1

57342

National Library
of Canada

Bibliothèque nationale
du Canada

CANADIAN THESES
ON MICROFICHE

THÈSES CANADIENNES
SUR MICROFICHE

NAME OF AUTHOR/NOM DE L'AUTEUR Lianne Marie Dwyer

TITLE OF THESIS/TITRE DE LA THÈSE Forest Floor Heterogeneity as a Functional
Component in Litter Decomposition

UNIVERSITY/UNIVERSITÉ Carleton

DEGREE FOR WHICH THESIS WAS PRESENTED/
GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE Ph.D.

YEAR THIS DEGREE CONFERRED/ANNÉE D'OBTENTION DE CE DEGRÉ 1978

NAME OF SUPERVISOR/NOM DU DIRECTEUR DE THÈSE Dr. H.G. Merriam

Permission is hereby granted to the NATIONAL LIBRARY OF
CANADA to microfilm this thesis and to lend or sell copies
of the film.

The author reserves other publication rights, and neither the
thesis nor extensive extracts from it may be printed or other-
wise reproduced without the author's written permission.

*L'autorisation est, par la présente, accordée à la BIBLIOTHÈ-
QUE NATIONALE DU CANADA de microfilmer cette thèse et
de prêter ou de vendre des exemplaires du film.*

*L'auteur se réserve les autres droits de publication; ni la
thèse ni de longs extraits de celle-ci ne doivent être imprimés
ou autrement reproduits sans l'autorisation écrite de l'auteur.*

DATED/DATE May 3, 1978 SIGNED/SIGNÉ Lianne Dwyer

PERMANENT ADDRESS/RÉSIDENCE FIXE R.R. 1

Kanata, Ontario

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis

**THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED**

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

**LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE**

FOREST FLOOR HETEROGENEITY
AS A FUNCTIONAL COMPONENT
IN LITTER DECOMPOSITION

by

LIANNE MARIE DWYER, B.Sc., M.Sc.

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario
April, 1978

The undersigned hereby recommend to the Faculty
of Graduate Studies acceptance of this thesis, submitted by
Lianne Marie Dwyer, B.Sc., M.Sc., in partial fulfilment of
the requirements for the degree of Doctor of Philosophy.

.....
Chairman, Department of Biology

.....
External Examiner

.....
Thesis Supervisor

ABSTRACT

The effect of topographic heterogeneity on the litter decomposition process was examined in a beech-maple woodlot near Ottawa. Topographic heterogeneity of the woodlot floor, consisting of rises, depressions and more extensive level areas, about 1 m in diameter with a 0.5 m vertical maximum, was a result of undulations in the underlying glacial till. The topographic sites are hereafter referred to as high, level, and low areas. This topographic heterogeneity affected structural and functional components of the litter system, and ultimately influenced the rate of litter decomposition and the incorporation of organic matter into surface soil.

Surface litter accumulation was the first litter system component affected by topographic heterogeneity. Average accumulations, measured from April to October, were 416.2 g/m^2 in high areas, 1209.9 g/m^2 in level areas and 2438.3 g/m^2 in low areas, a ratio of about 1:3:6. Wind and gravity redistributed the surface litter during the summer months. April accumulations in high, level and low areas approximated a 1:3:6 ratio but by September this widened to approximately 1:4:8; October litterfall narrowed the ratio of litter accumulation to approximately 1:2:4. Aged, or partially decomposed, litter contributions to this surface litter accumulation were 121.5 g/m^2 in high areas, 422.9 g/m^2 in level areas and 647.9 g/m^2 in low areas.

Greater litter weight and depth in low areas protected the underlying soil from desiccation. Average soil moisture contents (measured from April to October) were 19.10% (wet weight basis) in high areas, 26.44% in level areas and 38.47% in low areas. Mid-summer soil suction values rose to 54.88 centibars in high areas, whereas they did not exceed 7.03 centibars in low areas.

In low areas the temperature variability at the litter-soil interface was reduced by the surface litter and by the heat capacity of the greater moisture content. Average July temperatures (C) ± 1 S.D. were 17.90 ± 6.09 in high areas, 16.29 ± 3.96 in level areas and 15.74 ± 3.33 in low areas.

Larger populations of microbial sugar, cellulose and lignin decomposers were assayed in low areas. Average litter and soil populations (based on ten estimates made from April to October) were generally two to four times larger in low areas than on high areas. Sugar decomposing bacteria in litter were most abundant in all topographic areas, 135 million/g dry litter in high areas, 396 million/g in level areas and 456 million/g in low areas; lignolytic fungi were least abundant, 39100/g dry litter in high areas, 70000/g in level areas and 95400/g in low areas. Most assayed populations showed two population peaks, one in late May or June and one in late September or October. These peaks were related to physical conditions and possibly priming by soluble nutrients in litter.

Two litter decomposition experiments using the mesh bag technique measured decay as weight loss, organic loss and lignin gain. The first experiment ran 16 months, from July to November, and the second ran 6 months, from May to November. The 6-month experiment, dominated by rapid leaching, had an average exponential rate of weight loss (excluding herbaceous material) of -0.051 . The longer experiment was more influenced by slower decay processes such as invertebrate fragmentation and microbial degradation, and showed an exponential rate of weight loss of only -0.015 over 16 months. Topographic site and litter mixture (simulating leaf litter composition on high, level and low areas) affected decay processes and overall decay rates. The fastest exponential weight loss rate, monitored over 16 months, was measured for low litter mixtures decomposing on low sites (-0.027), and the slowest rate was measured for high litter mixtures decomposing on high sites (-0.004).

Fastest organic loss and lignin gain rates (-3.13 and 0.422 , respectively, measured over 16 months) were for high litter mixtures decomposing in low areas. Faster qualitative changes occurred in high litter mixtures because these mixtures contained only unaged leaves, which had larger initial organic and smaller initial lignin contents.

More organic matter, both in litter fragment and amorphous form, was incorporated into surface soil of low areas. Litter fragments made up 0.32% (by weight) of surface soil in high areas, 1.25% in level areas and 5.28% in low areas. After litter fragments

0

were removed, the organic content of soil in high areas was 4.96%, compared to 8.54% in level areas and 10.79% in low areas. Incorporation of organic matter into the surface soil was considered an indirect measure of long-term decomposition. Humus formation and accompanying changes in soil structure and nutrient retention capacity are discussed.

In addition to documenting levels of spatial heterogeneity in a litter decomposing system, this study mentions the significance of spatial heterogeneity in the context of a temporally fluctuating environment. The general contribution of system heterogeneity is considered.

ACKNOWLEDGMENTS

Dr. H.G. Merriam has been a continual source of ideas and encouragement; I thank him for his thorough and honest appraisal during all phases of my doctoral program.

Dr. C.A. Barlow has been a kind and willing critic of the developing project. I thank Dr. H. Yamazaki, Dr. K. Torrance and Dr. G. Lang for critical examination of this manuscript.

Dr. K.C. Ivarson generously gave advice and practical assistance in the analysis of microbial populations. His expertise was essential to this aspect of the program, and I gratefully acknowledge his contribution. I thank Mr. H. Malinowski for his expert identification of fungal genera.

I must also thank Mr. D. Omond for his ready technical assistance both in the field and in the lab, as well as fellow graduate students for their constructive discussions.

To Laurie Dwyer I express much appreciation for his help and understanding during the course of this program. I would also like to thank my parents for their continuing support and encouragement during my education.

Financial assistance was provided by NRC and Ontario Government Scholarships, and by teaching assistantships from Carleton University.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS	10
I. Study Area	10
II. Experimental Procedure	12
1. Surface Litter Accumulation	12
2. Physical Conditions	14
3. Surface Soil Characteristics	16
4. Microbial Populations	17
a. Serial dilution technique	18
b. Sample washing procedure	22
5. Litter Decomposition Measures	23
RESULTS AND DISCUSSION	28
1. Surface Litter Accumulation	28
2. Physical Conditions	41
3. Surface Soil Characteristics	57
4. Microbial Populations	63
(i) Group 1: Soluble carbon or sugar decomposers	64
(ii) Group 2: Cellulose decomposers	77
(iii) Group 3: Lignin decomposers	85
(iv) Summary of the microbial populations	89
5. Litter Decomposition Measures	92
(i) Litter decomposition measured as weight loss	94
(ii) Litter decomposition measured as organic loss and lignin gain	111
(iii) Litter decomposition measured as decreasing cation concentrations	121
(iv) Summary of litter decomposition	122
GENERAL DISCUSSION	126
APPENDICES	144
LITERATURE CITED	166

LIST OF TABLES

Table		Page
1.	Utilization of replicate sites for descriptive and experimental measurements.....	13
2.	Topographic distribution of standing crop of surface litter.....	29
3.	Depth of litter accumulation in three topographic areas in spring, summer and fall.....	33
4.	Qualitative separation of surface litter in the April collection.....	39
5.	Temperature at litter-soil interface and surface soil moisture measured between 900 and 1200h, April 28.....	42
6.	Monthly temperature means, standard deviations and ranges for each topographic area measured at the litter-soil interface.....	44
7.	Mean monthly moisture content of surface litter and surface soil in three topographic areas.....	46
8.	Soil moisture suction in three topographic areas.	48
9.	Temperature summary for five week-long periods chosen to exemplify seasonal differences in three topographic areas.....	50
10.	Temperature ranges for five representative periods during the growing season in three topographic areas.....	52

11.	Components of soil organic matter in the top 10 cm of three topographic areas.....	58
12.	Loss on ignition as a measure of soil organic matter in three topographic areas.....	60
13.	Particle size analysis of soil from three topographic areas.....	62
14.	Moisture content of samples used in microbial assays.....	68
15.	Fungi isolated from litter and soil fractions from three topographic areas.....	76
16.	Summary of microbial populations of sugar, cellulose and lignin decomposers in the litter and soil of three topographic areas.....	90
17.	Litter decomposition rates (measured as weight loss) during the July decay experiment.....	97
18.	Litter decomposition rates (measured as weight loss) during the May decay experiment.....	102
19.	Qualitative changes in litter during the July decay experiment.....	113
20.	Organic changes in litter monitored during the May decay experiment.....	117

LIST OF FIGURES

Figure		Page
1.	Qualitative separation of surface litter from the April collection, excluding woody material....	36
2.	Predictability indices (P) calculated from hourly temperature readings, and a breakdown of this index into the proportion due to constancy (C) and repeatability (M) in each topographic area during five week-long periods.....	54
3.	Temporal changes in litter bacterial populations from three topographic areas grown on sugar substrate.....	66
4.	Temporal changes in soil bacterial populations from three topographic areas grown on soil extract medium (which supports sugar decomposers).	69
5.	Temporal changes in litter fungal populations from three topographic areas grown on sugar substrate.....	71
6.	Temporal changes in soil fungal populations from three topographic areas grown on sugar substrate..	72
7.	Temporal changes in cellulolytic bacteria isolated from litter.....	79

8.	Temporal changes in cellulolytic bacteria isolated from soil.....	81
9.	Temporal changes in cellulolytic actinomycetes isolated from litter.....	83
10.	Temporal changes in cellulolytic actinomycetes isolated from soil.....	84
11.	Temporal changes in lignolytic fungi isolated from litter.....	87
12.	Temporal changes in lignolytic fungi isolated from soil.....	88
13.	Rate of litter decomposition (measured as weight loss) for two representative experimental treatments.....	95
14.	Flow diagram of the response of a litter system to the underlying topographic heterogeneity of the woodlot floor without feedback.....	127

INTRODUCTION

Nutrient cycling and energy flow are two inseparable ecological processes which are important in determining the structure and limiting the function of all ecological systems. The decomposition of litter, which is a major process of forest nutrient cycling, is no exception. Because decomposition processes and the availability of energy to detritus-feeding organisms are closely linked, nutrient cycles parallel the flow of energy through the community. The action of decomposer microorganisms illustrates the dependent nature of matter and energy in biological systems; these microorganisms make the chemical elements in organic compounds available to plants, but they do so only because they can obtain their own nutrient needs and metabolic energy from this conversion.

An approach considering the inseparable nature of nutrient cycles and the one-way flow of energy driving these cycles (Reichle et al. 1975a) has been less popular than analysis based on energy alone (Odum 1957, Slobodkin 1962, Colley 1965, Wiegert et al. 1970, Jordan 1971, Hughes 1971), or on nutrient cycling alone (Burges 1956, Ovington 1956, Attiwell 1968, Duvigneaud and Denaeyer-De Smet 1970, Likens et al. 1971, Woodwell et al. 1975, Carter and Cragg 1976). Although available nutrients are now recognized as limiting the productivity of most systems (Witkamp 1971, Tamm 1972), energy is the fuel which powers ecological processes. It has been hypothesized that

ecosystems adopt strategies to expend readily available energy to minimize the constraints of limited nutrients and water (Reichle et al. 1974).

Ovington (1962) and Macfadyen (1963) stated the significance of litter decomposition from an energy viewpoint; during the decomposition of organic plant and animal debris, the detritus food chain may process over half (in some instances as much as 70%) of the energy entering the ecosystem as primary production. However, perhaps a more important aspect of the decomposition process is found in the detail of this activity, the uptake and subsequent release of nutrients by the decomposers. The result is a decomposer food web in which essential elements are conserved within the ecosystem due to their temporary immobilization within decomposer bodies (Todd and Cromack 1972), which then become food for other decomposers. The temporary trapping of nutrients within decomposer biomass increases the nutrient retention capacity of the system, which otherwise would be restricted to the living biomass in the non-decomposer communities and the cation exchange capacity of the soil. Perhaps a major contribution of the microbial decomposers is this short-term storage of nutrients within their biomass and the ready availability of these nutrients to other microbes and to growing plants.

Nutrient conservation is a common theme in ecology: Odum (1971) emphasized the theoretical importance of nutrient conservation to a stable system; others, (Bormann and Likens 1967, Likens et al. 1977) have empirically described soil nutrient loss initiated by clearcutting

and the subsequent slow recovery of steady-state nutrient cycles with reforestation.

Pomeroy (1970) suggested that the ability of systems to conserve and concentrate nutrients forms a basis for succession: succession can be seen as a process through which enough nutrients are conserved, first in living biomass, then in the organic matter and flora of the soil, to support the rise of succeeding communities. Climax communities then perpetuate their stability in part by conserving essential nutrients. Marks and Bormann (1972) indicated a mechanism for the conservation of elements from an early successional stage. They determined that in early secondary successional growth, pin cherry (Prunus pensylvanica) was able to take up nutrients and conserve them in its biomass more efficiently than later vegetation. The trapping of nutrients in the cycle of autotrophic and decomposer biomass prevents their leaching, and hastens nutrient accumulation within the system. Vitousek and Reiners (1975) stated the temporary nature of this nutrient accumulation; in a steady-state system elemental outputs must come to equal elemental inputs. Lang (1974) detailed this expectation, as he monitored the variability around a steady-state average in a mature forest.

The complex process of decomposition can be separated into litter fragmentation, simple physical leaching, and chemical degradation carried out by microorganisms. Microbial decomposers (bacteria, fungi, actinomycetes and yeasts) are essential to litter decomposition because they have enzymes capable of degrading structural carbohydrates such as cellulose and lignin (Witkamp 1971). In fact, Macfadyen (1963) stated that microorganisms are capable of degrading up to 90% of the matter bound in litter.

Macrodecomposers, however, are more important to the decay process than this figure indicates. Edwards and Heath (1963) showed that the presence of macrofauna was essential for microbial decay. Other workers have also shown the importance of macrodecomposers, specifically invertebrates (Reichle 1971), in exposing more of the detritus surface area (Drift 1963), by mixing this organic matter with the mineral soil (Ovington 1962), and thereby encouraging higher microbial activity (Jackson and Raw 1966). In addition, litter and soil animals increase mobilization of nutrients from senescent fungal tissues, and generally influence a flow of energy many times that through their own bodies (Anderson 1973b). Some researchers believe that litter decomposes at a rate directly related to the number of invertebrates in the litter and underlying soil (Edwards et al. 1970).

Study of a process as complex as litter decomposition encourages all possible attempts at simplification. One of the major obstacles to simplification has been the spatial heterogeneity, or non-uniformity, of all major components of the decomposer system, including the environment, the decomposable substrates entering the system, and the nature and distribution of the decomposer organisms (Parkinson 1972).

This heterogeneity is not an uncommon experimental hazard in biological studies. The approach to this problem in litter decomposition studies has been similar to that in other systems; the environmental heterogeneity is usually treated as an unavoidable complication, and is dealt with by selective sampling and large-scale replication in an attempt to define the "average" condition. Levins (1969), in a short paper dealing with the selection of predators for biological control

programs, was one of the first to attack this approach; he emphasized that the spatial and temporal heterogeneity of an environment are real attributes of the system which must be considered in any study or manipulation of system processes.

Until now, the heterogeneity of environments has been recognized primarily by theoreticians and researchers considering the general relationships among environments, their biological diversity and system stability. Simpson (1964) hypothesized that the more complex and heterogeneous the physical environment, the more diverse its community. MacArthur (1972) and Pearson (1971) supported this view with findings that the more complex the vertical stratification of an environment, the more species of birds it would support. By contrast, Wiens (1974) found no relationship between bird species numbers and grassland heterogeneity; he suggested that such a simple relationship between spatial heterogeneity and populations was probably rare since other factors, such as climate, also imposed limits on avian populations. Connell and Orias (1964) emphasized the importance of these unpredictable factors to a developing community in their hypothesis that a stable environment would in itself result in greater species numbers.

May (1974) reviewed the implications of spatial heterogeneity on the stability of populations in a temporally changing environment; he concluded that, generally spatial heterogeneity of the environment is a stabilizing factor. Supporting this view is Birch's (1971) survey of examples in which spatially heterogeneous environments provide refuges for animals in adverse seasons, from which they recolonize intermittently

favourable regions. Paine (1969) cited the importance of refuges in the intertidal zone to survival of gastropods escaping their predators. Finally, Rosenzweig and Winakur (1969) demonstrated the stabilizing role of spatial heterogeneity in their work on the coexistence of desert rodents.

In the preceding examples, the spatial heterogeneity of the environment provides the inhabiting organisms with alternatives, whether the motivating force is provided by climatic changes, predation, or competition. Roughgarden (1974) examined the relationship between the spatial heterogeneity of the carrying capacity and equilibrium pattern of population abundance. He assumed that given the choice inherent in a heterogeneous environment, populations could "track" their preferred environment in the spatial matrix. Within the limits imposed by their dispersal ability and competitive restrictions, populations could migrate within the heterogeneity of the system to those sites which best met their requirements for that time. Roughgarden (1977) also examined population distributions in temporally fluctuating environments. He showed that spatial heterogeneity in the distribution of a population is an inevitable consequence of dispersal in a fluctuating environment, even if the fluctuations result in a random distribution of resources.

In much of the foregoing literature, consideration of the role of heterogeneity is theoretical, or recognition of its influence in environmental studies is ancillary to the main purpose. By contrast, Reice (1974) set out to examine the effect of spatial heterogeneity on a system function. He considered differences in bottom sediment and in leaf patches,

and the effect of this heterogeneity on the decomposition of leaf litter in a woodland stream. Reice concluded that the heterogeneous streambed was composed of a mosaic of component decomposer communities.

My study examines the role of spatial heterogeneity in the terrestrial decomposition process. The heterogeneity of the environment is initially provided by glacial deposits underlying the beech-maple woodlot study area. These deposits result in an undulating topography of the woodlot floor, with high and low areas approximately 1 m in diameter and 0.5 m maximum, vertically. The soil of the high areas typically contains till that is stonier than the soil of the level and low areas. These high areas are well-drained, to the extent that they provide quite an arid mesoenvironment for much of the growing season. Due to their lack of protection from wind they normally support only a small standing crop of decomposing litter. The low areas provide a much more moist mesoenvironment, partly due to their protected location among the high areas, but also because of the thick layer of decomposing litter which accumulates in them. The high and low areas, together with the approximately level areas within the woodlot, provide the original topographic heterogeneity of the decomposition system.

Effects of topography as a source of heterogeneity have been documented in a northern hardwood forest (Hart et al. 1962) and in tundra decomposition studies (Parkinson 1972). In my study, the effect of the original topographic heterogeneity is reflected in various levels of "derived" heterogeneity (Patterson 1972); that is, heterogeneity whose cause can be traced to the underlying topography, but which is expressed by other components in the system.

I will examine several levels of derived heterogeneity. The logic of the sequence is stated briefly here. The first level is a heterogeneous accumulation of surface litter, which I observed in an earlier study (Mack 1973). As the loose surface litter is moved by local winds and gravity it tends to accumulate in the protected low areas, with the result that these areas develop greater depth and diversity in their litter layer. Greater litter accumulation in low areas increases stability of the physical conditions (specifically litter moisture and temperature) (Drift 1963, Dickinson 1974). My study shows that there are significant differences in the variability of physical conditions experienced by organisms inhabiting different topographic areas. More stable physical conditions and a larger and more diverse litter resource in the low areas lead to increased decomposer activity; invertebrate activity increases the incorporation of organic matter in the surface soil of low areas (Ovington 1962, Wallwork 1970, Edwards et al. 1970).

Finally, greater surface litter accumulation, physical stability, and greater incorporation of organic matter into the soil in low areas combine to produce a larger and more active microbial community (Alexander 1961, Parkinson 1972). Spatial heterogeneity of all these major components of the decomposer system results in spatial heterogeneity of the decay process.

My study measures the rate of litter decay, and considers longer term incorporation of organic matter into the surface soil, in

✓

the context of the spatially heterogeneous environment outlined above. The role of spatial heterogeneity in the decomposer system is also considered in the context of temporally fluctuating climatic conditions. Roughgarden's (1974) concept of "tracking" as it applies to decomposer organisms is utilized in describing the effect of spatial heterogeneity on the process of decomposition throughout the woodlot.

In summary, this study is specifically designed to investigate the effect of spatial heterogeneity on the structure and function of a litter decomposing system. The results indicate that heterogeneity is an important functional factor in defining both physical and biotic components. Furthermore, interaction of the spatially heterogeneous litter system components with a temporally fluctuating environment produces a two dimensional heterogeneity which determines the decomposition process.

MATERIALS AND METHODS

I. Study Area

The site chosen to study the role of heterogeneity in litter decomposition is a predominantly beech-maple woodlot located south of Ottawa, Ontario. The site, about 13 ha, is bounded on all sides by pasture fields and is located between Woodroffe Avenue and Highway 16, 1.2 km north of the Jock River. The woodlot developed on glacial deposits of Grenville loam (Hills et al. 1944). The drainage is good throughout, and the soil has a neutral to mildly alkaline pH. Undulations of the underlying stoney greyish till produce high, level and low areas that are the original topographic heterogeneity of the litter system.

The study area, a fenced plot approximately 54 m x 40 m, is located in the interior of the woodlot. The canopy layer is dominated by beech (Fagus grandifolia) and sugar maple (Acer saccharum) trees, with an average DBH near 15 cm. A few basswood (Tilia americana) and some ironwood (Ostrya virginiana) are also present. Except for some regeneration by beech and maple saplings, the middle strata of the stand are quite open.

The distribution of the ground vegetation is influenced by the topography of the woodlot floor. In early spring, leeks (Allium tricoccum) appear to cover much of the woodlot floor; however, closer examination

reveals that they are found most frequently in high and level areas, and almost never in the low areas, which are still very moist from spring melt. A survey of 22 high areas, 22 level areas and 22 low areas made in late May (a time of maximum leek production) indicated that the average leek cover for high, level and low areas was approximately 31%, 27% and 3%, respectively.

In addition to this spatial heterogeneity, herbaceous cover changes dramatically through time. In the following few weeks before the canopy fills in, dogtooth violets or trout lilies (Erythronium americanum), trilliums (Trillium grandiflorum and Trillium erectum), squirrel corn (Dicentra canadensis), spring beauty (Claytonia virginica), bloodroot (Sanguinaria canadensis), wild ginger (Asarum canadense), jack-in-the-pulpit (Arisaema triphyllum), blue cohosh (Caulophyllum thalictroides) and beech and maple seedlings appear, and are apparently uniformly distributed. As the canopy fills in, most of the herbs produce seeds and their vegetative parts begin to decompose. During the summer months, only blue cohosh, wild ginger, jack-in-the-pulpit, and the beech and maple seedlings are present on the forest floor. A second survey made of the same sites in late July, indicated that blue cohosh was the dominant herbaceous plant, and that it was found more frequently on level and low sites than on high sites (14% cover on level sites, 6% on low sites and 3% on high sites).

Within the confines of this study area, 66 sites were chosen for experimental purposes. As has been mentioned, 22 sites were high

areas, 22 were low areas and 22 were located on level ground. All sites were chosen so that the topographic feature being selected was about 1 m in diameter. The 22 sites within each topographic category were considered replicates, as it was impossible to make all measurements and do all analyses and experiments on each site, without structurally destroying that site. Table 1 shows how the 66 sites were utilized during the three-year field study.

II. Experimental Procedure

1. Surface Litter Accumulation

A total of 30 sites were monitored for surface litter accumulation. Each site was sampled monthly from April through October. At each of these sampling times, the litter accumulation was determined for each site by collecting all distinguishable above-ground surface litter (including small fragments) from a different (15 x 15) cm plot. Each sample was dried at 100 C to a constant weight. The mean standing crop of surface litter was calculated (as dry g/m^2) for each topographic site, at monthly intervals throughout the growing season.

At three sampling times, May, July and October, the depth of surface litter was also measured at each site both in leaf layers and in cm.

Another collection made in April underwent further analysis. In addition to determination of the dried weight of the total sample from each site, each site's collection was separated into litter

Table 1. Utilization of replicate sites for descriptive and experimental measurements.

SITE NUMBERS

ALL TOPOGRAPHIC AREAS*

1	Physical Factor Measurement (Jun-Oct 1975)
2	
3	
4	
4	
6	Surface Litter Accumulation, Soil Organic Matter Incorporation,
7	Soil Textural Analysis
8	(Apr-Oct 1974)
9	
10, 12	
11	-extra control
13	
14	Decay Experiment I
15	(begun in July 1975)
16	-Be:Ma(spring)
17	-Be:Ma(fall)
18	-cohosh
19	-leeks
20	-mixed Be:Ma
21	Physical Factor Measurement (Jun-Oct 1975)
22	Microbial Analysis (Apr-Oct 1976; analysis - winter of 1976-1977)

-Soil pH Measurement 1974

LEVEL

LOW

HIGH

*

categories which reflected the type and age of accumulated litter. The proportion of each litter category, on a dry weight basis, provided a measure of the distribution and composition of litter within the three topographic areas.

In an attempt to determine the extent of litter movement over relatively short (i.e. one month) time intervals, a series of four screens was set out on top of the existing litter at each collection site in June. Each screen, consisting of a (15 x 15) cm piece of fibreglass membrane, was secured to the surface soil with 'staples' made from stovepipe wire. The litter which accumulated was collected from one of each series of four screens each month from July to October, inclusive. The oven-dried weight of the litter collected at each sampling time was determined, and the net change in litter weight for each monthly period was calculated for each collection site.

2. Physical Conditions

Two physical factors, litter temperature and moisture content, were measured in this study. Temperature at the litter-soil interface was monitored at six sites at hourly intervals throughout one growing season. Three YSI #44006 thermistors were placed at the litter-soil interface of each site. The thermistors were read by resistance bridges constructed by the Carleton University Science Workshop, and charted on Rustrak DC operated continuous paper chart recorders. A stepping switch read each thermistor in sequence; the time interval was set so that each thermistor was read at approximately hourly intervals. The accuracy of the thermistors was greater than the readability of the recorder, which was ± 0.5 C.

The six sites at which temperatures were monitored consisted of two high sites, two level sites and two low sites. Except for brief intervals during the summer, and a September breakdown of equipment servicing three sites, hourly temperatures were measured at all six sites. This frequency of measurement meant that both daily and seasonal fluctuations were monitored. In order to look at differences in diurnal variation among the three topographic areas without the added complexity of seasonal variations, five week-long time periods were selected for analysis. The five periods were chosen to represent distinct climatic periods during the growing season.

Each period was then analysed by the method of Colwell (1974) to determine the extent and sources of the predictability of diurnal fluctuations in the litter-soil interface temperatures. This provided an index of the repeatability or predictability of the environment in relation to the source of this predictability. For the temperature series to have a high level of predictability, it must either be relatively constant or strongly periodic. Both these circumstances could be reflected in a low variance over time, but the consequences for organisms living at these temperatures, and the strategies required of them, would be quite different. This method distinguishes between the constancy and periodicity of the temperatures. Monthly means, variances and ranges were also calculated for each topographic area so that an area could be characterized by an absolute range of temperatures, as well as an index of its predictability.

