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LITTER DECOMPOSITION AND NUTRIENT RELEASE
• IN A RED MAPLE WOODLOT
UNDER NATURAL CONDITIONS AND
UNDER INSECTICIDE AND HERBICIDE TREATMENTS

by

GREGORY CHARLES WEARY, B.Sc. (Agr.), 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

June, 1974

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ABSTRACT

Litter production and decomposition were measured in a red maple woodlot, in the vicinity of Ottawa. The disappearance of organic matter was monitored during two concurrent but distinct experiments designed to: permit the comparison of two techniques; allow a double appraisal of decay rates in the same system; and to evaluate the effect of two biocides on the rate of litter decomposition.

In the first experiment the litter layer was intensively sampled to provide an accurate estimate of the litter standing crop and to evaluate the effect of the insecticide carbofuran on the rate of decomposition and nutrient release.

In the second experiment the "litter bag technique" was used to monitor the decay of litter confined in nylon mesh bags and to measure the influence of the herbicide mixture 2,4-D: 2,4,5-T on litter decomposition.

Comparison of the two methods revealed that confined litter decays more slowly than under natural conditions and that techniques using unconfined litter produce a more accurate measure of decomposition rate.

Results indicated that both chemicals had a significant effect on litter decomposition and the rate of accumulation of organic matter on the forest floor. The herbicide, by accelerating litter decay, decreased the rate of organic matter accumulation, while the insecticide had the opposite effect by reducing the rate of litter breakdown.

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I. INTRODUCTION

Herbivores and their predators which constitute the grazing chain, are not necessarily essential components of every ecosystem; the decomposer organisms however, which make up the detritus chain, are indispensable. Without the continuous decomposition and ultimate mineralization of dead organic matter it would accumulate and the consequent reduction in nutrient availability would cause the community to become less and less fertile. The limiting case is found in raised bogs where Sphagnum mosses, growing on the barely decomposed debris of previous generations, depend on meteorological input for the majority of their nutrient supply.

The decomposer community plays a vital role in forest ecosystems. In the process of breaking down dead organic matter the detritus food chain may handle over half the energy flow entering the ecosystem through primary production (Ovington, 1962; Macfadyen, 1963). It is during the release of this energy that plant nutrients are made available for recycling to the system as a whole. In addition, the incorporation of organic matter improves the physical characteristics of forest soil and plays an important role in soil chemistry.

In many natural ecosystems but particularly in forests, mineral supply depends on remineralization of chemical elements that are returned to the soil as organic debris (Witkamp, 1971). The importance of this process is most evident in wet tropical forest

ecosystems where the heavily weathered and leached soils contain a limited pool of available elements. Clearing such a system destroys the mineral cycle allowing the rapid leaching of nutrients from the soil. In addition, the rapid laterization of cleared tropical soils, with exposure to sun and oxygen, soon makes them unsuitable for agriculture or reforestation (Ehrlich and Ehrlich, 1972). In temperate forests, it is likely that the slower rates of mineralization, and thus rates at which nutrients are made available, may actually limit forest production especially on poorer soils (Witkamp, 1971). This hypothesis may be substantiated by occasional high rates of productivity on alluvial sites with high nutrient influx in temperate and cold climates (Witkamp, 1971). Efficient nutrient cycling in forest ecosystems, via decomposition accounts in part for their low net nutrient requirements as compared to agricultural crops. It is by virtue of this efficiency that forest ecosystems remain stable and maintain their productivity (Pomeroy, 1970).

Many factors causing disruption of nutrient cycles are the direct or indirect results of human action. Bormann et al. (1967) found that clear cutting of a forest ecosystem in New Hampshire resulted in accelerated loss of nutrients. The amount of nitrogen lost during the first year was equivalent to the amount turned over annually prior to cutting, and losses of cations were from 3 to 20 times greater than from comparable undisturbed systems. Nutrient pools may also be depleted by the leaching of minerals upon the destruction of nutrient cycling mechanisms by man-made biocides,

or by losses resulting from accelerated decomposition or fire (Witkamp, 1971).

The use of biocides as management tools is widespread in both agriculture and forestry. The quantity of these chemicals used each year is being increased in an effort to maintain or increase production (Ehrlich and Ehrlich, 1972). This trend is, in many cases part of a positive feedback loop in which the biocide removes any biological controls which may exist, allowing survivors of the pest species to multiply; thus requiring additional treatments, frequently heavier than the first. There is growing concern not only about the apparent inefficiencies of these management techniques but also about the possible long term side effects of such massive applications of toxic materials to natural systems.

Because insecticides are selected for their toxicity to arthropods, they pose a serious threat to the soil fauna. There have been many studies demonstrating the adverse effects of pesticide residues on non-target soil organisms. Edwards (1964) has found that twelve commonly used insecticides cause a reduction in the numbers of ten soil dwelling orders. Davis et al. (1969) using the same chemicals has obtained similar results with additional groups of soil organisms.

Workers agree that insecticides can have a variety of effects on the soil community. It appears that while microbial activity may be disturbed by very large doses of most insecticides, amounts of this magnitude are not likely to occur even as accumulations

from frequent field applications. Some authors have found that microbial activity has been stimulated by applications of D.D.T. and parathion (Eno, 1958; Bollen, 1961).

While the direct effects of most herbicides are well known, a potential hazard exists in that they too may influence non-target groups or subsystems which play a role in maintaining ecosystem stability. A major fraction of the herbicides used in forests may flow through the decomposer subsystem. Sprays penetrating the canopy, rain washing treated surfaces and abscission of treated foliage all contribute to the litter community. The significance of these inputs together with the importance of the decomposition process has stimulated numerous studies of the potential toxicity of herbicides to specific decomposer species (Newman, 1947; Whiteside and Alexander, 1960; Caseley and Eno, 1966; Bakalivánov, 1972).

Unfortunately results of most of the work on biocides can not be synthesized into a basis for the prediction of the effects of toxic chemicals at the system level. This is primarily because the effects of biocides have most often been measured in terms of changes in numbers of test organisms. It is difficult to extrapolate from this type of information to functional changes at the system level.

To predict changes in a system function such as the decomposition process, many parameters must be taken into consideration simultaneously. These include fluctuation in numbers of individuals, changes in species interactions, alteration of successional trends, and changes in species function. Questions involving the function

of a system component are probably best achieved by studying the function itself rather than the individuals making up the community.

This study was designed to measure the rate of litter decomposition and nutrient release in a red maple woodlot. In addition, it was to evaluate the impact of an insecticide and a herbicide on the function of the forest decomposer community.

The disappearance of organic matter was monitored during two concurrent but distinct experiments. In the first, a new method was used to provide a more accurate estimate of decay rate and to measure the effect of the insecticide carbofuran on litter breakdown and nutrient release. In the second experiment, the standard litter bag technique was used to evaluate the effect of the herbicide mixture 2,4-D:2,4,5-T, on decomposer function. These two experiments permit the comparison of two techniques, allow a double appraisal of decay rates in the same system, and provide relative measures of the effect of two biocides on system function, simultaneously.

II. THE STUDY AREA

A. Location and Geology

The study area is located in the Ottawa Greenbelt bordering the Mer Bleue (45° 24' N, 75° 34' W), and is part of the Central Research Forest managed by the Canadian Forestry Service Environment Canada.

The C.R.F. is located on the floor of the late Pleistocene Champlain Sea (Gadd, 1963). When the Champlain Sea occupied this area, soft silty marine clay, now termed leda clay, accumulated in layers up to 200 feet thick. As the sea withdrew, the waters ceased to be purely marine. The change in salinity was due to a sudden influx of fresh-water from glacial sources, or more likely, by the sudden release of large volumes of silt laden water from the Great Lakes region (Gadd, 1963).

During this period, large quantities of sand were carried into the sea, by rivers, fed from the melting ice sheet. Only later, as the sea began to fall, did the sand spread over the lowland to mantle the clay. The ancestral Ottawa River flowing across these sand plains rapidly cut numerous channels through the sand deposits exposing the buried clay. Eventually these channels were abandoned, leaving island-like plateaus or ridges each with a flat topped core of marine clay capped with abandoned fluvial deposits of stratified, non-fossiliferous, buff sands (Gadd, 1963). The study site is located on one of two such ridges straddled by the Central Research Forest.

B. Site Selection and Description

Preliminary site selection was made using aerial photographs, with the help of the forest manager. Each potential site was visited and judged as to its suitability for the study. The site chosen was a .34 ha (.91 acres) stand of red maple (Acer rubrum) with uniform age composition. It forms part of a continuous red maple woodlot which has developed its present cover during 40 years of secondary succession from abandoned pasture (Salm, 1974 personal communication). Experimental plots centered in the stand were buffered from foreign litter input and physical fluctuations not typical of the stand.

The woodlot slopes from South to North with a gradient of 1/250 and is relatively flat, with the exception of several shallow depressions, which become water filled in the spring and after heavy rains. Experimental plots were located in the driest areas between shallow furrows running the length of the stand (Fig. 1).

Two plots, A and B, each 4 m by 9 m were established for the measurement of decomposition rate (Fig. 1). In addition they were to serve as treatment and control respectively for the testing of the pesticide carbofuran. The two plots were separated by an eight foot wide buffer strip down the center of which ran a plastic barrier four feet high and extending six inches into the ground. The buffer strip and barrier together with careful application of the pesticide were intended to eliminate contamination of the control plot. The

Fig. 1. Diagram of the red maple woodlot illustrating plot locations.
Dimensions: Overall length, 80 m, total width between furrows 55 m.

barrier would also prevent the movement of litter fauna from treated to untreated areas. Both plots were oriented parallel to the slope of the land to ensure that neither surface runoff nor ground water flow could move pesticide into the control area.

Each plot was subdivided as shown in figure 2. Two catwalks extending the length of the plot divided it into 3 strips, each 1 m wide and 9 m long, these walks ensured the litter was not disturbed during sampling. Each strip was subdivided into 0.5 m squares (36 blocks), the plot thus contained 108 blocks of equal size. All blocks could be easily reached either from outside the plot or from one of the catwalks.

A third plot enclosed an area of 500 m², between two furrows on the eastern border of the study area (Fig. 1). This level, well drained area, isolated from other study plots was used for the litter bag experiment designed to measure the relative decomposition rate of herbicide treated litter.

1. Vegetation

To adequately describe the vegetation within the study area, trees, saplings and seedlings were counted, measured, and identified in the central 0.04 ha (1/10 acre) of the site. In addition, examples of all ground flora were collected and identified. Biomass was calculated from the regression given by Heller (1971) for the relationship of biomass to diameter at breast height and tree height.

Fig. 2. One of the two identical plots used to measure the decomposition rate of unconfined litter, and to determine the effect of the insecticide carbofuran.

