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# ABSTRACT

# ARTHROPODS ASSOCIATED WITH BREAKDOWN OF CORN (ZEA MAYS) RESIDUES IN THE FIELD

By

Rosa Somera Quiachon

A preliminary field survey was made of animal populations associated with decomposing surface litter from a previous corn crop (*Zea mays*). Three collections from each of 12 sampling sites were made at 2-month intervals from May to September. No crop or growing vegetation was present at the sites sampled. Two types of litter had been deposited at each site and were sampled separately: 1) corn cobs and 2) corn stalks and leaves. The soil (0-5 cm) under each litter type was also sampled. Animals were extracted with heat (Berlese extraction). Dry matter changes in litter and changes in carbon and nitrogen in litter and soil were followed. Changes in mineral nutrients were followed in soil. Air, litter, and soil temperatures and soil moisture were recorded at the time of sampling and related to area weather records.

Animal populations encountered were similar to those reported for grasslands and for mull-type forest litter associations. Acarina and Collembola together comprised 90 to 97 percent of total arthropod numbers. The biomass represented by these two mesofaunal groups, however, would have been very much less than that of the dominant macroarthropods: Diptera, Coleoptera, Chilopoda and Araneida. Other arthropods present in substantial numbers only in certain samples included Psocoptera (May and July), Hemiptera (September), Hymenoptera (sporadic). A very few diplopods were found in May, mainly in cob litter. Isopods, present in both litters in May, were found only in soil under stalks in July and September.

A few earthworms (Annelida) were found in litter in May but not again until September when a few were recovered from soil.

All major meso- and macro-arthropod groups were already well established in both litter and soil in May. A much smaller proportion of the total Acarina populations was found in the soil at this time than in the case of Coleoptera, Diptera and Collembola. Acarina may have been deterred from moving into the soil by high moisture (in excess of field capacity) or by low temperature (10-12°C).

In later samplings, there was a marked shift in numbers of all major groups from litter to soil. The shift was greater at stalk sites than at cob sites. Several factors appeared to have influenced the observed patterns of increased residence in soil: 1) litter-soil temperature gradients, 2) differences in physical properties of the litter such that stalks and leaves lost moisture more rapidly after wetting than the cobs, and 3) differences in available energy content of organic materials translocated from litter into soil.

With regard to the last factor, dry matter in the litter layer disappeared more rapidly from cobs than from stalks and leaves (60% *vs*. 35% loss during the study period).

Due to the more rapid substrate utilization, it appeared that less available energy remained residually in September at cob sites than at stalk sites. Total site numbers (litter plus soil) were higher at cob sites in May but substantially lower than at stalk sites in September. A higher C/N ratio in the stalk litter was consistent

with the view that it was at a less advanced stage of decomposition, hence higher in residual energy content than the cobs.

Evidence that qualitative and quantitative changes occurred in available substrates and/or food chain structures during the study period was provided by a near linear replacement over time of Collembola by Acarina in the mesofaunal component of arthropod populations in both litters and in the soils underneath. This change was accompanied by release of basic cations and increasing pH.

The implications of these observations for critical research in relation to minimum tillage or no-till management systems are discussed. In the absence of tillage, animal activities may control the distribution of recycled nutrients and profoundly influence the rooting behavior and nutritional requirements of crops.

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TO MY P

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# INTRODUCTION

The soil in its natural state is not only a complex mixture of mineral matter and decaying organic substances, but is also the home of myriads of living moeities of various sizes and forms. Plant residue reaching the soil under natural field conditions undergoes decomposition involving many complex processes. During the decay process the litter loses weight, energy and minerals primarily through activities of the litter-soil biota.

Much research has been directed toward assessing the relative importance of soil fauna vs. the microflora in residue decay. It is becoming increasingly evident that soil animals play numerous important roles in the degradation of plant litter. Their contributions in specific situations may be of paramount importance.

Fragmentation of plant tissues by soil animals increases the surface exposed to leaching and to colonization by microflora. Physical changes associated with ingestion and defecation expose cellular contents and structure to attack by microbial populations in the gut and in the external environment.

Enzymatic alteration of certain substrates and the mixing of diverse substrates and nutrients during gut passage favors microbial utilization. These effects and the moisture retentiveness of feces favors their colonization by the soil microflora.

Soil animals also effect alterations in soil physical properties. Their burrows contribute to pore volume and to continuity of pore systems for gas exchange and water movement. Their traffic between litter and soil leads to translocation of litter fragments and fecal pellets into the mineral matrix where further decomposition and humification produces structure-stabilizing deposits of organic matter (humus). Soil animals are therefore active agents in the formation and the stabilization of friable soil structure.

Much of the data bearing on microflora-fauna interactions has come from non-agricultural habitats and microcosm experiments. Conventional tillage destroys the stratification characteristic of natural litter-soil associations and disrupts living spaces and traffic channels in the mineral matrix. Excessive mechanical tillage leads to progressive deterioration of soil structure. Where residues of the previous crop are left on the surface of the soil, there is an approach to natural litter systems in which the role of soil animals in development and stabilization of favorable soil structure may be an important factor in crop performance. There is current rapid trend toward "no till" management practices in many areas of the country. In many situations, success of these practices requires control of insect pests with chemicals. Since beneficial animals may also be reduced in numbers, it becomes important to identify them and evaluate their beneficial roles.