Moisture characteristics of the sites were determined by two methods. First, 4s percent moisture (% of wet weight) in litter and

surface soil which was determined as the difference between fresh and oven-dried weights of the litter and soil samples used for organic determinations. These monthly measures were supplemented by moisture determinations of the litter and soil samples which were assayed for microbial activity throughout the growing season.

Soil moisture also was measured as tension, measured in centibars of soil suction with 12-inch Soil Test soil moisture gauges (Evanston, Ill., USA). These instruments consisted of an air-tight, water-filled tube with a porous ceramic cup at the bottom and vacuum gauge near the top. Each unit was installed with the porous ceramic cup in firm contact with the soil, about 5 cm below the litter-soil interface. As the soil dried, moisture was sucked out of the porous ceramic cup and a vacuum was created in the system which was read on the vacuum gauge. When it rained and the soil became wet, the moisture from the soil moved back into the unit through the pores in the cup and the gauge showed a lower 'soil suction' reading. Two of these tensiometers were placed at each of the six sites designated for measurement of physical factors. They were read on most days from May to October.

3. Surface Soil Characteristics

The extent of incorporation of organic matter into the soil was determined from soil cores with a surface area of 5 cm^2 . After the surface litter was removed from each (15 x 15) cm plot, two soil cores were taken within the plot. Each core was taken to a depth of 15 cm, or rock, whichever came first, but only the top 10 cm were kept. Cores were oven-dried at 100 C to a constant weight, and a subsample

was muffled at 500 C for 5 hours to burn all organic matter (Paine 1971).

The May and June collections underwent further analysis. Each oven-dried core from these collections was hand-picked to remove the incorporated litter fragments which were distinguishable by naked eye. These fragments were weighed and the soil and litter fragments muffled separately at 500 C until all organic matter burned. The soil cores thus provided a measure of the spatial heterogeneity in the "standing crop" of organic matter which was litter fragments.

The soil pH of the three topographic areas was determined from a May collection of soil cores, two cores taken from each of 30 sites. After removing the surface litter, a soil core was taken at each site to a depth of 5 cm. The cores were returned to the lab and readings were made the same day with a glass electrode on a 1:2 fresh soil:water mixture equilibrated for 30 minutes (Gochenaur and Woodwell 1974).

4. Microbial Populations

Three sites, one high, one level and one low, were sampled frequently throughout the growing season to provide material for microbial analysis. The sampling technique was similar to that used for the measurement of organic accumulation. At each site the surface litter was collected from two (15 x 15) cm squares and then five soil cores, 5 cm² in area, were taken from within this area. Litter samples were collected and stored in tied plastic sandwich bags; soil collections

were made in sterilized 'Whirl-Pak' bags (Nasco). Since these samples were not analysed immediately after collection, they were stored at temperatures ranging from -5 C to -10 C. This range was chosen because Christensen (1969) found that samples frozen up to 9 months (at -7 C) showed no significant changes in numbers of fungi per gram dry soil, or in the frequencies and densities of dominant species. Shortly before analysis, the two litter samples and five soil samples from each site were lumped; microbial analysis was then done on the aggregated litter sample, and separately on the soil sample.

a. Serial dilution technique

The microbial populations themselves were determined by dilution plate estimation. This technique is based on the assumption that when soil (or litter) is dispersed in a liquid, the cells become detached from the litter or soil, and that when this cell suspension is mixed with an agar medium in a petri dish, each cell will grow and give rise to a discrete colony. By counting these colonies, the number of cells in the suspension can be determined, and hence the number of cells in the original sample estimated and compared with numbers in other samples (Jensen 1968). However, problems with this method may cause it to underestimate the total microbial community (Parkinson et al. 1971). First, not all cells may be released from the litter or soil, and clumps of cells may exist in the solution. In addition, not all cells grow on any one agar, so some populations may not be assayed. I attempted to overcome this last problem by replicate platings on several agar media.

Cell suspensions were made from subsamples of the aggregated soil and litter samples; it was therefore important to homogenize the samples as much as possible. This was done by working the samples by

hand through the protective plastic bags to mix the particles, fragment the surface litter (sticks and bark pieces were removed), and produce a sample with a homogeneous moisture content. A four-gram subsample was then removed from each litter sample and placed in a sterilized Waring blender. A total of 396 ml of sterile water was added to the sample to prepare a 1:100 dilution. First, just enough sterile water was added to wet the litter and the sample was mixed at high speed for two minutes. The remaining water was then added, and the blender was run at high speed for another five minutes. A 10-ml subsample of this suspension was immediately added to a dilution bottle and further dilutions were prepared from this. Before each subsequent dilution, the sample was shaken vigorously by hand for one minute to resuspend the particles. Litter dilutions of 1:1,000,000, 1:10,000,000, and 1:100,000,000 were prepared for bacterial analysis, whereas dilutions of 1:10,000, 1:100,000, and 1:1,000,000 were sufficient for fungal analysis.

The soil suspensions were prepared by weighing out a 10-g subsample from the homogenized soil sample, and immediately transferring this to a sterile dilution bottle containing 90 ml of distilled water to prepare a 1:10 dilution. Further dilutions were prepared from this bottle. For bacterial analysis, dilutions of 1:100,000, 1:1,000,000, and 1:10,000,000 were prepared, whereas fungal analyses were made on dilutions of 1:1,000, 1:10,000, and 1:100,000. Five pour plates were made for each dilution.

At the same time as litter and soil were subsampled for microbial analysis, duplicate subsamples of the same weight were taken.

These samples were dried at 100 C to a constant weight and the percent moisture of the samples was calculated. This information was used to express population estimates on a per g dry weight of substrate basis.

Both the litter and soil suspensions were pour-plated on four different agar media, as well as being used to inoculate a vanillin solution. The litter samples were plated on a rose bengal plus aureomycin medium to isolate fungal colonies (K.C. Ivarson, personal communication); a Peoria medium plus actidione was the substrate for a general bacterial count (Baker and Whittingham 1972); an egg albumen plus actidione medium was used for isolation of actinomycetes (Corke and Chase 1956); and a cellulose agar isolated cellulose-decomposing bacteria and fungi (Eggins and Pugh 1962). In addition, inoculation of a vanillin solution isolated those microbes capable of utilizing vanillin (an aromatic compound similar in structure to lignin) as a carbon source. Subsequent plating on Waksman's acidic agar selected the fungal component of this community (Henderson 1961).

Replicate plating thus provided a means of separating the microbial community into functional nutritional groups. The vanillin solution and subsequent plating supported only fungi capable of utilizing an aromatic compound as the sole carbon source. Similarly, only organisms capable of using cellulose as a carbon source grew on the cellulose agar. Since the Peoria and rose bengal media both contained dextrose, a readily metabolized carbon source, they could theoretically support all bacteria or fungi. In practice, since organisms which are primarily sugar decomposers grow much more quickly than cellulose or lignin decomposers on a simple sugar substrate, these dilution platings

strongly selected for sugar-decomposing organisms and under-estimated the others (Watson et al. 1974). The only difference between litter and soil plating media was that a special soil extract agar plus actidione (James 1958) replaced the Peoria plus actidione agar as a medium for soil bacterial growth. All media are documented in Appendix I,

All plates were stored, inverted, in aluminum storage boxes at room temperature (approximately 25 C). Plates were read on a Quebec colony counter after 6 or 7 days incubation. Dilutions yielding 50 - 80 bacterial colonies or 25 - 35 fungal colonies were counted to get population estimates; the two other dilutions provided 'back-up' counts. In addition, three control plates for each sample on each medium allowed identification of any contamination. Population numbers were calculated per g dry weight of sample.

One follow-up procedure was required to interpret dilution plating results. Although the egg albumen plus actidione medium was expected to isolate actinomycetes, other bacteria and even fungi were also found on these plates. In order to estimate the proportion of all colonies found on this medium which were actinomycetes, individual colonies were removed from egg albumen plates of the August 19 collection and isolated on a potato dextrose agar (Difco bacterial potato dextrose agar, pH 6.3 at 25 C). Fifty-five isolates were taken from each of the six samples and these were identified as actinomycete or non-actinomycete; a ratio of actinomycete:non-actinomycete was

calculated for each soil and litter sample and these were used as correction factors in estimating actinomycete populations from the egg albumen medium.

b. Sample washing procedure

As already described, fungal populations were estimated by the serial dilution technique, but it was not possible to tell from these platings which fungal colonies grew from mycelial cells that were active in the original sample, and which grew from spores that were dormant on their previous substrate. In order to examine the types of fungi that were active in the litter or soil, soil and litter fragments were washed to remove spores of most soil fungi (Parkinson et al. 1971). Samples, (approximately 1.0 g litter and 4.0 g soil) from the May 29 collection were washed in a modified Parkinson and Williams washing apparatus measuring (13 x 4 x 4) cm and containing three sieves (Williams et al. 1965).

Tap water (approximately 35 C) was run through the sieves (mesh sizes 1.00 mm, 0.75 mm, and 0.25 mm) for fifteen seconds, then the two coarser screens were removed and tap water was run through the third screen for three minutes. The apparatus was agitated by hand, and by cupping a hand over the bottom of the screen, water was made to rise to the top of the apparatus and then fall quickly, keeping the litter (or soil) fragments in nearly constant motion. This action removed most spores from the organic fragments. After three minutes of agitation, 2 l of sterilized water were poured over the sample and through the screen to remove any contamination from tap water. The remaining fragments were plated by surface inoculation on

rose bengal agar; they were distributed by agitation without the use of forceps. Fifteen replicate plates were made for each washed sample.

After incubation for one week at room temperature (25 C) fifty-five colonies were isolated from each sample and transferred to potato dextrose slants (made with Difco bacto potato dextrose agar, pH 6.3 at 25 C) to await identification. Identification was made using Clements and Shear (1973), Ainsworth et al. (1973) and Gilman (1957). This method did not allow enumeration of fungal colonies due to uncertainty about the amount of material lost during washing. However, it did provide a means of determining the relative abundance of those fungi which were active in the litter system.

5. Litter Decomposition Measures

Estimates of the rate of decay within the three topographic areas were made using the litter bag technique (Bocock and Gilbert 1957, Crossley and Hoglund 1962). Bags were made from flexible fibreglass reinforcing membrane with a mesh size of 2 mm x 1 mm (Flintkote 990-06), sewn with heavy polyester thread. Each bag was constructed so that the bottom (15 x 15) cm lay flush against the ground; the top was then cut larger than the bottom and 'pleats' were taken in this top piece so that the volume of leaves in the bag would not cause the bottom to curl away from the ground, as would occur with a pouch-style bag. Three sides of the bag were sewn, 10 cm on a side, and after the litter contents were added, the fourth side was closed with Ofrex No. 80 aluminum-coated staples. The surface litter was cleared from those sites used for the decay experiments, and the bottom 'side' of the bag

was anchored to the soil surface on all four sides with 'staples' of stovepipe wire. Good contact was maintained between the bag and the soil surface.

Two decay experiments were run; Experiment I ran for 16 months (July to November), while Experiment II ran for only 6 months (May to November). The sites used for the two experiments are outlined in Table 1.

Experiment I examined the effect of litter mixtures and environmental characteristics of the different topographic areas on the rate of litter decay. Litter, which was limited to leaf material for this experiment, was collected from the area surrounding the plot. The leaves were then air-dried and weighed into bag-size lots. The bag assortment of litter was composed according to previous determinations of surface litter composition in the three topographic areas. Bags containing high litter mixtures were filled with 1.0 g of litter consisting of 50% unaged beech leaves and 50% unaged maple leaves. Level mixtures contained 3.0 g of litter, 33.5% unaged beech leaves, 16.5% aged beech leaves, 33.5% unaged maple leaves, and 16.5% aged maple leaves. Low mixtures contained 8.0 g, consisting of 25% each of unaged beech leaves, unaged maple leaves, aged beech leaves and aged maple leaves. Unaged beech and maple leaves were complete and intact with no visible evidence of decay. Aged leaves of both species were defined as those that were at least 25% filamentous; that is, they were a more variable category, but at least 25% of the leaf matrix was decayed, leaving only the more persistent veining.

Before being put in place at the start of the decay experiment, the bags of air-dried leaves were remoistened. Bags were laid in a single layer on the woodlot floor between two large sheets of plastic, which also enclosed several evaporating dishes containing water. The bags were left in this high humidity for several days, until they no longer felt brittle to touch.

Litter bags, with contents simulating high, level and low litter accumulations, were distributed among the three topographic areas to form a factorial design of litter mixture and topographic site. Eighteen replicate bags were placed at each site in the factorial design, sixteen replicates were placed at each extra control site. At each sampling period, two (or occasionally four) bags were removed from each site. They were collected in individual plastic sandwich bags, and closed with a wire tie to maintain field moisture content. All bags were stored at temperatures ranging from -5 C to -10 C.

Analysis began by air-drying the contents of each bag and determining the moisture content and dry weight. The contents of each bag were then ground in a Wiley mill to pass through screen size #40. One 0.25 g subsample from each bag was used for organic matter determination (Paine 1971). The ash left after muffling underwent calcium, magnesium and potassium extraction (Jackson 1958). Calcium and magnesium were then read by atomic absorption on a Jarrell-Ash model JA82-270 spectrophotometer at wavelengths of 422.7 and 285.2 mμ, respectively. Potassium concentrations were read in the flame emission mode

at a wavelength of 766.5 m μ (Model JA82-270 Instruction Manual, 1968). A second subsample, ranging in size from 0.25 g to 0.50 g, depending on the availability of sample, was analyzed for lignin content (Van Soest 1963).

Decay Experiment II examined the rate of decay of specific litter mixtures when located in different topographic areas. All bags contained the same amount of litter, 3.0 g, simulating the amount of litter found on level sites. Five litter mixtures were examined: a 1:1 combination of unaged beech and maple leaves collected in the spring just before the May experiment began (Be:Ma(spring)); a 1:1 combination of unaged beech and maple leaves collected the previous fall, air-dried and kept during the winter (Be:Ma(fall)); cohosh leaves and stems collected the previous fall and air-dried (cohosh); leek leaves collected that spring (leeks); and a combination of one-third unaged beech leaves, one-third unaged maple leaves and one-sixth each of aged beech and maple leaves, all obtained that spring (mixed Be:Ma). Table 1 shows the positioning of the various litter mixtures among the topographic sites. Ten replicate bags were set out at each site.

The bags to be left in the woodlot were maintained the same as those in Experiment I. Litter bags were also monitored in an environmental chamber. These were placed in plastic trays, two to a tray; each tray was lined with about 2.5 cm of surface soil collected from the beech-maple woodlot; the bags were placed on this. The temperature in the chamber was programmable to simulate a constant day temperature, followed by a constant night temperature. For the first three months,

the day and night temperatures were both kept at 15 C, based on the mean maximum and minimum temperatures recorded during the month of May, 1975 by Environment Canada at Ottawa International Airport. During the last three months, the day temperature was 26 C and the night temperature remained at 15 C (based on August, 1975 mean max-min temperatures). The moisture content in the bags was maintained by watering each bag with 325 ml distilled water (pH 4-5) every two weeks.

Two, or occasionally four, bags were removed from each site at each sampling time. Their collection, storage, and analysis were the same as in Experiment I, except that cation content was not determined.

RESULTS AND DISCUSSION

1. Surface Litter Accumulation

Surface litter accumulation is the first litter system component influenced by topographic heterogeneity. Table 2 summarizes the standing crop of surface litter, measured in g/m^2 , collected from ten high, ten level, and ten low experimental sites. Since the collections were made at monthly intervals throughout one growing season, they reflect heterogeneity of surface litter accumulation through time, as well as in space.

As indicated by the monthly means in Table 2, the low areas contain more surface litter during each collection period than do the level areas, which contain more than do the high areas ($F=235.18$, $P<.001$). The approximate ratio of surface litter in high, level and low areas of 1:3:6 (dry g/m^2) is maintained for most sampling times. Deviations from this ratio become more extreme later in the growing season. The greatest difference in surface litter accumulation between high and low areas occurs in September, when the ratio of high, level and low areas approximates 1:4:8. The October sampling period reflects a reversal of this trend as the ratio of high, level and low litter accumulation drops to approximately 1:2:4. Because of the large variances associated with the monthly means, the only

Table 2. Topographic distribution of standing crop of surface litter (expressed as dry g/m²).The values are means $\pm$ 1 standard deviation, where N = 10.

COLLECTION TIME	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
APRIL	410.6 $\pm$ 213.7	1140.6 $\pm$ 656.6	2592.1 $\pm$ 780.0
MAY	423.1 $\pm$ 425.1	906.9 $\pm$ 417.6	2629.0 $\pm$ 996.1
JUNE	457.5 $\pm$ 325.0	1447.6 $\pm$ 420.7	2429.3 $\pm$ 1163.9
JULY	400.0 $\pm$ 357.8	1296.9 $\pm$ 668.8	2747.6 $\pm$ 1004.5
AUGUST	342.9 $\pm$ 245.9	1326.8 $\pm$ 770.9	2241.4 $\pm$ 1105.0
SEPTEMBER	273.8 $\pm$ 193.3	1078.2 $\pm$ 437.6	2179.6 $\pm$ 489.4
OCTOBER	605.3 $\pm$ 257.8	1272.0 $\pm$ 676.5	2249.4 $\pm$ 899.4
MONTHLY $\bar{x}$	416.2	1209.9	2438.3

significant temporal differences occur in the high areas, where there is a significant loss from June to September, and a significant increase in October ($F = 5.57$, $P < .01$).

The temporal pattern on high sites can be explained by the interaction of litter input and topography. Litter input is low from April to September in this beech-maple woodlot. Over 80% of the canopy leaf litter (which accounts for almost all input excluding the irregular input of woody material) falls in October (Merriam, unpublished). From April to September, the previous year's leaf litter input and the small input from the current year are redistributed over the woodlot floor by wind and gravity. Exposure of the high areas and protection of the low areas result in litter accumulation in low areas. This pattern is disrupted in October when the heavy leaf input temporarily covers all of the woodlot floor, and litter accumulation in high, level and low areas equalizes. Surface litter was not collected in November but much of the October litter input is apparently blown from high and level areas before snowfall; the April litter accumulations again approximate a 1:3:6 ratio among high, level and low areas.

My measurements of litter standing crop are in the range expected from previous studies, but there are few published records that specify the topographic distribution of surface litter. Earlier measurements of the standing crop of surface litter in my beech-maple study area, from unspecified topographic areas, ranged from 1306.3 g/m^2 to 858.6 g/m^2 (Merriam, unpublished).

John (1973) measured a total standing crop of 1300 g/m^2 in a tropical forest in West Africa, a value also in the middle of my range despite obvious, but unspecified, differences in litter input and decomposition rate. Lang (1974) monitored total litter and fermentation weights ranging from 468.2 g/m^2 to 670.4 g/m^2 in a mixed oak forest, with a relatively rapid litter and fermentation turnover time of 1.53 years.

Other researchers have measured litter input rather than standing crop. Phillipson et al. (1975) measured litter input (leaves, flowers, bud scales, fruits and twigs) for a 5-year period in a beech woodlot in England, and found that annual input ranged from $205 - 388 \text{ g/m}^2$. Table 2 shows an approximate increase in litter accumulation of between 70 and 330 g/m^2 for different areas during the peak litter input period from September to October. A general figure of $250 - 360 \text{ g/m}^2$ annual leaf litter production in temperate forest zones (Armentano and Woodwell 1976) also approximates the range of surface litter accumulated in my study between September and October, since between 77% (John 1973) and 84% (Anderson 1973a) of annual litter-fall is leaf material. Maldaque (1968) measured an annual input of 244 g/m^2 sugar maple (Acer saccharum) leaves in a Canadian forest with a climate similar to that of my study area. Gosz et al. (1972) made detailed collections of aboveground litter-fall in a mature hardwood forest; they collected an annual total of 570.2 g/m^2 , or 353.3 g/m^2 if all woody material is excluded. Lang (1974) measured a total annual litter input of

648.1 g/m², or 537.4 g/m² if all woody material is excluded, in a mixed oak forest on the New Jersey piedmont. Leaf litter input in my beech-maple study area totalled 551.7 g/m² in 1972 (80.3% of total litter excluding branches), and occurred almost exclusively in October (Merriam, unpublished). All the preceding litter input measurements indicate that litter accumulations listed in Table 2 are within expected ranges, considering that the final October sampling time was too early to include all fall leaf litter input.

Hart et al. (1962), working in a northern hardwood forest, examined the accumulation of litter in high and low areas. They found that the accumulation of fall leaf litter ranged from a mean of 165.7 g/m² on high sites to a mean of 618.1 g/m² on low sites. Since Hart et al. did not make collections until November, their measurements include all fall leaf litter input, as well as the relocation of litter which occurs after the final October collection of my study.

One of the effects of surface litter accumulation is the protection it affords the litter-soil interface from desiccation (Nielsen 1959, Drift 1963) and temperature extremes (Williams and Gray 1974, Dickinson 1974). Since litter depth is a more direct indication of this buffering potential than is weight, depth was measured in cm and in leaf layers at three times during the growing season. Table 3 summarizes these readings and indicates that the depth of litter, by either measurement, is greatest in low areas.

Table 3. Depth of litter accumulation in three topographic areas in spring, summer and fall.
 Values are depths first expressed in leaf layers, then in cm, where $N = 10$.

MEASUREMENT TIME	TOPOGRAPHIC AREA	
	HIGH	LEVEL
MAY	2.70, 0.75	7.00, 1.90
JULY	3.00, 0.49	6.60, 1.06
OCTOBER	7.80, 2.00	10.50, 3.50
		11.30, 4.45
		8.50, 1.94
		13.40, 7.50

The linear measure of depth was subject to compaction by trampling or rain, and could underestimate the effective depth. By similar logic, measurement of number of leaf layers alone could overestimate the buffering capacity of accumulated litter, since a wet mat of twenty leaf layers does not provide the insulation of twenty layers of dry leaves. Table 3 shows the necessity of two measures. In high areas the number of leaf layers increases slightly from May to July, while the depth in cm decreases by more than 30%. Compaction is also evident in level and low areas, where the linear depth decreases more than the number of leaf layers. Table 3 also shows the equalizing effect of October litterfall on litter accumulation in all three areas.

An attempt to measure the horizontal movement of surface litter using replicate surface screens (see Materials and Methods) was unsuccessful. The collecting technique was a major problem. In securing the collecting screens on top of existing litter at each site, the litter was compressed slightly, and the screens were slightly depressed relative to the surface of adjacent litter. For this reason, litter continued to accumulate until the screened area was no longer a small local depression; this overestimated litter input to all areas. In addition, the smooth surface of the collecting screens was a poor imitation of the woodlot floor, and leaves on these screens were more susceptible to movement by wind than was adjacent litter. The result is that the screen data do not accurately represent the changing distribution of

surface litter in the three topographic areas. Table 2 provides the best information on the distribution of surface litter.

In addition to the spatial heterogeneity in the depth and weight of surface litter per unit area, an analysis of the April collection indicates differences in the composition of the litter accumulated in high, level and low areas. Eight litter categories are considered (Figure 1).

Beech and maple leaves were separated because of their abundance in the study plot and their different decay rates. Shanks and Olson (1961) reported that beech leaves lose 21% of their weight during the first year after leaf fall, compared to a loss of 32% for sugar maple leaves; Gosz et al. (1973) and Coldwell and Delong (1950) also found a significantly greater weight loss from sugar maple leaves than beech leaves after 11 months. These two canopy leaf types were used as substrates in later decay experiments.

Since it was difficult to separate leaves older than one year into specific age categories, leaves were divided into "intact" and "aged" categories. The first category consisted of leaves showing only slight, or no, visible signs of decay, and the latter was made up of all leaves which lacked the fleshy matrix on 25% or more of their surface area. The petioles were not detached from these leaves, but a separate category of "petioles" was required for all those physically separated from their leaves before collection.

Figure 1. Qualitative separation of surface litter from the April collection. Woody material has been omitted.

PROPORTION
OF TOTAL LITTER

Herbaceous material was considered separately, and treated separately in decay experiments, because of its seasonal abundance and extremely rapid decomposition (Kuhnelt 1969). Due to an April sampling time, the Herbaceous material consisted of stems and a few leaves of blue cohosh from the previous fall. Also as a result of the sampling period, a category of "flowers and fruit" contained mostly bud scales, beech nuts and their husks. The last category, that of "unidentifiable fragments" consisted mostly of leaf fragments too small to identify, and was a general category for aged leaf material.

Figure 1 illustrates the distribution of "aged" and "intact" leaf material. A greater proportion of aged beech and maple leaf litter accumulated in low areas (6.95% and 9.99% for aged beech and maple in low areas compared to 3.64% and 5.44% for the same categories in high areas). By contrast, high areas have a slightly larger proportion of intact beech leaves than do low areas (23.83% compared to 21.72%), and a much larger proportion of intact maple leaves (33.53% as compared to the low areas' 17.35%).

The distribution of "aged" and "intact" leaf litter indicates two things. First, since all aged categories are scarce in high areas, these areas are dominated by intact beech and maple leaves. Second, the lower proportion of intact maple leaves in the low areas indicates that they are more susceptible to fragmentation and decay than beech leaves, particularly when accumulated in low areas.

Another indication of the accumulation of aged or partly decayed plant material in low areas is the larger proportion of detached petioles and "unidentifiable fragments" found there.

The two remaining categories, "herbaceous material" and "flowers and fruit" do not show evidence of greater accumulation in low areas. As mentioned, the "herbaceous material" at this time of year is mainly cohosh stems and leaves. The aboveground parts of this species die in the fall, and typically they dry, turn brown, but the stems remain standing through the winter. They enter the litter in the spring directly where they grew.

Distribution of beech nuts and their husks is principally a function of small mammal movement, and follows a different pattern.

One more litter category, "woody material", was separated. But this category accounts for such a large proportion of the standing crop (26%, 30% and 53% in high, level and low areas, respectively) that it obscures comparison of intact and aged leaf material among areas. This is a significant problem since leaf material was the substrate chosen for further decomposition studies, and woody material, which may take many years to decompose (McFee and Stone 1966), was not dealt with in any detail by this relatively short-term experiment. Figure 1, therefore, omits "woody material", but Table 4 includes this more resistant litter category.

Table 4 lists the weights of each litter category per unit area. It makes four points not illustrated in Figure 1.

Table 4. Qualitative separation of surface litter in the April collection.

The values are means $\pm$ 1 standard deviation, where $N = 10$, expressed in g/m^2 .

LITTER CATEGORIES	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
INTACT Be LEAVES	72.6 $\pm$ 29.1	167.7 $\pm$ 185.6	299.8 $\pm$ 185.8
AGED Be LEAVES	11.1 $\pm$ 7.5	17.9 $\pm$ 8.8	47.9 $\pm$ 42.0
INTACT Ma LEAVES	93.0 $\pm$ 25.8	128.3 $\pm$ 43.6	210.5 $\pm$ 126.5
AGED Ma LEAVES	25.7 $\pm$ 8.1	43.6 $\pm$ 16.3	121.2 $\pm$ 32.6
PETIOLES	7.2 $\pm$ 4.3	20.6 $\pm$ 5.7	46.0 $\pm$ 16.1
HERBACEOUS MATERIAL	1.7 $\pm$ 0.6	12.8 $\pm$ 3.2	11.4 $\pm$ 3.7
FLOWERS & FRUIT	15.8 $\pm$ 12.7	65.2 $\pm$ 44.8	43.4 $\pm$ 27.5
UNIDENTIFIABLE FRAGMENTS	77.5 $\pm$ 80.9	340.8 $\pm$ 385.5	432.8 $\pm$ 240.5
SUBTOTAL	304.6	796.9	1213.0
WOODY MATERIAL	106.0 $\pm$ 158.6	343.7 $\pm$ 197.4	1379.1 $\pm$ 733.7
TOTAL	410.6	1140.6	2592.1

First, the total accumulation of litter is least on high areas, greater on level areas, and greatest in low areas, and with the exception of "herbaceous material" and "flowers and fruit", all individual categories show the same trend. Second, it indicates the enormous contribution of woody material, particularly to low areas. Third, the standard deviations around the mean weight of each litter type are a measure of the huge variability in litter accumulation among replicate sites. Despite this variability, weights in most categories tested (all except "herbaceous material" and "flowers and fruit") were significantly larger in low areas than on high areas ($P < .05$); furthermore, there were significant differences ($P < .05$) among all three areas for all categories except intact beech and maple leaves, and aged beech leaves. Finally, although the proportion of intact beech and maple leaves in the low areas appears to be equal to or smaller than proportions in the other two areas (Figure 1), Table 4 indicates that there are 510.3 g/m^2 of these intact leaves in low areas compared to only 165.6 g/m^2 on high areas. The significance of this difference in fresh litter resources for decomposing organisms will be discussed later.