LYSIMETER

THROUGHFALL TRAP

Table 1 illustrates that although numerous species of woody and herbaceous vegetation are to be found in the woodlot, red maple is the dominant and most significant in terms of above ground biomass and litter production. The dominance of red maple in the woodlot ensured a homogeneous distribution and quality of litter, thus minimizing variance in subsequent measurement of litter input and decomposition.

2. Soil Characteristics

The soil on which the woodlot has developed is classified by the Carleton County soil survey (1944) as Uplands Sand, an excessively drained acid sand low in organic matter (O.M.) and available plant nutrients. Soil cores from within the study site indicate that some differentiation has occurred in the soil profile, forming a mini humo-fernic podzol, soil type 4.32 in the Canadian system of soil classification. The profile type is L, E, H, Ae, Bf, C and includes all the diagnostic (underlined) horizons of group 4.32 (C.S.S.C.). Colorimetric examination of the Bf horizon using the Munsell color notation, measured a "reddish yellow" soil color (10 YR 3/2;3/3 moist) also consistent with this group. The Ae horizon is indistinct (salt and pepper). The Bf horizon contains less than 5% O.M., further confirming the classification. The podzol has developed under mixed forest vegetation on acid parent material which is well, to imperfectly drained. Other soil characteristics are summarized in table 2.

Table 1. A list of trees, shrubs and herbs found in the red maple woodlot and their relative importance in terms of biomass and litter production.

	SPECIES	NUMBER /.04HA (.1 ACRE)	ABOVE GROUND BIOMASS KG/.1 ACRE	PERCENT OF TOTAL LITTER PRODUCTION
Trees (> 8.4cm)	<u>Acer rubrum</u>	35	54,249.20 kg	— 94.5%
	<u>Populus tremuloides</u>	1	2,618.00 kg	
Saplings (2.5-8.4cm)	<u>Acer rubrum</u>	3	27.61 kg	5.5%
Seedlings (< 2.5cm)	<u>Acer rubrum</u>	11	.243 kg	
	<u>Fraxinus pennsylvanica</u>	1		
	<u>Populus tremuloides</u>	1		
	<u>Prunus virginiana</u>	11		
	<u>Prunus serotina</u>	1		
	<u>Ulmus americana</u>	15		
Herbs	<u>Achillea millefolium</u>			
	<u>Aster macrophyllus</u>			
	<u>Botrychium multifidum</u>			
	<u>Dryopteris disjuncta</u>			
	<u>Dryopteris spinulosa</u>			
	<u>Equisetum arvense</u>			
	<u>Lycopodium complanatum</u>			
	<u>Lycopus uniflorus</u>			
	<u>Maianthemum canadense</u>			
	<u>Medeola virginiana</u>			
	<u>Onoclea sensibilis</u>			
	<u>Osmunda clatonia</u>			
	<u>Osmunda regalis</u>			
	<u>Polygonatum pubescens</u>			
	<u>Pyrola elliptica</u>			
	<u>Rubus hispidus</u>			
	<u>Sedge</u>			
	<u>Viola incognita</u>			

(Taxonomic classification according to the new Britton and Brown illustrated flora of the North Eastern United States and adjacent Canada by H.A. Gleason Hafner publ. co. 1968.)

Table 2. Summary of the chemical and physical characteristics of the surface soil in the red maple woodlot.

<u>SOIL CHARACTERISTIC</u>	<u>H LAYER</u>	<u>Bf LAYER</u>
p H	4.2	4.5
Bulk Density	0.119 g/cc	1.05 g/cc
Field Capacity	-	16.3 H ₂ O
Ca	9.20 meq/100g	4.75 meq/100g
Mg	0.16 meq/100g	0.42 meq/100g
K	0.18 meq/100g	0.09 meq/100g
C.E.C.	14.45 meq/100g	4.5 meq/100g

C. Litter Input

Litter input was measured to determine the amount of nutrient entering the system and to establish the relationship which exists between the input and loss rates which govern the standing crop of litter on the forest floor. Litter traps suitable for the continuous collection of canopy debris were constructed according to the recommendations of Medwecka-Kornas (1970). The traps were cotton bags 1.0 m deep; each had a metal hoop in the rim to maintain a circular opening of 500 cm². The bags were supported 1.5 m above the forest floor; as they were freely permeable to water they drained and dried quickly. Twenty-two traps were placed at random through the study area giving a sampling density of 59 traps per ha.

The frequency of litter collection varied with the season. Traps were emptied every two weeks during spring and summer, but during the autumn period of heavy litter input, collections were made weekly. Weathering of debris in the traps was not desirable and collection was more frequent during times of high precipitation. Litter collected from each trap was dried at 80° C to constant weight, held in a desiccator and weighed. The total weight of all samples was used to calculate the litter input since the previous sampling.

The litter traps are designed to measure leaf litter originating in the canopy. They clearly can not sample litter input originating below 1.5 meters, nor are they suited for quantitative collection of debris larger than one half the trap diameter (Medwecka-Kornas, 1970).

Branch fall was measured monthly using four nets, each 2 m² in area, suspended 0.25 m above the forest floor. Branches only partially within the net were cut with a hand saw. The appropriate portion was returned to the laboratory dried and weighed.

The litter contribution of the understory and ground flora was measured separately using 22 randomly selected clip plots. Each of these plots covered 500 cm² of the forest floor and included all vegetation to the height of 1.5 m (the height of the litter traps). Prior to the onset of leaf fall, after the period of peak growth, all leaves on woody species, and all herbaceous ground cover within each of these plots was harvested, dried and weighed. A single estimate of spring production by short lived herbaceous perennials was made in 1974 and was assumed to be applicable to preceding years.

The temporal distribution of litter input is illustrated in figures 3 and 4. The monthly input of leaf litter monitored over three years is relatively consistent. The maximum occurs in either October or November; at least 75% of the annual litter is deposited during these two months. Litter fall is minimal during the month of August contributing only two percent of the annual input. The input of seeds and bud scales during spring and early summer, was measured in 1972 and 1973, this type of debris accounts for between five and eight percent of the total "leaf" input during the year. The average contribution of ground flora less than 1.5 m in height, is six percent of the total annual leaf litter input.

Fig. 3. Monthly litter input collected during 1971, 1972 and 1973, excluding stem, branch and bark (g/m^2).

☆ - Total input from all vegetation less than 1.5 m in height.

Branch input was sporadic, and is presented in figure 4 as yearly totals. The low value in 1971 results from the use of the small traps to measure twig input. This is a poor method, and to improve the estimate of branch fall, 2 m² nets were installed during the fall of 1971. The increase in the amount of wood deposited in 1973 over 1972 is primarily due to a larger than average input during the winter of 1972-1973. This input of nearly 600 g/m² was not closely associated with any measured climatic variable. Mean monthly wind velocities measured by the Forestry Service did not differ between the November to June periods for which branch fall was different. Precipitation differences however suggested that storms, freezing rain and associated maximum wind velocities may have contributed to the difference in branch fall. Weather data confirmed that during the periods in question thunderstorms and freezing rain had been more common in the spring of 1973 and may have caused the peak branch input. Data collected during three years suggest that the pattern of leaf litter input is relatively consistent temporally, qualitatively, and quantitatively. It is difficult however to determine the pattern of branch input which changed radically in temporal distribution as well as in quantity during the 2 years for which reliable data exist.

Fig. 4. Total stem branch and bark input during 1971, 1972 and 1973.

D. Microclimate

Temperature and humidity were both monitored in the litter layers of the study area. Relatively continuous temperature data were obtained over a two year period. Humidity measurements were taken sporadically during the summer of 1971.

A resistance bridge designed and built in the Carleton University Science Workshop, automatically monitored twelve Y.S.I. #44006 thermistors. The voltage output from the bridge was recorded by a Cole Parmer Mk VII potentiometric chart recorder, providing a permanent record of air, litter and soil temperatures at each of three stations.

Relative humidity within the litter layer was measured using an Atkins' thermistor psychrometer model 3Z02B. A plastic garden flat from which the bottom had been removed was permanently imbedded in the soil. A second flat inverted over the first and sealed with stopcock grease, effectively enclosed a volume of air which could be drawn into the Atkins' gun via a tube passing into the upper flat. Tables 3 and 4 summarize the temperature and humidity data obtained during the course of the study.

Table 3. Maximum, minimum and mean temperatures recorded for eight consecutive months in the red maple woodlot.

MONTH and YEAR	AIR TEMPERATURE 15 cm above Litter(shaded) [°C]		LITTER TEMPERATURE L layer [°C]		SOIL TEMPERATURE 2.5 cm below surface [°C]	
	Range	Average	Range	Average	Range	Average
7 - 71	23.5 11.5	16.9	21.0 12.5	17.0	19.0 12.5	16.7
9 - 71	21.5 5.0	12.8	16.5 9.0	12.2	14.5 10.5	12.0
10 - 71	11.0 6.0	8.3	10.5 8.5	9.1	10.0 9.0	9.2
11 - 71	0.0 -0.5	-0.25	3.0 0.25	1.7	4.0 1.5	2.8
12 - 71	7.0 -0.5	2.4	3.5 3.0	3.1	3.5 3.0	3.4
1 - 72	0.0 -20.0	-11.8	1.0 0.0	0.66	1.5 1.0	1.27
2 - 72	-3.0 -10.5	-6.1	1.0 0.5	0.611	1.0 0.5	0.833

Table 4. Relative humidity of the air (at 30 cm) and the surface litter in the red maple woodlot.

DATE	TIME	AIR (% R.H.)	LITTER (% R.H.)	REMARKS
26-7-71		72	83	
27-7-71	12am	75	94	
	6pm	55	80	
28-7-71	10am	70	85	
	12am	58	85	
29-7-71		95	97	Rained earlier in the day
30-7-71		89	94	
2-8-71		67	71	
3-8-71		88	86	Light rain falling
6-8-71	3:30pm	45	64	
	8:30pm	48	77	
10-8-71		89	91	Light rain falling
11-8-71		54	82	
12-8-71	9am	56	89	
	12am	64	82	
13-8-71	3pm	79	83	
	8pm	86	81	
17-8-71		62	74	
18-8-71		77	82	
20-8-71		97	95	Light rain falling
23-8-71		70	88	
24-8-71		71	81	
26-8-71		78	84	
28-8-71		100	94	Raining heavily
30-8-71		95	90	
31-8-71		64	85	
1-9-71	10:30am	81	89	
	12am	75	85	
3-9-71	12am	81	81	
4-9-71	5pm	83	79	Light rain falling
28-9-71		87	88	
14-10-71		94	94	Clearing after 3 days of rain.
15-10-71		94	97	
26-10-71		97	97	
1-11-71		61	87	
20-6-72		88	74	Warm and Humid
12-7-72		97	97	
13-7-72		86	86	
17-7-72		95	95	
18-7-72		78	78	Light rain falling
20-7-72		86	91	
21-7-72		83	80	

III. THE DECOMPOSITION OF UNCONFINED LITTER

This experiment had two goals: to monitor accurately the rate of litter decay under natural conditions in a red maple woodlot and to measure the effect of the pesticide carbofuran on the decomposition process and concurrent nutrient release.