The objective of the present study was to effect a preliminary gross characterization of animal populations and seasonal successions associated with surface litter from corn (*Zea mays*). Two different types of litter were considered (corn cobs, and corn stalks and leaves), since these present a different array of substrates and physical properties which might influence their selection and colonization by different animals. Changes in C/N ratio of litter and soil and in available nutrients in soil were followed. Relationships to seasonal changes in temperature and moisture were observed.

# REVIEW OF LITERATURE

Early in the development of biology as a science, the heterotrophic microflora were recognized as principal agents in the chemical breakdown of organic matter. More recent studies of the fauna in soils and litter has not changed this basic concept. However, these studies have revealed important, frequently essential, direct and indirect effects of the fauna on the rate of breakdown, the nature and distribution of products, and on the environment in which these changes occur.

Chemical and physical effects of the larger invertebrates were recognized early and have been studied extensively. At the other end of the scale, the protozoa and their activities as secondary consumers have been subjects for investigation since the early days of microbiology. It is only within comparatively recent times that critical studies have been directed to soil and litter animals of intermediate size: the mesofauna.

It has long been recognized, in general terms, that soil and litter animals are integral links in the overall cycling of energy and nutrients, that important activities include comminution of litter and translocation of organic and mineral materials, and that synergistic interactions occur between fauna and flora in decomposer food chains.

Recently, functional studies have been initiated to quantify the ecological impact of soil invertebrates living in the organic horizons at or near the soil surface. The invertebrates that have been studied most frequently in this context include acarine mites, collembola, nematodes, annelid and enchytraeid worms, millepedes, centipedes and insects, mainly dipterous flies, beetles, and their larvae.

## Role of Soil Arthropods in Decomposition of Litter

The fertility of soils beneath the fresh litter depends on the rate and nature of the decomposition of plant residue. Studies of the primary decomposition of fresh plant litter in the field offer evidence of the importance of animal activity in this process.

Kurcheva (1962) used naphthalene to prevent the participation of invertebrates in the decomposition

processes in an oak forest litter. Naphthalene drives away animals but does not inhibit bacterial and fungal activity. Under these conditions oak litter lost only 9% of its original weight in 140 days whereas untreated litter lost 55% in the same time. Crossley and Witkamp (1964) found that 55% by weight of oak leaf litter was retained after 1 year in plots treated with naphthalene, whereas untreated control plots retained only 40%.

Edwards and Heath (1963) exposed litter contained in nylon bags of different mesh sizes to various sections of the fauna and to microorganisms alone. Litter disappeared three times faster from bags to which earthworms had access than from bags from which they were excluded. When animals were completely excluded for nine months, no visual breakdown occurred.

Heath _et al_. (1966) found that allowing earthworms to feed on them considerably accelerated rates of disappearance of "tough" leaves such as beech and oak, whereas animal activity did not affect the rate of disappearance of "soft" leaves such as kale, beet and lettuce. Curry (1969b) made a study of the role of soil animals in the decay and the disappearance of grassland herbage confined in nylon bags of different mesh sizes in the soil and on the soil surface. The size of the animals admitted was controlled by mesh size. Animal activity contributed little to the rate of decay and disappearance of grassland herbage on the soil surface and did not accelerate decay of herbage in the soil.

The rate at which soil arthropods consume litter depends on many factors. It is believed that the suitability of litter for saprophages depends on the chemical composition (nitrogen content, C:N ratio, Ca content, presence of flavored and tannic substances), mechanical properties and moisture content of the litter (Dunger, 1958). Wallwork (1958) noticed that factors affecting food preferences are particle size, stage in chemical decay of food, and moisture content.

Handley (1961) suggested that phenolic compounds precipitate protein complexes, rendering the residual leaf proteins resistant to decomposition and forming a protective layer on the cellulose of the cell walls. Heath and Arnold (1966) suggested also that the food preferences of soil fauna probably depend on the palatability of leaf material rather than its digestability. The unpalatability of leaf material rich in polyphenols may be because of its astringence. On the other hand, sugars or readily hydrolyzed carbohydrates likely enhance palatability. Edwards and Heath (1963) and Satchell and Lowe (1969) suggest that fresh leaf litter remains unpalatable to soil fauna until polyphenols become leached out. King and Heath (1967) showed that the amount of polyphenol found was inversely proportional to the rate at which leaves disappeared, and that "hard" leaves had more polyphenolic substances than "soft" ones.

The rate at which soil invertebrates consume litter depends also on the temperature and the amount of moisture in the litter (van der Drift, 1951; Gere, 1956). Seasonal variations are observed in the activity of soil arthropods. Crossley and Hoglund (1962) found a good correlation between the number of microarthropods in litter bags and the rate of litter disappearance. They also found that the number of arthropods depended on the moisture content of the litter. Edwards and Heath (1963) observed that, after heavy rain, leaf discs disappeared more rapidly than in dry periods. Van der Drift (1962) suggested that moisture was more important than temperature in litter decay.

