15/75	Y = -1.4834 E-02 + 9.6412 E-02 x (MC)	8	0.708****
		Y = -4.5051 E-01 + 2.7037 E-02 x (LT) + 1.4237 E-01 x (MC)		0.846****
29+36	5/24/74-10/20/74	Y = 6.2066 E-02 + 1.0189 E-01 x (MC)	18	0.795*
		Y = -1.2910 E-01 + 1.1031 E-02 x (LT) + 1.0605 E-01 x (MC)		0.814*
17	5/24/74-10/20/74	Y = 7.8369 E-02 + 1.1528 E-01 x (MC)	9	0.972*
17	10/20/74-4/20/75	$Y = 9.8182 E-02 + 2.3435 E-02 x (AT)^2$	7	0.912*
17	4/20/75-8/15/75	Y = -1.4925 E-01 + 1.9784 E-02 x (AT) + 6.4661 E-02 x (MC)	8	0.888***
25	5/24/74-10/20/74	Y = 1.0637 E-01 + 6.8624 E-02 x (MC)	9	0.865*
		Y = -1.0873 E-02 + 6.9615 E-03 x (AT) + 7.2070 E-02 x (MC)		0.896**
25	10/20/74-4/20/75	Y = 1.1870 E-01 + 1.8438 E-02 x (AT)	9	0.782***

(Continued on next page)

Appendix Table 4. (Continued)

Site	Date	Regression model	No. of samples	Correlation coefficient (r)
17+25	5/24/74-10/20/74	Y = 9.2259 E-02 + 9.1534 E-02 x (MC)	18	0.893*
		Y = 1.7394 E-02 + 4.3859 E-03 x (AT) + 9.4460 E-02 x (MC)		0.900*
17+25	10/20/74-4/20/75	Y = 1.0906 E-01 + 2.0879 E-02 x (AT)	16	0.845*

[1]Litter temperature

[2]Air temperature

[3]Moisture content

*Denotes $p < 0.01$

**Denotes $p < 0.02$

***Denotes $p < 0.05$

****Denotes $p < 0.10$