There is no completely satisfactory technique for measuring the decomposition of litter. Estimates of decay rates obtained from litter bag studies are biased toward lower rates while teathered leaves overestimate the natural rate of breakdown due to losses of segments which have not decayed (Witkamp and Olson, 1963). An additional disadvantage of these techniques is that they are only applicable to fresh, initially undecomposed litter, they cannot be used to monitor changes in the litter layer as a whole. Numerous authors, however, have used both teathered and confined litter to provide information on the relative rates of litter breakdown under different experimental treatments (Woodwell and Marples, 1968).

Several studies have measured changes in the total amount of organic matter on the forest floor by periodically removing and weighing the litter from sample quadrats. (Wiegert and Evans, 1964; Zavitkovski and Newton, 1971). This technique is useful in long term studies with low density sampling. The replication required to monitor monthly changes in litter weights, and to increase precision sufficiently to distinguish between treatments over a relatively short term, would cause considerable habitat destruction and involve

a great deal of labour. It would also be impractical to maintain a consistent quality of sample by removing feces, invertebrates and soil aggregates from each of these relatively large quadrats.

In this study a new method was used to obtain accurate estimates of the litter standing crop and to compare decomposition rates under treated and natural conditions. The technique is to sample the litter layer intensively at frequent intervals using a small core sampler. This method overcomes most of the problems encountered with earlier techniques; it permits repeated high density sampling with little habitat disturbance; it allows free litter movement during decay, and at the same time provides material from the entire organic horizon.

A. Materials and Methods

1. Litter Sampling

To measure the in situ rate of decomposition, numerous litter samples were required to obtain a good estimate of the amount of litter on the forest floor. In addition these had to be removed with little disturbance of the habitat. Several authors have used small cylindrical cores to census populations of soil organisms. Capstick (1962) studied the suitability of these samplers for estimating the amount of litter on the forest floor. He found that as sampler size was increased from 1 cm² to 42 cm² the coefficient of variation of the estimates obtained was reduced by less than one

third. He found no significant difference between samplers of 1 cm^2 , and 2.63 cm^2 which are the only ones suitable for routine use when large numbers of samples are required. Capstick also demonstrated that estimates obtained using 1.0 cm^2 cores are well within the 95% confidence interval of traditional quadrat sampling techniques. He concludes that the use of corers with a cross-sectional area of 1.0 cm^2 has advantages in economy of material, speed of sampling and provides excellent estimates of the amount of litter on the forest floor.

Based on these recommendations a coring device and sample holder (Fig. 5) were designed to facilitate the removal and handling of the many litter samples taken each month. The corer was constructed of stainless steel rod, drilled and machined to cut a core of one square centimeter in area and 2.5 cm in length. A brass plunger within, limited the length of the core and functioned to expel the sample from the corer.

To obtain a sample, the corer was pushed through the litter layer with a twisting motion. As the core was cut and entered the tube, the plunger moved upward in the body of the corer. When withdrawn, the corer held the sample in the tube, moderate pressure on the plunger was sufficient to expel the core.

The sample holders, fabricated from a 2.5 cm thick block of plexiglass, were designed so the cores could be injected into them with the corer, and removed intact, for analysis. Each of the two sample holders had 108 holes drilled completely through its thickness,

Fig. 5. The coring device and sample holder used in the sampling of unconfined litter on the forest floor.

each hole corresponding to a sample location in the field. Each row of holes was provided with a common bottom of plexiglass held in place with screws. Similarly each row had a common top of aluminium sheeting which snapped in place. During a sampling run all bottom strips were screwed in place, as each row was filled the metal covers were snapped in place preventing further disturbance of the samples.

Litter sampling began in June 1972 immediately prior to pesticide treatment and occurred monthly thereafter with the exception of the winter months until November 1973. To ensure that the heterogeneity within each plot was adequately sampled each month, a single core was removed at random from each of the 108 plot subunits (Fig. 2). Two hundred and sixteen cores per month uniformly sampled the total area of plots A and B. The system worked very well in the field, litter and small roots were cut cleanly with little effort, and all 216 cores could be cut in less than four hours.

2. Litter Analysis

Samples brought in from the field were dried at 50°C for 48 hours to facilitate their removal from the sample holder. Cores were systematically transferred into sample cups by sliding the bottom strips from under each core in turn allowing it to fall into the sample cup.

Each core consisted of three visible layers, litter, humus and mineral soil. While the distinction between humus and mineral soil was made on the basis of color and texture, the separation of

litter and humus layers required meticulous hand sorting. The operational definition of litter for the purpose of this study was any recognizable leaf fragment regardless of species. In fact, however, the only litter items specifically discarded were twigs, roots and animal fragments. The litter layer was carefully separated from the humus with fine surgical forceps. Accurate sorting of each core required from five to ten minutes, for the complete removal of all litter, including particles as small as 0.5 mm in diameter. Humus, twigs, roots and animal litter were stored in sealed vials for future study.

The organic content of the herbaceous litter was determined by a rigidly controlled muffling technique described by Paine (1971) and Reiners and Reiners (1972). By carefully controlling the temperature and duration of combustion, losses of inorganic elements can be minimized (Paine, 1971). In the following pages it is assumed that weight loss on ignition (L.O.I.) under these conditions is approximately equal to total organic weight, and that the terms can be used synonymously.

Litter was processed in lots of 36 samples, each of which was dried to constant weight at 80°C and cooled in a metal desiccator. Individual samples were weighed into crucibles which had been cleaned in 36N chromic acid, heated at 500°C for four hours, and cooled in a desiccator. The samples were placed in a preheated oven, covered, ashed at 500°C for four hours. The oven temperatures were recalibrated with a Simpson meter and thermocouple after each use to

guarantee uniform ashing. The crucibles containing the ashed samples were cooled in desiccators and weighed. Weights of crucible, crucible plus sample, and crucible plus ash were recorded for each litter sample. A fortran program was written to calculate sample weight, ash weight, L.O.I. (= organic weight), percent ash and percent L.O.I. (= percent organic) for each sample.

3. Nutrient Sampling

The quantity of nutrient released from the litter by decomposition can be calculated if input and loss rates are known. The major input of nutrient ions to the litter layer, other than litter itself is by throughfall. Nutrients deposited on foliage by rainfall or dry fallout are carried downward by throughfall or may be absorbed by plants (Carlisle *et al.*, 1966). Nutrients may also be leached from the leaves by precipitation and deposited on the forest floor (Monk, 1971). Nutrient loss from the litter layer is predominately by the leaching of organic compounds (Nykvist, 1963) and inorganic elements (Attiwill, 1968) released by decomposition or deposited by throughfall.

In this study eight throughfall traps intercepted precipitation which had passed through the canopy, and sixteen lysimeters were used to collect leachate samples from beneath the organic horizons. Both types of sampler were based on the same design incorporating a 16 ounce mason jar. The lids of the jars were replaced with discs of 0.79 mm nylon mesh epoxied inside the

the sealing rings. Five cm sections of 6.9 cm i.d. plexiglass tube were machined with a rebate to fit over the sealing rings and were epoxied in place. All metal parts of the assembly were coated with epoxy to prevent contamination.

In each plot, 4 throughfall traps were mounted on wooden platforms for stability and distributed as shown in figure 2. The rim of the trap was 25 cm above the litter layer. The lysimeters were completed in the field, each received a 6.9 cm core of the litter and humus layer, which fit snugly into its plexiglass collar. The tight fit between core and lysimeter ensured that throughfall deposited on the 37 square centimeters of litter contained by the lysimeter would percolate through the core. The lysimeters, distributed as shown in figure 2 were buried with their rims flush with the litter layer.

Within 24 hours of each rainfall all throughfall traps and lysimeters were emptied. Each sampler was lifted from its location and the lid assembly unscrewed from its jar. In the case of the lysimeters, this procedure prevented the disturbance of the soil core. The throughfall or leachate sample was poured into a storage bottle, the jar was rinsed in distilled water and shaken dry. The sampler was reassembled and replaced in its location. Precipitation and leachate samples from successive collections were pooled by location, and stored in the dark at 4°C. During periods of light precipitation, monthly accumulation was frequently insufficient to provide the 100 ml required for complete analysis. Consequently samples were often pooled

over periods of several months. Each sample was analysed for Ca, Mg, and K, when sufficient volume had been collected. The total volume of water collected by each sampler was recorded to calculate the absolute amount of nutrient being deposited in or carried from the stand.

4. Nutrient Analysis

Analysis of all precipitation and leachate samples obtained in 1972 and 1973 was performed by the Canada Centre for Inland Waters, Burlington, Ontario. Calcium and magnesium were determined by atomic absorption on a Perkin Elmer model 403 spectrophotometer at wavelengths of 422.7 and 285.2 m μ respectively. Potassium concentrations were obtained in the emission mode at a wavelength of 766.5 m μ .

5. Pesticide Application

The pesticide was applied to plot A on June 6, 1972 soon after litter cores had been removed. A portable, compressed air sprayer was used to apply the chemical at the recommended rate of 278 cc in 370 litres of water per ha (24 oz/100 gal/acre). The entire plot and a 2.0 m strip of soil around it were sprayed with the pesticide. Extreme caution was taken to avoid contamination of the control plot; spraying was done in the early morning, the spray head was kept within 30 cm of the ground and delivered a coarse spray less subject to drift. Treatment was repeated according to directions.

one month after initial spraying and again in June 1973. Immediately prior to each treatment, the control plot was sprayed with an equal volume of water. Information concerning the chemicals used during the experiment is given in the Appendix.

B. Results.

1. Litter Decay Under Natural Conditions.

The rate of decomposition is described during three distinct intervals: summer 1972, winter 1972-73, and summer 1973. This is a valid approach biologically as it has been shown that decay rates change considerably and quite abruptly in the spring and fall (Witkamp, 1971; Smith and Douglas, 1971). In addition however, the distinction between the two summer periods and the intervening winter is required as weight data were obtained by different techniques for the winter and are not strictly comparable.