## Changes in the Chemical Composition of the Litter Due to Animal Activities

In evaluating the role of soil invertebrates in the decomposition of litter, important factors include, not only the amount of litter eaten by the animals, but also the qualitative changes in the chemical composition of the litter due to their activities. Two general mechanisms must be distinguished in assessing the effects of soil arthropods on chemical properties of plant litter. First is change directly dependent on the animals' metabolism and second is indirect participation of invertebrates through their action on microflora, where the role of the animal is more like the action of a catalyzer (MacFadyen, 1961).

According to recent data, direct participation by invertebrates in the decomposition of plant litter is on a very small scale. From approximate estimates of MacFadyen (1961), of the total calories contained in dead plant remains entering the soil in a temperate zone pasture, 85 percent was freed by microbial activities and only 15 percent by the activities of soil animals. Feeding experiments with larvae on forest oak litter showed that 93 percent of the consumed food was defecated and only 7 percent was assimilated (van der Drift, 1970).

The change in chemical composition of litter that passes through the alimentary canal of animals has been investigated. Several workers have found that feces immediately after excretion differ little in chemical composition from the litter eaten (Dunger, 1963; Bocock, 1963). On the other hand, van der Drift (1970) reported that the non-cellulosic decomposable carbohydrate content of oak litter was reduced significantly in the excrement.

While comminution and incorporation of organic matter into the mineral soil is an important contribution of the soil mesofauna, this is perhaps secondary to their effect on the decomposer microflora. McBrayer and Reichle (1971) showed that approximately 60 percent of the total biomass of the soil fauna was contained in the fungivore trophic level. At an average feeding rate of 7.1 percent dry wt day$^{-1}$, this trophic level would remove by grazing nearly 24 mg fungus m$^{-2}$ day$^{-1}$. Additional quantities of microflora would be ingested by surface-feeding saprophages. Burges (1967) reported that maximal faunal activity occurred immediately following fungal blooms in litter. Engelmann

(1961) suggested that grazing by Oribatei stimulated the microfloral population as a whole and thus promoted decomposition.

The indirect action of soil dwelling animals on the process of decomposition is well illustrated by data of Anstett (1951). He found that, when worms were removed after having been in the test boxes for a long time, the rate of decomposition of grape vines was still much higher than in the control boxes where the worms had never been. Microbial analysis showed that the population density of microflora in the test boxes was five times as high as in the controls. Obviously, earthworm activities had greatly increased the availability of energy and otherwise altered the nutritional environment in ways which stimulated activities of the microflora. Reyes and Tiedje (1973) found a more rapid and extensive mineralization of $^{14}C$-labeled yeast by an animal-microbial system than when either was acting independently.

Investigations by several authors have shown that the number of microorganisms is much higher in animal excrement than in the soil (van der Drift et al., 1960; Ghilarov, 1963). It is not clear where the increase in reproduction of the microorganisms takes place, whether in the alimentary canal of the animals or in their excrement, which does afford a favorable environment for the development of microflora (Day, 1950).

Atlavinyte (1971) suggested that arrival of fecal material from both arthropods and earthworms in the more favorable moisture conditions in deeper strata, the opening of cell contents, and a usual rise of litter pH during gut passage induce rapid microbial growth, particularly by bacteria. Van der Drift (1970) found the pH changed from 4.3 in oak leaves to 6.7 in the fecal pellets of larva. Stebaev (1968) suggested that feces could be enriched with vitamins promoting the growth of other organisms. Rangaswarmi (1966) reported that proteins in the form of enzymes associated with the excrements provide favorable nutrients to enhance microbial growth. When feeding on forest litter and other plant litter, invertebrates break it up finely and mix it with soil, and so create conditions for more intensive microbial activity. The action of microarthropods is particularly effective in that respect. According to several estimates (Sukachev and Dylis, 1964), oribatids, when feeding on pine needles, increased the surface area of the ingested material to approximately 10,000 times the original figure.

The soil is inhabited by a multitude of animals that feed on microorganisms, but they are also capable of beneficial action on the activity of microflora. When invertebrates are introduced into a soil culture, widespread senile deterioration of fungi and bacteria (due, it is believed, to the presence of antibiotics in the soil) is arrested (Witkamp, 1960). It is proposed that animals that eat microbes are able to intensify the activity of microflora, i.e. to accelerate energy transfer by breaking up the compactness of colonies of bacteria and fungi (MacFadyen, 1961).

In addition, soil animals aid in the distribution of microorganisms. Experiments with four species of fungi have shown (Hutchinson and Kamel, 1956) that the rate of dispersal of microorganisms in sterile soil was substantially higher when earthworms were introduced. Similar results were obtained in experiments with Oribatidae, which inoculate the soil with microorganisms, carrying them on the body surface and in the alimentary canal. It has been shown that fungus spores remain viable after passing through the intestinal tracts of Collembola (Poole, 1959).

## Action of Invertebrates on the Physical Properties of Soil and on Soil Formation

By moving about in search of food or in migrations due to unfavorable climatic conditions, animals open up systems of burrows and passageways which increase the total porosity of the soil matrix and the continuity of pore systems for rapid exchange of gases and movement of water. These physical rearrangements in mineral matrix geometry create conditions favorable for plant root function and for aerobic microbial processes and rapid decomposition of organic matter and release of mineral nutrients.