The three areas have both quantitatively and qualitatively different litter layers. The greater proportion of aged litter in low areas indicates that not only does more litter accumulate, it remains for longer periods; a greater diversity of aged litter provides a more diverse food resource for decomposer organisms (Parkinson 1972). In addition, the accumulated litter in low

areas modifies physical conditions of these sites. The next section examines the moderating effect of accumulated litter on moisture and temperature conditions at the litter-soil interface.

2. Physical Conditions

Temperature and moisture levels of the litter and surface soil were monitored because they were the physical factors with the most direct effect on decomposer activity, and hence decay rate (Alexander 1961, Kononova 1966, Witkamp 1966, Witkamp 1971, Edwards 1975, Schlesinger 1977). Temperatures at the litter-soil interface were measured hourly to detect diurnal patterns, while the most frequent record of soil moisture (as soil suction) was taken daily.

Table 5 shows the relationship between temperatures at the litter-soil interface and surface soil moisture for three topographic areas on a single morning in late April. The first point that is apparent from Table 5 is that high and level areas have warmer mean temperatures than do low areas, but that the smallest variance is associated with temperatures in low areas. As a result of the large variances in high and level areas only the cooler temperatures of low areas can be statistically separated from those in other topographic areas ($F=14.70$, $P<.001$). Timing of the measurement program dictates that the variability in temperatures has both a spatial and temporal component; part is due to differences among the 22 replicate sites, but part is also due to the gradual rise in temperature between 900 and 1200h.

Table 5. Temperature at litter-soil interface (C) and surface soil moisture (% wet soil weight) measured between 900 and 1200h, April 28, 1975.

The values are means $\pm$ 1 standard deviation, where N = 22.

PHYSICAL CONDITION	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
TEMPERATURE	8.86 $\pm$ 3.68	9.54 $\pm$ 3.48	6.41 $\pm$ 1.60
SOIL MOISTURE	24.19 $\pm$ 4.48	33.16 $\pm$ 4.19	47.36 $\pm$ 6.73

The second point shown in Table 5 is that the soil moisture content of the low areas is statistically greater than that in the other topographic areas ($F=117.57$, $P<.001$). The result is that temperatures in the moist low areas are moderated, and they do not reflect the rising ambient temperatures between 900 and 1200h as quickly as the other topographic areas do; temperatures in low areas remain cooler, and they have the least variability in temperature because the temporal component of their variance is reduced.

Temporal changes in temperature from June to October are summarized in Table 6. Three main points can be made. First, although mean temperatures of the litter-soil interface show no statistically significant trend from June to October, temperatures in September and October are cooler than in previous months. Second, and more important, most temperatures monitored in low areas have smaller variances and narrower ranges. Finally, the smaller variance and narrower range of October temperatures are attributed to the shorter, 19-day sampling time for October.

Temporal changes in moisture content were measured as percent moisture (percent of wet weight) in litter and soil (Table 7), and in soil, as soil suction, stated in centibars (Table 8). Both measurements indicate greater soil moisture in low areas during all measurement periods.

Table 7 also allows comparison of litter and soil moisture contents; it shows greater variability in the moisture content of surface litter compared to more constant soil moisture in all areas. However, interpretation of this trend requires

Table 6. Monthly temperature means, standard deviations and ranges (in C) for each topographic area measured at the litter-soil interface.

Calculations were made from hourly temperature readings taken from 1000 to 1400h and 000 to 400h daily.

Monthly mean air temperatures (in C) were obtained from Environment Canada measurements made at Ottawa International Airport.

TOPOGRAPHIC AREA							
PERIOD	HIGH		LEVEL		LOW		AIR TEMP.
	$\bar{x} \pm 1 \text{ S.D.}$	RANGE	$\bar{x} \pm 1 \text{ S.D.}$	RANGE	$\bar{x} \pm 1 \text{ S.D.}$	RANGE	
JUNE	17.45 $\pm$ 4.06	9.00-27.25	17.19 $\pm$ 3.17	10.75-25.25	15.12 $\pm$ 2.41	9.75-21.50	25.0
JULY	17.90 $\pm$ 6.09	9.25-27.75	16.29 $\pm$ 3.96	9.00-25.50	15.74 $\pm$ 3.33	9.25-23.00	27.9
AUGUST	17.59 $\pm$ 3.63	10.00-27.25	14.40 $\pm$ 3.14	7.75-22.25	14.31 $\pm$ 2.08	9.50-19.50	26.1
SEPTEMBER	12.15 $\pm$ 2.74	6.00-18.75	11.30 $\pm$ 2.13	6.00-16.75	11.14 $\pm$ 3.06	5.50-16.00	18.1
OCTOBER (ends Oct 19)	11.98 $\pm$ 1.73	8.25-17.75	12.32 $\pm$ 1.88	8.25-19.25	11.98 $\pm$ 1.50	8.00-16.50	13.6
SEASONAL $\bar{x}$	15.41		14.30		13.66		

7

explanation of the data sets from May, June and October. At these measurement times surface litter moisture contents are unusually large compared to soil moisture. Field notes for May and June sampling days indicate that it began to rain shortly after sampling began. Therefore, many of the litter samples were wetted, but the rain did not affect the underlying soil before cores were taken. A similar explanation is suggested for October, although no field note was made.

Standard deviations of means for each month were not included in Table 7 because most were 15 - 25% of the mean, regardless of the area sampled. Surface litter moisture content is less variable through time in low areas than in level and high areas (Table 7). It was also noted that the underlying litter layers in low areas remained moist to the touch for long periods following a rain, while litter in high and level areas dried more rapidly. Table 7 therefore indicates the importance of litter depth to the maintenance of litter and soil moisture.

Temporal trends in moisture content are not obvious from Table 7 because of the sampling technique used. Ten replicate sites were sampled in each area, but collections were made only once each month. Thus, these measurements are strongly influenced by the timing and volume of the last rainfall, and do not represent true monthly averages. Table 8 overcomes this problem, since it summarizes daily measurements of soil suction over monthly intervals.

Table 7. Mean monthly moisture content (% wet weight) of surface litter and surface soil in three topographic areas (N = 10).

PERIOD	SURFACE LITTER			SURFACE SOIL		
	HIGH	LEVEL	LOW	HIGH	LEVEL	LOW
APRIL	24.40	33.34	45.56	22.64	29.06	39.33
MAY	44.90	38.29	62.39	19.78	29.85	41.07
JUNE	36.75	32.55	63.55	18.74	23.64	29.38
JULY	18.48	22.34	44.94	14.93	24.93	38.59
AUGUST	19.06	30.15	37.33	15.64	24.95	38.63
SEPTEMBER	16.40	27.57	44.59	18.04	26.03	38.87
OCTOBER	43.83	57.03	58.85	23.90	26.62	43.40
SEASONAL $\bar{x}$	29.12	34.47	51.03	19.10	26.44	38.47

Table 8 illustrates both spatial and temporal trends in soil suction. A smaller soil suction was consistently measured in low areas, indicating more water in the soil pores of these areas, although the soil was never saturated. Soil suction varies little from May to October in low areas. In high and level areas, however, soil suction increases in the summer months, reaching a maximum in August, and then decreases in September and October. These results indicate that the surface soils of more exposed level and high areas become drier during the warmer summer months, whereas the low areas remain moist.

The constant moisture regime of the low areas buffers against daily and seasonal temperature extremes and produces the small variances and narrow temperature ranges shown in Table 6. The low areas also have slightly, but consistently, cooler monthly mean temperatures than do level and high areas. The moderating effect of moisture on daily or seasonal warming trends is longer lasting than moderation of cooler temperatures. The result is that the narrower monthly ranges of temperatures in low areas are almost entirely due to elimination of warmer temperatures.

The inconsistent temporal pattern in monthly temperatures observed in Table 6 is also at least partly attributable to litter and soil moisture levels. Air temperatures measured by Environment Canada at Ottawa International Airport, 5.5 km from the woodlot, show an expected slight warming trend in midsummer, and gradual cooling in the fall. During the summer period the mean litter-soil interface temperatures do not show a similar warming trend, and

Table 8. Soil moisture suction (centibars) expressed as monthly means of daily readings ± 1 standard deviation in three topographic areas.

PERIOD	TOPOGRAPHIC AREA		
	HIGH	LÉVEL	LOW
MAY	16.50 $\pm$ 2.70	8.97 $\pm$ 2.57	6.74 $\pm$ 1.59
JUNE	28.79 $\pm$ 17.51	28.95 $\pm$ 19.82	5.93 $\pm$ 3.44
JULY	25.76 $\pm$ 15.67	25.44 $\pm$ 17.47	3.94 $\pm$ 3.94
AUGUST	54.88 $\pm$ 16.77	44.86 $\pm$ 17.20	7.03 $\pm$ 5.87
SEPTEMBER	35.71 $\pm$ 15.41	32.18 $\pm$ 15.50	2.25 $\pm$ 1.57
OCTOBER	11.24 $\pm$ 5.72	7.45 $\pm$ 3.32	5.11 $\pm$ 5.30
SEASONAL $\bar{x}$	28.81	24.64	5.17

they remain consistently lower than air temperatures. The canopy layer, herbaceous vegetation, surface litter, and soil moisture all oppose the heating effects of dry sunny days and temperatures at the soil surface remain cooler (Kuhnelt 1969). Moist litter and soil found in low areas have the greatest moderating effect.

By October, insulation of the litter layer and heat capacity of the soil moisture may result in litter-soil interface temperatures which are warmer, rather than cooler, than ambient. Although the mean litter-soil temperatures for October are cooler than the air temperatures, the coolest litter-soil temperature recorded is 8.0 C. By contrast, daily minimum air temperatures for the first nineteen days of October fall below 0 C three times, once as low as -2.3 C.

From January to March, snow provides additional insulation, and temperatures at the litter-soil interface of both high and low areas are consistently warmer than ambient temperatures (Merriam and Wegner, personal communication). Similar temperature modification under the snow has been discussed by Hart et al. (1962) and Fahey and Lang (1975).

Table 9 lists the means and standard deviations of hourly temperatures for five separate week-long periods. These periods were selected to exemplify distinct climatic periods that were observed within the growing season. These selected periods were analysed to examine diurnal temperature patterns in the three areas. The timing and short duration of each selected period insured that seasonal climatic changes did not occur within a period, and only diurnal temperature fluctuations remained.

Table 9. Temperature summary for five week-long periods chosen to exemplify seasonal differences in three topographic areas.

The values are mean $\pm$ 1 standard deviation (N = 168) calculated from hourly temperatures recorded at each site.

PERIOD	LOCATION	TOPOGRAPHIC AREA		
		HIGH	LEVEL	LOW
JUN 5-12				
	1	14.82 $\pm$ 1.94	*14.27 $\pm$ 1.57	13.90 $\pm$ 1.28
	2	15.02 $\pm$ 2.78	15.73 $\pm$ 2.62	13.74 $\pm$ 1.16
	3	14.91 $\pm$ 2.15	*13.88 $\pm$ 1.81	14.32 $\pm$ 1.38
	4	*13.24 $\pm$ 2.58	12.54 $\pm$ 2.10	11.55 $\pm$ 0.72
	5	*13.27 $\pm$ 2.73	13.06 $\pm$ 3.27	*12.15 $\pm$ 1.25
	6	12.62 $\pm$ 1.99	11.61 $\pm$ 1.69	*12.27 $\pm$ 1.44
JUL 1-8				
	1	20.12 $\pm$ 1.82	*19.25 $\pm$ 1.37	*18.59 $\pm$ 1.69
	2	21.28 $\pm$ 2.77	*19.73 $\pm$ 1.80	20.06 $\pm$ 2.04
	3	20.36 $\pm$ 2.00	20.30 $\pm$ 2.35	18.76 $\pm$ 1.02
	4	*20.49 $\pm$ 2.92	19.46 $\pm$ 2.97	16.34 $\pm$ 0.76
	5	*20.74 $\pm$ 3.04	20.63 $\pm$ 3.83	17.53 $\pm$ 1.15
	6	19.52 $\pm$ 2.17	17.80 $\pm$ 1.78	*18.04 $\pm$ 1.49
AUG 17-24				
	1	13.86 $\pm$ 1.42	11.00 $\pm$ 2.28	10.10 $\pm$ 1.80
	2	13.04 $\pm$ 2.00	*13.88 $\pm$ 2.16	9.06 $\pm$ 1.30
	3	13.19 $\pm$ 1.56	11.93 $\pm$ 1.67	*13.26 $\pm$ 1.92
	4	15.86 $\pm$ 2.95	14.51 $\pm$ 2.40	*13.37 $\pm$ 1.28
	5	*15.72 $\pm$ 2.74	14.97 $\pm$ 2.88	13.71 $\pm$ 1.28
	6	*15.02 $\pm$ 2.49	*13.49 $\pm$ 1.74	14.21 $\pm$ 1.50
AUG 31-SEP 7				
	1	14.43 $\pm$ 1.34	11.26 $\pm$ 2.15	10.40 $\pm$ 1.67
	2	13.36 $\pm$ 1.76	14.20 $\pm$ 1.56	9.26 $\pm$ 1.54
	3	*13.38 $\pm$ 2.13	*12.60 $\pm$ 1.52	13.53 $\pm$ 1.88
	4	*13.14 $\pm$ 2.37	*12.15 $\pm$ 1.66	12.19 $\pm$ 0.38
	5	12.72 $\pm$ 2.03	12.24 $\pm$ 2.13	*12.08 $\pm$ 1.34
	6	12.39 $\pm$ 2.02	11.23 $\pm$ 1.24	*12.60 $\pm$ 0.92
OCT 12-19				
	1	*12.05 $\pm$ 1.01	*11.87 $\pm$ 0.94	*11.58 $\pm$ 0.92
	2	*11.44 $\pm$ 1.00	*12.00 $\pm$ 0.94	*12.11 $\pm$ 0.82
	3	---	11.55 $\pm$ 0.99	---
	4	---	---	---
	5	---	---	---
	6	---	---	---

* Indicates sites selected to exemplify the temperature conditions of each area in further analyses.

The first period, June 5 - 12, was chosen because it was the earliest period for which hourly temperatures were obtained following spring melt. July 1 - 8 represents early summer, when warmer, drier summer conditions began. August 17 - 24 represents mid-summer, a warm dry period. August 31 - September 7 marks the beginning of fall, with its cooler, damper conditions, but before the period of peak leaf input. October 12 - 19 is the latest period for which hourly temperatures were obtained, and it includes the time of peak litterfall.

Table 9 shows that temperatures measured in different topographic areas are not obviously different on the basis of their weekly means. Although means measured in low areas are slightly cooler than those in other topographic areas, the difference is very small.

The other point to be made from Table 9 is that, in general, standard deviations of temperature measurements for low areas are smaller than those for level or high areas. The variability of temperatures is also expressed in terms of ranges for two sites with similar means within each area in each time period (Table 10). Both measures of variability of weekly temperature data indicate that diurnal temperature variation is least in low areas, and greatest on high areas. Before further analysis was done, the spatial and temporal components of temperature variability were separated.

As Table 9 shows, temperature means and standard deviations vary little among replicate sites; however, analysis of variance

Table 10. Temperature ranges (in C) for five representative periods during the growing season in three topographic areas.

PERIOD	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
JUNE 5 - 12	9.00 - 22.25	10.75 - 18.25	9.75 - 15.75
JULY 1 - 8	14.75 - 27.75	16.50 - 24.00	15.00 - 21.75
AUGUST 17 - 24	10.00 - 23.00	9.25 - 18.75	9.50 - 17.75
AUGUST 31 - SEPTEMBER 7	7.50 - 18.75	8.50 - 16.75	8.75 - 16.00
OCTOBER 12 - 19	9.25 - 15.00	10.00 - 14.50	9.75 - 14.25

done on the six sites within each topographic area indicate that all sites are separable ($P < .001$). Due to the large number of temperatures recorded, and the small variance around temperature means within each site, small spatial differences among replicate sites appear very significant. In order to eliminate most of the spatial variability in temperature readings, and also reduce the number of readings for further analysis, two sites were chosen to represent each area in each time period. The two sites chosen within each area met three criteria: they had similar standard deviations, similar means, and their means were closest to the mean of the six site means for the topographic type. Selecting these pairs of sites minimized the spatial variance so that the remaining temporal variation in temperature could be analysed using data from each of these pairs of sites.

The pattern of diurnal variations in temperature was examined in more detail by a method of Colwell (1974). A predictability index (P) was calculated for each weekly series of temperatures. The components of P are constancy (C) and contingency or cyclic repeatability (M) of temperatures.

Figure 2 shows the predictability indices and the contribution of their components. This figure makes two main points. First, the predictability of temperatures is always greatest in the low areas and least in the high areas. Second, the contribution of constant temperatures is greatest to the low areas, whereas a larger proportion of the high areas' predictability is due to cyclic repeatability of the temperatures. Further differences

Figure 2. Predictability indices (P) calculated from hourly temperature readings, and a breakdown of this index into the proportion due to constancy (C) and repeatability (M) in each topographic area during five week-long periods.

PREDICTABILITY

HI LEV LO

JUN 5-12

HI LEV LO

JUL 1-8

HI LEV LO

AUG 17-24

HI LEV LO

AUG 31-SEP 7

HI LEV LO

OCT 12-19

during the season are attributable to the interaction of air temperature with changing litter depth and soil moisture levels.

June 5 - 12 temperatures are cool. Low areas, and to a lesser extent, level and high areas, still retain the moisture of spring melt, and relatively constant temperatures are an important source of predictability.

By the first of July, warmer, drier conditions prevail. All areas reflect the diurnal temperature pattern in their increased cyclic repeatability component. Only the moist low areas retain a strong constancy component, and they smooth diurnal fluctuations by eliminating the warmest temperatures.

All areas show a drop in predictability August 17 - 24. Level areas show smaller predictability values because their constancy component has decreased. By contrast, low areas show a substantial reduction in repeatability of temperatures, and their constancy component declines only slightly. A possible explanation for the decrease in temperature repeatability from July to August is that ambient temperatures show less diurnal fluctuation as nights remain warm. Moist low areas further smooth these reduced fluctuations. Decline of constancy in level areas is attributable to mid-summer dryness. The high areas show a change only in the repeatability component because they lacked litter and had already begun to dry in July.

The greatest differences in temperature predictability among the three areas occur in early fall, August 31 - September 7. Fall soil moisture levels are high in all areas, and the constancy component of the predictability index rises accordingly. However,

since this period is before litterfall, only the low areas have a deep litter layer, and these areas have the most predictable temperatures; high areas have little surface litter, and the constancy and overall predictability of their temperatures is least. Predictability in level areas remains the same as during the previous period, but the constancy component has become larger.

The last period, October 12 - 19, occurs during leaf fall. The buffering capacity of this new litter layer, and the cool, wet climatic conditions are reflected in a very large constancy component in all areas. Since predictability (P) is the sum of constancy (C) and repeatability (M), the proportion of P due to repeatability continues to decrease during this period.

I have compared predictability indices among areas and in time, yet I have not formally calculated their variance. This is because my sampling technique and the format used to compute the index eliminated spatial and temporal variability. I earlier explained the selection of sites to eliminate spatial variation. Temporal variability within the index was eliminated by choosing time and temperature intervals so that within one time interval a change of only one temperature interval was possible. The time interval was one hour, and the chosen temperature interval was 2.0 C. Since a 2.0 C change in temperature cannot occur at the litter-soil interface in less than one hour, the complete temperature universe was measured, and no allowance for temporal sampling was needed in calculating the predictability indices. Thus, both spatial and temporal variability were eliminated from the analysis, and no variance measure was required for the predictability indices.

3. Surface Soil Characteristics

Incorporation of organic matter into the surface soil is a function of the overlying layer of surface litter, and the decomposition of this litter, effected primarily by invertebrate and microbial activity (Drift 1969, Ghilarov 1969). Therefore, incorporation of organic matter into the soil is a reflection of the long-term outcome of the litter decomposition process, and as such will be considered the final level of derived heterogeneity in this study. However, this same measure, as an indicator of soil structure, affects early decomposer populations. Therefore, soil organic content measurements will be presented at this stage.

Table 11 lists the proportion of the soil fraction made up by litter fragments in high, level and low areas in spring. Despite the large sample size, the variances in fragment proportions are enormous, an indication of the real substrate variability within replicate sites. Nevertheless, the means indicate that low areas contain many (16.5) times more litter fragments than do high areas. But in high areas the proportion of these "litter" fragments which is made up of roots (many of which were alive at the time of sampling) exceeds 50%, twice the percentage root contribution in low areas. Table 11, therefore, overestimates the contribution of decomposable litter fragments to high areas; the actual difference between litter fragments incorporated into high and low areas is greater than 16.5 times.

Table 11. Components of soil organic matter in the top 10 cm of three topographic areas.

The values are means $\pm$ 1 standard deviation, where $N = 40$, expressed as percent of total dry weight.

INCORPORATED ORGANIC MATTER	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
LITTER FRAGMENTS IN SOIL INCLUDING ROOTS	0.32 $\pm$ 0.41	1.25 $\pm$ 2.17	5.28 $\pm$ 6.66
LITTER FRAGMENTS IN SOIL EXCLUDING ROOTS	0.15	0.66	3.86
ORGANIC CONTENT OF SOIL MINUS LITTER FRAGMENTS	4.96 $\pm$ 2.78	8.54 $\pm$ 2.48	10.79 $\pm$ 3.49

After removing litter fragments, the remaining surface soil from low areas has twice the organic content of soil from high areas (Table 11). This amorphous soil organic material, which bears no trace of the anatomical structure of the plant residue from which it was derived, is termed humus (Russell 1961). The significance of humus to soil structure, and its role in litter decomposition and nutrient retention, will be considered in the General Discussion.

Table 12 lists the temporal changes in soil organic matter content in three topographic areas. Although there is considerable variability among the sites, in each of the three areas, the monthly and seasonal means indicate a larger proportion of soil organic matter in low areas, less in level areas, and least in high areas. There is no apparent pattern in temporal changes in soil organic matter. The monthly means in high areas are not separable ($P > .05$). There are significant differences ($P < .05$) in the organic matter content of soil cores taken in level areas from May to June, July to August, and August to September, and in low areas from May to June, and June to July, but there is no logical explanation for these differences. Accumulation of soil organic matter is a slow continuous process (Pomeroy 1970, Witkamp 1971), and monthly changes are not expected. The fact that means of 20 replicate samples show these monthly fluctuations is further evidence of the gross variability in soil organic content among replicate sites.

A simple textural analysis of the three areas, done on the September soil collection, is summarized in Table 13. Since soil

Table 12. Loss on ignition as a measure of soil organic matter in three topographic areas, expressed as percent of the total dry weight of soil and stated as means $\pm$ 1 standard deviation, where N = 20.

COLLECTION TIME	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
APRIL	5.76 $\pm$ 3.86	12.28 $\pm$ 4.22	18.27 $\pm$ 7.03
MAY	6.04 $\pm$ 3.70	10.66 $\pm$ 2.79	15.57 $\pm$ 5.03
JUNE	4.24 $\pm$ 1.50	7.60 $\pm$ 1.89	9.32 $\pm$ 2.39
JULY	3.08 $\pm$ 1.47	9.47 $\pm$ 4.14	17.68 $\pm$ 6.51
AUGUST	6.20 $\pm$ 4.18	16.95 $\pm$ 6.40	22.25 $\pm$ 6.35
SEPTEMBER	4.50 $\pm$ 3.38	11.67 $\pm$ 4.13	20.86 $\pm$ 7.78
OCTOBER	6.13 $\pm$ 3.32	11.09 $\pm$ 2.55	22.22 $\pm$ 4.95
MONTHLY $\bar{x}$	5.14	11.39	18.02

crumbs were not disaggregated before analysis, an aggregate rather than particle size analysis was performed. The most conspicuous result is that all areas are dominated by their coarse aggregate fractions. The level and low areas have between 40 and 50% of their material (by weight) in the two coarsest categories, and the low area has almost 30% of its material in the coarsest fraction.

The United States Department of Agriculture classification (Kilmer and Alexander 1949) considers all particles >2.0 mm as gravel, but in my aggregate analysis this fraction contained soil crumbs and litter fragments, as well as stones. These organic components were most important in low areas, where they made up 16.9% of the coarsest fraction by weight. In level areas, the coarsest fraction was 5.0% organic, and in high areas it was only 1.3% organic. By contrast, the total contribution of coarser sand and stones was much greater in high areas, 27.64%, as compared to 15.65% in low areas. The coarser sand and stones were >0.5 mm in diameter, and so were found in the three largest size classes. In summary, the coarsest categories in the low areas contain considerable organic material in the form of soil crumbs and litter fragments, whereas on high areas these fractions contain more stoney material.

None of the smaller size classes contained appreciable organic matter. This indicates that humic organic matter aggregated with the mineral component, and formed soil crumbs (Buckman and Brady 1969).

Soil in low areas contains more organic material, in both fragment and humus form, and soil crumbs are a more prevalent formation. These soil crumbs result in potentially good aeration and rainfall penetration (Schnitzer and Khan 1972).

Table 13. Particle size analysis of soil from three topographic areas.

The values are means $\pm$ 1 standard deviation, where $N = 10$, expressed as the percent by weight in each size category.

PARTICLE SIZE CATEGORIES	TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW
>2.00 mm gravel and soil crumbs	7.89 $\pm$ 2.97	17.31 $\pm$ 11.28	29.10 $\pm$ 11.73
1.00 - 2.00 mm coarse sand	11.32 $\pm$ 5.03	25.83 $\pm$ 3.44	24.46 $\pm$ 2.47
.210 - 1.00 mm medium sand	49.60 $\pm$ 4.54	40.24 $\pm$ 7.20	33.79 $\pm$ 7.74
.105 - .210 mm fine sand	21.03 $\pm$ 4.97	11.38 $\pm$ 3.65	7.83 $\pm$ 2.71
.063 - .105 mm very fine sand	3.23 $\pm$ 2.40	2.03 $\pm$ 1.08	2.06 $\pm$ 0.80
<.063 silt and clay	<u>6.93 $\pm$ 2.27</u>	<u>3.21 $\pm$ 1.28</u>	<u>2.76 $\pm$ 0.69</u>
TOTAL	100	100	100

The feedback linking the formation and effects of an organic surface horizon (L-F-H) and an organic-enriched A (A_h) horizon in mineral soils can be briefly summarized. Incorporation of more resistant litter fragments into surface soil is initially accomplished primarily by soil invertebrates (Edwards et al. 1970, Dickinson 1974). Further physical and chemical modification of these litter fragments is carried out by microorganisms (Ghilarov 1969). Products of this microbial activity combine with resistant litter compounds to form humus (Martin and Haider 1971). The resultant development of a friable organic soil completes the cycle and encourages further invertebrate and microbial activity on fresh litter (Alexander 1961, Jackson and Raw 1966). The next section compares microbial populations in the three topographic areas.

4. Microbial Populations

Three functional groups of microbes were assayed by plating samples of litter and soil taken from each topographic area between April and October. The functional groups were separated on the basis of their ability to metabolize increasingly resistant carbon compounds. The first group of microorganisms utilizes only soluble carbon, or a sugar substrate, the second group can derive its energy from the metabolism of cellulose, and the third group consists of those fungi able to decompose highly resistant lignin compounds. Decomposer microorganisms were divided into these three main functional groups because the associated substrates represent successive stages of litter decay (Garrett 1951, Schlesinger 1977),

and because the chemical and physical structure of litter have important effects upon its microbial decay rate (Alexander 1961). However, the successional pattern of decomposer microorganisms in a litter substrate rarely follows a linear progression from sugar, to cellulose, to lignin decomposing organisms (Saito 1956, Frankland 1966, Hudson 1968). Further complexity is added by the fact that substantial microbial decomposition may occur prior to deposition of plant litter on the ground (Hudson 1968, Harley 1971).

(1) Group 1: Soluble carbon or sugar decomposers

Figures 3, 4, 5 and 6, and Table 15 show temporal changes in the sugar decomposers. Figures 3 and 4 illustrate bacterial populations in samples taken from litter and soil, respectively, and Figures 5 and 6 show changes in fungal numbers in the same litter and soil samples. All media used for these assays were capable of supporting a large variety of sugar decomposing microorganisms. The Peoria medium used to assay bacteria on litter, and the rose bengal-aureomycin medium used for fungal counts on litter and soil samples, contained significant dextrose (Appendix I). Bacteria in soil were plated on a soil extract medium, to which dextrose was not added. However, Lockhead and Chase (1943) found that soil extract media also support sugar decomposers.