Figure 6 illustrates the change in the amount of organic matter in the litter layer during two summers and the intervening winter from June 2, 1972 to November 6, 1973. The weight of organic litter in grams per square meter is plotted against sampling date. Unless otherwise stated organic weights given in the following pages refer to ash free organic weights, as determined by weight loss on ignition (Paine, 1971; Reiners and Reiners, 1972). Each data point is the mean of 108 samples. The variation bars show one standard error of the mean.

Ordinary least squares regression analysis was used to determine the best linear model of the decomposition process during each of the three intervals studied. Slopes were tested using the F statistic ($F_{1,n-2}$) which demonstrated that decay rates during the summer periods differed significantly from zero ($p < .005$).

Fig. 6. The rate of litter decomposition under natural conditions during two summers and the intervening winter from June 2, 1972 to November 6, 1973.

At the beginning of the study, on June 2, 1972, the amount of organic litter on the floor of the woodlot was estimated at 599 ± 23 g/m² (Fig. 6a). Subsequent sampling at intervals of 33, 69 and 114 days indicated a progressive decrease in the amount of litter on the ground. Over the first three sampling intervals the weight of the litter layer decreased by 2.9 grams per square meter per day. The estimate of the amount of "old litter" remaining on November 6, 1972, is high. This apparent increase in the litter standing crop from September to November, 1972, is an artifact of the technique used, and is described below. While the accuracy of this data point is questionable it was included in the regression to calculate the minimum rate of decay for the first summer shown in figure 6a.

The decomposition rate of litter from the time of litter fall until May 2, 1973, is illustrated in figure 6b. Data available for this period is presented separately as it was obtained indirectly. The last core samples prior to the winter were removed on November 6, 1972, after litterfall was complete, the litter was next sampled May 2, 1973. It was hoped, that by careful sorting, recently fallen litter could be separated from old material, thus doubling the information available from each core and providing two data points for each sampling. In this way it would be possible to follow a cohort of 1972 litter into 1973, and simultaneously by adding new and old litter weights, monitor the decay of the total litter layer from

November 1972 onward. Each of the 216 cores taken in November and May were sorted as usual, in addition however, the litter was separated into two categories; recently fallen and old litter.

This subjective distinction was made with relative confidence in November as the litter categories were usually quite different in appearance and texture. New litter was light colored and flexible compared with the dark, brittle leaves which had spent a year on the ground. In the few instances where its age could not be determined with certainty the leaf material was classified as old litter. In May the distinction proved to be more difficult as the litter layer had become more uniform in quality and it was difficult to recognize recent litter with certainty.

These sorting difficulties, which in November classified doubtful cases as old litter, and which in May were clearly biased in favour of the "old" category, resulted in overestimates in the amount of old litter on the forest floor. For these reasons the possibility of following the old litter cohort from 1972 to 1973 was discounted, however the estimate of the amount of old litter on the forest floor prior to leaf fall, has been included in figure 6a.

To obtain estimates of the total amount of litter on the forest floor in November and May, the organic weights of old and new litter were summed (Fig. 6b). The rate of decomposition during the winter, from November 1972 until May 2, 1973, is insignificant. The slope of the regression line fitted to the data is 0.098 and coincides with the line joining the means shown in figure 6b.

During the second summer of the study, the litter layer was sampled June 1, July 11, August 1 and November 6, estimates of the total organic weight are plotted against sampling interval in figure 6c. The weight of organic litter on the forest floor June 1, 1973 was estimated to be $518 \pm 18 \text{ g/m}^2$ significantly less than the amount present a year earlier. The average rate of decay during the second summer was nearly $1.5 \text{ g/m}^2/\text{day}$ and did not differ significantly from the rate for the previous summer.

2. Comparison of Decay Rates Between Treated and Untreated Litter.

The decomposition rate of pesticide treated litter is illustrated in figure 7. As in the previous figures, the weight of litter in g/m^2 is plotted against time in days on the X axis.

During the summer of 1972 treatment with pesticide reduced the rate of litter breakdown from $2.2 \text{ g/m}^2/\text{day}$ to $1.3 \text{ g/m}^2/\text{day}$. The apparent difference in slope of the decay curves 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 individual treated and untreated core weights were plotted over time. The slope of the regression line passing through these points was found to be significantly greater than zero at the 95% level of confidence thus the slopes of the two lines are different and the

Fig. 7. The decomposition rate of insecticide treated litter during two summers and the intervening winter from June 2, 1972 to November 6, 1973. The insecticide was applied June 2, 1972 only.

A Y intercept

B slope

F variance ratio statistic

p probability level

lines are divergent.

During the winter period from November 6, 1972 to May 2, 1973, there is no measurable difference in the decomposition of treated and untreated litter. While neither regression coefficient was significantly different from zero they were of opposite sign. The hypothesis that their slopes were different was rejected at the 95% level of confidence (Draper and Smith, 1966).

From June 1, to November 6, 1973, the decay rates of treated and untreated litter averaged $0.99 \text{ g/m}^2/\text{day}$ and $1.48 \text{ g/m}^2/\text{day}$ respectively. These rates were not significantly different at the 95% level of confidence normally used, they were different however at the 90% level (Draper and Smith, 1966). This decrease in the degree of confidence with which the null hypothesis is rejected is, in part, due to an experimental error. In 1972 the plot was treated twice according to manufacturer's recommendations, in 1973 however, due to an oversight the plot was sprayed only once.

3. Nutrient Flux

Concentrations of calcium magnesium and potassium in throughfall and leachate were compared between treated and control plots. The average concentration of these elements, standard deviation of the data and "t" ratios of inter-plot differences are listed in table 5. The lack of any consistent, significant difference in the nutrient content of either throughfall or leachate between plots

Table 5. Concentration of calcium, magnesium and potassium in throughfall and leachate, in both treated and control plots. (Sample volumes collected in treated and control plots were approximately equal).

DATE	ELEMENT	LEACHATE					THROUGHFALL				
		TREATMENT		CONTROL		t STATISTIC	TREATMENT		CONTROL		t STATISTIC
		$\bar{x}$	s.d.	$\bar{x}$	s.d.		$\bar{x}$	s.d.	$\bar{x}$	s.d.	
1-6-72	Ca	8.30	1.38	8.10	1.20	0.34	0.29	0.96	2.40	0.41	1.06
	Mg	1.38	0.29	1.28	0.24	0.85	0.48	0.11	0.40	0.07	1.37
7-18-72	K	4.83	1.51	4.40	0.83	0.71	2.92	0.74	2.90	0.78	0.04
7-18-72	Ca	5.95	1.11	6.30	0.53	0.89	2.40	0.41	2.70	0.27	1.30
	Mg	0.92	0.18	1.01	0.12	1.31	0.42	0.08	0.40	0.07	0.40
8-18-72	K	6.82	2.67	3.97	0.93	3.17*	1.36	0.30	2.04	0.23	4.00*
8-18-72	Ca	6.35	1.27	8.39	0.91	4.10*	3.50	0.38	6.60	3.80	1.80
	Mg	1.37	0.30	1.75	0.31	2.70	0.58	0.11	0.59	0.05	0.73
10-25-72	K	6.37	3.17	2.77	1.56	3.21*	1.12	0.22	1.24	0.70	0.36
4-1-73	Ca	6.97	1.72	5.41	0.97	2.20	4.23	0.24	4.80	0.25	0.66
	Mg	1.52	0.23	1.10	0.16	4.10*	0.93	0.13	0.98	0.05	0.73
6-5-73	K	4.77	1.80	2.33	0.74	3.50*	2.65	0.77	2.75	0.68	0.19
6-5-73	Ca	5.06	1.82	4.50	1.79	0.62	1.87	0.25	2.12	0.25	1.40
	Mg	1.05	0.30	0.94	0.29	0.76	0.53	0.05	0.60	0.001	3.00
7-12-73	K	5.05	1.41	3.76	1.54	1.70	1.80	0.69	2.28	0.52	1.00
7-12-73	Ca	10.23	4.10	14.26	4.09	1.70	3.70	0.25	3.40	0.42	1.10
	Mg	2.20	0.89	2.80	0.78	1.27	0.72	0.09	0.65	0.06	1.30
11-14-73	K	8.13	2.50	6.00	2.10	1.80	1.35	0.58	1.10	0.22	0.72

* Significant at the 95% confidence level.

indicates the treatment had no consistent effect on nutrient flux through the litter layer with the possible exception of potassium.

Table 6 summarizes the data on the total flux of calcium, magnesium and potassium through the litter layers of the red maple stand. As no significant differences could be demonstrated between treated and control plots, only those results obtained in plot B, which describe the nutrient dynamics under natural conditions, have been presented. The data derived from concentrations in throughfall and leachates are expressed in kg/ha.

From the table, it is evident that the total weight of each element leached from the litter exceeds that deposited by throughfall. The net loss of these elements, directly attributed to the biological and physical decomposition of organic matter, is given in column 5.

The relative importance of throughfall and litter decay in recycling these three nutrients is also shown in the totals. In 1973 the input of these three elements from litter decomposition actually exceeded the amount recycled by throughfall. In 1972 the relative contribution of each was equal, with the exception of the potassium input from throughfall, which was greater. The totals for each also show that although these elements appear in different amounts for each process, they appear in the same order by weight. In each case more calcium appears than potassium, and more potassium than magnesium.

During the summers of 1972 and 1973, 25.5 cm and 32.2 cm of throughfall were intercepted in the stand. This amounts to only 42% and 43% respectively of the gross precipitation measured 2 km away

Table 6. Nutrient flux through the litter layer of a red maple stand.

DATE	NUTRIENT	WEIGHT IN LEACHATE Kg/ha	WEIGHT IN THROUGHFALL Kg/ha	WEIGHT RELEASED BY DECOMPOSITION Kg/ha
6-1-72	Ca	4.23	1.63	2.60
to	Mg	0.68	0.27	0.41
7-18-72	K	2.30	1.97	0.33
7-18-72	Ca	5.57	2.90	2.67
to	Mg	0.89	0.42	0.47
8-18-72	K	3.53	2.19	1.34
8-18-72	Ca	6.63	3.60	3.03
to	Mg	1.42	0.57	0.85
10-25-72	K	2.38	1.31	1.07
Total input	Ca	16.43	8.13	8.30
June-Nov.	Mg	2.99	1.26	1.73
1972	K	8.21	5.47	2.74
4-1-73	Ca	8.78	3.37	5.41
to	Mg	1.79	0.68	1.11
6-5-73	K	3.74	1.93	1.81
6-5-73	Ca	4.24	2.28	1.96
to	Mg	0.87	0.65	0.22
7-12-73	K	3.58	2.50	1.08
7-12-73	Ca	19.00	7.74	11.26
to	Mg	3.73	1.48	2.25
11-15-73	K	7.99	2.50	5.49
Total input	Ca	32.02	13.39	18.63
April-Nov.	Mg	6.39	2.81	3.58
1973	K	15.31	6.93	8.38

at the Central Research Forest weather station. The ratio of throughfall to gross precipitation is a variable dependent upon canopy density, storm intensity and stem characteristics. (Helvey and Patric, 1965). While typical ratios are in the order of 70 to 75%, (Helvey and Patric, 1965) Voigt (1960) reported a ratio of only 66% in a beech stand with a 100% canopy cover. Estimates obtained in my woodlot may consistently underestimate the volume of throughfall, however it is likely that the closed canopy and numerous smooth tree trunks actually reduce throughfall via interception and increased stemflow (Helvey and Patric, 1965).