A structural effect of even greater significance in some situations derives from the fact that all soil-dwelling invertebrate saprophages, while feeding on plant litter, ingest at the same time a certain proportion of soil mineral particles. These mineral particles, mixed in the animals' alimentary canal with finely divided and partially digested plant matter, are excreted in the form of small crumbs that constitute durable structural aggregates (Sukachev and Dylis, 1964).

The amount of excrement discharged by black millepedes during a single season, in the forest belts planted in the north of the steppe zone, may be as much as 686 kg/ha (Sokolov, 1957). This author also estimates that earthworms on soddy, medium-podzolized soil in Moscow Province are able to work over the entire mass of soil in the 0-20 cm layers in the course of six years. The part of their excrement discharged as casts on the surface alone amounts to 16 tons $ha^{-1}$ $yr^{-1}$ (Ponomareva, 1950).

The contribution to water infiltration capabilities of this surface deposition of stable aggregates and of traffic channels opening at the surface of the soil would be difficult to assess, but would be of the greatest significance.

Soil animal activity also is important in the downward transportation of litter fragments and fecal pellets into the mineral matrix, where further microbial decomposition produces structure-stabilizing deposits of residual organic matter (humus) that is relatively resistant to further decomposition (van der Drift, 1970). Thus, soil animals not only create structural arrangements (pore systems) essential for aeration, permeability to water and moisture retention, but they contribute to the stabilization of these structures as well.

Vertical redistributions of organic materials and minerals by soil animals are important soil forming processes. Variations in faunal composition can lead to unique variations in horizon development (Ghilarov, 1971; van Rhee, 1969). Large invertebrates (earthworms, large insect larvae, diplopods, etc.) can influence the development of pedological features directly and to great depth (Sukachev and Dylis, 1964). In the absence of these larger animals, direct effects of the meso- and micro-fauna (springtails, mites, nematodes, etc.) extend to, at most, a few centimeters below the litter-soil interface.

A number of important forest soil types are differentiated on the basis of the extent to which animals influence the fate of surface litter: its accumulation, comminution and incorporation with mineral soil (Wood, 1962).

In the absence of comminution, litter accumulates as raw humus, or mor (the L layer in gleyed, podzolic earths). Accumulation and comminution, without incorporation leads to the formation of moder (F and H layers in gleyed, podzolic brown earths). Comminution and mechanical incorporation with mineral soil at the surface produces mull-like moder fabrics (mull-like rendzinas and the A horizon of brown earths). Where the litter is comminuted and mixed with mineral soil, and conditions are favorable for further rapid decomposition by the microflora, chemical incorporation of residual humified matter with soil minerals leads to the formation of mull.

Mull formation is associated with plant species and with soil and environmental conditions where litter fall is quickly and completely decomposed year by year. There is a high annual flux of nutrients, and vegetative production is characteristically high. Large invertebrates and their mixing function appear to be key factors in the rapid turnover of nutrients, as well as in the organic enrichment of mineral horizons to greater depth in these situations.

Ghilarov (1968) has proposed that the productivity of many forest ecosystems can be increased by management directed toward increasing populations of beneficial invertebrates. For this purpose, there are experimental data in support of such practices as mulching, liming and drainage. Once limiting environmental factors have been identified and corrected, it would be feasible to introduce beneficial animals where they are absent.

## Action of Invertebrates on the Chemical Properties of the Soil and Mineral Cycling

Soil dwelling invertebrates not only break down plant litter and mix it with the mineral part of the soil but also, change its chemical composition. Their excrement, as experiments with earthworms have demonstrated, contains a greater total amount of organic matter, of partially converted humates, of available forms of N, and of mineral nutrients required by plants, than does the soil, and it also contains higher total of assimilated (immobilized) elements (Sukachev and Dylis, 1964).

Where invertebrates are represented mostly by small forms (Acarina, Collembola and other microfauna) which live mainly in litter and the surface layer of humus, their role in transporting organic and mineral matter is negligible and is limited to a depth of a few centimeters in the topmost soil layers. Larger animals may go down to the subsoil, later bringing to the surface mineral particles containing elements of value for plant nutrition. Where carbonates lie not far from the surface earthworms bring them to the topmost layers (Sokolov, 1956). In addition, they enrich the soil with secretions from their oesophageal (lime) gland (Ponomareva, 1950) which helps to neutralize acid soils.

The ability to change soil reaction is observed also in ants. Ants tend to neutralize soil reaction by their excretions which are highly buffered at a slightly alkaline pH (Sukachev and Dylis, 1964).

In ecosystems in which litter constitutes an important storage reservoir for minerals, the activities of microflora and fauna in soils may control the rate of mineral cycling. Natural reforestation and natural successions of vegetation usually depend upon the activity of soil animals which are an obligatory link in mineral turnover (Ghilarov, 1968).