Media used to assay the sugar decomposers were also capable of supporting cellulose and lignin decomposers, since most can also metabolize sugars (Garrett 1951, Gyllenberg and Eklund 1974). However, the slower growth of cellulose and lignin decomposers

meant that fast-spreading sugar decomposers covered most of the plate area and prevented the establishment of decomposers of more resistant compounds (Parkinson et al. 1971, Watson et al. 1974). Therefore, although Figures 3, 4, 5 and 6 do not exclude cellulose and lignin decomposers completely, they represent sugar decomposers very well.

Figure 3 shows the large fluctuations in bacterial populations isolated from litter of the three topographic areas. Although the variance of each sample is large (Appendix II, Table 1), significantly fewer bacteria are found in litter from high areas ($F=6.10$, $P=.02$). Temporal changes in bacterial numbers are not synchronous over the three areas, but all populations reach their minimum value between late June and mid September. Populations of all areas peak twice during a growing season, once in the spring and again in the fall. Population maxima for litter bacteria occur in late May, and late September in high areas, in late June and mid October in level areas, and in late May and late October in low areas. This temporal pattern in bacterial numbers is generally related to the moisture content of the samples (Table 14); however, the fact that samples with the greatest moisture content do not always have the largest bacterial populations suggests that other factors are involved in limiting bacterial numbers. These other factors include litter depth, which also influences the relative exposure of the three areas to temperature extremes, and litter quality, which determines the availability of food resources to microorganisms.

Figure 3. Temporal changes in litter bacterial populations from three topographic areas grown on sugar substrate.

NO. BACTERIA
($\times 10^6$ /G DRY WT.)

The spring bacterial population maxima reflect a period of favourable physical conditions caused by warming temperatures as summer approaches, and moist litter due to the recent spring melt (Edwards 1975). The fact that bacteria in level areas apparently peak a month later than those in other topographic areas is probably a function of infrequent sampling times. The moisture content of litter sampled at the end of May is the lowest measured in the level area during the spring period (Table 14), and therefore populations peak at a later, more moist, sampling time. Although other litter and soil measurements made in the level area during May do not indicate a lack of moisture (Tables 7 and 8), samples for bacterial assays are taken on a single day from within a single 1 m^2 plot, and short-term local variations may be reflected. Cutler et al. (1923) showed that soil microorganisms can respond to short-term physical changes. They found that microbial population numbers may fluctuate as much over one three-day period as they do over a season, although when they averaged bacterial counts over two-week periods, they also showed two seasonal maxima, one in June and one in November. My microbial analysis will deal with seasonal trends based on seasonal changes in substrate and physical conditions.

Figure 4 shows temporal fluctuations in soil bacteria sampled from the three topographic areas. Three main points are apparent. First, bacterial numbers are approximately an order of magnitude lower in soil than in corresponding litter fractions. Second, all topographic areas show two peaks in population numbers,

Table 14. Moisture content (% wet weight) of samples used in microbial assays.

SUBSTRATE	SOURCE AREA	SAMPLING TIME									
		APR 28	MAY 13	MAY 29	JUN 16	JUN 29	JUL 23	AUG 19	SEP 21	OCT 18	OCT 28
LITTER	HIGH	24.14	14.11	33.38	38.08	32.95	19.91	28.30	25.82	18.94	18.74
	LEVEL	48.19	47.23	34.23	47.46	55.87	30.81	34.80	31.17	48.96	49.07
	LOW	51.48	56.25	53.53	46.04	66.29	46.55	43.66	35.30	40.76	52.34
SOIL	HIGH	22.85	22.18	25.40	21.55	24.02	14.77	19.33	21.16	25.04	26.13
	LEVEL	31.70	25.59	27.50	28.69	28.60	25.12	26.60	30.24	30.17	29.62
	LOW	40.54	42.96	39.80	42.58	39.97	39.00	33.53	41.87	38.35	33.02

Figure 4. Temporal changes in soil bacterial populations from three topographic areas grown on soil extract medium (which supports sugar decomposers).

NO. BACTERIA
($\times 10^6$ /G DRY WT.)

one in May and one in October. Third, there is no significant difference in soil bacterial populations among the three areas, except at peak times.

Both litter and soil microbial populations are apparently stimulated by the addition of new plant residues to the litter system (Laura 1975), but the larger autumn increase in soil microbial populations is caused specifically by rapid leaching of soluble compounds from the fresh litter into the soil (Witkamp 1966, Gosz et al. 1973). A second obvious soil microbial peak occurs in late May in high areas. It is the result of the spring warming trend which affects litter microorganisms earlier on high areas because these areas have a lower moisture content (Tables 7, 8 and 14), and warming air temperatures are not moderated. In addition, litter input does not stimulate microbial growth on high areas in autumn because fresh litter is too transient on these sites (Table 2). The burst of soil microbial growth following spring melt on high areas may, therefore, be due to soluble compounds leached from the small but stationary litter mat compacted under the snow.

Temporal changes in fungal populations are shown in Figures 5 and 6. Fungal population estimates in both litter and soil are approximately two orders of magnitude lower than corresponding bacterial estimates. Smaller fungal populations are expected in these mildly acidic soils (Waksman 1922). The mean and standard deviation of 60 soil pH measurements in the beech-maple study area is 5.95 ± 0.36 in high areas, 6.01 ± 0.22 in level areas, and 6.12 ± 0.42 in low areas. Furthermore, these fungal counts are

Figure 5. Temporal changes in litter fungal populations from three topographic areas grown on sugar substrate.

—————	high populations
- - - - -	level populations
- - - - -	low populations

NO. FUNGI
($\times 10^4$ /G DRY WT.)

Figure 6. Temporal changes in soil fungal populations from three topographic areas grown on sugar substrate.

———— high populations
----- level populations
- - - - - low populations

NO. FUNGI
($\times 10^4$ /G DRY WT.)

probably an overestimate since the dilution plate technique (used to produce Figures 5 and 6) does not differentiate between fungi actively colonizing plant debris, and dormant spores (Gochenaour and Woodwell 1974).

Figures 5 and 6 show population estimates based on colony counts. Although the population numbers cannot be assumed to represent active decomposers, they do estimate the total number of fungi in the active vegetative and dormant spore forms. Since the strategy of sugar decomposing fungi is known to be extensive production of resting forms, followed by rapid "burst" growth under favourable substrate and environmental conditions (Garrett 1951, Gray and Williams 1971), population estimates which include these resting stages may be more indicative of decomposition potential.

Figures 5 and 6 make three points about the size and distribution of fungal populations in litter and soil from the three topographic areas. First, fungal populations in soil fractions are almost two orders of magnitude lower than those in litter fractions, a result comparable to that obtained in the previous bacterial assay (Figures 3 and 4), and by other fungal researchers (Baker and Whittingham 1972). Second, there is no significant difference in fungal numbers in litter collected from high and low areas except during peak periods, but fungal populations from the soil are significantly larger in samples collected from the low area ($F=16.75$, $P<0.001$). Finally, most samples show two fungal population peaks, one in late spring, and one in late fall.

Comparison of population peaks on high areas in Figures 4 and 5 shows an obvious difference in timing between the dominant litter fungal peak, occurring in October (Figure 5), and the main soil bacterial peak, occurring in May (Figure 4). I hypothesize that whereas the fresh litter was too transient to allow significant leaching to the underlying soil during the autumn, the litter itself was readily colonized. Therefore, although large litter fungal populations were assayed on the high areas in October, this litter, and its associated microflora, did not remain on the site long enough for appreciable soluble nutrients to be leached to the soil before snowfall.

Only unpredictable spatial and temporal differences were anticipated in Figures 5 and 6 because these fungal populations include both vegetative and sporing stages, and fungal spores are always present in soil and air (Waksman 1922). Instead, the population pattern shown in Figures 5 and 6 is approximately that expected from assay of active vegetative fungi, in which populations increase during periods of favourable substrate and environment. Furthermore, the variability in fungal counts (Appendix II, Table 2) is less than would be expected from a spore count (Waksman 1922). Therefore, the dominant contributors to Figures 5 and 6 apparently are fungi which were in the vegetative state when sampled; contributions from dormant spores are restricted, perhaps by the time they require to form vegetative hyphae on assay plates (Gochenaur and Woodwell 1974).

Table 15 eliminates uncertainty about the activity of assayed fungi. It lists the fungi which remain after most resting spores are washed away, and therefore includes only the most active fungal genera in the three topographic areas. The one dominant genus in all litter and soil samples is Penicillium, a common and abundant genus in beech litter (Saito 1956), and cool temperate regions generally (Ivarson, personal communication). Although Penicillium is not a member of the Mucorales or "sugar fungi", it is commonly associated with members of this group such as Mortierella, Trichoderma and Mucor, as it is in Table 15 (Baker and Whittingham 1972). Two other abundant litter genera in Table 15 are Alternaria and Cladosporium. These are well documented as early colonizers (Webster 1957, Hogg and Hudson 1966, Hudson 1971, Baker and Whittingham 1972). In fact, Hogg and Hudson (1966) found that some beech leaves are substantially colonized by Alternaria, Cladosporium, and Coniothyrium even before leaf fall, and that they persist for much of the decomposition period. The two remaining genera in Table 15, Phoma and Fusarium are also important initial colonizers (Garrett 1951, Hudson 1968) although they have not been reported on living green leaves.

Soil samples contain fewer genera than do corresponding litter samples (Table 15), a result previously noted by Baker and Whittingham (1972). Again, Penicillium, Mortierella, Trichoderma and Mucor are present. Two additions, Gliocladium and Botrytis are also early colonizers (Garrett 1951, Ainsworth et al. 1973); in fact, a species of Botrytis has been recorded on living leaves (Hudson 1971, Pugh 1974).

Table 15. Fungi isolated from litter and soil fractions from three topographic areas.

LITTER SUBSTRATE		SOURCE AREA	SOIL SUBSTRATE	
GENUS	CONTRIBUTION (% by numbers)		GENUS	CONTRIBUTION (% by numbers)
Penicillium	.48	HIGH	Penicillium	.35
Alternaria	.15		Mortierella	.32
Cladosporium	.15		Trichoderma	.22
Mortierella	.05		Mucor	.11
Trichoderma	.05			
Mucor	.05			
Fusarium	.05			
Phoma	.01			
Coniothyrium	.01			
Penicillium	.46	LEVEL	Penicillium	.33
Alternaria	.20		Mortierella	.24
Cladosporium	.15		Gliocladium	.21
Trichoderma	.10		Trichoderma	.15
Mucor	.04		Mucor	.07
Phoma	.02			
Fusarium	.02			
Coniothyrium	.01			
Penicillium	.45	LOW	Penicillium	.28
Alternaria	.15		Gliocladium	.27
Cladosporium	.12		Mortierella	.22
Trichoderma	.10		Trichoderma	.15
Mucor	.10		Botrytis	.04
Fusarium	.05		Mucor	.04
Coniothyrium	.03			

Table 15 shows no significant functional difference in fungal populations of the three topographic areas; although Gliocladium is absent from high areas, and a significant contributor to level and low communities, it is also a pioneer genus. All areas are dominated by pioneer genera. It is interesting that even the earliest colonizers Alternaria and Cladosporium are capable of utilizing cellulose in pure culture (Yadav and Madelin 1968), and that sugar fungi may not become dominant until litter has been on the ground nine to ten months (Baker and Whittingham 1972). Microbial pioneer species are, therefore, not necessarily short-lived, but only early, and perhaps persistent, colonizers.

Similar fungal communities are found in all three topographic areas. All areas have a variety of litter types, which decay at different rates. Although litter remains longer in low areas, resulting in accumulation of more resistant compounds such as cellulose and lignin, most organisms which decompose cellulose and lignin can also utilize sugar. Therefore, no shift in dominant genera is observed among topographic areas.

(ii) Group 2: Cellulose decomposers

Two dilution plate media were used to estimate cellulose decomposers in litter and soil. The first was a medium containing ball-milled cellulose filter paper as the sole carbon source (Eggins and Pugh 1962). This method was intended to isolate cellulolytic fungi, but since the cellulose was not acid-treated, bacteria also grew on this medium. In fact, since bacteria are numerically more.

2

abundant in litter and neutral or mildly acidic soil, and are therefore found in greater numbers in serial dilutions (Waksman 1922), they dominated the cellulose plates. The second medium used to isolate cellulolytic decomposers was chosen specifically to isolate actinomycetes, since these organisms were known to be important in cellulose decomposition (Alexander 1961, Imshenetsky 1968, Buchanan and Gibbons 1974, Goodfellow and Cross 1974). However, the egg albumen medium of Corke and Chase (1956), which was intended to isolate actinomycetes, also allowed bacterial growth; therefore, a separate isolation and identification process was necessary to estimate actinomycete populations from growth on this medium.

Figure 7 illustrates three main aspects of spatial and temporal patterns in cellulolytic bacterial populations in litter. First, cellulolytic decomposer populations measured from April to October are significantly smaller on high areas than they are in low areas ($F=6.42$, $P=.02$) (calculated from data in Appendix II, Table 3). Second, populations in all three topographic areas are small during the summer period, between June 29 and September 21. Third, all three populations have two maxima, one in late spring and one in late fall, although these maxima are not as obvious in samples taken from high areas.

These cellulolytic population maxima may be due to the priming effect of fresh soluble carbon substrates. Gray and Williams (1971) suggest that the arrival of readily available nutrients in fresh litter may stimulate autochthonous (persistent) as well as zymogenous (opportunistic) decomposer activity. Therefore, input of

Figure 7. Temporal changes in cellulolytic bacteria isolated
from litter.

_____ high populations
----- level populations
- - - - - low populations

NO. CELLULOSE BACTERIA
($\times 10^6$ /G DRY WT.)

fresh litter may stimulate decay of more resistant materials. The fact that population maxima in cellulolytic bacteria, particularly in level and low areas (Figure 7), parallel maxima in sugar decomposing bacteria (Figure 3), suggests that both groups may be stimulated by nutrients leached from fresh litter.

Figure 8 follows temporal changes in cellulolytic bacteria in soil. With the exception of a large population peak in low areas in late fall, temporal fluctuations are small, and no significant pattern is detectable. Furthermore, there are no significant differences among populations from the three topographic areas. The one clear maximum on October 28 may be the result of priming by readily available nutrients. The fact that only soil in low areas supports a peak population may reflect a lack of resistant organic compounds in the other areas. Since cellulolytic bacteria cannot compete with sugar decomposers (Parkinson et al. 1971), cellulolytic population increases could be short-lived and easily missed by sampling, in the absence of resistant compounds. In addition, soil bacteria in general (Figure 4) are limited by a lack of available nutrients (Jensen 1971).

Figures 9 and 10 show temporal fluctuations in actinomycete populations in litter and soil. Although actinomycetes are classified as an order of bacteria, and are known cellulolytic decomposers, they were rarely included in population estimates illustrated in Figures 7 and 8. As with fungi, most counts of actinomycetes are spore counts (Gray and Williams 1971), and since spores require more time for development on dilution plates, bacteria generally out-compete

Figure 8. Temporal changes in cellulolytic bacteria isolated from soil.

NO. CELLULOSE BACTERIA
($\times 10^6$ /G DRY WT.)

actinomycetes on cellulose plates. Even on egg albumen plus actidione (a fungal inhibitor), a medium selected for encouragement of actinomycetes, most colonies were fast-growing bacteria. Figures 9 and 10 plot only those dilution plate colonies which were identified as actinomycetes.

Figure 9 shows a temporal pattern for actinomycetes in litter very similar to that for other cellulolytic bacteria (Figure 7). Populations in all three topographic areas are small during the summer period, between June 29 and September 21. Level and low populations have two maxima, one in late spring and one in late fall. Actinomycete populations on high areas do not achieve a fall maximum, although they have a wide gentle peak from August 19 to October 18. Actinomycete populations parallel cellulose bacteria populations closely, particularly in level and low areas. On these sites, actinomycete and cellulolytic bacteria peaks occur on exactly the same dates, perhaps due to stimulation by the same supply of available nutrients. Unlike other cellulolytic bacteria populations, actinomycete populations do not differ significantly among topographic areas except during population peaks (Appendix II, Table 4).

Actinomycete populations in soil (Figure 10) show more pronounced peaks than do other soil cellulolytic bacteria (Figure 8). Actinomycetes in high and low areas have two distinct peaks, one in May and one in October. Populations in level areas have a May peak, but no clear fall maximum.

Figure 9. Temporal changes in cellulolytic actinomycetes isolated
from litter.

———— high populations
----- level populations
- - - - - low populations

NO., ACTINOMYCETES
($\times 10^6$ /G DRY WT.)

Figure 10. Temporal changes in cellulolytic actinomycetes isolated from soil.

———— high populations
----- level populations
- - - - - low populations

NO. ACTINOMYCETES
($\times 10^6$ /G DRY WT.)

The fact that both high and low areas support large soil actinomycete populations in spring and fall while other cellulolytic bacteria populations only peak in low areas emphasizes the importance of the sporulating nature of actinomycetes. A lack of resistant organic compounds in high areas may eliminate most cellulolytic bacteria from these sites as they cannot compete with sugar decomposers for readily available nutrients. Actinomycetes can remain on these sites as dormant spores and may be primed in spring and fall by any excess of available nutrients. It is possible that sporulation by actinomycetes enables these decomposers to remain dormant when substrate is scarce, yet they are present to utilize readily available substrate when it does not require competition with sugar decomposers; after priming by readily available nutrients, actinomycetes remain active by metabolizing cellulose.

(iii) Group 3: Lignin decomposers

The final functional group to be assayed consists of microorganisms capable of attacking lignin, a major constituent of wood and all secondarily thickened plant tissues. Lignin is known to be actively decayed by several fungi, but by few if any bacteria (Garrett 1951, Jackson and Raw 1966). Therefore, the assay method used here (Henderson 1961) aims at isolating only fungi capable of utilizing vanillin. Vanillin was chosen as a substrate because it is an aromatic compound similar in structure to lignin; therefore, fungi capable of metabolizing vanillin are assumed to be capable of breaking down lignin (Henderson 1961). Earlier attempts to incorporate

more natural resistant compounds, such as tannic acids, into an assay medium were unsuccessful in selecting organisms capable of utilizing lignin-related compounds (Henderson 1960).

Figures 11 and 12 follow temporal changes in lignolytic fungi isolated from litter and soil of the three topographic areas. These populations are one to two orders of magnitude smaller than total fungal populations isolated from corresponding samples (Figures 5 and 6). Furthermore, assays of both litter and soil samples indicate that lignolytic populations are slightly, but consistently, larger in low and level areas than they are on high areas. Temporal patterns are similar to those for sugar and cellulose decomposing populations. Despite relatively high variances (Appendix II, Table 5), Figures 11 and 12 show that populations from all three topographic areas, but particularly those from level and low areas, have two clear maxima, one in late spring and one in late fall.

Figures 11 and 12 apparently further support the theory suggested by Gray and Williams (1971) that readily available nutrients stimulate all microorganisms; once these readily available nutrients are utilized, some of the microorganisms are capable of attacking more resistant compounds such as lignin. In this way, an input of soluble nutrients may also stimulate decay of resistant compounds. However, it is not possible to deduce decay activity from fungal counts (Schlesinger 1977), particularly when some fraction, though probably a small fraction for lignolytic fungi (Garrett 1951), is contributed by spores. Therefore, another interpretation of the decay process is that small, persistent (autochthonous) populations

Figure 11. Temporal changes in lignolytic fungi isolated from
litter.

———— high populations
----- level populations
- - - - - low populations

NO. LIGNIN FUNGI
($\times 10^4$ /G DRY WT.)

Figure 12. Temporal changes in lignolytic fungi isolated from soil.

———— high populations
----- level populations
- - - - - low populations

NO. LIGNIN FUNGI
($\times 10^4$ / G DRY WT.)

of lignolytic fungi are responsible for most lignin decay. The brief bursts of population growth in late spring and late fall may be ineffective in significantly decomposing resistant compounds. This second interpretation suggests that each topographic area supports an autochthonous fungal population whose relatively constant size is governed by the accumulation of resistant compounds and the physical suitability of the area.

One further point about lignolytic decomposers is that this study did not investigate basidiomycete populations. Although this fungal class is well known for its lignin decomposing capability (Garrett 1951, Hering 1967, Gray and Williams 1971, Witkamp 1971a), no technique to quantitatively isolate members of the Basidiomycetes has been recorded (Katz and Lieth 1974).

(iv) Summary of the microbial populations

Microbial population results show both a spatial and temporal pattern. The spatial pattern is apparent from the summary of population levels of the three microbial functional groups in three topographic areas (Table 16). Most functional groups have larger populations in low areas than on high areas, and for many assayed populations this topographic difference is significant ($P < .05$). All functional groups also show a temporal pattern, consisting of spring and fall population peaks, regardless of their topographic origin (Figures 3 to 12).

Several quantitative differences have also been found within and among functional groups which do not contribute directly to the

Table 16. Summary of microbial populations ($\times 10^6$) of sugar, cellulose and lignin decomposers in the litter and soil of three topographic areas.

The values are means of 10 estimates.

FUNCTIONAL GROUP	SUBSTRATE					
	LITTER			SOIL		
	TOPOGRAPHIC AREA			TOPOGRAPHIC AREA		
	HIGH	LEVEL	LOW	HIGH	LEVEL	LOW
SUGAR DECOMPOSERS:						
BACTERIA	135.	396.	456.	4.00	2.73	9.03
FUNGI	2.70*	1.91	1.99	.0234	.0252	.0435
CELLULOSE DECOMPOSERS:						
BACTERIA	51.6	218.	219.	1.37	1.29	6.46
ACTINOMYCETES	10.6	22.9	19.0	.919	.733	2.72
LIGNIN DECOMPOSERS:						
FUNGI	.0391	.0700	.0954	.0407	.0636	.0715

* one very high value has raised the mean.

general spatial pattern, although these differences are all apparently related to the availability of resource substrates. For example, soil typically supports bacterial and fungal populations one to two orders of magnitude lower than corresponding populations grown on a litter substrate (Table 16), and fewer fungal genera occur in the soil (Table 15). Jensen (1971) ascribed this difference to a general lack of available nutrients in the soil. Cellulolytic and lignolytic populations are also consistently smaller than sugar decomposing populations; lignolytic fungi may be two orders of magnitude lower than sugar fungi (Table 16). These differences may also be related to substrate differences, such as a lack of aged litter in most areas, as well as slower growth of microorganisms on these more resistant substrates. Even within the group of sugar decomposers, fungal populations may be two orders of magnitude lower than those of bacteria. However, this numerical difference may underestimate the contribution of fungi to the decomposing community. Fungal vegetative growth is extensive, and hyphae can produce a biomass 62 times that of bacterial colonies in the same volume of soil (Satchell 1971).

Qualitative differences in microbial communities in the topographic areas were not elucidated. The three topographic areas show no difference in community structure (Table 15). All major genera are generalists, capable of utilizing soluble or more resistant compounds, depending on substrate availability. However, future investigation of the distribution of Basidiomycetes, well known lignolytic specialists, might reveal spatial differences in the pattern of microbial communities.

Spring and fall population peaks generally occur from late May to June and late September to October, in all functional groups. The synchrony of these peaks suggests similar causes. Timing of these peaks is attributable to a combination of favourable physical conditions (Drift 1963), and priming by a supply of readily available nutrients (Macura et al. 1963). Whereas I have monitored the physical conditions and can relate them to population fluctuations, I have only literature reports to substantiate the contribution of nutrient priming. However, the fact that all functional groups peak at about the same times supports the theory that soluble compounds stimulate all microbial activity, and that once the soluble compounds are utilized, those populations capable of more resistant degradation remain active (Williams and Gray 1971).

Spatial and temporal patterns in microbial populations are in response to other levels of heterogeneity in the litter system, especially topographic and seasonal differences in physical conditions and decomposable substrates. The sequence of this influence will be detailed in the General Discussion.

5. Litter Decomposition Measures

Rate of litter decomposition was monitored to assess the functional response of the litter system to spatial heterogeneity of its components. The rate of decomposition in the three topographic areas was measured using the mesh bag technique (Bocock and Gilbert 1957). Two decay experiments were run, one beginning in

July, running 16 months, and one beginning in May, running 6 months. Changes in dry weight, organic matter content (determined as LOI), lignin content, and cation concentration (calcium, magnesium and potassium) were used to monitor decomposition changes in the litter; cation concentrations were only measured in litter samples from the decay experiment begun in July.

Although Witkamp and Olson (1963) and Suffling and Smith (1974) have shown that the mesh bag technique may inaccurately estimate the actual rate of decomposition, the method has been used successfully to index decay rates, and to evaluate the effect of specific treatments on the litter community (Shanks and Olson 1961, Crossley and Hoglund 1962, Edwards and Heath 1963, Woodwell and Marples 1968, Wiegert 1974).

A common problem with the mesh bag technique has been that poor contact between bagged litter and the underlying soil caused artificially dry litter. Litter bags generally simulate microenvironmental characteristics of surface litter layers, but do not follow breakdown and decomposition patterns of the leaf litter year class from which the experimental material was drawn (Anderson 1973b). Another artificial constraint imposed by the small mesh size of some litter bags is the inaccessibility of the bagged litter to invertebrates. Since invertebrates are essential to the natural decomposition process, this is a serious constraint (Edwards and Heath 1963, Heath et al. 1966, Ghilarov 1971). I designed the bags used in this study to minimize these problems (see Materials and Methods).

(i) Litter decomposition measured as weight loss

Weight loss through time was the prime measure of the decomposition process. Weight loss as a function of decay is usually best represented by a linear regression on a semi-logarithmic plot (Olson 1963, Witkamp and Olson 1963, Minderman 1968, Schlesinger 1977). Figure 13 is a representative plot showing the natural logarithm of percent of litter weight remaining, over time, for two of the litter treatments. A least squares regression on such semi-log plots was used to determine the best linear model of the decomposition process for each combination of litter and site. All slopes were tested using the F statistic, which demonstrated that during both the 16-month and 6-month experiments, decay rates for all experimental treatments differed significantly from zero ($P < .005$) (Tables 17 and 18).

The difference in slope of decay curves for various treatments was tested by a simple regression technique using the original data, a more powerful method than comparing the regression coefficients of the calculated lines (Draper and Smith 1966). The differences between mean empirical values used to plot the two decay curves at each time interval were calculated and plotted over time. If the slope of the regression line passing through these mean differences was found to be significantly greater than zero ($P < .05$), it was concluded that the slopes of the original two lines were different.

Figure 13. Rate of litter decomposition (measured as weight loss)
for two representative experimental treatments.

Two general results in Table 17 indicate the effect of litter mixture and topographic site on decay rate. First, the loss rate calculated from low litter (simulating the leaf litter composition on low sites) was greater than that from high litter (simulating litter on high sites), when both were kept on a high site ($F=7.32$, $P=.035$). Furthermore, low litter had a greater rate of weight loss on all topographic sites than did high litter. Second, each of high, level and low mixtures of litter showed their greatest rates of weight loss when kept on low topographic sites.

Although these relationships between litter mixture and topographic site are apparent in Table 17, practical problems arose in testing their statistical significance. As mentioned earlier, comparison of regression slopes required a pairing of values from two decay curves (Draper and Smith 1966). In my experiments, two or four replicate weight measurements were made at each time interval. Since there was no logical method of pairing replicate measurements from two decay curves, a mean was calculated for each time interval, and only these means were paired for comparison of regression slopes; this resulted in a severe reduction from 22 to 7 data points used to compare decay rates. Since each curve is based on information from all 22 data points, it is unnecessarily stringent to require F statistics calculated from compared decay curves to achieve confidence levels dictated by the reduced sample size. Table 17 includes F statistics for each pair of compared curves. Since sample size and statistical

Table 17. Litter decomposition rates (measured as weight loss) during the July decay experiment.

Three litter types and three topographic sites were factorially combined to produce nine treatments.

Bracketed treatments are pairs compared.

TREATMENT	% WEIGHT REMAINING	EXPONENTIAL LOSS RATE (b)*	F STATISTICS**	F STATISTICS FOR COMPARISONS
HIGH LITTER:				
in HIGH area	89.32	-.00432	11.26	3.86
in LEVEL area	72.02	-.0155	19.87	
in LOW area	67.81	-.0231	140.55	
LEVEL LITTER:				7.32
in HIGH area	88.86	-.00704	124.58	3.10
in LEVEL area	74.76	-.0135	42.69	
in LOW area	66.28	-.0209	142.09	
LOW LITTER:				.093
in HIGH area	86.36	-.00809	118.24	2.70
in LEVEL area	71.32	-.0165	106.12	
in LOW area	56.73	-.0270	55.27	

* Exponential weight loss (b) is estimated from a semi-logarithmic regression (base e) of weight loss (N = 22).

** All slopes differ significantly from zero ($P < .005$)

treatment were the same for all comparisons, these F statistics are a useful index of the degree of difference between decay rates.