The results of numerous authors who have studied the chemical constituents of throughfall are summarized in Table 7. Considering the duration of each study and the diversity of forest types investigated, throughfall measurements are reasonably consistent. The total amounts of potassium and magnesium deposited on the litter layer of the red maple stand are similar to those values reported in other temperate deciduous forests, a notable exception being an extremely high value for potassium measured by Eaton et al., (1973). The amount of calcium leached from the red maple canopy in throughfall is large relative to weights reported by Nihlgard, (1970) and Reiners, (1972) for beech and oak forests respectively. On the other hand, extrapolation of the value obtained by Eaton et al. in mixed forest including maple, indicates that large amounts of calcium may be lost from the canopy on an annual basis.

Table 7. The amount of calcium, magnesium and potassium contributed to the litter layer by throughfall as reported in the literature and as measured during this study. Values are in Kg/ha for the stated number of months only.

AUTHOR	FOREST TYPE	TIME [Months]	THROUGHFALL [cm]	Ca Kg/ha	Mg Kg/ha	K Kg/ha
Attiwill 1966	Eucalyptus	12	63	5.3	1.9	11.4
Nihlgard 1970	Beech	12	66	9.0	3.0	9.9
Reiners 1972	Oak	12	43*	7.5	3.0	-
Eaton <u>et al.</u> 1973	Beech, Birch Maple	5	45	6.7	2.0	30.0
Weary 1973	Red maple	8	32	13.4	2.8	6.9

* Estimated as 70% of reported gross precipitation.

The relatively high amounts of calcium reported in this study and by Eaton, Likens and Bormann (1973), may be due in part to the improved analytical techniques used. Likens et al., (1967) have demonstrated that the determination of calcium by atomic absorption may produce low values unless a lanthanum buffer is used to reduce interference by Al and SiO_2 . Without this buffer previous authors may have underestimated the amount of calcium in their samples.

C. Discussion

1. Decomposition Under Natural Conditions

a. Litter Decomposition Rates

As illustrated in figure 6a, the rate of decomposition during the first summer is $2.19 \text{ g/m}^2/\text{day}$. Expressed as a proportion of the amount of litter on the forest floor at the beginning of the interval, the rate of loss amounts to $0.36\%/\text{day}$. This rate of litter breakdown is considerably greater than rates measured in the laboratory, (Johnston, 1953; Ivarson, 1972 unpublished) it also exceeds estimates obtained in the numerous investigations using the litter bag technique to determine the rate of decomposition in the field (Bocock and Gilbert, 1957; Witkamp and Olson, 1963).

Johnston (1953) in a laboratory study, measured a 34% loss in the weight of oak leaves over 360 days. My results indicate that decomposition proceeds much more quickly when all the physical and biological factors which contribute to litter breakdown are allowed to operate. A 34% loss in weight occurs in only 93 days, one third the time required under laboratory conditions. It has been generally accepted that the elimination of large invertebrate decomposers drastically reduces the rate of decomposition (Cragg, 1968; Witkamp, 1971). Edwards and Heath (1963) found that without the larger invertebrates the rate of litter breakdown dropped three fold. The absence of invertebrate decomposers is undoubtedly an important factor contributing to the low decay rate measured in Johnston's

study. It is doubtful if even the most elaborate laboratory facilities can simulate the conditions required to maintain the diversity of decomposer organisms found in the field. For this reason, laboratory studies are prone to produce under-estimates of decay rate under the best of conditions.

The use of litter bags has been a common method of monitoring decay rate in the field. With this technique, Witkamp and Olson (1963) measured the half life of red maple litter as 357 days. Based on my results, obtained by periodically sampling the litter layer, the half life for soft maple litter is 137 days, only 38% that of his bagged litter. Witkamp and Olson (1963) have compared decomposition rates of confined and unconfined deciduous litter. They found that tethered leaves decayed 2 to 3 times as fast as bagged litter. The half life for tethered red maple was found to be 127 days, very close to my estimate for red maple. These authors conclude that both techniques provide biased estimates of the rate of decomposition. While the litter bags tend to under-estimate the rate, due to exclusion of some organisms and the moderation of physical disturbances, the tethering technique may produce an over-estimate due to the loss of fragments which remain undecomposed. They add, however, that the rapid decay rates calculated on the basis of tethered leaves cannot be interpreted simply as over-estimates of true breakdown rates because the consumption and decay of detached fragments continues. In fact, decay of small fragments may proceed even more rapidly as they sift down through the litter and eventually

come in contact with humus or mineral soil (Saito, 1956; Witkamp and van der Drift, 1961).

Confirmation of their observations is found in my results. While periodic sampling of the litter layer indicated a decomposition rate of 0.36%/day, a litter bag experiment carried out simultaneously revealed a rate of 0.15%/day. These rates are in the same ratio as Witkamp and Olson (1963) found to exist between confined and unconfined litter, and indicate that confined litter does decay more slowly than under natural conditions. Most important, however, is the fact that while the teathering technique may be suspected of producing an overestimate, the coring method is not so biased. It is likely, therefore, that techniques using unconfined litter produce the most accurate measures of decay rate.

During the winter, decomposition proceeds very slowly and there is no measurable change in the amount of litter on the floor of the stand (Fig. 6b). This is due in part, to the relatively low temperatures measured in the litter layer over the period. Between November 1971 and March 1972, litter temperatures ranged from -0.5°C to $+4^{\circ}\text{C}$, far below ideal for active decomposition (Smith and Douglas, 1971) and too cold to permit extensive leaching of the litter. While these findings are in apparent contrast with results obtained by some workers who suggest that decay does proceed during the winter, the difference lies in the varying limits that have been placed on the "winter" period. Most authors follow changes in the amount of organic matter by sampling at regular intervals; in so doing they

often include periods of relatively high decomposer activity at the beginning and end of their "winter" period. Bleak (1970) studying the disappearance of plant material under a winter snow cover has reported losses of 29 to 51% for certain grasses. Because his sample period ran from October to the following June, he concedes that this loss "takes place during the late fall, winter or early spring". As observed by Kucera (1959) and Nykvist (1959) the leaching of water soluble compounds can result in a weight loss of up to 33% in some litter. Bleak (1970) observed that most of the snow cover melted during a relatively short period in April and May, he feels that while insects do not seem to be an important factor in litter disappearance under the snow, water from melted snow may leach large quantities of soluble material. It is probable then, that much of his reported weight losses did not occur during the winter but during the spring. Further confirmation of low decomposition rates during the winter period was found by Smith and Douglas (1971). They report that organic matter placed in the soil when temperatures have dropped below 4°C, and retrieved before the soil warms in the spring, loses very little weight through decomposition.

The winter period in the present study began in November and terminated in May. Cores were taken after the first snow had fallen and again before it had melted in May. Litter temperatures averaged less than 4°C during the interval and there had been no opportunity for leaching due to the lack of free water. It is not surprising, therefore, that there was no measurable amount of decomposition over the interval.

b. Standing Crop Estimates

The standing crop of litter in a forest ecosystem is a complex system parameter influenced by a spectrum of physical and biological variables. Differences in species, diversity, successional status, macro- and microclimate all influence rates of production and decomposition and, consequently, the standing crop of litter. It is difficult to make meaningful comparisons of litter standing crops reported in the literature as they have been measured at different times of the year and under a wide range of conditions. Table 8 shows the variation which is typical of these estimates, and suggests that values for the standing crop of red maple litter obtained in this study are well within the possible range. The estimates of standing crop even in temperate forests may vary by an order of magnitude. Maldague (1968) measured a very large accumulation of 2012 g/m² in a mor sugar maple stand while Zavitkovski and Newton (1971) estimated the total accumulation in an alder thicket to be 190 g/m² at equilibrium. There does, however, seem to be a measure of central tendency with all other estimates in the range of 575 ±175 g/m². The similarity between my estimates and those obtained by Maldague in a maple moder is particularly interesting considering the proximity of the study sites, the similarity of climate and the independence of the two estimates. Monthly estimates of the amount of litter on the forest floor are given in table 9.

As observed in Results the rate of litter breakdown during the second summer is not significantly different from that measured

Table 8. The standing crop of litter in a variety of forest types as reported in the literature, and as measured in this study.

AUTHOR	LOCATION	SPECIES	STANDING CROP Annual Range g/m ²
Bocock and Gilbert 1957	England	Birch Lime Oak	400
Greenland and Kowal, 1960	Ghana	Numerous	221
Van der Drift 1963	Netherlands	Mixed Hardwood	600 - 280
Madge 1965	Nigeria	Numerous	1700 - 245
Maldaque 1968	Quebec	Maple mul Maple moder Maple mor	460 682 2012
Woods and Gallegos 1970	Panama	Numerous	902 - 447 1000 - 547
Zavitkovski and Newton 1971	Oregon	Alder	190
Weary 1973	Ontario	Red Maple	706 - 275

Table 9. Standing crop of litter on the floor of the red maple woodlot prior to ignition. (in g/m²)

<u>YEAR</u>	<u>DATE</u>	<u>PLOT A (treated)</u>	<u>PLOT B (control)</u>
1972	June 2	574	706
	July 5	504	608
	August 10	507	568
	September 24	421	304
	November 6 (old litter)	295	348
	November 6 (total litter)	538	568
1973	May 2	549	592
	June 1	528	616
	July 11	457	336
	August 1	370	348
	November 6 (old litter)	333	275

during the first. However, the standing crop of litter measured in June 1973 was estimated to be 80 g/m^2 less than the amount available the year before, a significant change at the 95% level of confidence. Due to the similarity of decay rates during the two periods, this relationship is maintained over the second summer, and the standing crop is smaller than at any corresponding time during the summer of 1972. This does not contradict the theories of Jenny et al. (1949) which postulate an increasing accumulation of organic matter on the forest floor until an equilibrium is reached at the climax, nor does it refute the data of Zavitzkovski and Newton (1971) who have actually documented this accumulation over 50 years in alder stands of increasing age. Van der Drift (1963) in a six year study of decomposition rate has recorded fluctuations in the standing crop of litter. In a histogram of annual litter standing crops designed to illustrate decay rates, van der Drift has indirectly demonstrated a gradual increase in the total amount of litter accumulated on the forest floor in spite of periodic declines.