The two main mechanisms in mineral turnover are mineral transfer via litter consumers and mineral release by microbial decomposers. Witkamp and Frank (1970) used a series of microcosm experiments to study mineral transfer relative to system structure and environment. In general, temperature appeared as the most influential environmental variable in forest-floor processes where moisture is not limiting for long periods of time. The major factor in mineral transfer appeared to be the physico-chemical and biological properties of minerals. Leachable and normally plentiful K was leached out, $^{137}C_s$ with a strong affinity for sand remained in the soil, biologically essential Mg apparently was immobilized in the humus, whereas most of the organic carbon lost from the leaves eventually ended up as $CO_2$ released to the atmosphere.

## Distribution of Arthropods

Usher (1969) observed three types of distribution of arthropods within a block of samples: 1) uniform, 2) random, and 3) aggregated. Using a coordinate technique for specifying locations, numbers and distance between aggregations, he concluded that aggregation resulted from some field attribute of the species such as size of the egg cluster, or availability of a food niche.

It is generally known that the horizontal patterns of animal populations are not random, but are aggregated or clumped (MacFadyen, 1952; Haarlov, 1960; Poole, 1961; Block, 1966; and Gerard, 1966). Klopfer (1969) has suggested that heterogeneity of the environment has resulted in reduced interaction between species, consequently permitting more species to coexist. If the environment was uniform, interspecific competition would be intensified resulting in a reduced number of different species. Other factors, biotic and abiotic that may affect, in different degrees, the distribution and abundance of soil animals are (1) competition for food, (2) reproduction behavior, (3) mutual attraction for other individuals of the same species, (4) response to daily and seasonal weather changes, and (5) increased survival of the species through clumping. Individuals in groups often experience a lower mortality rate during periods of stress (such as attacks of other organisms) than do isolated individuals, because the surface area exposed to the environment is less in proportion to the mass and because the group may be able to favorably modify the microclimate or microhabitat (Allee, 1931; 1959).

Seasonal abundance of soil organisms has been correlated by numerous authors with such parameters as moisture and temperature (MacFadyen, 1952; Block, 1966). Madge (1965a,b) showed that tropical leaf litter disappeared most rapidly during the wet season due mainly to activity of mites and collembola. The effects of cultivation, moisture temperature and many other factors have been reviewed thoroughly by Christiansen (1964) and Burges and Raw (1967).

According to Ghilarov (1965), composting during autumn encourages invertebrate development during the winter. Also, composting of urban wastes is promising. Various organic wastes with the addition of soil and sewage sludge have almost the same life forms as can be observed in leaf composts.

# MATERIALS AND METHODS

## Experimental Area

In the spring of 1969, 12 plots were laid out just to the east of the Baker Woodlot on the University Farm (Fig. 1). The area had been planted to experimental corn breeding materials the year before. The corn had been planted in blocks of 25-foot (7.6 m) rows and harvested with a 1-row picker-sheller. The corn cobs had been dumped in a pile at the end of each row.

The area was not plowed in 1969 so that arthropod populations could be studied in surface litter and the soil underneath. The 12 plots for the study were selected to contain 6 uniform rows of stalks and their associated corn cobs (Fig. 2). The plots were arranged to provide sampling sites at 4 incremental distances from the edge of the woodlot, with 3 replications at each distance (Fig. 3). This was done in consideration of the possibility that the woodlot might serve as a source of colonizing species or that a

Fig. 1. General view of the experimental area, looking west toward Baker Woodlot. May 11, 1969.

Fig. 2. Condition of corn trash at representative sample site. July 22, 1969. Note soil thermometer, right foreground.