Interpretation of F statistics for compared curves reinforces the two points made previously regarding patterns in loss rates in Table 17. In addition, this index indicates the similarity in exponential loss rates from high litter and low litter when both are decomposing in low areas ($F=.093$).

In general, Table 17 indicates the interactive effect of litter composition and decay site on decomposition. The standing crop of leaf litter in the three topographic areas differs both qualitatively and quantitatively, and litter mixtures used in the decay experiments simulate these differences. Not only does low litter contain aged beech and maple leaves, which are absent from high litter, it also contains eight times the dry weight of high litter. Since the contact area of the experimental decay bags is the same, regardless of their contents, the number of leaf layers is greatest in bags containing low litter. Furthermore, aged litter was placed beneath unaged litter in the bags to more closely simulate the natural condition.

The combination of greater leaf depth in low, and to a lesser extent, level, litter bags, and the delicate filamentous structure of aged leaves, results in greater compaction of these bagged leaves, and particularly of the aged leaf layers. The aged leaf layers are therefore closely associated with the soil. As a result of this close association, as well as the more

absorptive nature of aged leaf tissue after its waxy cuticle has been broken down (Verona and Lepidi 1972, Cromack 1973), the aged leaves maintain a high moisture content. Due to this moisture content of aged leaves in low litter bags, the unaged contents of the bag are also kept moist. Since moisture loss is usually the limiting factor in surface litter decay (De Boois 1974), and is a well documented limitation of litter bag experiments using unaged leaves (Crossley and Hoglund 1962, Anderson 1973b), the moisture maintaining capability of low litter mixtures is of importance to litter breakdown.

Field observations indicate that litter bags with low litter mixtures buffer moisture and temperature conditions for their contents, much as the larger habitats of low topographic areas provide protection for their inhabitants from periods of desiccation and abrupt temperature changes. Low litter mixtures therefore maintain a microenvironment more conducive to invertebrate fragmentation and microbial decomposition.

It follows that the slowest weight loss rate occurs in bags of high litter maintained in high areas, and the fastest weight loss occurs in bags of low litter maintained in low areas, since these are the factorial combinations which allow the effects of site and litter mixture to reinforce each other. Furthermore, if a significant difference is to be found between any decay curves, paired so as to have one factor common, it would be expected between sites where the buffering capacities of the bagged litter mixtures will be most significant. Hence, the greatest difference

in-decay curves is between high and low litter mixtures, both maintained on high sites. Similar logic dictates that litter mixture will be least important in low areas because these sites provide stable moisture and temperature conditions, and make the additional buffering potential of bagged litter unnecessary; hence, the observed similarity in decay curves of high and low litter mixtures maintained in low areas.

Table 17 requires one more word of explanation. In addition to listing exponential weight loss rates for each litter/site combination, Table 17 lists the percent weight remaining at the end of the experiment. These weights are the means of four replicate measurements taken at the end of 16 months. They are included to indicate the extent of weight loss. Table 17 shows that although the magnitude of the slope is inversely proportional to the percent of the litter weight remaining, the statistical significance of the difference between slopes of different treatments is not proportional to the difference between their final weights. This is not surprising, since the weight remaining is calculated from only four measurements taken at 16 months, whereas the decay slope is the best fitting line calculated from measurements made over the full course of the experiment. The F statistic takes into account the goodness of fit between the calculated line and all measured points during the experiment. Therefore, the best indicators of significant differences between treatments are those based on measurements taken throughout the experiment; that is, the decay slopes of the different treatments, and F statistics calculated from them.

Table 18 shows the weight loss of five mixtures of bagged litter maintained in three topographic areas, and also in a temperature-programmed environmental chamber (see Materials and Methods). Five litter/site treatment effects can be seen. Most obvious is the rapid rate of weight loss of spring leek leaves, regardless of the decomposition site. The second fastest rate of loss on all topographic sites is also from herbaceous litter, blue cohosh leaves and stems. The third point to note is that weight loss rates of all litter mixtures are slowest in the chamber, and the faster decay rates of herbaceous material are most inhibited by the chamber conditions. Fourth, no significant difference exists between decay rates of mixtures of unaged beech and maple leaves collected in the fall, air-dried and stored until May (Be:Ma(fall)), and unaged beech and maple leaves left on the woodlot floor and collected just prior to the May experiment (Be:Ma(spring)). Finally, mixed beech and maple litter, which consists of two-thirds unaged leaves and one-third aged leaves, all collected in the spring, shows a loss rate which is greatest on low sites and slower on level and high sites.

The faster weight loss of herbaceous leaves has been well documented (Shanks and Olson 1961, Kuhnelt 1969). The speed of decomposition of leek leaves is verified by several seasons of field observations. Cohosh leaves also decay quickly; the cohosh material was collected in the fall, air-dried and stored over the winter, because it was impossible to find identifiable cohosh leaves on the woodlot floor by spring. The decay rates listed for

Table 18. Litter decomposition rates (measured as weight loss) during the May decay experiment.

Five litter types and three topographic sites and one environmental chamber resulted in 20 combinations.

AREA	LITTER COMBINATION	% WEIGHT REMAINING	EXPONENTIAL LOSS RATE (b)*	F STATISTICS**
HIGH	Be:Ma(spring)	79.75	-.0366	21.30
	Be:Ma(fall)	80.52	-.0407	35.16
	cohosh	69.34	-.0607	39.50
	leeks	4.34	-.600	86.80
	mixed Be:Ma	78.42	-.0427	59.25
LEVEL	Be:Ma(spring)	78.30	-.0417	21.33
	Be:Ma(fall)	80.80	-.0352	86.41
	cohosh	63.00	-.0790	63.18
	leeks	3.58	-.680	18.41
	mixed Be:Ma	76.25	-.0444	69.76
LOW	Be:Ma(spring)	70.50	-.0623	48.96
	Be:Ma(fall)	67.25	-.0709	36.66
	cohosh	55.50	-.102	57.50
	leeks	3.83	-.0642	18.97
	mixed Be:Ma	66.34	-.0811	32.44
CHAMBER	Be:Ma(spring)	81.24	-.0355	63.19
	Be:Ma(fall)	77.85	-.0402	50.25
	cohosh	77.95	-.0401	88.50
	leeks	7.42	-.441	71.19
	mixed Be:Ma	77.64	-.0418	131.29

* Exponential weight loss (b) is estimated from a semi-logarithmic regression (base e) of weight loss (N = 14).

** All slopes differ significantly from zero ($P < .001$)

cohosh material in Table 18 are for a 1:1 mixture (by weight) of leaves and stems, and are much slower than would be found for leaves alone. At the end of the 6-month period it was rare to find anything but stems remaining in the cohosh decay bags.

I suspect that the slow loss rates of all litter categories in the chamber were caused by periodic desiccation of the bagged litter. Although the samples were watered every two weeks (see Materials and Methods), bags of litter were maintained on only 2.5 - 3.75 cm of soil, and circulating fans within the chamber dried these litter and substrate systems between waterings. Decay rates in chambers are similar to rates on high sites except for herbaceous litter mixtures; herbaceous rates are slower in the chamber, although the difference is insignificant ($P < .10$). The slower decay rates for litter in chambers illustrate the importance of environmental moisture for both physical leaching and microbial decomposition (Eggleton 1938, Nielsen 1959).

The fact that no significant difference exists between decay rates for beech and maple leaves collected in the fall, dried and stored, and those left on the woodlot floor until spring, suggests that no significant loss occurs during the winter and early spring months. This is apparently in contradiction to Anderson (1973b) who found that up to 75% of the first year's weight loss was due to leaching, and Gosz et al. (1973) who found such a rapid and variable rate of leaching in the first month after leaf fall that they did not begin calculating decay rates until the second month. In general, physical leaching maximizes in late

fall before freezing, during winter thaws, and in early spring during snow melt. Therefore, beech and maple leaves in the woodlot during this period (Be:Ma(spring)) might lose a portion of their water soluble contents, and then have a significantly slower decay rate in the subsequent months of measurement (May to November). However, Weary and Merriam (in press) found no overwintering weight loss from red maple leaves in a woodlot near my study area. I suggest that a combination of negligible decay rates during the coldest part of the winter, and the criterion used to select unaged leaves which minimized fall and spring leaching effects, accounts for the similarity in decay rates.

Although beech and maple leaves collected in the spring (Be:Ma(spring)) were potentially well leached, only leaves which did not appear leached or fragmented were selected. These leaves were usually collected from high areas and were the top-most leaves on the litter surface; they were minimally exposed to physical weathering. The reason for this selection was that it was impossible to consistently distinguish age classes of leached litter. Thus, in order to ensure inclusion of only the previous year's leaves, I selected leaves that were less weathered than was normal for their year class, and consequently spring and fall beech and maple leaves (Be:Ma(spring) and Be:Ma(fall)) are essentially replicates.

The mixed beech and maple litter of Table 18 (mixed Be:Ma) is similar in make-up to the low litter mixtures in Table 17. This "mixed" combination also decayed fastest on low sites (Table 18).

Since all mixtures in Table 18 contain only the weight of litter characteristic of level sites, they do not have the depth of bagged litter found in low litter mixtures. Therefore, bagged litter in Table 18 does not modify physical conditions to the extent that the low litter mixture does in Table 17. The depth of litter accumulated in hollows is especially important in providing favourable decomposition conditions to bagged litter mixtures in Table 18. Therefore, it is predictable that all 6-month litter mixtures, with the exception of leeks, show faster decay rates on low sites than on high sites ($P < .10$) (Table 18).

Mixed beech and maple rates of loss measured over the 6-month period begun in May are double those measured over the 16-month period begun in July, measured in high and level areas. The 6-month rate measured in the low area is four times that measured over 16 months. Although it is not possible to state why the short-term rate was as fast as it was in the low area, comparison of Tables 17 and 18 indicates that the "mixed" litter mixture consistently lost weight faster in the first 6 months of the experiment than in the following 10 months. Weight loss data for the 16-month experiment begun in July and the 6-month experiment begun in May are presented in Appendix III, Tables 1 and 2.

A fast initial weight loss followed by more gradual reduction is a pattern seen in many decomposition studies. The fact that early weight losses are well represented by semi-log plots of weight against time (Olson 1963), indicates potentially great non-linearity in the decay process. As previously mentioned, these

early losses are almost entirely a result of leaching (Bocock et al., 1960, Witkamp 1971, Anderson 1973b, Gosz et al. 1973). Later, the remaining organic accumulation is composed largely of relatively resistant compounds such as cellulose, lignin, cutins, suberins and waxes (Minderman 1968). At this stage, the decay process is too slow for exponential decay curves to accurately represent the decay process (Witkamp 1971). Anderson (1973b) has indicated that exponential decay curves are good estimates of weight loss from chestnut leaves for periods up to about 20 months following leaf fall in an English woodlot. Since my study was carried out in a region of colder winters, soluble compounds may remain past 20 months.

Tables 17 and 18 indicate that rapid weight loss from leaching dominates all of the 6-month and the early months of the 16-month experiment; the expected reduced leaching from the aged litter component is obscured. Slower rates for the 16-month experiment are a reflection of the slower decomposition processes which follow the initial leaching period, and begin as early as the fourth month. Since the slope of the regression line is determined by the goodness of fit throughout the 16-month experiment, the initial rapid weight loss is reduced in importance, and the over-all slope decreases accordingly.

Since my litter types are generally mixtures of species and/or ages, it is difficult to compare their weight loss rates with simplified categories in the literature. Table 17 shows beech and maple litter mixtures with 16-month weight losses of between 10.68% and 43.27% depending on litter/site combination. Table 18

shows 6-month losses from unaged beech and maple mixtures ranging from 19.20% to 32.75%; "mixed" aged/unaged mixtures (similar to the low litter mixture in Table 17) lose from 21.58% to 33.66%. Shanks and Olson (1961) found approximately comparable annual weight losses of 32% for unaged sugar maple leaves and 21% for unaged beech leaves (Fagus grandifolia) in the southern Appalachian Mountains.

Several researchers have noted the faster rate of decay of sugar maple leaves as compared to beech leaves (Coldwell and Delong 1950, Shanks and Olson 1961, Gosz et al. 1973). This is partly because beech has significantly less water-soluble organic material and significantly more hemicellulose, cellulose and lignin than sugar maple (Melin 1930), and is more resistant to leaching (Gosz et al. 1973), microbial activity (Lewis and Starkey 1968) and invertebrate fragmentation (Edwards and Heath 1963).

Anderson (1973b) calculated decay constants from semi-log plots of percent of litter weight remaining against time (in months) and obtained rates over 13 months of -0.00142 and -0.00159 for unaged chestnut leaves, and -0.00024 and -0.00070 for unaged beech leaves; all rates were measured from bags with a mesh size of 175 μ . Table 17 shows decay rates, measured from bags with a substantially larger mesh size of 1 mm x 2 mm, which allowed access to all microorganisms and all invertebrates except the largest earthworms (Edwards and Heath 1963). Although Anderson states that he found no difference in decay rates calculated from bags with mesh sizes of 7 mm, 1 mm and 175 μ , he mentions that earthworms play an

important part in removing litter fragments, particularly chestnut litter, from coarse mesh bags; he also emphasizes the importance of abiotic fragmentation to litter bag losses. Therefore, I suggest that although Anderson's rates should be faster because of milder winters, my rates are more rapid primarily because of the greater accessibility of my bagged litter to invertebrate and abiotic fragmentation.

Gosz et al (1973) also calculated exponential decay constants for unaged leaves, and for leaves left on the woodlot floor to leach for one month. They used bags with a mesh size of 3 mm. Decay constants calculated from semi-log plots of percent litter weight remaining, over time, ranged from -0.33 for sugar maple to -0.27 for beech leaves over an 11-month period (following one month leaching). Their monthly rates, comparable to those in Table 17, are -0.0300 for sugar maple and -0.0245 for beech leaves. These rates are slightly higher than those in Table 17, probably as a result of greater losses of litter fragments through the larger mesh size used by Gosz et al.

The major difference between my litter mixtures and litter used by other researchers to monitor the decomposition process is that most of my litter mixtures contain two leaf species, often at two stages of decay. Decomposition of these mixtures requires consideration of all four processes involved in the mineralization of leaf litter: leaching, abiotic breakdown by fragmentation, biotic breakdown resulting from feeding activities of litter and soil animals, and decomposition by microorganisms (Anderson 1973b). Litter

decomposition data obtained from experiments with a single unaged species in mesh bags can be explained in terms of leaching and abiotic fragmentation, particularly if the mesh size eliminates most invertebrate activity, but decomposition of realistic litter mixtures is more complex. The increased complexity can best be seen in Table 17.

Table 17 lists decay rates for litter mixtures consisting of aged and unaged beech and maple leaves. Since aged leaves have undergone a longer period of leaching prior to the experimental period, they might be expected to reduce the over-all decay rate. However, Table 17 shows that low litter mixtures which contain the greatest proportion of aged litter, have the fastest decay rates, indicating greater losses from aged litter by biotic and abiotic fragmentation and by microbial decomposition. Therefore, although litter mixtures containing aged litter may have a reduced rate of leaching because of the predominance of their resistant compounds, that reduction may be more than compensated because the delicate filamentous structure of aged leaves predisposes them to greater fragmentation, particularly with high invertebrate activity in the litter.

Evidence exists for the preference of invertebrates for aged litter. Minderman and Daniels (1967) compared the palatability of aged and unaged leaf litter to soil animals and found a preference for aged litter, apparently because of its larger concentration of microbes. This preference is fortuitous since soil animals are dependent on microorganisms for most of their nutrition

(Nielsen 1962). Other researchers have related invertebrate preference for aged litter to the chemical quality of the litter. Satchell and Lowe (1967) showed earthworm preference for aged litter with a reduced polyphenol (tannin) content. However, this preference is also related to microbial biomass since tannins inhibit bacterial growth (Basaraba and Starkey 1966, Lewis and Starkey 1968); aged litter has a reduced polyphenol content and supports a larger number of microorganisms. 7

Litter and soil animals actively fragment (Ghilarov 1969) and chemically modify (Marcuzzi and Lafisca 1975) the plant litter, and thereby increase the surface area exposed to subsequent microbial breakdown and oxidation (Ghilarov 1971). The degree of fragmentation of litter by litter and soil animals, especially invertebrates, is important in litter bag studies because litter is susceptible to loss from the bags when fragments are less than mesh size (Howard 1967). Much of the subsequent microbial decomposition leading to mineralization is carried out beneath the bag, in the fermentation and upper soil layers (Witkamp 1971, Schlesinger 1977).

The mesh bag technique limits study to the early stages of decay prior to fragmentation loss from the litter bags. I monitored chemical changes occurring in bagged leaf litter prior to this fragmentation, and the next sections present the results of the qualitative analyses.

(ii) Litter decomposition measured as organic loss and lignin gain

Organic loss and lignin gain were the two major qualitative patterns examined during decay. Organic analysis (as LOI)- facilitated comparison of the organic or decomposable fractions of litter through time without consideration of ash fractions. Lignin was analysed because it is known to be a resistant constituent of litter (Peevy and Norman 1948, Pinck et al. 1950, Alexander 1961, Christensen 1973), and it has recently been suggested as an index of decay (Cromack 1973).

Plant materials high in lignin are very resistant to decomposition by microorganisms, and it has been found that materials with a high lignin content are decomposed more thoroughly when incorporated in soil than when in the surface litter. This is thought to be a result of differences between microorganisms in the litter and soil; perhaps organisms that bring about a slow attack on lignified tissues in the soil are unadapted to the highly aerobic and drier conditions in surface litter (Peevy and Norman 1948). Therefore, lignin is not decomposed to any extent in litter bag experiments. Leaching and microbial decay of the more soluble and easily decomposable materials from the bags will increase the lignin proportion of the remaining litter. The increase in lignin proportion is therefore an indirect indicator of litter losses due to leaching and microbial degradation. Changes in the proportional lignin content of litter do not assay litter lost by abiotic fragmentation, and do not measure removal by invertebrates unless a specific tissue type is removed.

Table 19 shows calculated rates of organic loss and proportional lignin gain for the 16-month decay experiment, and Table 20 shows only organic loss rates for the 6-month experiment. In general, variability of these qualitative measurements was great. Although most treatments showed a linear loss of organic matter through time, lignin analysis results were so scattered that a significant linear regression of lignin content on time could not always be demonstrated.

Table 19 lists organic loss rates for three litter mixtures located on three topographic sites for a maximum of 16 months. Again, the three litter mixtures simulate high, level and low litter. Two general patterns are apparent. First, contrary to weight loss rates (Table 17) which were greatest for low litter and least for high litter mixtures, organic loss rates were greatest for high litter mixtures, and generally decreased for level and low litter. (The single rate for low litter in high areas is inexplicably high). Second, loss rates are greatest on low sites and least on high sites for all litter types (again excluding the organic loss rate of low litter in high areas).

The greater organic losses from the high litter mixtures are a result of the higher organic content of this litter mixture at the start of the experiment (98.34%, compared to 94.62% for low litter). Since high litter is composed entirely of unaged leaves, the loss of readily soluble carbon compounds from this litter would be expected to exceed loss from low litter, containing previously leached aged litter. Since high litter is normally too

Table 19. Qualitative changes in litter during the July decay experiment.

Rate of decline in organic content of litter and rate of increase in lignin content were estimated from simple linear regressions of percent organic and percent lignin over 16 mo (N = 20).

TREATMENT	QUALITATIVE MEASUREMENT			
	ORGANIC CONTENT		LIGNIN CONTENT	
	LOSS RATE	F STATISTIC	GAIN RATE	F STATISTIC
HIGH LITTER:				
in HIGH area	-1.63	18.99*	.411	13.49*
in LEVEL area	-1.16	21.16*	.425	14.94*
in LOW area	-3.13	98.58*	.422	12.14**
LEVEL LITTER:				
in HIGH area	-.890	3.42****	.154	1.68****
in LEVEL area	-.940	9.54**	.160	2.68****
in LOW area	-1.84	13.33*	.226	4.10***
LOW LITTER:				
in HIGH area	-2.26	17.93*	.202	4.13***
in LEVEL area	-0.617	2.65****	.186	2.46****
in LOW area	-.757	9.60**	.280	3.49****

* All slopes differ significantly from zero ($P < .001$)
 ** " " " " " " ($P < .01$)
 *** " " " " " " ($P < .05$)
 **** " " " insignificantly " " ($P > .05$)

transient to undergo intensive leaching, the faster leaching rates obtained here are largely an artifact of the litter bag technique. The faster loss of organic material from litter in low areas is due to the same conditions that produced faster rates of weight loss in low areas. The physical protection afforded by the low areas, and by the litter which accumulates over top of decay bags in these areas, produces a habitat conducive to invertebrate fragmentation and microbial degradation. Appendix III, Table 3 shows organic data for the 16-month decay experiment begun in July.

Table 19 also lists the results of lignin analyses for the 16-month decay experiment begun in July. Almost half the calculated lignin gain rates are insignificant ($P > .05$). However, the gain rates for all high litter mixtures are faster than those for level and low litter mixtures. This result is consistent with organic loss rates. Since lignin gain and organic loss are related decay measures, the more rapid loss of organic matter from high litter mixtures (Table 19) predicts a faster rate of lignin gain in these same mixtures.

By the same logic, lignin levels should be least in initial high litter mixtures, which have a larger organic content, and greatest in low litter mixtures; but measured lignin contents were approximately the same in all initial litter mixtures. I suggest that the lignin values obtained for low litter are not representative of these mixtures. Since the proportion of aged litter increased from high to low litter, and since lignin remains

resistant to decay while other leaf compounds are more easily metabolized and lost from the litter mass during aging (Peevy and Norman 1948), the proportion of lignin should be greatest in low litter. Although insufficient aged material was available for additional lignin analyses, earlier samples of high, level and low litter were analysed for carbon:nitrogen ratios. Since these ratios are an alternate index to the extent of decay of plant litter (Alexander 1961, Witkamp 1971), I will report them here to substantiate the qualitative differences among initial high, level and low litter mixtures.

Carbon:nitrogen ratios are 44.96 in high litter, 36.77 in level litter and 32.67 in low litter. Generally, aged litter should have a narrower carbon:nitrogen ratio because of the export of carbon as carbon dioxide by metabolizing decomposers (Witkamp 1971); therefore, these ratios reflect the greater proportion of aged litter in the low litter mixtures. Changes in proportional lignin content and carbon:nitrogen ratios are correlated in aging litter (Cromack 1973); lignin content increases as carbon:nitrogen ratios decrease. Therefore, carbon:nitrogen results for the different litter mixtures indicate the probability of larger initial lignin contents in low litter mixtures than those measured. Larger initial lignin values for low litter are compatible with slower lignin gain and organic loss rates measured for this mixture. However, intermediate carbon:nitrogen ratios, and hence predicted intermediate lignin contents, of the level litter mixture are not compatible with the slowest lignin gain rates

20 calculated for this mixture. Since organic loss rates for level litter are intermediate between those for high and low litter, and the lowest lignin regression rates are insignificant ($P > .05$), the logic is retained, and insignificant lignin rates are discarded.

Table 19 also shows that lignin gain rates are consistently faster in low areas than on high areas, a finding compatible with faster loss of organic matter and weight in low areas (Tables 17 and 19). Therefore, despite obvious problems caused by the variability of lignin results, lignin gain rates are generally consistent with organic loss rates, and both qualitative measures indicate the importance of topographic site and associated litter mixtures to chemical decomposition. Appendix III, Table 4 shows results of lignin analyses for the July experiment.

Interpretation of qualitative analyses of the 6-month decay experiment begun in May is hindered by small sample size ($N=12$ for organic analysis and $N=5$ for lignin analysis). Table 20 lists only the organic loss rates for each litter/site combination.

The most obvious result is the very rapid loss rate measured for leeks maintained in the chamber. Even this loss rate is an underestimate since the chamber was observed to slow decomposition; in fact, a loss rate was calculated for leeks only in the chamber because it was the one site at which sufficient sample remained for analysis. Other rapid organic loss rates obtained for beech and maple litter mixtures (Be:Ma(fall)), especially in high areas, are inexplicable.

Table 20. Organic changes in litter monitored during the May decay experiment.

Rate of decline in organic content of litter was estimated from simple linear regressions of percent organic over 6 mo ($N = 12$).

TREATMENT			
AREA	LITTER MIXTURE	LOSS RATE	F STATISTIC
HIGH	Be:Ma(spring)	-2.68	11.49**
	Be:Ma(fall)	-3.06	9.88**
	cohosh	-1.58	6.52***
	mixed Be:Ma	-1.70	10.39**
LEVEL	Be:Ma(spring)	-1.29	7.68***
	Be:Ma(fall)	-4.53	6.63***
	cohosh	-1.26	27.25*
	mixed Be:Ma	-1.31	27.23*
LOW	Be:Ma(spring)	-1.52	11.14***
	Be:Ma(fall)	-1.95	8.48***
	cohosh	-1.04	6.48***
	mixed Be:Ma	-1.13	4.77***
CHAMBER	Be:Ma(spring)	-1.13	11.98**
	Be:Ma(fall)	-1.06	6.25***
	cohosh	-0.91	7.99***
	leeks	-4.69	55.64*
	mixed Be:Ma	-0.97	24.31*

* All slopes differ significantly from zero ($P < .001$)

** " " " " " " ($P < .01$)

*** " " " " " " ($P < .05$)

A second, consistent result is that cohosh, the other herbaceous material, has the slowest rate of organic loss (Table 20). The contrast between the two herbaceous categories is at first surprising, and the slow rate for cohosh appears in contradiction to the general conclusion that herbaceous litter decays rapidly (Shanks and Olson 1961, Kuhnelt 1969). I suggest that there is no contradiction, and that the slow loss rate can be largely explained by extensive leaching and possibly microbial decay prior to cohosh collection in the fall. Qualitative changes occurring during the May to November experiment therefore reflect the slower decay of more resistant compounds (Minderman 1968, Anderson 1973b).

Initial lignin values for cohosh, which are approximately two times initial leek values (Appendix III, Table 6), and the lower organic content of cohosh material (Appendix III, Table 5) support this hypothesis. However, initial cohosh lignin and organic levels also predict faster organic loss rates for cohosh than for canopy leaf mixtures, and this is not demonstrated (Table 20). Therefore, preliminary leaching and decay of cohosh material is only sufficient to explain differences between organic loss rates of cohosh and leeks. Leeks experience minimal decay losses prior to collection because the brevity of the leek senescent period dictates that they be collected while still green; delay of only a few days allows enough decay to make leek collection impossible. Comparison of organic losses from cohosh and canopy leaf mixtures requires further consideration of the nature of the initial cohosh material.

Unlike other litter mixtures which contain only leaf material, the cohosh category is a 1:1 mixture (by weight) of stems and leaves. As mentioned earlier, decay losses from leaves and stems are very different, and at the end of 6 months most decay bags contain only stems. The delicate nature of cohosh leaves was also observed; and much of the weight loss from cohosh bags was ascribed to physical and invertebrate fragmentation of cohosh leaves. Because fragmentation losses are not reflected in the qualitative composition of the remaining litter, cohosh organic and lignin levels remain relatively constant. Therefore, a combination of delicate leaf, and resistant stem structure, and the importance of fragmentation in litter bag experiments, accounts for the extremely slow rate of organic loss from cohosh material.

A third result is that the effect of topographic site on short-term decay in Table 20 is opposite to that found in Table 19; in Table 20, faster organic loss rates occur on high sites. This indicates that leaching, which is generally the most important decay process operating in the first months (Anderson 1973b, Gosz et al. 1973), is most efficient on rises. A possible explanation is that when nutrients are released by rainwater from litter on these drier, relatively bare sites, there is less likelihood of nutrients being reabsorbed by the surface litter (Witkamp 1969), or trapped by a microbial biomass in the litter (Witkamp 1971, Cromack et al. 1975), or by humus in the soil (Schnitzer and Khan 1972), than there would be if litter was decomposing on low sites. Differences between high and low sites may therefore be artifactual.

Although leaching losses from surface litter are the same in both areas, reabsorption by other components of the litter system retain these nutrients in the low areas.

Finally, "mixed" beech and maple mixtures in Table 20 (mixed Be:Ma) have a slower organic loss rate than do the unaged beech and maple mixtures (Be:Ma(spring) and Be:Ma(fall)). The explanation is the same as that for the slower loss rate of low litter mixtures in Table 19. "Mixed" beech and maple litter contains aged litter which has been leached prior to the experiment; the starting organic content of this "mixed" litter is only 91.39% compared to 93.53% for unaged beech and maple leaves. Unaged beech and maple (Be:Ma(spring) and Be:Ma(fall)) therefore contain a slightly larger proportion of soluble compounds which they quickly lose during the experiment.