2. Decomposition of Treated Litter

Carbofuran is the approved common name of 2,3-dihydro - 2,2-dimethyl - 7-benzofuranyl methylcarbamate, one of a class of pesticides known as N-methyl carbamates. Harris (1973) in an evaluation of materials used as soil insecticides found that carbofuran had the broadest spectrum of activity of any insecticide

tested. He has also shown that its biological activity persists for up to 16 weeks (Harris, 1969). Both he and Landis (1965) agree that the half life of the chemical is similar to other moderately persistent insecticides, approximately eight weeks.

Carbofuran is a reversible cholinesterase inhibitor which causes systemic toxic effects when inhaled or ingested (Niagara, 1970). Evidently carbofuran has little influence on microbial activity. Harnish and Wendler (1972) found that concentrations of up to 1000 ppm did not substantially affect the number or types of microorganisms isolated from the soil nor was there any effect on soil respiration. Metcalf (1971) working in small model ecosystems concluded that carbofuran is readily biodegradable and that ecological magnification does not occur. These conclusions must be interpreted cautiously considering reports by other authors which suggest that carbofuran does have a considerable impact on invertebrate populations. Despite a claim by Niagara (1970) that "carbofuran is one of the least toxic compounds to earthworms" Thompson (1971) found that it drastically reduced numbers and biomass of earthworms in the field. Dondale (1971, 1972) found that carbofuran reduced the numbers of phytophagous insects by 71%, their natural enemies by 56%, and the decomposer fauna by 58%. While most groups recovered rapidly, the decomposers had recovered by only 45% in 3 months. His specific recommendation that the decomposer fauna receive further investigation has not been followed in subsequent studies, and has not been discussed even in the most comprehensive study of the impact of carbofuran on the

environment (Niagara, 1972).

Considering the information concerning the biological activity of carbofuran, it is not surprising that the decay rate of treated litter is reduced. The increase in decay rate associated with the application of some pesticides is due to the elimination of a predator and the subsequent multiplication of the prey. Edwards and Heath (1963) found that an increased decay rate resulted from the application of D.D.T. to litter. They attributed this to an increase in the numbers of springtails. This phenomenon is less likely to occur with a broad spectrum pesticide such as carbofuran as it is toxic to the majority of the soil fauna including mites and collembola.

The reduction in the decomposition rate observed during the first summer after treatment is almost certainly due to the reduction in numbers or activity of more than one decomposer species. During the study the presence of numerous decomposer groups was noted, in addition to bacterial and fungal decomposers; collembola, acarina, lepidoptera, coleoptera, myriapoda and annelida were abundant. While there certainly are other decomposers contributing to the decay process, these are the most significant in terms of litter disappearance due to their role in the initial fragmentation of litter. All of these groups have been shown to be susceptible to carbofuran and may have been affected by the treatment (Dondale, 1971; Thompson, 1971; Johansen and Baird, 1972; Harris, 1973). It would be of considerable interest to see which groups were most influenced by the

treatment. However, to approach the problem on both a functional and taxonomic level would require a considerable effort and should be the subject of a co-operative study.

The rate of litter decay is an important factor governing the rate of accumulation of organic matter on the forest floor. All else being constant, a reduction in the rate of decomposition should be reflected by an increase in the standing crop of organic matter. Such an increase is evident when one compares litter accumulation in treated and control plots. As discussed previously, the measured rate of ~~litter~~ decay under natural conditions was greater than litter input during the study. The standing crop of litter available in June and November 1973 was significantly less than that present at the same time the previous year. While under the natural regime there was a measured reduction in the accumulation of ~~organic~~ matter, estimates of litter standing crop in the insecticide treated plot increased over the same period. Although there was no significant change from June 1972 to June 1973, there was a net increase by November 1973.

These changes which were coincident with the application of the pesticide cannot be judged as beneficial or deleterious in themselves on the basis of a two year study. The alteration of decomposition rates and standing crops measured during this study may appear to be of minor importance. Over the long term, however, a sustained increase in the rate of litter accumulation will result in decreased nutrient cycling and an unusually rapid accumulation of

organic matter in the litter layer. The long term effects of these changes on system structure and function are not easily predictable, and will be discussed later.

IV. THE DECOMPOSITION OF CONFINED LITTER

This experiment was designed to provide data on the natural rate of decomposition which would be comparable with information available in the literature, it was also intended to evaluate the effect of the herbicide 2,4-D:2,4,5-T on the function of the decomposer community in a red maple woodlot. A litter bag technique was used to measure decay rates of treated and untreated litter. Dry weighed leaves were placed in nylon mesh bags on the forest floor, half were treated with the herbicide and the remainder served as a control. Weight loss was measured periodically as an index to decomposition rate.

Although Witkamp and Olson (1963) have demonstrated that this technique is biased towards underestimates of the true rate of decomposition, the method has been used successfully in numerous studies to provide relative estimates of decay rate and to evaluate the effect of specific treatments on the litter community (Edwards and Heath, 1963; Woodwell and Marples, 1968). In addition to permitting evaluation of the impact of the herbicide on litter decomposition the litter bag technique provides base data on decay rates which are comparable with existing data. Furthermore as a standard technique it provides a basis of comparison for decay rates measured by the coring technique previously described.

A. Materials and Methods

1. Sample Preparation

The apparent simplicity of the litter bag technique as described in the literature had suggested that it would be ideal to measure relative rates of decomposition. Preliminary work however revealed several additional procedures required to ensure conclusive results. A review of the literature indicated that selection of mesh size is a critical factor in this technique. Edwards and Heath (1963) compared enclosures of various mesh sizes. They found that as mesh was decreased from 7.0 to 1.0 mm the rate of litter decomposition dropped three fold. They concluded that the rate differences were due to the exclusion of the larger invertebrates. Crossley and Hoglund (1962) concur and have used 1.0 mm mesh bags in a study of microarthropods which required the exclusion of larger invertebrates.

To determine the maximum size of invertebrate decomposers in the experimental area, 50 pit traps were placed in two transects across the site. In addition to this, over 50 m² of forest floor were searched with the goal of collecting any decomposer organisms large enough to be excluded from a mesh bag yet not sampled by pit trapping. The largest organisms obtained were earthworms, millipedes, beetle larvae, fly larvae and snails. Each of these in turn was placed under a 5.0 mm mesh bag containing maple litter. Without exception the organisms were able to penetrate the mesh and enter

the bag. The results of our field trials and the literature survey suggested that a 5.0 mm nylon mesh was suitable for the experiment.

To ensure detectability of results the initial amount of litter per sample had to be sufficient so that losses would be measurable assuming a minimum rate of decomposition. The literature reports a wide variety of decomposition rates, depending on temperature, humidity, latitude, altitude, and species (Jenny, Gessel and Bingham, 1949; Shanks and Olson, 1961; Witkamp and van der Drift, 1961; Wiegert and Evans, 1964). With some subjective interpretation of their results, the minimum rate of decomposition was estimated to be 3% per month. The greater the initial amount of litter the more easily one can detect a three percent change in weight. Given that it was desirable to keep the amount of litter per unit area "normal", bag size would have to be appropriate to enclose sufficient litter so that a three percent change in weight would be detectable.

The amount of litter on the forest floor was determined using the coring technique described earlier. Two hundred small cores, 1 cm² in area were taken within the study site, the litter layer was removed and weighed. The amount of litter was estimated to be 523 ± 53 g/m² assuming the minimum rate of decomposition, monthly loss would be nearly 1.5 g/ft², (16.3 g/m²) an easily detectable weight change. The size of the mesh bags to be used was thus fixed at one square foot (.093 m²). One hundred and thirty bags were made from 5.0-mm mesh nylon minnow netting. Each bag was

sewn with nylon thread, labelled with a metal tag and finally weighed.

On May 8, 1972 several bushels of maple leaf litter were gathered from the study site, only the most recently deposited litter was collected. The litter was returned to the laboratory and air dried at 20°C and 20% RH. until constant weight was attained. The mild drying conditions were used to minimize qualitative changes in the litter. The dry litter was hand sorted and only entire, unfragmented maple leaves were selected for use. Approximately 50 grams of the dry leaves were carefully placed in each of the 130 weighed nylon mesh bags, which were then sewn closed with nylon fishing line. Completed bags were held under drying conditions until all were ready. Immediately prior to placing the bags in the field, final total weights were taken and the actual weight of the litter was calculated.

As weight loss was to be the major index of decomposition, losses due to fragmentation were reduced. Mesh bags filled with whole leaves were transported in plastic bags to retain fragments which would escape during handling. The weight of these fragments was deducted from the actual weight of litter placed in the field.

2. Herbicide Application

It was important that the bags which were to be treated with herbicide were dosed equally and accurately. To ensure this they were laid out in an area remote from the study plot. A

previously calibrated, compressed air sprayer was used to deliver the appropriate dose of 13.5 pints/acre (2.6 l/ha). The control bags were similarly sprayed with water (see Appendix).

Before a bagged sample was placed on the forest floor all litter was removed from the square foot that was to receive it. This procedure solved two problems; primarily it was intended to facilitate retrieval of fragments dropping from the bag during the experiment. More important however was the fact that in this way the amount of litter subject to decomposition was kept at a normal level, not doubled as it would be if bags were placed on top of existing litter.

On the 8th of June 1972, treated and control bags were paired and distributed through the plot. Sample locations were chosen at random on a 20 x 25 meter grid laid over the plot. Treated and control bags were placed adjacent to each other but separated by a metal barrier to prevent contamination of the control bag.

In the fall of 1972 the experiment was duplicated using 30 bags filled with fresh litter. The goal of this run was to measure the rate of decomposition of leaf litter over winter, prior to the time when herbicide treatment is usually applied.

3. Sample Analysis

At monthly intervals a predetermined number of bags was removed from the study plot. Before being moved, each bag was cleaned of litter which had fallen on it since it had been placed in the field. It was then carefully lifted by one corner to expose the many small roots which had invaded the litter, these were cut to free the bag from the soil.

The mesh bag was returned to the laboratory in a plastic bag and dried to constant weight at 20°C and 20% relative humidity. Each litter sample was hand sorted to remove any material which had entered during the experiment. Seeds, twigs, roots, invertebrates, feces and mineral soil aggregates were separated from leaf material. A flotation technique was devised to separate organic and inorganic components less than 2.0mm in diameter, a fraction which became more important as decomposition progressed. After hand sorting, the remaining mixture of soil, feces and litter fragments was dusted over a water-filled tray to which several drops of soap had been added to reduce surface tension. While the soil and feces sank to the bottom the litter floated and was poured off into a filter funnel to which suction was applied. The litter collected was washed, dried and added to the main litter sample which was then redried to constant weight. The weight lost by each sample was calculated as a percent of its original weight to correct for the effect of unequal starting weight.