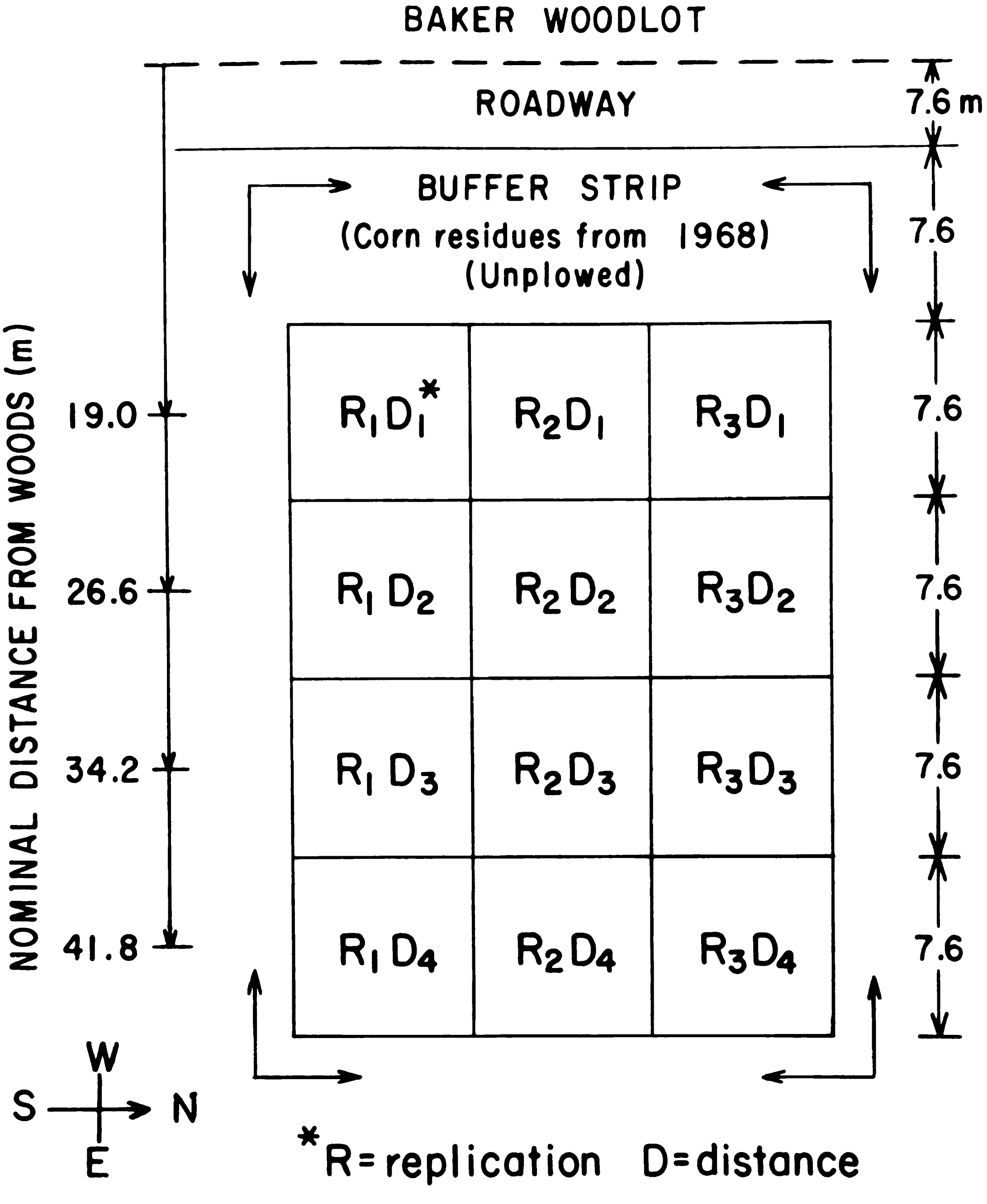

FIG. 3. DIAGRAM SHOWING THE 12 SAMPLING AREAS WHICH WERE TREATED AS REPLICATES WHEN NO SIGNIFICANT EFFECTS OF DISTANCE FROM WOODLOT COULD BE SHOWN. CORN ROWS RAN EAST AND WEST. SAMPLING AREAS VARIED FROM 8 TO 10 ROWS (8.5 TO 10.6 M, SOUTH TO NORTH).

micro-climate gradient might be associated with proximity to the woodlot.

The soil is classified as: Berrien fine sandy loam (Aquic Udipsament, sandy, mixed Mesic).

## Sampling

Arthropod populations in litter and in soil to a 2-in depth under the litter were estimated three times during the season (May 22-24, July 15-17, September 14-16). On each collection date, one of the six corn rows on each plot was selected at random for sampling.

Corn cobs were sampled separately from the portions of corn stalks and leaves which had been beaten to the ground by the action of the picker-sheller and of snow and rain (Fig. 2). These two types of litter are distinguished hereafter as "cobs" and "stalks."

Litter over a square foot of ground surface was collected, using a 12 x 12-inch steel frame (930 $cm^2$) and a knife to trim away litter outside the sample area (Fig. 4). An undisturbed soil core, 16 $in^2$ (103 $cm^2$) to a depth of 2

Fig. 4. Collection frame (12" x 12") used in obtaining cob samples (top) and stalk samples (bottom).

in. (5.08 cm) was taken immediately under the litter sample at each site (Fig. 5).

Litter samples were placed in plastic bags, soil samples were placed in wax-coated cake boxes and sealed. Samples were placed immediately in a styrofoam chest containing ice to keep them cool until they could be transported to the laboratory for extraction (Fig. 6).

## Extraction and Identification of Arthropods

Extraction was initiated on the day of collection. Each litter sample was emptied on the screen in the wide portion of a Tullgren-Berlese funnel (Fig. 7). The soil cores were transferred to standard Berlese funnels, with care to avoid damaging their structural integrity. A marked vial containing 95% ethanol was placed beneath each funnel exit to collect the arthropods falling from the sample. A light bulb (25 watt) fixed at the top of the funnel provided a source of heat. The drying and heating effects of the light bulb forces the soil animals to seek more moderate temperature and humidity regimes toward the

Fig. 5. Collecting undisturbed soil core after removal of litter sample. Top: 4 x 4 x 2 1/2 in core frame inserted to 2-in depth within area delineated by litter-sampling frame. Bottom: Excised soil core being transferred to waxed carton for transport to laboratory.

Fig. 6. Collection tools and samples of litter and soil (top) and ice-cooled styrofoam chest (bottom) used to transport samples to the laboratory.