Comparison of organic losses from low litter mixtures (Table 19) and the similar "mixed" litter of Table 20 again indicates the slower losses measured over 16 months than those measured over 6 months. Therefore, much of the early organic loss is a result of leaching of soluble compounds; slower decay processes are more important to organic loss rates in the longer 16-month experiment.

The fact that fall canopy litter (Be:Ma(fall)) has a consistently faster organic loss rate in all topographic areas than does canopy litter collected the following spring (Be:Ma(spring)) is inexplicable. The two mixtures have almost identical initial organic contents and similar lignin contents, and as previously explained, criteria used for spring collections ensured that leaves

for Be:Ma(spring) mixtures underwent minimal additional leaching prior to collection. Comparison of these two mixtures casts further doubt on the validity of the fast organic loss rates calculated for Be:Ma(fall) mixtures.

Almost none of the lignin gain rates for May litter mixtures are significant ($P > .05$) because of large sample variation and small numbers of replicates. Results of lignin analysis for the May experiment are presented in Appendix III, Table 6; lignin gain rates, corresponding to the organic loss rates of Table 20, are listed in Appendix III, Table 7.

(iii) Litter decomposition measured as decreasing cation concentrations

Litter concentrations of calcium, magnesium and potassium were measured only during the 16-month decay experiment begun in July. The only cation that showed a significant linear relationship over time was calcium, and it did so only in level and low litter mixtures. Calcium, expressed as meq/100 g litter, experienced a linear loss rate between -0.60 and -2.80, with no pattern related to litter mixture or topographic site. This range is within that expected, since calcium is a structural component of organic material, and calcium release is known to approximate dry weight loss (Thomas 1970, Witkamp 1971, Gosz et al. 1973). However, too many variables affect leaching of cations from litter, and retention of cations by microorganisms and invertebrates, to allow cation content to be an accurate index of the decomposition process (Todd and Cromack 1972, Cromack et al. 1975, Carter and Cragg 1976).

(iv) Summary of litter decomposition

Litter decomposition results indicate that decay rates depend on topographic site and litter mixture. The mesh bag technique was used to estimate litter decay, but litter bags and the experimental program were designed to approximate natural decomposition as closely as possible. High, level and low topographic sites have characteristic litter accumulations, physical conditions, incorporated soil organic matter and microbial populations. Litter mixtures simulate the mixture of aged and unaged leaves found in different topographic areas. Additional herbaceous litter mixtures are not specific to topographic site, but are considered significant to general decay because of the relative rapidity of their decomposition. All decomposition processes, leaching, abiotic and biotic fragmentation, and microbial breakdown are involved in the realistic decay treatments. The effect of topographic site and litter mixtures is reflected in weight loss rates summarized in Tables 17 and 18, and in organic loss and lignin gain rates in Tables 19 and 20.

Weight loss rates for both the 16-month (Table 17) and 6-month (Table 18) decay experiments, and organic loss and lignin gain rates measured over 16 months (Table 19), are greatest in low areas. Faster decomposition in low areas is a function of predictable moisture and temperature conditions in these areas, which encourages microbial and invertebrate activity. However, faster organic losses were measured in high areas during the short

6-month experiment (Table 20). This apparent contradiction emphasizes the changing contribution of different decay processes through time. During the first 6 months, leaching is the dominant process (Gosz et al. 1973), and the only short-term process, affecting organic measurements, and it is apparently more efficient on high areas. Weight loss measured over the same 6 months is influenced by fragmentation as well as leaching, and the total loss is greatest in low areas.

Comparison of 6-month and 16-month decay rates indicates the early importance of leaching, and to a lesser extent, abiotic fragmentation losses. Decay rates calculated over 6 months are consistently faster than those calculated over 16 months, whether measured as weight (Tables 17 and 18) or organic loss (Tables 19 and 20). Rates for the 16-month experiments are influenced less by early rapid losses from leaching and abiotic fragmentation, and more by slower biotic fragmentation and microbial degradation.

The effect of litter mixtures, simulating litter on different topographic sites, is shown in Tables 17 and 19. Low litter mixtures lose weight faster on all topographic sites (Table 17). This result is attributable to two characteristics of the aged litter component of low litter. First, aged litter has greater moisture retention capabilities, and bags containing this component have more stable moisture and temperature conditions, similar to those found in low topographic sites. Aged litter is also qualitatively different than unaged litter, and despite its large content of resistant compounds, is more palatable to

invertebrates (Minderman and Daniels 1967, Satchell and Lowe 1967). Therefore, low litter mixtures encourage microbial and invertebrate activity, much as do low topographic sites.

Table 19 shows that organic loss and lignin gain rates are greatest for high litter mixtures. Again, this apparent contradiction emphasizes the importance of all decay processes. Since high litter mixtures contain only unaged litter they do not provide mock low decay sites within their bags. However, high litter has a larger initial organic content and smaller lignin content than does low litter. Therefore, high litter mixtures undergo rapid leaching of soluble compounds and microbial degradation of easily metabolized substrates. Invertebrate fragmentation, which is an important process to low litter mixtures, is not generally reflected in qualitative measurements, and microbial degradation of aged litter is slower than degradation of unaged litter. The result is that faster qualitative changes occur in high litter mixtures.

The herbaceous species monitored, leeks and cohosh, exhibit fast weight and organic losses in all topographic areas. "Mixed" aged and unaged beech and maple leaves, similar to low litter mixtures, exhibit a rate of weight loss exceeded only by herbaceous species, but this same mixture shows a slower organic loss rate than do unaged beech and maple leaves, because of initial differences in organic levels.

Litter decomposition rates are therefore affected by topographic site conditions and the litter mixtures which accumulate at these sites. Decomposition of soluble compounds, such as those

abundant in leeks and cohosh leaves, are not restricted to any one topographic site; however, breakdown of more resistant compounds, such as those found in aged beech leaves, is most common in low topographic areas. The General Discussion will consider the importance of topographic characteristics to the decomposition process in more detail.

GENERAL DISCUSSION

This study shows that spatial and temporal heterogeneity are functional components of the decomposition process and are therefore necessary to its understanding in a system context. Local structural and functional differences are related to topographic heterogeneity of the woodlot floor; Figure 14 illustrates the sequence of the influence of topography on these structural and functional components of the litter system, and ultimately on the rate of litter decomposition and development of soil structure.

The first level of heterogeneity derived from topography is spatial heterogeneity of surface litter accumulation. Surface litter is both quantitatively and qualitatively different on high, level and low areas. Specifically, the standing crop of surface litter in low areas is greater by weight (Table 2), and in depth (Table 3) than on level and high sites; litter also accumulates for longer periods in low areas and these areas have a greater proportion of aged litter (Table 4, Figure 1).

Differential accumulation of surface litter is substantiated by several seasons of field observation. Wind action and gravity are two physical factors responsible for the distribution pattern of surface litter. Table 2 lists the net result of litter movement at monthly intervals. Analyses of these monthly standing crop

Figure 14. Flow diagram of the response of a litter system to the underlying topographic heterogeneity of the woodlot floor without feedback.

Original Heterogeneity

TOPOGRAPHY

LITTER ACCUMULATION

INCORPORATED
SOIL ORGANIC
MATTER

MICROBIAL
and

INVERTEBRATE
POPULATIONS

LITTER
DECOMPOSITION

DECOMPOSITION ENVIRONMENT
(PHYSICAL CONDITIONS)

Derived Heterogeneity

measurements indicate that the ratio of surface litter located in high, level and low areas changes from approximately 1:3:6 in April to 1:4:8 in September. Since there was no significant input of new litter before October (Merriam, unpublished), this change in ratio reflects the net movement of surface litter from high to low areas. Once in the low areas, this large standing crop of surface litter is maintained throughout the season (Table 2). Hart et al. (1962) also noted the independence of litter accumulation and litterfall. They measured a spatial variability in litter accumulation - the result of more litter accumulating in low areas - that was five times greater than spatial variability in litterfall.

The first effect derived from spatial heterogeneity in litter accumulation is a spatial heterogeneity in the physical conditions, such as temperature and moisture, at the litter-soil interface, and in their variability. Depth of surface litter influences the physical conditions of the decomposing system in two distinct, but related, ways. First, surface litter accumulation protects the underlying litter and soil from desiccation (Nielsen 1959, Drift 1963), and second, it moderates environmental temperature extremes at the litter-soil interface (Hart et al. 1962, Williams and Gray 1974, Dickinson 1974).

In my study, the surface soil in low areas remains moist (Tables 7 and 8), and because the top litter layers protect underlying litter layers from drying wind and sun, the underlying litter in low areas also maintains a greater moisture content than in other topographic areas (Table 7). Low areas also show

the least variability in litter temperatures (Tables 6 and 10), which is reflected in higher temperature predictability in these areas (Figure 2). The greater predictability of temperatures in low areas is qualitatively different than temperature predictability in other topographic areas in that constancy plays a larger role (Figure 2).

Moist conditions in low areas are a direct result of the physical protection provided by a greater depth of surface litter. However, more constant litter temperatures are attributable both to the thermal insulation provided by surface litter, and to the heat capacity of the high soil moisture content. Low areas moderate environmental temperature changes most effectively, and these areas have more constant litter temperatures.

Absolute litter temperatures also vary with topographic site. During spring and summer, the moist low areas have slightly, but consistently, cooler temperatures than do other topographic areas (Table 6). This is a reflection of the moderating effect of moisture levels in low areas on daily and seasonal warming trends from June to September. Merriam and Wegner (personal communication) found litter-soil temperatures slightly warmer in low areas than in other topographic areas from January to March. However, the latter result is not directly attributable to differences in moisture levels. All areas typically have a high moisture content in fall (Table 8) that remains through winter, but low areas obtain better insulation from their deeper snow cover and litter layer than do other topographic areas (Hart et al. 1962).

Spatial heterogeneity in microbial populations is the third level of derived heterogeneity since these populations are affected by both of the previous levels (Figure 14). Quantitative and qualitative differences in accumulated litter provide microbial resource substrates that differ in abundance and decomposability (Parkinson 1972); these substrates may therefore determine microbial numbers, as well as type and diversity. Moisture and temperature conditions have a strong influence on microbial metabolic rates, and are therefore important in determining microbial activity (Alexander 1961). Since spatial differences in litter accumulation and physical conditions are related to topographic site in the present study, microbial populations also differ among topographic areas.

There is a greater proportion of aged litter in low areas, because litter remains for longer periods in these areas. Aged litter is qualitatively different than fresh litter (Alexander 1961, Satchell and Lowe 1967, Schlesinger 1977). Typically, fresh litter loses its soluble carbon compounds quite rapidly by leaching (Anderson 1973b, Gosz et al. 1973) and by microbial activity (Alexander 1961). Aged litter, therefore, contains a higher proportion of resistant compounds, such as cellulose and lignin (Melin 1930). Since not all bacterial organisms are efficient at breaking down these more resistant compounds, bacterial populations may be distributed according to the availability of soluble and resistant substrates (Alexander 1961). Therefore, more cellulose and lignin decomposers might be expected in low areas.

Three functional groups of microorganisms were assayed in each topographic area on the basis of their ability to metabolize increasingly resistant compounds; they are sugar, cellulose and lignin decomposers. Table 16 summarizes the results of all microbial analyses. In general, all functional groups are most abundant in low areas. One exception is noted in Table 16, and is attributable to the very large contribution of a single peak population. However, the main conclusion from Table 16 is that distribution of microbial functional groups is not related to the age of accumulated surface litter. Cellulolytic and lignolytic microorganisms are not more abundant in low areas than sugar decomposers.

Identification of major fungal genera in the three topographic areas leads to the same conclusion; no significant functional differences were found in fungal populations identified from the three areas (Table 15). All identified genera were generalists, and a few had been previously noted by other researchers on living leaves. Although these genera were grown on a sugar substrate, resulting in a strong selection for sugar decomposers, all colonies from several plates were identified, and even a single colony of specialized cellulose or lignin decomposers would have been noted.

My results indicate what others in the literature have suggested; most resistant compounds are broken down by generalist microorganisms that can degrade both soluble and resistant compounds, depending on the availability of substrate (Gray and Williams 1971,

Baker and Whittingham 1972). Therefore, distribution of fresh and aged leaf litter is not reflected in microbial community composition, and there is no qualitative difference among microbial communities in the three topographic areas.

However, the microbial assay program of the present study excluded one group of decomposers that is very important to the decay of resistant compounds. Because of inadequacy of assay techniques and limitations imposed by the scope of this study, basidiomycete populations were not investigated, although their lignolytic capabilities are well known (Garrett 1951, Hering 1967, Gray and Williams 1971). Since Basidiomycetes are typically found in moist habitats, like those provided by low areas (Table 8), and work on the long-term decay of aged leaf and woody material, also abundant in low areas (Table 4), their presence would be expected in these soils (Christman and Oglesby 1971). Therefore, although long-term decomposition is outside the scope of this study, there is indirect evidence that, in such a context, the low areas may support a qualitatively different microbial community. The limitations of short-term surface litter decomposition studies will arise again in discussion of decomposition rates and incorporation of organic matter into the surface soil.

In contrast to the demonstrated qualitative uniformity of microbial communities, all microbial analyses indicate quantitative differences among the three topographic areas; microbial populations are generally larger in low areas (Table 16). This result is attributed to two characteristics of the low areas. First, these

areas have abundant resources for microorganisms in the large mass of their accumulated surface litter, whereas the thin and transient litter on high areas is frequently inadequate to support a large microbial population (Table 2); second, the low areas provide a stable physical environment during the summer months, characterized by predictable moisture and temperature (Table 8, Figure 2).

The importance of temperature and moisture to microbial activity has been well established (Alexander 1961, Witkamp 1966, Wiant 1967, Reiners 1968, Witkamp 1971, Reichle et al. 1975).

It is generally accepted that under controlled conditions, soil and litter respiration, assumed to be mainly attributable to microbial respiration, will double for each 10 C increment ($Q_{10}=2$), within the normal range of field temperatures (Wiant 1967). However, litter and soil respiration studies have measured Q_{10} values ranging from 1.6 (Kucera and Kirkham 1971) to 3.2 (Anderson 1973c). Witkamp (1969) found that the daily cycle of soil respiration paralleled the diurnal temperature cycle with a predawn minimum and an afternoon maximum, and a $Q_{10} \approx 2.5$.

By contrast, moisture does not have a continuous predictable effect on microbial activity; its only direct influence is exerted when it is outside the organisms' tolerance ranges. This can occur when it is too low for microbial metabolic requirements, and also when it is in excess, and diminishes the oxygen supply to aerobic microorganisms (Alexander 1961). Typically, moisture adversely affects decomposer organisms during periods of summer drought (Schlesinger 1977) and spring snow melt (Mack 1973). Moisture

conditions are generally adequate for microbial activity in temperate forests (Cromack 1973), but in drier areas, soil moisture often is a factor in determining microbial activity (Kozlov 1967). De Boois (1974) noted that moisture generally affects the litter layer, whereas temperature is of importance in the more moist fermentation and humus layers. Only under acceptable moisture conditions are litter decomposition rates controlled primarily by temperature (Witkamp 1971).

Results of my summer monitoring program indicate that moisture levels are often inadequate, particularly on high areas (Tables 7 and 8). Periodic lack of moisture limits microbial activity directly (Alexander 1961), and also exposes the decomposing system to warmer daily temperatures (Table 10), which further desiccate the litter and inhibit future microbial attack (Drift 1963). The combined effect of temperature and moisture has been noted by other researchers (Witkamp and Drift 1961, Reiners 1968), and in my study (Table 5). Consideration of both physical factors is essential to interpretation of microbial population patterns.

During the spring and summer months, cooler temperatures in low areas reduce microbial respiration, and based on temperature alone, microbial activity should be greater on high areas. However, during the summer months high areas have a thin litter cover, and although warm, their litter and soil are dry. Therefore, summer microbial populations are generally smaller and less active on high areas than in low areas (Appendix II). Brief exceptions occur when microbial populations peak. With few exceptions, all populations isolated

from litter and soil in all three topographic areas show a spring and fall peak. Since timing of these population maxima may differ by one or two weeks among the topographic areas, high areas may briefly support a larger microbial population than the other topographic areas (Figures 3 to 12).

Timing of microbial population peaks is also dependent on temperature and moisture. Typically, the spring peak occurs in all areas in late May or early June. This is a period of favourable physical conditions caused by warming temperatures as summer approaches, and moist litter conditions remaining from the recent spring melt. Field observations indicate that high and most level areas lose their snow cover by mid-April, whereas the snow remains in low areas until the beginning of May. But although high and level areas may provide favourable moisture conditions at a time when low areas are still too wet, they do not show earlier microbial peaks; population maxima occur at about the same time in all areas because ambient air temperatures remain limiting until late May.

Fall population maxima cannot be explained by favourable physical conditions. These peaks are largely a result of the "priming effect" of fresh litter (Laura 1975), although high, and to a lesser extent, level, areas are dependent on fall moisture levels.

Moisture has another effect on microbial activity that is not dependent on its interaction with temperature. Periodic desiccation of the high areas, alleviated by summer rains, may

stimulate microbial activity. During the drying phase, microbial populations decline and certain soil qualities, particularly amino acid availability, are altered. Increased nutrient availability favours microbial metabolism when water is again available (Stevenson 1956, Soulides and Allison 1961, Van Schreven 1967). It is suspected that fragmentation of dry soil colloids results in an increased surface area for subsequent decomposition (Birch 1958, Jager 1967). Upon rewetting, the diminished microbial population shows a burst of activity because the surviving microorganisms are in an active growth stage (Birch 1958), and nutrients are temporarily abundant.

Since I did not synchronize microbial collections with rainfall I do not have direct evidence of the drying-rewetting phenomenon occurring on high areas. However, conditions are suitably dry, and this process is a possible means of maintaining a slow rate of soil microbial activity on the high areas during the summer months.

In summary, results from this short-term study indicate that variability in physical conditions is more important than diversity of substrate resources to microbial community composition. Therefore, there is no direct evidence that distribution of the three functional groups of microorganisms is related to the diversity of litter in the three topographic areas, but there is evidence that all functional groups thrive in the more stable decomposition environment of the low areas.

The two remaining levels of heterogeneity, litter decomposition, and incorporation of organic matter into surface soil,

are derived from all previous levels of heterogeneity. However, litter decomposition is most directly affected by spatial heterogeneity of microbial organisms, and soil organic incorporation is mainly affected by litter decomposition and surface litter accumulation (Figure 14). Both litter decomposition and soil organic incorporation are measures of decomposition, but their time frames differ.

Litter decomposition summarizes estimates of surface litter decomposition obtained by the mesh bag technique. Incorporation of organic matter into the surface soil follows litter fragments after they have passed through the mesh of the litter bags and entered the fermentation and humus layers. Although decomposition of litter fragments and formation of soil humus are outside the scope of this study, these long-term decomposition processes are integral to the functioning of a litter system (Schlesinger 1977). Spatial heterogeneity of soil organic incorporation is indicative of the heterogeneity of the long-term decomposition process over the woodlot floor, and it emphasizes the importance of some areas for the decay of resistant compounds and the development of a well-structured organic soil.

Two major generalizations can be made about surface litter decomposition in relation to topography. First, all litter types and litter mixtures exhibit faster weight and organic losses, and lignin gains, in low areas (Tables 17, 18 and 19), with the exception of short-term organic losses which are greatest on high areas (Table 20); second, litter mixtures simulating litter

accumulation in low areas lose weight ~~fastest~~ on all topographic sites (Table 17), but have the slowest organic loss and lignin gain rates (Table 19). Both these conclusions are attributable to levels of heterogeneity derived from the original topographic heterogeneity.

The first generalization indicates the importance of topographic site to litter decomposition. Since decomposition measures were made on imported bagged litter, the most important attributes of the topographic sites in the first few months were their physical conditions and native microbial and invertebrate populations; during the latter stages of the decay experiments, protection provided by differential accumulation of litter became significant.

The stable moisture and temperature conditions and large microbial and invertebrate populations of the low areas have been detailed; low sites provide the best decomposition environment for microbial (Alexander 1961) and invertebrate (Kuhnelt 1976) activity. During the early experimental months, bagged litter provides the only protective layer of surface litter. However, wind and gravity continue to redistribute surface litter, and in time the differential accumulation of litter buries bagged litter in low areas, while leaving litter bags on high areas exposed. The increased protection and insulation provided by the added surface litter in the low areas maintains stable temperature and moisture conditions, and encourages continued microbial and invertebrate activity.

Two other processes resulting in litter bag losses are leaching and abiotic fragmentation. Leaching is of particular importance in the first months of decay (Gosz et al. 1973), and there is the possibility of more complete leaching losses from high areas. Therefore, short-term organic losses are fastest on these areas (Table 20). Abiotic fragmentation is of equal importance in all topographic areas; its contribution varies in response to differences in litter quality.

The second generalization, that low litter mixtures lose weight faster in all topographic areas, while exhibiting the slowest organic loss and lignin gain rates, reflects the effect of litter quality on litter decay processes. Leaching, microbial degradation, and invertebrate and abiotic fragmentation are involved in decay of these realistic litter mixtures. Since low litter contains a greater proportion of aged litter, it has a lower proportion of soluble carbon compounds. Therefore, both leaching and microbial decay rates are slow, and hence qualitative changes in litter are slow. However, the physical delicacy of aged litter, and its greater palatability to invertebrates, results in increased abiotic and invertebrate fragmentation, and weight losses from litter bags are rapid.

Therefore, the physical and biotic characteristics of a topographic site, and the quantity and quality of accumulated litter, determine the rate and extent of litter decay. Unaged litter,

especially leaf material with a high water-soluble content, may be leached, fragmented, and superficially broken down by non-specialist microbial populations on all topographic sites.* However, these processes, which are most important to early litter losses, are relatively ineffectual in reducing resistant substrates. Therefore, aged litter, which has already lost most of its soluble material, is dependent on combined invertebrate and microbial activity to begin degradation of more resistant compounds. This later stage of litter decomposition is dependent on the stable decomposing environment and large microbial and invertebrate populations found in low areas. Thus, low sites, which accumulate litter long enough for it to be aged, also provide the decomposing environment and decomposer organisms necessary for long-term decay processes.

It is unfortunate that over-all measures of litter decomposition place artificial boundaries on the decay process. The litter bag technique only monitors decay until litter fragments are small enough to pass through the mesh (Howard 1967). It typically allows only short-term conclusions, such as the early importance of leaching and abiotic fragmentation (Gosz et al. 1973, Anderson 1973b), since it can only describe changes in litter tissue that remains intact during the experimental treatment. Therefore, in my experiment, long-term degradation could only be predicted from large microbial populations in low areas (Table 16), and the high humus content of these areas (Tables 11 and 12).

Humus formation is slow and poorly understood (Harris et al. 1972, Schnitzer and Khan 1972), but it is a natural continuation of surface litter decomposition. Reduced to its simplest terms, humus formation begins with the incorporation of plant remains (as well as excrement and microbial and animal bodies), by invertebrates, into the lower organic surface horizons and organic-enriched soil horizons. Therefore, this incorporation is directly affected by the abundance of surface litter (Figure 14). Much of the subsequent degradation is carried on by autochthonous microorganisms (Gray and Williams 1971). These organisms continue to degrade the litter material to smaller molecules, which they use as carbon and energy sources; microorganisms also synthesize and excrete products, such as phenols and amino acids. Resistant material, particularly lignified tissues, may be only superficially altered by microbial attack, and these resistant compounds are thought to combine with polymerized microbial products to form humus (Martin and Haider 1971, Schnitzer and Khan 1972, Flaig et al. 1975).

Humus is important both to soil structure and soil fertility. As mentioned previously, humus improves soil crumb structure, aeration and drainage; because of its sorptive capacity, humus also greatly increases the water and nutrient retention capacity of the soil (Buckman and Brady 1969, Schnitzer and Khan 1972). Low areas are the main sites for humus formation, and they are essential to the development of soil structure and nutrient retention.

My study concentrates on the effects of spatial heterogeneity during the growing season, late April to late October, and I have detailed the sequence of influence of topography on structural and functional components of the litter system during this time. Results indicate that low areas are the most important topographic areas for long-term decomposition, and that they provide the most favourable litter decomposing environment during the growing season. However, the litter system functions in a seasonally fluctuating environment, and there are indications that other topographic areas may provide temporarily significant decomposer habitats. I have, therefore, briefly outlined the changing significance of topographic areas through one year.

During the winter, insulation of a greater depth of litter and snow in the low areas maintains temperatures above freezing (Merriam and Wegner, personal communication), whereas the more exposed soil on high areas may freeze (Hart et al. 1962); therefore, only low areas allow a slow rate of winter microbial activity. However, in early spring, low areas remain wet and cold from spring melt, after high areas have begun to dry. Cool air temperatures reduce microbial and invertebrate metabolic rates, but drier high areas may provide refuges for invertebrates as they "track" their most favourable environment (Kuhnelt 1969, Roughgarden 1974). During the summer months, from June to September, low areas are again the main decomposing areas. High areas become dry and bare of litter, whereas low areas maintain a thick litter layer, and show stable moisture and temperature conditions. Microbial populations cannot "track" their preferred environment, as more mobile invertebrates do, but

their heightened growth and activity reflect favourable conditions; both microorganisms and invertebrates are more abundant in low areas during most of the growing season. Late fall is the time of peak litterfall and cooler, damper weather. For a short period prior to freezing temperatures, all topographic areas support rapid leaching and microbial activity.

Evidence of spatial heterogeneity in a litter system, and reflection of this heterogeneity in the decomposition process, has applicability outside the study of litter decomposition. Too often, in attempting to define the "average" state of a system, researchers ignore or obscure the natural heterogeneity which may be a functional characteristic of a system. But evidence is accumulating that spatial heterogeneity is a system attribute (Levins 1969, Reice 1974, Levin 1976) and even a regional characteristic (Patterson 1972, Wegner 1976, Merriam 1978). In my study of the decomposition process, recognition of topographic heterogeneity is necessary to evaluate critical areas and spatial relationships within the system through time. In general, consideration of inherent heterogeneity, especially in the context of a temporally fluctuating environment, is essential to any interpretation or manipulation of natural structure and function.

APPENDICES

- I. Media for Microbial Analysis.
- II. Microbial Populations (Tables 1 to 5).
- III. Litter Decomposition Measurements (Tables 1 to 7).

APPENDIX I

Media for Microbial Analyses

1. Rose bengal and aureomycin medium (Ivarson, personal communication)

Dextrose	10.0g	MgSO ₄ ·7H ₂ O	0.5g
Peptone	5.0g	Agar	20.0g
KH ₂ PO ₄	1.0g	Water	1000.0ml

Before sterilization, a solution containing 0.0333g rose bengal is added to each liter of medium. (This equals 1:30,000).

Solution is sterilized at 15 psi for 15 min. After sterilization 10ml of a filter-sterilized solution of aureomycin containing 7.5mg aureomycin is added to each 250ml of medium.

2. Peoria nutrient agar (Baker & Whittingham, 1972)

Dextrose	1.0g	Agar	20.0g
Bacto-peptone	5.0g	Water	1000.0ml
Yeast extract	3.0g		

Solution is sterilized at 15 psi for 15 min. After sterilization, 1ml of a fungal inhibitor actidione (250mg/25ml water solution) is added to each 250ml of medium. (Addition of actidione is a modification of Baker and Whittingham's medium).

3. Egg albumen and actidione medium (Corke & Chase, 1956)

Dextrose	1.0g	Egg albumen	0.25g
K ₂ HPO ₄	0.5g	Agar	15.0g
MgSO ₄ ·7H ₂ O	0.2g	Water	1000.0ml
Fe ₂ (SO ₄) ₃	trace		

Egg albumen is first dissolved in water and made alkaline to phenolphthalein with 0.1N NaOH. Final pH of the medium should be 6.8. Solution is sterilized at 15 psi for 15 min. After sterilization, 1ml actidione (250mg/25ml water solution) is added to each 250ml of medium.

4. Cellulose agar (Eggins & Pugh, 1962)

Cellulose (powdered)	10.0g	MgSO ₄ ·7H ₂ O	0.2g
(NH ₄) ₂ SO ₄	0.5g	CaCl ₂	0.1g
L-asparagine	0.5g	Yeast extract	0.5g
KH ₂ PO ₄	1.0g	Agar	20.0g
KCl	0.5g	Water	1000.0ml

Cellulose is prepared as a 4% suspension in water of Whatman's standard grade cellulose powder for chromatography, ball-milled for 72 hours. This suspension of ball-milled cellulose is added to the other constituents of the medium after they have been steamed, and before sterilization. Medium is sterilized for 15 min at 15 psi. Final pH of the medium is 6.2.