B. Results

The results indicate that the treatment of forest litter with the herbicide mixture, temporarily stimulates the decomposition process, and reduces the standing crop of organic matter on the forest floor. In figure 8, cumulative percent weight loss is plotted against duration of exposure. Each data point represents the mean weight of 5 litter bags. The variation bars show one standard error of the mean.

As in the previous experiment, ordinary least squares regression analysis was used to determine the best linear model of the decomposition process during each of three phenologically distinct intervals; summer I; (days 0-158), winter; (days 158-348), and summer II (days 348-528). The F statistic tested the significance of the slope in the linear regression models.

The calculated rates of litter decomposition for treated and untreated litter, during the first summer, were 0.30 and 0.26 %/day respectively. These decay rates were significantly different from zero at the 95% level of confidence. The apparent difference in the slopes of the curves indicates that treated litter disappears more rapidly than untreated litter. The significance of this difference was tested using the regression technique described earlier (Draper and Smith, 1966). This test demonstrated that the decomposition rates were different ($p < .005$). Comparison of the individual slopes, reveals that the herbicide treatment increases the rate of litter breakdown by 15% during the first five months after

Fig. 8. The influence of herbicide on the rate of litter decomposition measured during two summers and the intervening winter of 1972-1973.

spraying.

Decay rate over the winter period was calculated on the basis of samples obtained November 15, 1972 and May 11, 1973. Figure 8 shows that during the winter period from day 158 to day 348 there was a reduction in the rate of decomposition for both treated and untreated litter. The ordinary least squares method was used to fit regression lines to the winter data. From the slope of the fitted lines, decay rates of 0.016 and 0.0047 were calculated for treated and control samples respectively, neither rate was significantly different from zero. When similarly tested the individual rates of decomposition did not differ at the five percent level of significance. During this period the decomposition of treated litter closely parallels the natural rate of litter breakdown. Similar results were obtained in the preceeding experiment.

During the second summer after treatment, from day 348 to day 528, an increase in the decay rate of all samples was evident (Fig. 8). The calculated decomposition rates of 0.089 and 0.087 %/da for treatment and control, were both significant at the 95% level of confidence. The rates, however, were not different from each other ($p > .05$), indicating that the decay rates of treated and untreated litter are similar, one year after treatment.

Figure 9 illustrates the results of the parallel experiment designed to measure the rate of weight loss from immediately after leaf fall until early June when the herbicide is applied. Cumulative percent weight loss is plotted against duration of exposure. The

Fig. 9. The average rate of decomposition of confined red maple litter during the first seven months after abscission. The solid line does not imply that interpolation will accurately describe the decay process during this interval (see figure 10).

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slope of the least squares regression line is 0.157 and differs significantly from zero ($p < .005$). This experiment indicates that untreated litter decomposes at an average rate of 0.157% per day during the first seven months after leaf fall. A more accurate description of the decay process during this period is given in the following discussion.

C. Discussion

1. The Decomposition of Confined Litter

From the litter bag data a composite model of the decay process was prepared (Fig. 10). The model describes the decomposition of 100 grams of litter during 752 days from the time it is deposited on the forest floor as litter. The quantity of litter lost from an initial 100 grams at abscission, is plotted against exposure time. The amount remaining (the standing crop) at any time x , can be calculated from the equation, $R_x = 100 - Y_x$. The bottom, solid line is a linear approximation of the process under natural conditions. The broken line represents a hypothetical decay curve during the first winter, and the upper, solid line illustrates the influence of the herbicide treatment on the decomposition process.

The autumn litter input decays rapidly during its first 7 months on the forest floor, at an average rate of 0.157 g/day and has lost 35 g by June of the subsequent year (day 224).

Few authors have followed litter decay during the first autumn and winter after abscission. However there is evidence to suggest that rates are initially high, but decline during the winter months. Substantial quantities of water soluble organic and mineral substances are leached from the litter soon after it falls, prior to the onset of winter (Bocock et al., 1960; Gilbert and Bocock, 1960). At the same time the rapid utilization of sugars, starches and pectins by resident microbial populations removes the majority

Fig. 10. A model of the decomposition process; describing the decay of 100 grams of litter, during two years from the time it is deposited on the forest floor.

of these substances within a short period further increasing weight loss (Burgess, 1967). Kucera (1959) has determined that the removal of all water soluble components from leaf litter would result in a weight loss of from 33 to 46 percent for hard maple and american elm respectively. Earlier work by Nykvist (1963) demonstrated that in only three days, the loss of water soluble organic compounds by leaching amounted to ten percent of the initial weight of litter.

While data collected at the beginning and end of the initial winter period can only produce an average rate of decay over the interval, more frequent sampling (prohibited by ice layers over the bags) would have provided a more accurate picture of the actual process. The broken line is a hypothetical curve of weight loss during the first winter. Although it is speculative it is consistent with information available in the literature.

As modelled in figure 10, during the first summer the litter spends on the ground (day 224 to 382) it loses 41% of the amount available in the spring, (day 224) losing a total of 61.65 g during the first year (382 days) after leaf fall. It is during this period that the herbicide has the effect of increasing decomposition rate. The significance of this influence is discussed later.

By the beginning of the second winter the remaining litter has changed qualitatively, having lost the majority of the sugars present and from sixty to eighty percent of the sodium and potassium it originally contained (Attiwill, 1968). The resistant residue decays very little, 0.0047 percent per day, and by May, (day 572)

has only lost an additional 0.57 grams for a total loss of 62.12 grams. The winter decay rate, and all other rates discussed here are regression statistics as explained under Results. The regression coefficient, or slope, of the decay process during the second winter is not significantly different from zero. Thus there was in fact no measurable decay over winter.

During the second and final summer of the study the decomposition rate averaged 0.087 percent per day over 180 days. The loss amounted to 10.14 grams for the season, and totaled 72.26 grams after two year's decay. It is interesting to note that the rate of decomposition over the second summer is approximately one third that maintained during the first. This difference was not related to a microclimatic change between the two periods. It is undoubtedly due to the qualitative change in the litter after it has spent one full year on the forest floor.

Van Cleve (unpublished) has found that fresh aspen and birch litter is high in carbohydrate, lipid and starch but relatively low in lignin content. Partially decomposed litter however, is low in the first three but relatively high in lignin. Witkamp and van der Drift (1961), Cromack (1973) and Van Cleve (unpublished) stress that decomposition rates are negatively correlated with lignin concentration. It follows that as lignin content increases during decomposition, the rate of litter breakdown will decrease.

As shown in figure 10, under natural conditions red maple litter loses 35%, 61% and 72% of its initial weight after 6, 12 and 24 months respectively.

The literature reports a wide variety of decomposition rates varying with the species of litter, (Shanks and Olson, 1961) the soil type, (van der Drift, 1963) latitude, (Jenny, Gessel and Bingham, 1949) altitude, (Shanks and Olson, 1961) and environmental factors (Witkamp and van der Drift, 1961). Bocock (1964) one of the few authors to measure loss rates from the time of litter fall, found that Fraxinus excelsior lost 90% of its initial weight in a single year. Shanks and Olson (1961) on the other hand, report that sugar maple loses only 35% of its weight in the same period of time.

Two studies are of particular interest in that they have measured rates similar to those presented here for red maple. Bocock and Gilbert (1957) report that C.K. Capstick and D.C. Twinn (unpublished) have used a direct measure of litter loss to estimate decay rate. They found that during the seven month interval, December 1955 to June 1956, Quercus petraea litter lost 38% of its initial weight. In the second study, Witkamp and Olson (1963) found that bagged red maple leaves initially decomposed at a rate of 0.194 percent per day.

2. The Influence of the Herbicide on Decomposition Rate

The increase in decomposition rate subsequent to the application of the herbicide mixture may be due to both direct and indirect effects of the chemical on decomposer populations. Both 2,4-D and 2,4,5-T are chlorinated phenoxy acids and as such exert a direct influence on plants via their hormone-like activity in growth

regulation (Audus, 1963; Ashton and Crafts, 1973).

The chlorophenoxy herbicides, differ in their persistence and toxicity. Their mode of action, however, is similar in that they have profound effects on growth and structure, influencing almost every biological activity of a plant. The biochemical mechanism by which the chlorophenoxy compounds affect plants has proven to be very elusive. Their main action seems to involve a complex series of reactions initiated by derepression of the gene regulating synthesis of the enzyme RNase (Ashton and Crafts, 1973). The resultant synthesis of RNA and protein is accompanied by massive cell proliferation giving rise to tumorous tissues, excessive production of buds and root initials, softening of root cortex and general disintegration. Where concentrations are not sufficient to cause direct mortality, crushing and plugging of vascular tissues may result in slower death from lack of nutrients.

The majority of workers have been concerned with the possible negative influence of herbicides on non-target species. In a review of the effect of herbicides on soil micro-organisms, Fletcher (1960) finds general agreement that at the rates used in agricultural practice 2,4-D and 2,4,5-T have no adverse effect on the total number of micro-organisms in the soil; Anderson and Baker (1950) reported that 2,4-D enhanced the growth of fungi in the soil. Similar stimulatory effects have been observed for 2,4,5-T on soil fungi (Roberts and Bollen, 1955; Newman and Downing, 1958). In ~~these~~ amounts 2,4-D stimulates the same broadleaved plants it kills in

higher concentrations (Ashton and Crafts, 1973). Bakalivanov (1972) reports that 2,4-D stimulates the vegetative development of five widespread fungi including three species of Aspergillus and one of Penicillium.

Thus although the impact of herbicides on the function of an intact litter community has never been documented, it seems clear that these chlorinated phenoxy acids may enhance the growth and reproduction of many types of decomposer organisms. This would account, at least in part, for the increased rate of litter breakdown observed during the course of this study.

The increased decomposition rate of herbicide treated litter may result from an additional but indirect effect of the chemical. In a multispecies system it has been shown that unilateral elimination of a predator which usually performs a regulatory function in the system may permit the prey populations to expand rapidly (Paine, 1966). Alternatively, a reduction in the effectiveness of a competitor can have a similar effect (Hardin, 1960; Paine, 1966).