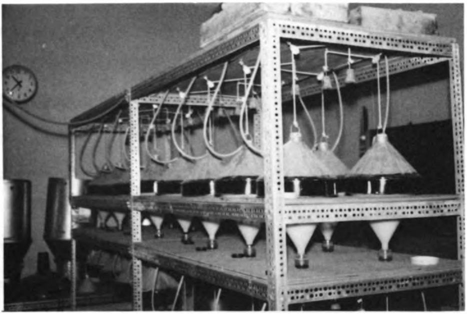

Fig. 7. Extraction apparatus: Tullgren-Berlese funnels (against rear wall), used for extraction of soil animals from larger litter samples; standard Berlese funnels (on rack in foreground), used for extraction of undisturbed soil cores and smaller litter samples.

narrow mouth of the funnel where they eventually fall into the collecting vials. Extraction of the arthropods was allowed to proceed for 4 days for the litter samples and 5 days for the soil samples.

The vials containing the arthropods were cleared of debris and mineral matter that fell through the screen by employing a modified flotation method. Ethanol in the collection vial was replaced with water. Magnesium sulfate was added to separate the organic from the mineral material. The buoyant organic materials were decanted and treated with xylene to separate the arthropods from the other organic debris. The arthropod cuticle is wetted by xylene and they accumulate in the xylene-layer which settles out on the water surface. The xylene-water interface was scanned under a low power stereoscope and the arthropods were picked out. They were then brought back in 95% ethanol.

The above procedure posed the risk of losing some of the smallest arthropods but extra care was exercised to minimize such loss. Considering the preliminary nature of the study, no attempt was made to recover very small arthropods that may have been lost by entanglement in debris.

The arthropods were sorted, counted, and recorded to the smallest readily recognizable group: to order or family for the insects, to species for springtails, and to class or morphological group for the other arthropods.

## Soil Analyses

After extraction of arthropods, the 4 soil samples from each replication were composited, passed through a 2-mm sieve and sub-sampled. Soil pH, K, Ca, Mg, and P were determined according to routine methods of the Soil Testing Laboratory, Michigan State University.

Soil pH was determined in a 1:1 water suspension, using a Beckman Zeromatic glass electrode pH meter. Phosphorus was extracted with Bray P-1 reagent using a 1:8 soil to solution ratio; available K, Ca, and Mg with 1.0 N $NH_4OAc$ (pH 7.0) using a 1:8 soil to solution ratio.

The determination of exchangeable $NH_4^+$-N and $NO_3^-$-N was done by semi-micro distillation according to Bremner (1965), using Devarda's alloy to reduce $NO_3^-$ to $NH_4^+$. (It was assumed that rapid drying in the Berlese extractors would have minimized microbial transformation of mineral and organic N.)

Moisture content determination was accomplished by measurement of loss of weight of a field-moist sub-sample after oven drying for 48 hours at 110°C. Water capacity at 1/3 atm tension was determined using the method described by Klute (1965).

## Total Nitrogen of Soils and Litter

The semi-micro Kjeldahl method of Bremner (1965) was used to determine total N in soils and litter except that in the $K_2SO_4$-catalyst mixture, HgO was used as catalyst instead of $CuSO_4$. This necessitates the addition of $NA_2S_2O_3$ to the alkali solution used in the distillation step.

One-half gram of finely ground soil (80-mesh) or 50 mg of litter (dried at 65°C and ground to pass a 40-mesh sieve) was wrapped in a cigarette paper and added as a package into a 100-ml Kjeldahl flask. After adding 2 ml of distilled water the flask was allowed to stand for 30 minutes. Then 1.1 gm of $K_2SO_4$-catalyst mixture and concentrated $H_2SO_4$ (3 ml for soil and 2 ml for litter) were added. The mixture was digested until clear (2-1/2 hrs. for soil and 1 hr for litter). The digested mixture was made alkaline with 40% NaOH-$Na_2S_2O_3$ solution and distilled for 5 minutes into 2% boric-acid-methyl purple indicator solution. The $NH_3$ liberated was estimated by titration with 0.01 N HCl and is reported as total N.

## Total Carbon of Soils and Litter

Total carbon in soils and litter was determined with a Leco carbon analyzer (Model 70). Sub-samples for analysis were ground to pass an 80-mesh screen. One-hundred mg of soil (10 mg of litter) was weighed into a combustion crucible. Approximately 1 gm each of iron chips and tin catalyst were added. Combustion in the induction furnace occurred in a stream of $O_2$ at 1670 °C. Combustion products in the $O_2$ carrier stream was passed through a purification train to remove particulate matter, water and $SO_2$ and to convert CO to $CO_2$. Purified $O_2$ + $CO_2$ was collected terminally in the analyzer cylinder at 45 °C where $CO_2$ was estimated from the change in thermal conductivity relative to pure $O_2$. The thermistor signal on this instrument is read out digitally as % carbon in a 1-gm sample and must be converted to actual size of the combusted sample.

## Air and Soil Temperature

Air temperatures at the experimental area were observed during each sampling period. Soil temperatures at the surface and at a 2-inch depth under both cobs and stalks were likewise measured and recorded.

# RESULTS

## Major Animal Groups

A preliminary analysis of variance showed no significant effects of proximity to Baker Woodlot or variation in numbers of any animal group. Examination of the grid distribution of the numerically dominant groups (Acarina, and Collembola) showed non-uniform distributions at each sampling, but centers of concentration were distributed in a random fashion.