5. Soil extract agar (James, 1958)

K ₂ HPO ₄	0.2g
Agar	15.0g
Soil extract	1000.0ml

Soil extract is prepared by adding to 500g of fertile soil the amount of water, predetermined for the soil used, necessary to yield 1000ml of extract. This amount is usually 1200-1500ml. The soil suspension is heated in an autoclave at 121°C for 30 min. After cooling, it is filtered through paper or cloth. The first cloudy portion of the filtrate is refiltered by returning it to the same filter. To 1000ml of the extract, K₂HPO₄ and agar are added. The pH is adjusted to 6.8. After sterilization, 1ml actidione (250mg/25ml water solution) is added to each 250ml of medium. (Addition of actidione is modification of James' medium).

6. Vanillin method (Henderson, 1961)

Modified Turfitt's medium (Turfitt, 1944):

NH_4NO_3	1.0g	NaCl	0.005g
K_2HPO_4	0.25g	Vanillin	0.10g
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	0.25g	Water	1000.0ml

Dispensed in 20ml volumes to small Erlenmeyer flasks and sterilized for 15 min at 15 psi.

1ml of 1:100 litter or soil dilution is used to inoculate suspensions. After incubation at room temperature for 7 days, the flasks are shaken by hand for 1 min and 1ml from each flask is transferred to a replicate flask and incubated for a further 7 days. After incubation the flasks are again shaken for 1 min, and 1ml portions of the resulting suspensions are used to prepare dilutions used to inoculate Waksman's acidic agar.

Modified Waksman's acidic agar (Waksman, 1922):

Dextrose	10.0g	MgSO_4	0.5g
$(\text{NH}_4)_2\text{SO}_4$	2.5g	Agar	25.0g
KH_2PO_4	1.0g	Water	1000.0ml

Enough 1N H_2SO_4 is added to make the reaction equivalent to pH 3.6-3.8. 25g of agar are then added and dissolved by boiling. The medium is then sterilized at 15 psi for 15 min. The reaction of the medium after sterilization should be pH 4.0.

APPENDIX II Table 1. Bacterial populations in Litter and Soil ($\bar{x} \pm 1S.D.$, where $n=5$)
NOTE: Populations are tabled values $\times 10^6$

SAMPLE SITE	SAMPLING TIME									
	APR 28	MAY 13	MAY 29	JUN 16	JUN 29	JUL 23	AUG 19	SEP 21	OCT 18	OCT 28
<u>LITTER</u>										
HIGH	83.2 $\pm$ 17.1	34.0 $\pm$ 14.5	314. $\pm$ 22.7	244. $\pm$ 18.6	44.6 $\pm$ 11.3	115. $\pm$ 10.9	166. $\pm$ 46.0	251. $\pm$ 33.7	92.6 $\pm$ 4.42	9.08 $\pm$ 1.86
LEVEL	479. $\pm$ 71.8	374. $\pm$ 110.	242. $\pm$ 103.	305. $\pm$ 120.	402. $\pm$ 35.1	112. $\pm$ 33.5	306. $\pm$ 22.7	266. $\pm$ 25.2	1250. $\pm$ 485.	223. $\pm$ 70.7
LOW	458. $\pm$ 81.6	274. $\pm$ 125.	1730. $\pm$ 264.	362. $\pm$ 108.	333. $\pm$ 92.7	172. $\pm$ 83.8	244. $\pm$ 66.4	220. $\pm$ 25.3	231. $\pm$ 77.0	539. $\pm$ 21.3
<u>SOIL</u>										
HIGH	.780 $\pm$.138	1.06 $\pm$.083	21.0 $\pm$ 2.01	.941 $\pm$.171	1.16 $\pm$.132	.838 $\pm$.024	1.93 $\pm$.806	2.46 $\pm$.770	3.31 $\pm$ 1.05	6.52 $\pm$ 1.17
LEVEL	1.45 $\pm$.126	2.34 $\pm$.534	4.77 $\pm$.565	.962 $\pm$.121	1.38 $\pm$.140	1.29 $\pm$.237	2.81 $\pm$.792	3.38 $\pm$.218	4.93 $\pm$.990	3.95 $\pm$.638
LOW	1.76 $\pm$.368	8.14 $\pm$ 1.98	5.88 $\pm$.583	2.18 $\pm$.145	3.27 $\pm$.673	2.92 $\pm$.269	3.85 $\pm$.920	3.72 $\pm$.628	5.78 $\pm$ 1.55	52.8 $\pm$ 15.0

APPENDIX II Table 2. Fungal Populations in Litter and Soil ($\bar{x} \pm 1S.D.$, where $n=5$)
NOTE: Populations are tabled values $\times 10^4$

SAMPLE SITE	SAMPLING TIME									
	APR 28	MAY 13	MAY 29	JUN 16	JUN 29	JUL 23	AUG 19	SEP 21	OCT 18	OCT 28
<u>LITTER</u>										
HIGH	136. $\pm$ 25.8	28.9 $\pm$ 10.3	159. $\pm$ 38.4	98.4 $\pm$ 20.9	24.6 $\pm$ 2.21	94.4 $\pm$ 9.22	165. $\pm$ 27.2	182. $\pm$ 20.0	1670. $\pm$ 323.	145. $\pm$ 20.8
LEVEL	102. $\pm$ 10.5	213. $\pm$ 25.7	244. $\pm$ 46.6	287. $\pm$ 23.2	251. $\pm$ 41.8	80.1 $\pm$ 11.2	131. $\pm$ 25.8	140. $\pm$ 24.2	292. $\pm$ 31.1	167. $\pm$ 47.9
LOW	106. $\pm$ 10.0	496. $\pm$ 49.4	180. $\pm$ 46.2	110. $\pm$ 31.1	36.9 $\pm$ 4.36	57.0 $\pm$ 21.5	200. $\pm$ 31.6	81.9 $\pm$ 9.61	315. $\pm$ 43.1	406. $\pm$ 60.2
<u>SOIL</u>										
HIGH	1.94 $\pm$.750	1.52 $\pm$.476	3.54 $\pm$.960	1.68 $\pm$.140	2.50 $\pm$.617	1.24 $\pm$.377	1.41 $\pm$.368	3.10 $\pm$.759	3.57 $\pm$.913	2.95 $\pm$.731
LEVEL	2.90 $\pm$ 1.45	2.15 $\pm$.886	1.68 $\pm$ 1.21	1.85 $\pm$.826	1.93 $\pm$.509	2.72 $\pm$.665	2.34 $\pm$.620	3.12 $\pm$ 1.07	5.19 $\pm$.880	1.36 $\pm$.277
LOW	3.23 $\pm$ 1.39	5.09 $\pm$ 1.05	3.29 $\pm$ 1.07	3.69 $\pm$.988	4.33 $\pm$.943	4.89 $\pm$ 1.54	3.88 $\pm$.550	3.89 $\pm$.866	7.47 $\pm$ 2.70	3.70 $\pm$.827

APPENDIX II Table 3. Cellulolytic Bacterial Populations in Litter and Soil ($\bar{x}$ $\pm$ S.D., where $n=5$)

NOTE: Populations are tabled values $\times 10^6$

SAMPLE SITE	TIME									
	SAMPLING					TIME				
	APR 28	MAY 13	MAY 29	JUN 16	JUN 29	JUL 23	AUG 19	SEP 21	OCT 18	OCT 28
<u>LITTER</u>										
HIGH	79.2 $\pm$ 22.3	10.4 $\pm$ 7.46	114. $\pm$ 21.7	62.9 $\pm$ 36.5	26.2 $\pm$ 4.91	23.9 $\pm$ 6.99	48.8 $\pm$ 14.4	56.6 $\pm$ 9.02	89.5 $\pm$ 27.8	4.38 $\pm$.585
LEVEL	165. $\pm$ 37.9	108. $\pm$ 40.7	231. $\pm$ 48.2	211. $\pm$ 32.2	98.3 $\pm$ 29.2	19.9 $\pm$ 4.58	92.7 $\pm$ 25.9	58.2 $\pm$ 18.0	961. $\pm$ 215.	240. $\pm$ 66.6
LOW	253. $\pm$ 49.8	126. $\pm$ 40.0	706. $\pm$ 104.	144. $\pm$ 24.1	93.2 $\pm$ 12.7	31.2 $\pm$ 15.7	139. $\pm$ 88.5	47.9 $\pm$ 5.87	226. $\pm$ 76.8	428. $\pm$ 50.7
<u>SOIL</u>										
HIGH	.363 $\pm$.131	.378 $\pm$.117	3.62 $\pm$.933	.533 $\pm$.122	.466 $\pm$.178	.284 $\pm$.056	1.59 $\pm$.521	.957 $\pm$.104	3.41 $\pm$.809	2.14 $\pm$.463
LEVEL	.867 $\pm$.211	.968 $\pm$.093	2.32 $\pm$.869	.508 $\pm$.056	.527 $\pm$.045	.700 $\pm$.123	2.70 $\pm$.424	1.27 $\pm$.210	1.58 $\pm$.817	1.46 $\pm$.179
LOW	.837 $\pm$.095	2.74 $\pm$ 1.56	1.23 $\pm$.720	.700 $\pm$.138	.837 $\pm$.104	1.58 $\pm$.143	3.07 $\pm$.880	1.02 $\pm$.149	8.38 $\pm$ 1.90	44.2 $\pm$ 6.73

APPENDIX II Table 4. Actinomycete Populations in Litter and Soil ($\bar{x}$, where $n=5$)
 NOTE: Populations are tabled values $\times 10^6$

SAMPLE SITE	SAMPLING TIME									
	APR 28	MAY 13	MAY 29	JUN 16	JUN 29	JUL 23	AUG 19	SEP 21	OCT 18	OCT 28
LITTER										
HIGH	8.71	1.88	44.6	11.6	5.48	4.19	10.5	10.2	7.60	.990
LEVEL	8.68	29.9	49.6	30.8	16.0	1.72	13.4	6.26	42.6	29.8
LOW	8.72	12.6	93.8	8.92	6.0	2.39	8.60	4.40	13.6	30.6
SOIL										
HIGH	.174	.296	3.10	.322	.319	.200	.690	.473	1.31	2.31
LEVEL	.461	.710	1.02	.322	.307	.342	1.00	.914	1.06	1.19
LOW	.406	2.71	1.60	.858	1.10	.798	1.10	.740	1.84	16.0

APPENDIX II Table 5. Lignolytic Fungal Populations in Litter and Soil ($\bar{x} \pm 1S.D.$, where $n=5$)

NOTE: Populations are tabled values $\times 10^4$

SAMPLE SITE	SAMPLING TIME									
	APR 28	MAY 13	MAY 29	JUN 16	JUN 29	JUL 23	AUG 19	SEP 21	OCT 18	OCT 28
<u>LITTER</u>										
HIGH	2.05 $\pm$ 0.359	3.74 $\pm$ 0.954	5.58 $\pm$ 1.61	4.71 $\pm$ 1.62	3.21 $\pm$ 0.517	4.61 $\pm$ 1.14	2.81 $\pm$ 1.43	3.62 $\pm$ 1.43	3.54 $\pm$ 0.912	3.25 $\pm$ 0.740
LEVEL	2.37 $\pm$ 1.87	4.25 $\pm$ 2.73	14.4 $\pm$ 4.82	7.02 $\pm$ 4.90	8.41 $\pm$ 2.61	6.32 $\pm$ 1.21	3.71 $\pm$ 0.915	4.62 $\pm$ 2.51	6.98 $\pm$ 2.43	12.0 $\pm$ 6.97
LOW	3.26 $\pm$ 1.87	9.26 $\pm$ 3.09	16.4 $\pm$ 4.74	10.6 $\pm$ 4.21	9.25 $\pm$ 5.31	7.64 $\pm$ 3.22	5.51 $\pm$ 1.75	5.72 $\pm$ 2.43	9.65 $\pm$ 4.32	18.1 $\pm$ 6.73
<u>SOIL</u>										
HIGH	1.63 $\pm$ 0.598	4.21 $\pm$ 1.31	5.73 $\pm$ 1.22	4.62 $\pm$ 1.27	2.66 $\pm$ 1.01	1.43 $\pm$ 0.810	3.74 $\pm$ 2.15	5.66 $\pm$ 1.77	6.99 $\pm$ 2.43	4.04 $\pm$ 1.63
LEVEL	2.52 $\pm$ 0.395	4.76 $\pm$ 1.43	10.6 $\pm$ 4.13	7.93 $\pm$ 2.61	5.14 $\pm$ 2.25	4.31 $\pm$ 1.76	4.54 $\pm$ 1.21	7.31 $\pm$ 2.22	7.45 $\pm$ 3.21	9.61 $\pm$ 3.94
LOW	2.84 $\pm$ 0.996	3.22 $\pm$ 1.04	5.65 $\pm$ 1.28	11.7 $\pm$ 4.03	8.72 $\pm$ 3.21	4.50 $\pm$ 1.98	5.61 $\pm$ 3.20	8.32 $\pm$ 7.41	9.31 $\pm$ 6.43	11.6 $\pm$ 5.21

APPENDIX III Table 1. Weight measurements (as % of starting sample) for July decay experiment

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)							
	0	3	4	5	9	14	15	16
<u>HIGH LITTER</u>								
HIGH site	100	98.34	87.69	92.02	94.67	95.90	91.85	94.27
"	"	98.41	97.28	92.68	92.03	95.14	90.95	84.36
"	"	99.02						95.22
"	"	98.67						93.88
LEVEL site	100	82.03	66.04	85.68	76.36	77.87	69.00	77.42
"	"	85.79	74.12	73.31	79.42	72.13	64.42	68.44
"	"	79.46						73.24
"	"	72.83						69.00
LOW site	100	86.58	80.12	84.38	79.26	64.64	71.03	67.14
"	"	93.42	77.85	79.32	76.53	67.66	65.01	62.31
"	"	89.67						68.55
"	"	85.31						73.24
<u>LEVEL LITTER</u>								
HIGH site	100	94.66	97.54	96.87	90.58	89.54	89.69	92.22
"	"	97.89	98.31	95.32	92.42	91.33	90.88	89.48
"	"	98.43						85.32
"	"	95.31						88.41
LEVEL site	100	87.87	86.37	87.05	81.42	84.55	81.12	79.85
"	"	91.63	80.12	82.31	84.50	79.36	75.60	73.33
"	"	82.31						68.54
"	"	84.66						77.32
LOW site	100	83.50	83.04	81.28	76.72	74.24	71.47	64.48
"	"	88.62	80.01	83.54	78.51	73.34	69.99	66.32
"	"	81.33						70.90
"	"	85.50						63.42
<u>LOW LITTER</u>								
HIGH site	100	93.52	96.57	96.38	91.47	91.79	88.58	87.85
"	"	97.83	95.42	97.30	93.33	90.48	90.37	82.31
"	"	98.86						89.54
"	"	97.02						85.76
LEVEL site	100	86.83	86.59	86.46	83.20	78.99	73.03	71.55
"	"	82.40	84.32	83.92	84.54	81.52	75.63	68.32
"	"	87.38						75.49
"	"	85.41						69.91
LOW site	100	70.07	70.45	70.86	69.36	64.20	51.92	54.70
"	"	74.52	68.52	69.32	72.54	68.31	60.52	53.62
"	"	69.32						60.14
"	"	75.21						58.47

APPENDIX III Table 2a. Weight measurements (as % of starting sample) for May decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)				
	0	3	4	5	6
<u>HIGH SITE</u>					
Be:Ma(spring)	100	87.00 85.33	88.33 80.52	90.00 83.24	72.33 88.33 70.33 88.00
Be:Ma(fall)	"	87.33 86.67	72.67 84.63	76.83 76.67	82.43 73.00 84.32 82.32
cohosh	"	86.67 79.33	77.00 88.00	76.54 73.42	75.67 56.00 78.67 67.00
leeks	"	11.33 18.67	4.33 10.00	1.67 3.37	6.00 7.67 1.67 2.00
mixed Be:Ma	"	90.00 88.93	73.00 86.94	80.00 78.93	76.33 76.00 77.67 83.67
<u>LEVEL SITE</u>					
Be:Ma(spring)	100	85.33 88.00	88.33 90.33	82.34 77.67	86.33 87.67 75.86 63.33
Be:Ma(fall)	"	89.67 89.67	88.67 93.33	81.00 85.36	83.54 81.33 75.34 82.93
cohosh	"	78.00 81.00	68.33 74.67	65.33 70.00	76.00 61.33 64.33 50.33
leeks	"	0.33 2.00	1.00 2.67	0.67 1.33	6.33 2.67 0.33 5.00
mixed Be:Ma	"	81.67 94.67	82.00 86.00	85.33 78.00	74.00 72.00 76.67 82.33

APPENDIX III Table 2b. Weight measurements (as % of starting sample) for May decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)				
	0	3	4	5	6
<u>LOW SITE</u>					
Be:Ma(spring)	100	82.33	75.00	63.00	64.33
		94.33	85.67	75.00	79.67
					70.00
					68.00
Be:Ma(fall)	"	70.33	71.33	68.67	69.67
		65.67	61.33	61.00	57.67
					68.33
					73.33
cohosh	"	66.00	64.00	66.67	46.00
		62.00	59.33	50.00	51.67
					55.67
					68.67
leeks	"	1.00	2.00	0.33	6.33
		2.00	0.67	2.67	2.00
					5.00
					2.00
mixed Be:Ma	"	75.00	69.67	53.33	66.67
		76.33	78.00	50.67	58.67
					66.33
					75.67
<u>CHAMBER SITE</u>					
Be:Ma(spring)	100	85.33	83.67	82.67	84.64
		90.33	86.00	83.00	73.92
					86.84
					79.67
Be:Ma(fall)	"	97.00	85.33	81.67	83.94
		82.67	87.00	87.33	80.01
					74.67
					72.78
cohosh	"	83.67	85.67	87.33	81.64
		88.00	87.00	79.33	72.93
					76.57
					80.67
leeks	"	14.00	10.00	14.67	10.00
		8.00	8.67	9.00	5.00
					4.67
					10.00
mixed Be:Ma	"	82.67	83.67	78.67	76.94
		88.00	88.33	82.67	73.67
					81.64
					78.33

APPENDIX III Table 3b. Organic matter analysis (as % dry weight) for July decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)						
	0	3	4	5	9	14	15
LEVEL LITTER							
HIGH site	92.88 90.98	59.00 62.53 50.83 63.39 37.87 43.34 40.16 37.80	58.06 45.95 42.51 40.31	58.69 39.47 34.95 37.74	71.66 72.01 56.87 71.31	35.01 61.82 24.19 31.39	51.54 66.47 60.45 39.81 40.70 48.22 63.26 35.68 20.78 39.42
LEVEL site	92.88 90.98	65.17 79.91 83.07 78.91 73.64 77.75 82.83 74.19	71.34 74.59 78.21 82.23	68.27 63.07 60.99 79.12	70.79 64.60 76.81 78.83	85.16 61.61 80.22 78.55	53.23 82.94 72.00 60.32 65.89 77.40 59.01 79.51 44.55 43.56
LOW site	92.88 90.98	78.58 63.42 53.43 65.70 76.45 74.07 61.06 79.34	62.53 26.42 71.81 74.19	43.10 34.80 75.21 71.70	68.37 53.18 80.50 75.07	44.09 35.63 61.86 59.75	40.55 28.25 54.56 40.61 30.64 24.22 73.49 66.54 56.62 40.23

APPENDIX III Table 3c. Organic matter analysis (as % dry weight) for July decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)									
	0	3	4	5	9	14	15	16		
<u>LOW LITTER</u>										
HIGH site	94.56	63.66	52.59	41.36	66.20	43.72	25.10	50.79		
	94.69	49.21	56.12	43.26	62.32	48.07	30.54	17.47		
		58.53						34.52		
		49.11						42.62		
LEVEL site	94.56	72.17	58.75	71.55	76.59	70.43	70.48	62.45		
	94.69	70.10	60.93	55.97	81.67	64.24	67.33	67.26		
		60.05						67.99		
		78.08						67.31		
LOW site	94.56	78.63	85.12	78.58	81.43	74.69	63.61	83.00		
	94.69	80.60	74.63	73.64	79.20	83.10	73.18	73.18		
		77.86						65.00		
		76.32						74.32		

APPENDIX III Table 4a. Lignin analysis (as % dry weight) for July decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)						
	0	3	4	5	9	14	15
HIGH LITTER							
HIGH site							
23.80	24.60	27.48	24.59	23.26	29.42	26.65	25.04
20.96	24.30	24.90	28.66	31.74	26.04	30.43	37.81
20.05	31.39						26.32
19.99	26.36						28.94
21.45							
20.65							
LEVEL site							
23.80	33.09	22.80	30.91	28.11	29.68	28.32	32.32
20.96	23.75	26.17	25.49	28.57	34.83	26.54	29.82
20.05	29.84						28.94
19.99	28.38						26.52
21.45							
20.65							
LOW site							
23.80	23.11	26.95	25.24	22.55	29.29	31.67	29.83
20.96	30.70	31.56	31.51	33.97	26.26	26.24	25.75
20.05	27.96						32.07
19.99	26.55						34.13
21.45							
20.65							

APPENDIX III Table 4b. Lignin analysis (as % dry weight) for July decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)							
	0	3	4	5	9	14	15	16
LEVEL LITTER								
HIGH site	25.18 23.63	28.42 28.82 19.61 26.47 23.62 17.99 17.34 16.18	24.16 21.97 24.99 20.59	22.35 31.80 23.52 21.89	24.94 30.53 28.87 27.69	23.57 27.59 28.52 29.14	29.35 27.05 22.28 24.20	23.68 18.82 26.96 26.57 28.26 16.98
LEVEL site	25.18 23.63	26.38 29.40 29.19 23.22 32.37 29.81 26.61 21.44	22.30 34.23 23.39 23.94	28.08 25.08 25.55 23.52	28.90 31.07 25.85 25.52	31.87 21.52 28.82 25.48	26.26 30.68 29.25 28.85	26.92 28.08 26.86 24.17 32.73 32.19
LOW site	25.18 23.63	23.69 31.99 24.91 28.35 25.76 29.07 29.56 26.72	19.86 25.15 35.53 24.42	25.15 21.75 28.00 29.77	25.20 32.98 27.56 29.13	27.64 32.94 26.24 29.40	21.36 29.78 32.69 27.64	31.66 28.28 21.87 33.64 34.56 30.90

APPENDIX III Table 4c. Lignin analysis (as % dry weight) for July decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)						
	0	3	4	5	9	14	15
<u>LOW LITTER</u>							
HIGH site	24.17	26.12	20.56	25.64	26.30	27.20	22.38
	20.54	22.31	23.04	20.27	20.88	28.78	24.40
		22.05					
		19.95					
LEVEL site	24.17	25.13	22.55	32.01	25.58	26.11	28.44
	20.54	25.82	29.21	21.32	21.65	24.88	30.78
		24.30					
		28.26					
LOW site	24.17	22.54	25.62	29.82	26.76	25.48	27.20
	20.54	30.49	32.97	34.20	30.67	33.63	35.61
		26.66					
		22.63					

APPENDIX III Table 5a. Organic matter analysis (as % dry weight)
for May decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)				
	0	3	4	5	6
<u>HIGH SITE</u>					
Be:Ma(spring)	93.42	84.82	81.13	84.58	76.61
		86.96	74.26	87.03	65.67
					77.76
					83.93
Be:Ma(fall)	93.65	83.27	86.23	72.54	75.84
		90.67	70.71	90.53	70.88
					84.38
					69.45
cohosh	94.39	88.41	92.38	90.94	90.49
		97.30	95.73	91.62	86.02
					80.46
					81.50
leeks	96.61	---	---	---	---
mixed Be:Ma	91.39	78.57	78.56	77.52	83.33
		80.54	82.22	83.56	75.13
					84.04
					77.91
<u>LEVEL SITE</u>					
Be:Ma(spring)	93.42	89.00	89.87	80.93	81.53
		88.99	91.83	84.23	85.31
					90.91
					88.68
Be:Ma(fall)	93.65	88.42	64.76	79.25	46.59
		90.27	77.62	55.29	64.72
					86.68
					81.00
cohosh	94.39	92.80	87.64	86.52	87.72
		92.92	88.95	88.65	86.70
					88.20
					87.39
leeks	96.61	---	---	---	---
mixed Be:Ma	91.39	88.17	89.51	86.18	80.94
		85.66	84.14	85.45	83.02
					82.99
					85.62

APPENDIX III Table 5b. Organic matter analysis (as % dry weight).
for May decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)				
	0	3	4	5	6
<u>LOW SITE</u>					
Be:Ma(spring)	93.42	88.13 91.80	86.72 89.52	89.96 84.85	85.41 80.74 79.78 90.93
Be:Ma(fall)	93.65	90.47 91.99	89.72 87.89	82.01 84.41	79.80 72.95 88.43 90.77
cohosh	94.39	90.90 94.36	94.91 87.12	88.16 88.67	87.15 88.41 93.34 85.88
leeks	96.61	---	---	---	---
mixed Be:Ma	91.39	88.94 90.33	86.13 83.83	89.00 82.33	84.07 79.02 92.87 84.31
<u>CHAMBER SITE</u>					
Be:Ma(spring)	93.42	90.77 93.51	89.77 93.57	87.91 92.68	85.35 84.28 88.79 87.81
Be:Ma(fall)	93.65	88.05 83.35	90.02 84.18	87.55 83.84	87.78 88.85 88.01 82.31
cohosh	94.39	91.68 94.33	91.62 93.17	92.69 85.98	87.97 90.39 91.05 88.18
leeks	96.61	78.73 70.75	75.00 73.75	71.28 74.39	60.08 72.32 69.34 64.72
mixed Be:Ma	91.39	87.66 90.78	86.23 89.26	85.99 85.48	87.33 85.16 87.23 84.01

APPENDIX III, Table 6. Lignin analysis (as % dry weight) for
May decay experiment.

LITTER/SITE COMBINATIONS	ELAPSED TIME (mo)				
	0	3	4	5	6
<u>HIGH SITE</u>					
Be:Ma(spring)	28.45	30.53	31.69	31.62	35.46
Be:Ma(fall)	27.41	27.62	28.70	24.68	36.36
cohosh	21.93	22.68	23.34	25.72	27.17
leeks	10.20	---	---	---	---
mixed Be:Ma	34.68	35.04	32.52	37.07	39.88
<u>LEVEL SITE</u>					
Be:Ma(spring)	28.45	35.41	38.00	39.12	35.10
Be:Ma(fall)	27.41	33.20	31.29	28.37	30.52
cohosh	21.93	29.51	28.59	32.02	30.30
leeks	10.20	---	---	---	---
mixed Be:Ma	34.68	33.47	38.31	36.10	42.42
<u>LOW SITE</u>					
Be:Ma(spring)	28.45	32.92	27.43	32.13	32.18
Be:Ma(fall)	27.41	30.09	33.08	31.33	38.99
cohosh	21.93	25.41	24.94	31.65	38.51
leeks	10.20	---	---	---	---
mixed Be:Ma	34.68	36.10	34.90	36.72	40.63
<u>CHAMBER SITE</u>					
Be:Ma(spring)	28.45	30.99	34.62	30.72	36.64
Be:Ma(fall)	27.41	28.86	30.64	34.59	31.71
cohosh	21.93	20.64	25.47	28.88	30.95
leeks	10.20	10.38	11.27	14.17	13.62
mixed Be:Ma	34.68	35.49	35.60	37.82	38.01

APPENDIX III Table 7. Lignin changes in litter monitored during the May decay experiment. Rate of increase in lignin content was estimated from simple linear regressions of percent lignin over 6 mo (N = 5).