Most authors agree, that at the rates of application normally used, there is little likelihood that serious changes in soil animal populations will result from the use of 2,4-D and 2,4,5-T (Rapoport and Cangioli, 1963; Fox, 1964; Edwards, 1970). There is evidence, however, that herbicides do release certain species from their predators allowing them to flourish. Ilin (1961) suggests that the increase in bacterial numbers he observed in herbicide treated soils results from the decreased abundance of

protozoa. Adams (1960) and Adams and Drew (1965) demonstrated that the application of 2,4-D increased aphid infestations as a result of depressing the activities of coccinellid beetle predators. Other authors have shown 2,4-D to increase reproduction rates of certain soil nematodes (Webster, 1967) and to increase aphid fecundity (Maxwell and Harwood, 1960). Clearly the mechanisms exist by which the herbicide could increase the rate of litter decomposition, either by direct stimulation of a wide range of decomposer groups, or indirectly via the elimination of regulatory mechanisms such as predation or competition.

In this study the herbicide exerted a significant influence on the rate of litter breakdown only during the five months subsequent to its application. By November of the first year, rate differences between treated and untreated litter were insignificant at the five percent level. This return to a normal rate of decomposition is almost certainly due to the gradual degradation of the herbicide by soil organisms and by abiotic processes involving the transformation of herbicides by humic and fulvic acids in the soil (Stevenson, 1972a, 1972b).

While the rate of herbicide degradation varies with its formulation and the type of litter it is applied to (Norris and Greiner, 1967), Sheets and Harris (1965) have reported persistence times of one month for 2,4-D and up to three months for 2,4,5-T. The fact that the herbicide influences decomposition rates over a five month period suggests that the mixture may be more persistent

in our soils or that the decomposer community requires approximately two months to re-establish an equilibrium.

While the herbicide seems to have only a short term influence on decay rate the effect of accelerated decomposition is evident over a longer period. Figure 10 illustrates that the standing crop has been reduced by the treatment and remains low for the duration of the experiment. Under natural conditions where the annual litter input is added to the standing crop this difference would not remain constant as in figure 10, but would gradually be reduced over a number of years beginning with the first litter input subsequent to herbicide treatment.

V. GENERAL DISCUSSION AND CONCLUSIONS

Olson (1963) and others have proposed models which predict the time required for the standing crop of organic matter to return to steady-state once that state has been disturbed. All such models assume climax systems with constant annual litter increments and constant decay rates. Because of these assumptions the models are not applicable to an early successional forest. However, they can help to establish the significance of changes in decay rates and litter standing crops.

The general model formulated by Jenny, Gessel and Bingham (1949) depicts the oscillation in the amount of organic matter on the forest floor as the accumulation eventually returns to the steady-state (Fig. 11). The inset depicts the annual pattern of increase. Litter input A , which is assumed to be constant from year to year, increases the amount of litter on the forest floor from F_x to f_x . During the interval Δt , which is usually one year, a specific fraction of f_x is decomposed. This fraction, the decomposition constant, k' , is assumed to apply throughout the life of the forest. F_{x1} is the amount of organic matter remaining in the litter layer prior to the next litter fall. At equilibrium, input equals loss, ($A = k'f_x$). It is from this equation that k' is calculated initially, A and f_x being measured in a climax forest at equilibrium.

The model is inadequate to describe the accumulation of litter in subclimax seral stages for two reasons; primarily because

Fig. 11. Gradually rising exponential curve for litter accumulation in an idealized deciduous ecosystem (Olson, 1963).

Fig. 12. Field to forest succession in the Eastern United States (Woodwell and Whittaker, 1968). Some oscillations in the climax are assumed.

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the annual production of litter is not constant, but increases yearly, and secondly, due to the fact that with seral changes in species dominance, decay rates cannot remain static. Since litter input is related to the quantity of photosynthetic machinery in the ecosystem, it is likely that the fundamental shape of the accumulation curve changes as succession proceeds, and is similar to the curve of increasing standing crop given by Woodwell and Whittaker (1968) (Fig. 12). Early in succession, the increasing biomass will produce larger litter inputs annually. This, combined with the probable low diversity of decomposer organisms would accelerate the accumulation of organic matter on the forest floor. As net production, (the slope of the curve in Fig. 12) approaches zero in the climax stage, litter accumulation would be reduced, and the standing crop would stabilize as predicted in Olson's model. The shape of this accumulation curve is controlled by changing rates of both litter input and decomposition. It is possible that different systems may exhibit different patterns of organic matter accumulation as succession proceeds.

Weary (1971) proposed a model based on the calculations of Jenny et al. (1949), and Olson (1963) to simulate the sigmoid accumulation of organic litter through succession. The model is always sigmoid in form, but the shape can be controlled by varying three separate functions which determine rate of change in the lag, log, and stationary phases of litter accumulation. In the simplest form of the model, litter fall (A) and decay rate (k') are dynamic input variables which change through succession. The calculation of

litter production and decomposition each include an independently chosen random variable. A low litter production combined with a high rate of decomposition produces a net loss of organic matter from the litter layer. The opposite relationship between input and decay results in a net litter accumulation. This randomization, although it reduces the short term predictability of the accumulation process, does not influence the long term trend of gradual accumulation, despite occasional net decreases in the standing crop of organic matter. It does however, better describe the actual build-up of organic matter on the forest floor, by allowing for some fluctuation in the total amount of litter, as documented by van der Drift (1963). Earlier models have assumed predictable annual increments to the litter layer and a steady accumulation at a predetermined rate.

Models of this type are of limited use in predicting the long term effects of changes in system function, because of a lack of data on the functions themselves. They are, however, useful as guides when considering the effects of various impacts on forest systems. In terms of these two litter accumulation models, it is unlikely that the red maple stand has achieved a steady-state. While an increase in litter standing crop was evident only in the pesticide treated plot, it is certain that there is an overall accumulation if branch input is included; the contribution of branchfall to the total organic accumulation was from one to two times that of leaf litter. This, together with the slower decay rate of woody material (McFee

and Stone, 1966; Gosz et al., 1973) indicates that organic matter is accumulating in the stand.

As succession proceeds, the quality and species composition of the litter in the woodlot will change. Although these changes are not easily measured over a short period in a forest ecosystem, an increase in diversity of dominant species is evident in older, neighbouring woodlots. The large input of maple branches and stemwood in my stand may indicate a similar trend toward co-dominance with one or more other species. The concurrent changes in the production and quality of litter, microtopography and microclimate during succession, will alter the relationship between litter input and decay until at some stage they are equal and accumulation stops.

Minor perturbations of this steady-state only temporarily alter the standing crop of organic matter on the forest floor; resulting in oscillation around a mean value as illustrated in figure 12. The steady-state value of litter accumulation may be permanently displaced to either higher or lower levels by major physical and successional changes. For example, if the maple stand began to dry, the species dominance would change and decay rate could increase. This would result in a lower standing crop of organic matter in the litter layer as is evident in nearby beech-maple stands. On the other hand, a trend toward a wetter site would undoubtedly cause a further accumulation of undecomposed litter by reducing the opportunity for aerobic decomposition.

The sigmoid model has demonstrated that if the rate of loss exceeds the rate of input during a single year, the steady-state is re-established over a number of seasons. It is evident that small, discrete decreases in the accumulated standing crop, such as result from the application of herbicide, are more quickly made up during the early stages of succession than near the climax where rate of accumulation is slower.

If the litter layer of the forest floor in a climax temperate forest is stripped of all organic debris, Jenny et al. (1949) estimate that it will take from 25 to 50 years to return to a steady-state. By comparison, the 10% decrease in the standing crop of litter due to the herbicide treatment in the red maple stand is small. Assuming there is no sustained increase in the decomposition rate as would result from a second herbicide treatment, an increase of 10% in a single leaf fall, (or of 3% in the total leaf and branch input), would balance the deficit completely in one season. Increases of this magnitude occurred in both 1972 and 1973.

The present trend in the woodlot is toward increased accumulation of the total amount of organic matter in the litter layer, despite the decline in the standing crop of leaf litter measured from 1972 to 1973. Thus, while the increase in the amount of litter in the insecticide treated plots is significant relative to the loss suffered under natural conditions, it is not abnormal in terms of the overall pattern of litter and nutrient accumulation in the red maple stand. The effect, however, would be more important

and serious in a climax stage when an equilibrium in the organic and mineral pool has been achieved. Excessive accumulation at the climax could deprive the plant community of essential nutrients. The impact would be particularly serious if accumulation continued over an extended period due to repeated applications of the insecticide.

This study is the first to have used intensive sampling of unrestrained litter to evaluate the impact of experimental treatments on the function of an intact decomposer community. Results indicate that the technique overcomes the problems associated with other methods and is capable of providing the precise estimates of litter standing crop which are required to distinguish small but significant weight changes over short periods of time.

The experiment has demonstrated that it is possible to obtain a direct measure of the effectiveness of the decomposer system, a major parameter of a vital ecological process. This has proven to be a powerful tool in determining the effect of two toxic chemicals on ecosystem function, an effect not subject to measurement using the conventional species or component approach.

Specifically, in addition to describing the naturally occurring rates of litter input and decomposition, this study has demonstrated that the herbicide mixture 2,4-D : 2,4,5-T, and the insecticide carbofuran, have significant effects on the decomposition process in a red maple woodlot. The herbicide, by accelerating litter decomposition, decreases the rate of organic matter accumulation, while the insecticide has the opposite effect by reducing the rate of

litter breakdown.

The results of this study illustrate that ecosystems integrate the variable and often insignificant effects of toxic materials, (as measured at the species level) to produce measurable changes in community function. The possibility that minor changes in ecosystem function may also be integrated and magnified by biological systems, deserves serious consideration and further study. Future studies must approach environmental problems from a functional viewpoint which attempts to answer questions involving system function at the ecosystem level of organization. This approach is vital if we are to obtain sound data on ecosystem function and truly long term solutions to the complex environmental problems confronting us today.

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VII. APPENDIX A

Table 1. Information concerning the chemicals used during this study.

	INSECTICIDE	HERBICIDE
Supplier	Niagara Chemical Co. Burlington, Ontario	Niagara Chemical Co. Burlington, Ontario
Common Name	Furadan	Brushkiller
Active Ingredient	Carbofuran	2,4-D and 2,4,5-T in a 2:1 ratio
Chemical Name	2,3-dihydro-2,2- dimethyl-7-benzofuranyl -N-methyl carbamate	(2,4-dichlorophenoxy) acetic acid (2,4,5-trichlorophenoxy) acetic acid
Composition as Supplied	Carbofuran 44% Clay 4% Water 20% Suspending Agent 30% Emulsifier 1% Wetting Agent 1%	2,4-D 56% 2,4,5-T 27% Varsol 13% Emulsifier 4%
Dose per Acre	24 fl. oz. Furadan .72 lb. Carbofuran in 100 gallons of water	270 fl. oz. Brushkiller 6.7 lb. 2,4-D and 3.3 lb. 2,4,5-T in 150 gallons of water

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