TREATMENT			
AREA	LITTER MIXTURE	GAIN RATE	F STATISTIC
HIGH	Be:Ma(spring)	1.00	14.15***
	Be:Ma(fall)	0.85	0.74****
	cohosh	0.85	11.31***
	mixed Be:Ma	0.70	1.50****
LEVEL	Be:Ma(spring)	1.44	5.32****
	Be:Ma(fall)	0.32	0.35****
	cohosh	1.52	14.07***
	mixed Be:Ma	1.07	2.89****
LOW	Be:Ma(spring)	0.52	0.90****
	Be:Ma(fall)	1.60	7.88****
	cohosh	2.48	8.59****
	mixed Be:Ma	0.77	3.63****
CHAMBER	Be:Ma(spring)	1.12	4.82****
	Be:Ma(fall)	0.98	6.15****
	cohosh	1.58	8.56****
	leeks	0.66	6.46****
	mixed Be:Ma	0.58	11.20***

*** all slopes differ significantly from zero ($P \leq .05$)

**** " " " insignificantly " " ($P > .05$)

LITERATURE CITED

- Ainsworth, G.C., F.K. Sparrow and A.S. Sussman (ed.) 1973. The fungi: an advanced treatise. Vol. IVA. Academic Press. New York. 621 pp.
- Alexander, M. 1961. Introduction to soil microbiology. Wiley Publishing Co. New York. 472 pp.
- Anderson, J.M. 1973a. Stand structure and litterfall of a coppiced beech (*Fagus sylvatica*) and sweet chestnut (*Castanea sativa*) woodland. *Oikos* 24(1): 128-135.
- Anderson, J.M. 1973b. The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. I. Breakdown, leaching and decomposition. *Oecologia* 12(3): 251-274.
- Anderson, J.M. 1973c. Carbon dioxide evolution from two temperate deciduous woodland soils. *J. Appl. Ecol.* 10: 361-378.
- Armentano, T.V. and G.M. Woodwell. 1976. The production and standing crop litter and humus in a forest exposed to chronic gamma irradiation for twelve years. *Ecology* 57: 360-367.
- Attiwell, P.M. 1968. The loss of elements from decomposing litter. *Ecology* 49: 142-145.
- Baker, L.E. and W.F. Whittingham. 1972. Microfungal population changes associated with decomposition of oak forest leaf litter. Eastern Deciduous Forest Biome, Memo Report 72-105.
- Basaraba, J. and R.L. Starkey. 1966. Effect of plant tannins on decomposition of organic substances. *Soil Sci.* 101(1): 17-23.
- Birch, H.F. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10: 9-31.
- Birch, L.C. 1971. The role of environmental heterogeneity and genetical heterogeneity in determining distribution and abundance. In P. J. den Boer and G.R. Graywell (ed.) Dynamics of populations. Centre for Agricultural Publishing. Wageningen. 611 pp.

OF/DE

- Bocock, K.L. and O.J.W. Gilbert. 1957. The disappearance of leaf litter under different woodland conditions. *Plant 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.
- Bormann, F.H. and G.E. Likens. 1967. Nutrient cycling. *Science* 155: 424-429.
- Buchanan, R.E. and N.E. Gibbons (ed.) 1974. *Bergey's manual of determinative bacteriology* (eighth edition). The Williams and Wilkins Co. Baltimore. 1268 pp.
- Buckman, H.O. and N.C. Brady. 1969. The nature and properties of soils. The Macmillan Co. Toronto. 653 pp.
- Burges, A. 1956. The release of cations during the decomposition of forest litter. Sixth International Congress of Soil Science. Vol. B. Paris. 741-745.
- Carter, A. and J.B. Cragg. 1976. Concentrations and standing crops of calcium, magnesium, potassium and sodium in soil and litter arthropods and their food in an aspen woodland ecosystem in the Rocky Mountains. (Can.) *Pedobiologia* 16(5): 379-388.
- Christensen, M. 1969. Soil microfungi of dry to mesic conifer-hardwood forests in northern Wisconsin. *Ecology* 50: 9-27.
- Christensen, N.L. 1973. Fire and the nitrogen cycle in California chaparral. *Science* 181: 66-67.
- Christman, R.F. and R.T. Oglesby. 1971. Microbiological degradation and the formation of humus. In K.V. Sarkonen and C.H. Ludwig (ed.) *Lignins: occurrence, formation, structure and reactions*. Wiley Interscience. Toronto. 916 pp.
- Clements, F.E. and C.L. Shear. 1973. The genera of fungi. Hafner Publishing Co. New York. 496 pp.
- Coldwell, B.B. and W.A. Delong. 1950. Tree leaves before and after partial decomposition. *Scientific Agriculture* 30: 456-465.

- Colwell, R.K. 1974. Predictability, constancy and contingency of periodic phenomena. *Ecology* 55: 1148-1153.
- Connell, J.H. and E. Orias. 1964. The ecological regulation of species diversity. *Am. Nat.* 98: 399-414.
- Corke, C.T. and F.E. Chase. 1956. The selective enumeration of actinomycetes in the presence of large numbers of fungi. *Can. J. Microbiol.* 2: 12-16.
- Cromack, K. Jr. 1973. Litter production and decomposition in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina. Ph. D. thesis, University of Georgia, Athens, Georgia. 160 pp.
- Cromack, K. Jr., R.L. Todd and C.D. Monk. 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol. Biochem.* 7: 265-268.
- Crossley, D.A. and M.P. Hoglund. 1962. A litter-bag method for the study of microarthropods inhabiting leaf litter. *Ecology* 43: 571-573.
- Cutler, D.W., L.M. Crump and H. Sandon. 1923. A quantitative investigation of the bacterial and protozoan population of the soil, with an account of the protozoan fauna. *Philos. Trans. R. Soc. Lond. Biol. Sci.* 211: 317-350.
- De Boois, H.M. 1974. Measurement of seasonal variations in oxygen uptake of various litter layers of an oak forest. *Plant Soil* 40: 545-555.
- Dickinson, C.H. 1974. Decomposition of litter in soil. In C.H. Dickinson and G.J.F. Pugh (ed.) *Biology of plant litter decomposition 2*. Academic Press. New York.
- Draper, N.R. and H. Smith. 1966. *Applied regression analysis*. Wiley Publishing Co. New York. 407 pp.
- Drift, J. van der. 1963. The disappearance of litter in mull and mor in connection with weather conditions and the activity of the macrofauna. In J. Doeksen and J. van der Drift (ed.) *Soil organisms*. Holland Publishing Co. Amsterdam. 453 pp.
- Drift, J. van der. 1969. Problems in soil ecology requiring most urgent attention. In J. Phillipson (ed.) *Methods of study in soil ecology*. UNESCO. Paris. 303 pp.

- Duvigneaud, P. and S. Denaeyer-De Smet. 1970. Biological cycling of minerals in temperate deciduous forests. In D.E. Reichle (ed.) Analysis of temperate forest ecosystems. Springer-Verlag. New York. 304 pp.
- Edwards, C.A. and G.W. Heath. 1963. The role of soil animals in breakdown of leaf litter. In J. Doeksen and J. van der Drift (ed.) Soil organisms. North Holland Publishing Co. Amsterdam, 453 pp.
- Edwards, C.A., D.E. Reichle and D.A. Crossley, Jr. 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In D.E. Reichle (ed.) Analysis of temperate forest ecosystems. Springer-Verlag. New York. 304 pp.
- Edwards, N.T. 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Am. Proc. 39: 361-365.
- Eggins, H.O.W. and G.J.F. Pugh. 1962. Isolation of cellulose-decomposing fungi from the soil. Nature 193: 94-95.
- Eggleson, W.G.E. 1938. The influence of environmental factors on numbers of soil microorganisms. Soil Sci. 46: 351-363.
- Fahey, T.J. and G.E. Lang. 1975. Concrete frost along an elevational gradient in New Hampshire. Can. J. For. Res. 5: 700-705.
- Flaig, W., H. Beutelspacher and E. Rietz. 1975. Chemical composition and physical properties of humic substances. In J.E. Gieseking (ed.) Soil components. Volume 1. Organic components. Springer-Verlag. New York. 534 pp.
- Frankland, J.C. 1966. Succession of fungi on decaying petioles of Pteridium aquilinum. J. Ecol. 54: 41-63.
- Garrett, S.D. 1951. Ecological groups of soil fungi: a survey of substrate relationships. New Phytol. 50(2): 149-166.
- Ghilarov, M.S. 1963. On the interrelation between soil dwelling invertebrates and soil microorganisms. In J. Doeksen and J. van der Drift (ed.) Soil organisms. North Holland Publishing Co. Amsterdam. 453 pp.

- Ghilarov, M.S. 1969. Soil biocoenoses. In J. Phillipson (ed.) Methods of study in soil ecology. UNESCO. Paris. 303 pp.
- Ghilarov, M.S. 1971. Invertebrates which destroy the forest litter and ways to increase their activity. In P. DuVigneaud (ed.) Productivity of forest ecosystems. UNESCO. Paris. 707 pp.
- Gilman, J.C. 1957. A manual of soil fungi. Iowa State College Press. Iowa.
- Gochenaour, S.E. and G.M. Woodwell. 1974. The soil microfungi of a chronically irradiated oak-pine forest. Ecology 55: 1004-1016.
- Golley, F.B. 1965. Structure and function of an old-field broom-sedge community. Ecol. Monogr. 35: 113-131.
- Goodfellow, M. and T. Cross. 1974. Actinomycetes. In C.H. Dickinson and G.J.F. Pugh (ed.) Biology of plant litter decomposition 2. Academic Press. New York.
- Gosz, J.R., G.E. Likens and F.H. Bormann. 1972. Nutrient content of litter fall on the Hubbard Brook Experimental Forest, New Hampshire. Ecology 53: 769-784.
- Gosz, J.R., G.E. Likens and F.H. Bormann. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monogr. 43: 173-191.
- Gray, T.R.G. and S.T. Williams. 1971. Microbial productivity in soil. In D.E. Hughes and A.H. Rose (ed.) Microbes and biological productivity. University Press. Cambridge.
- Gyllenberg, H.G. and E. Eklund. 1974. Bacteria. In C.H. Dickinson and G.J.F. Pugh (ed.) Biology of plant litter decomposition 2. Academic Press. New York.
- Harley, J.L. 1971. Fungi in ecosystems. J. Ecol. 59: 653-668.
- Harris, W.F., P. Sollins, N.T. Edwards, B.E. Dinger and H.H. Shugart. 1972. Analysis of carbon flow and productivity in a temperate deciduous forest ecosystem. In D.E. Reichle, J.F. Franklin and D.W. Goodall (ed.) Productivity of world ecosystems. National Academy of Sciences. Washington. 163 pp.

- Hart, G., L.E. Leonard and R.S. Pierce. 1962. Leaf fall, humus depth and soil frost in a northern hardwood forest. Forest Research Note No. 131. Northeastern Forest Experiment Station. U.S. Department of Agriculture. 3 pp.
- Heath, G.W., M.K. Arnold and C.A. Edwards. 1966. Studies in leaf litter breakdown. I. *Pedobiologia* 6: 1-12.
- Henderson, M.E.K. 1960. Studies on the physiology of lignin decomposition by soil fungi. In D. Parkinson and J.S. Waid (ed.) The ecology of soil fungi. Liverpool University Press. Liverpool. 324 pp.
- Henderson, M.E.K. 1961. Isolation, identification and growth of some soil hyphomycetes and yeast-like fungi which utilize aromatic compounds related to lignin. *J. Gen. Microbiol.* 26: 149-154.
- Hering, T.F. 1967. Fungal decomposition of oak leaf litter. *Trans. Br. Mycol. Soc.* 50(2): 267-273.
- Hills, G.A., N.R. Richards and F.F. Morwick. 1944. Soil survey of Carleton County, Province of Ontario. Report No. 7, Ont. Soil Survey, Toronto. 103 pp and map.
- Hogg, B.M. and H.J. Hudson. 1966. Microfungi on leaves of Fagus sylvatica. I. The micro-fungal succession. *Trans. Br. Mycol. Soc.* 49: 185-192.
- Howard, P.J.A. 1967. A method for studying the respiration and decomposition of litter. In O. Graff and J.E. Satchell (ed.) *Progress in soil biology*. North Holland Publishing Co. Amsterdam. 656 pp.
- Hudson, H.J. 1968. The ecology of fungi on plant remains above the soil. *New Phytol.* 67: 837-874.
- Hudson, H.J. 1971. The development of the saprophytic fungal flora as leaves senesce and fall. In T.F. Preece and C.H. Dickinson (ed.) *Ecology of leaf surface micro-organisms*. Academic Press. New York.
- Hughes, M.K. 1971. Seasonal calorific values from a deciduous woodland in England. *Ecology* 52: 923-926.

- Imshenetsky, A.A. 1968. Decomposition of cellulose in the soil. In T.R.G. Gray and D. Parkinson (ed.) The ecology of soil bacteria. University of Toronto Press. Toronto. 681 pp.
- Jackson, M.L. 1958. Soil chemical analysis. Prentice-Hall, Inc. Englewood Cliffs, New Jersey. 498 pp.
- Jackson, R.M. and F. Raw. 1966. Life in the soil. Edward Arnold Publishers Ltd. London. 59 pp.
- Jäger, G. 1967. Changes in the activity of soil microorganisms influenced by physical factors (drying-remoistening, freezing-thawing). In O. Graff and J.E. Satchell (ed.) Progress in soil biology. North Holland Publishing Co. Amsterdam. 656 pp.
- James, N. 1958. Soil extract in soil microbiology. Can. J. Microbiol. 4: 363-370.
- Jarrell-Ash. 1968. Model JA82-270 instruction manual.
- Jensen, V. 1968. The plate count technique. In T.R.G. Gray and D. Parkinson (ed.) The ecology of soil bacteria. University of Toronto Press. Toronto. 681pp.
- Jensen, V. 1971. The bacterial flora of beech leaves. In T.F. Preece and C.H. Dickinson (ed.) Ecology of leaf surface microorganisms. Academic Press. New York.
- John, D.M. 1973. Accumulation and decay of litter and net production of forest in tropical West Africa. Oikos 24(3): 430-435.
- Jordan, C.F. 1971. Productivity of a tropical forest and its relation to a world pattern of energy storage. J. Ecol. 59: 127-142.
- Katz, B.A. and H. Lieth. 1974. Seasonality of decomposers. In H. Lieth (ed.) Phenology and seasonality modelling. Ecological studies 8. Springer-Verlag. New York. 444 pp.
- Kilmer, V.J. and L.T. Alexander. 1949. Methods of making mechanical analyses of soils. Soil Sci. 68: 15-24.
- Kononova, M.M. 1966. Soil organic matter: its role in soil formation and in soil fertility. Oxford: Pergamon. 554 pp.
- Kozlov, K.A. 1967. Microbe cenose in the soils of some landscapes of south-eastern Trans-Baikal area and their dynamics. In O. Graff and J.E. Satchell (ed.) Progress in soil biology. North Holland Publishing Co. Amsterdam. 656 pp.

- Kucera, C.L. and D.R. Kirkham. 1971. Soil respiration studies in tallgrass prairie in Missouri. *Ecology* 52: 912-915.
- Kuhnelt, W. 1969. Structural aspects of soil-surface-dwelling biocoenoses. In J. Phillipson (ed.) *Methods of study in soil ecology*. UNESCO. Paris. 303 pp.
- Kuhnelt, W. 1976. *Soil biology, with special reference to the animal kingdom*. Michigan State University Press. East Lansing. 483 pp.
- Lang, G.E. 1974. Litter dynamics in a mixed oak forest on the New Jersey Piedmont. *Bull. Torrey Bot. Club* 101(5): 277-286.
- Lauria, R.D. 1975. On the "priming effect" of organic materials. *Soil Sci. Soc. Am. Proc.* 39: 807-808.
- Levin, S.A. 1976. Population dynamic models in heterogeneous environments. In R.F. Johnston, P.W. Frank and C.D. Michener (ed.) *Annu. rev. ecol. syst.* 7. Annual Reviews, Inc. Palo Alto, California. 540 pp.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15: 237-240.
- Lewis, J.A. and R.L. Starkey. 1968. Vegetable tannins, their decomposition and effects on decomposition of some organic compounds. *Soil Sci.* 106: 241-247.
- Likens, G.E., F.H. Bormann, R.S. Pierce and D.W. Fisher. 1971. Nutrient-hydrologic cycle interaction in small forested watershed-ecosystems. In P. DuVigneaud (ed.) *Productivity of forest ecosystems*. UNESCO. Paris. 707 pp.
- Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton and N.M. Johnson. 1977. *Biogeochemistry of a forested ecosystem*. Springer-Verlag. New York. 146 pp.
- Lockhead, A.G. and F.E. Chase. 1943. Qualitative studies of soil microorganisms. V. Nutritional requirements of the predominant bacterial microflora. *Soil Sci.* 55: 185-195.
- MacArthur, R.H. 1972. *Geographical ecology*. Harper and Row Publishers. New York. 269 pp.

- Macfadyen, A. 1963. Animal ecology, aims and methods. Sir Isaac Pitman and Sons. London. 344 pp.
- Mack, L.M. 1973. The role of component heterogeneity in integrated beech-maple and poplar litter systems. M. Sc. thesis. Carleton University. Ottawa. 234 pp.
- Macura, J., J. Szolnoki and V. Vancura. 1963. Decomposition of glucose in the soil. In J. Doeksen and J. van der Drift (eds.) Soil organisms. North Holland Publishing Company. Amsterdam. 453 pp.
- Maldaque, M. 1968. Vitesse de décomposition de litières d'érable à sucre (*Acer saccharum* Marsh.) de la région de Québec. Nat. Can. (Que.) 95: 259-286.
- Marcuzzi, G. and M.T. Lafisca. 1975. Observations on the digestive enzymes of some litter-feeding animals. In J. Vanek (ed.) Progress in soil zoology. Dr. W. Junk Publishers. The Hague. 630 pp.
- Marks, P.L. and F.H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady state nutrient cycling. Science 176: 914-915.
- Martin, J.P. and K. Haider. 1971. Microbial activity in relation to soil humus formation. Soil Sci. III(1): 54-63.
- May, R.M. 1974. Ecosystem patterns in randomly fluctuating environments. In R. Rosen and F.M. Snell (ed.) Progress in theoretical biology 3. Academic Press. New York. 349 pp.
- McFee, W.W. and E.L. Stone. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Sci. Soc. Am. Proc. 30: 513-516.
- Melin, E. 1930. Biological decomposition of some types of litter from North American forests. Ecology 11: 72-101.
- Merriam, H.G. 1978. Changes in aspen parkland habitats bordering Alberta sloughs. Can. Field-Nat. 92(2):
- Minderman, G. 1968. Addition, decomposition and accumulation of organic matter in forests. J. Ecol. 56: 355-362.
- Minderman, G. and L. Daniels. 1967. Colonization of newly fallen leaves by micro-organisms. In O. Graff and J.E. Satchell (ed.) Progress in soil biology. North Holland Publishing Company. Amsterdam. 656 pp.

- Nielsen, C.O. 1959. Soil fauna and moisture regime of its environment. Proc. 15th Int. Congr. Zool. 349-350.
- Nielsen, C.O. 1962. Carbohydrases in soil and litter invertebrates. *Oikos* 13: 200-215.
- Odum, E.P. 1971. Fundamentals of ecology. W.B. Saunders Company. Philadelphia. 574 pp.
- Odum, H.T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.* 27: 55-112.
- Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322-331.
- Ovington, J.D. 1956. The composition of tree leaves. *Forestry* 29: 22-28.
- Ovington, J.D. 1962. Quantitative ecology and the woodland ecosystem concept. In J.B. Cragg (ed.) *Adv. in ecol. res.* 1. Academic Press. New York. 203 pp.
- Paine, R.T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. *Ecology* 50: 950-961.
- Paine, R.T. 1971. The measurement and application of the calorie to ecological problems. In R.F. Johnston (ed.) *Annu. rev. ecol. and syst.* 2. Annual Reviews, Inc. Palo Alto, Calif. 510 pp.
- Parkinson, D. 1972. Terrestrial decomposition. In D.E. Reichle, J.F. Franklin and D.W. Goodall (ed.) *Productivity of world ecosystems.* National Academy of Sciences: Washington. 163 pp.
- Parkinson, D., T.R.G. Gray, J. Holding and H.M. Nagel-de-Boois. 1971. Heterotrophic microflora. In J. Phillipson (ed.) *Methods of study in quantitative soil ecology.* IBP Handbook 18. Blackwell Scientific Publications. Oxford. 297 pp.
- Patterson, J.H. 1972. The role of wetland heterogeneity in the regulation of duck populations in eastern Ontario. Ph. D. thesis, Carleton University, Ottawa. 133 pp.
- Pearson, D.L. 1971. Vertical stratification of birds in a tropical dry forest. *Condor* 73: 46-55.

Peevy, W.J. and A.G. Norman. 1948. Influence of composition of plant materials on properties of the decomposed residues. *Soil Sci.* 65: 209-226.

Phillipson, J., R.J. Potman, J. Steel and S.R.J. Woodall. 1975. Litter input, litter decomposition and the evolution of carbon dioxide in a beech woodland, Wytham Woods, Oxford. *Oecologia* 20(3): 203-217.

Pinck, J.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.

Pomeroy, L.R. 1970. The strategy of mineral cycling. In R.F. Johnston, P.W. Frank, C.D. Michener (ed.) *Annu. rev. ecol. syst.* 1. Annual Reviews, Inc. Palo Alto, Calif. 406 pp.

Pugh, G.J.F. 1974. Terrestrial fungi. In C.H. Dickinson and G.J.F. Pugh (ed.) *Biology of plant litter decomposition* 2. Academic Press. New York.

Reice, S.R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. *Ecology* 55: 1271-1282.

Reichle, D.E. 1971. Energy and nutrient metabolism of soil and litter invertebrates. In P. DuVigneaud (ed.) *Productivity of forest ecosystems*. UNESCO. Paris. 707 pp.

Reichle, D.E., J.F. McBroyer and S. Ausmus. 1975. Ecological energetics of decomposer invertebrates in a deciduous forest and total respiration budget. In J. Vanek (ed.) *Progress in soil zoology*. Dr. W. Junk Publishers. The Hague. 630 pp.

Reichle, D.E., R.V. O'Neill and W.F. Harris. 1975a. Principles of energy and material exchange in ecosystems. In W.H. van Dobben and R.H. Lowe-McConnell (ed.) *Unifying concepts in ecology*. Dr. W. Junk B.V. Publishers. The Hague. 302 pp.

Reichle, D.E., R.V. O'Neill, H.H. Shugart and W.F. Harris. 1974. Principles of energy and material exchange in ecosystems. In W.H. van Dobben and R.H. Lowe-McConnell (ed.) *Structure, functioning and management of ecosystems*. Centre for Agricultural Publishing and Documentation. The Hague.

- Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. *Ecology* 49: 471-483.
- Rosenzweig, M.L. and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50: 558-572.
- Roughgarden, J.R. 1974. Population dynamics in a spatially varying environment: how population size "tracks" spatial variation in carrying capacity. *Am. Nat.* 108: 649-664.
- Roughgarden, J.R. 1977. Patchiness in the spatial distribution of a population caused by stochastic fluctuations in resources. *Oikos* 29: 52-59.
- Russell, E.W. 1961. Soil conditions and plant growth. Longmans. London. 635 pp.
- Saito, T. 1956. Microbiological decomposition of beech litter. *Ecol. Rev.* 14(2): 141-147.
- Satchell, J.W. 1971. Feasibility study of an energy budget for Meathop Wood. In P. Duvigneaud (ed.) Productivity of forest ecosystems. UNESCO. Paris. 707 pp.
- Satchell, J.W. and D.G. Lowe. 1967. Selection of leaf litter by Lumbricus terrestris. In O. Graff and J.W. Satchell (ed.) Progress in soil biology. North Holland Publishing Co., Amsterdam. 656 pp.
- Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. In R.F. Johnston, P.W. Frank and C.D. Michener (ed.) Annu. rev. ecol. syst. 8. Annual Reviews, Inc. Palo Alto, Calif. 490 pp.
- Schnitzer, M. and S.V. Khan. 1972. Humic sunstances in the environment. Marcel Dekker Inc. New York. 327 pp.
- Shanks, R.E. and J.S. Olson. 1961. First-year breakdown of leaf litter in southern Appalachian forests. *Science* 134: 194-195.
- Simpson, G.G. 1964. Species density of North American recent mammals. *Syst. zool.* 13: 57-73.
- 57
L

- Slobodkin, L.B. 1962. Energy in animal ecology. In J.B. Cragg (ed.) Adv. ecol. res. 1. Academic Press. New York. 203 pp.
- Soulides, D.A. and F.E. Allison. 1961. Effect of drying and freezing soils on carbon dioxide production, available mineral nutrients, aggregation and bacterial populations. Soil Sci. 91: 291-298.
- Stevenson, I.J. 1956. Some observations on the microbial activity of remoistened air-dried soils. Plant Soil 8: 170-182.
- Suffling, R. and D.W. Smith. 1974. Litter decomposition studies using mesh bags: spillage inaccuracies and the effects of repeated drying. Can. J. Bot. 52(10): 2157-2163.
- Tamm, C.O. 1972. Plant nutrients as limiting factors in ecosystem dynamics. In D.E. Reichle, J.F. Franklin, D.W. Goodall (ed.) Productivity of world ecosystems. National Academy of Sciences. Washington. 163 pp.
- Thomas, W.A. 1970. Weight and calcium losses from decomposing tree leaves on land and in water. J. Appl. Ecol. 7: 237-241.
- Todd, R.L. and K. Cromack. 1972. Concentration of phosphorus, potassium, calcium and magnesium by mixed deciduous litter-inhabiting fungi and bacteria (Coweeta Research Site). Eastern Deciduous Forest Biome Report 72-8.
- Turfitt, G.E. 1944. Microbiological agencies in the degradation of steroids. J. Bacteriol. 47: 487-493.
- Van Schreven, D.A. 1967. The effect of intermittent drying and wetting of a calcareous soil on carbon and nitrogen mineralization. Plant Soil 26: 14-32.
- 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. J. Assoc. Off. Agric. Chem. 46: 829-835.
- Verona, O. and A.A. Lepidi. 1972. Decomposition of the outward waxing film of wheat straw by soil microorganisms. In J. Szegi (ed.) Proceedings of the symposium on soil microbiology. Akademiai Kiado. Budapest. 454 pp.
- Vitousek, P.M. and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25(6): 376-381.

- Waksman, S.A. 1922. The growth of fungi in the soil. *Soil Sci.* 14: 153-157.
- Wallwork, J.A. 1970. *Ecology of soil animals.* McGraw Hill. New York. 283 pp.
- Watson, E.S., D.C. McClurkin and M.B. Honeycutt. 1974. Fungal succession on loblolly pine and upland hardwood foliage and litter in North Mississippi. *Ecology* 55: 1128-1134.
- Weary, G.C. and H.G. Merriam. 1978. Litter decomposition in a Red Maple woodlot under natural conditions and under insecticide treatment. *Ecology* 59, in press.
- Webster, J. 1957. Succession of fungi on decaying cocksfoot culms. Part II. *J. Ecol.* 45: 1-30.
- Wegner, J.F. 1976. Corridors for birds and small mammals in hedgerows adjoining a beech-maple farm woodlot. M. Sc. thesis, Carleton University, Ottawa. 93 pp.
- Wiant, H.V. Jr. 1967. Influence of temperature on the rate of soil respiration. *J. For.* 65: 489-490.
- Wiegert, R.G. 1974. Litterbag studies of microarthropod populations in three South Carolina old fields. *Ecology* 55: 94-102.
- Wiegert, R.G., D.C. Coleman and E.P. Odum. 1970. Energetics of the litter-soil subsystem. In J. Phillipson (ed.) *Methods of study in soil ecology.* UNESCO. Paris. 303 pp.
- Wiens, J. 1974. Habitat heterogeneity and avian community structure in North American grasslands. *Amer. Midl. Nat.* 91(1): 195-213.
- Williams, S.T. and T.R.G. Gray. 1974. Decomposition of litter on the soil surface. In C.H. Dickinson and G.J.F. Pugh (ed.) *Biology of plant litter decomposition 2.* Academic Press. New York.
- Williams, S.T., D. Parkinson and N.A. Burges. 1965. An examination of the soil washing technique by its application to several soils. *Plant Soil* 22: 167-186.
- Witkamp, M. 1966. Decomposition of leaf litter in relation to environment, microflora and microbial respiration. *Ecology* 47: 194-201.

- Witkamp, M. 1969. Environmental effects on microbial turnover of some mineral elements. I. Abiotic factors. II. Biotic factors. *Soil Biol. Biochem.* 1: 167-184.
- Witkamp, M. 1971. Soils as components of ecosystems. In R.F. Johnston, P.W. Frank, C.D. Michener (ed.) *Annu. rev. ecol. syst.* 2. Annual Reviews, Inc. Palo Alto, Calif. 510 pp.
- Witkamp, M. 1971a. Forest soil microflora and mineral cycling. In P. DuVigneaud (ed.) *Productivity of forest ecosystems.* UNESCO. Paris. 707 pp.
- Witkamp, M. and J. van der Drift. ~1961. Breakdown of forest litter in relation to environmental factors. *Plant Soil* 15(4): 295-311.
- Witkamp, M. and J.S. Olson. 1963. Breakdown of confined and non-confined oak litter. *Oikos* 14: 138-147.
- Woodwell, G.M. and T.G. Marples. 1968. The influence of chronic gamma irradiation on production and decay of litter and humus in an oak-pine forest. *Ecology* 49: 456-465.
- Woodwell, G.M., R.H. Whittaker and R.A. Houghton. 1975. Nutrient concentrations in plants in the Brookhaven oak-pine forest. *Ecology* 56: 318-332.
- Yadav, A.S. and M.F. Madelin. 1968. The ecology of microfungi on decaying stems of Urtica dioica. *Trans. Br. Mycol. Soc.* 51: 249-259.

END

05 02 79

FIN