Analysis of aggregation or migration phenomena was not among the objectives of this study. Therefore the 4 distances from the woodlot were combined with the 3 field replications (Fig. 1) to give 12 replications for factorial comparison of animal numbers in relation to litter sites (cobs *vs*. stalks), strata (litter *vs*. soil), and sampling date (Table 1).

The probabilities in Table 1-C show significant main effects of both sampling date and stratum for all groups except those present in low or transient numbers.

TABLE 1.--Numbers of principal animal groups in litter and soil by sampling dates.

| LITTER SITE | DATE | ANIMAL GROUPS | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Acarina | Araneida | Chilopoda | Coleoptera | Collembola | Diplopoda | Diptera | Hemiptera | Hymenoptera | Isopoda | Psocoptera | Annelida | Total Arthropods |
| A. Individuals $m^{-2}$ in litter (12-plot means) | | | | | | | | | | | | | | |
| *Corn* ***cobs*** | May 22-24 | 1685 | 7 | 80 | 163 | 7,739 | 4 | 230 | 0 | 3 | 5 | 5 | 5 | 9,921 |
| | Jul.15-17 | 1263 | 14 | 16 | 33 | 2,200 | 0 | 9 | 1 | 1 | 3 | 8 | 8 | 3,548 |
| | Sep.14-16 | 5846 | 35 | 41 | 25 | 653 | 0 | 13 | 15 | 14 | 1 | 0 | 0 | 6,643 |
| *Corn* ***stalks*** | May 22-24 | 786 | 6 | 35 | 129 | 4,618 | 1 | 102 | 1 | 2 | 8 | 243 | 4 | 5,931 |
| | Jul.15-17 | 1112 | 20 | 9 | 35 | 2,550 | 0 | 0 | 2 | 3 | 0 | 8 | 0 | 3,739 |
| | Sep.14-16 | 3997 | 27 | 19 | 17 | 400 | 0 | 5 | 6 | 5 | 0 | 0 | 0 | 4,476 |
| *LSD (05)* ***dates within sites*** | | ns[1] | ns | ns | ns | 4,279 | ns | 158 | ns | ns | ns | 75 | ns | -- |
| *LSD (05)* ***sites within dates*** | | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | 70 | ns | -- |
| B. Individuals $m^{-2}$ in soil to 5 cm under litter (12-plot means) | | | | | | | | | | | | | | |
| *Soil under cobs* | May 22-24 | 186 | 24 | 32 | 260 | 4,558 | 8 | 153 | 0 | 0 | 0 | 16 | 8 | 5,237 |
| | Jul.15-17 | 8179 | 57 | 153 | 89 | 8,631 | 0 | 105 | 0 | 65 | 0 | 81 | 0 | 17,360 |
| | Sep.14-16 | 8373 | 65 | 129 | 105 | 2,178 | 0 | 57 | 40 | 24 | 0 | 0 | 8 | 10,971 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Soil under stalks* | May 22-24 | 113 | 24 | 73 | 242 | 5,235 | 0 | 48 | 0 | 32 | 0 | 0 | 0 | 5,767 |
| | Jul.15-17 | 9236 | 97 | 178 | 73 | 9,793 | 0 | 40 | 0 | 0 | 16 | 40 | 0 | 19,473 |
| | Sep.14-16 | 45592 | 97 | 210 | 153 | 3,654 | 0 | 65 | 0 | 48 | 8 | 0 | 8 | 49,827 |
| *LSD (05) dates within sites* | | 8904 | 64 | 79 | ns | 4,279 | ns | ns | 26 | ns | ns | 75 | ns | -- |
| *LSD (05) sites within dates* | | 26748 | ns | 77 | ns | ns | ns | ns | ns | 41 | ns | ns | ns | -- |

C. Probabilities (P) for significance of F associated with replications, dates, sites and strata

| Category | df[2] | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Reps(R)* | 11/22 | .508 | .500 | .808 | .062 | .645 | .477 | .325 | .513 | .418 | .745 | .242 | .644 |
| *Dates(D)* | 2/22 | .080 | .031 | .076 | <.0005 | .007 | .104 | .002 | .069 | .414 | .828 | .006 | .311 |
| *Sites(S)* | 1/11 | .287 | .427 | .499 | .334 | .939 | .214 | .055 | .205 | .795 | .233 | .091 | .497 |
| *S x D* | 2/11 | .322 | .784 | .748 | .276 | .376 | .221 | .097 | .178 | .205 | .778 | .016 | .624 |
| *Strata(s)* | 1/88 | .085 | .001 | <.0005 | .002 | .002 | .676 | .658 | .557 | .006 | .706 | .127 | .285 |
| *s x D* | 2/88 | .222 | .349 | <.0005 | .215 | .001 | .839 | .010 | .530 | .697 | .197 | <.0005 | .259 |
| *s x S* | 1/88 | .213 | .295 | .013 | .513 | .205 | .531 | .370 | .203 | .986 | .189 | .001 | .659 |
| *s x S x D* | 2/88 | .265 | .784 | .572 | .398 | .753 | .674 | .226 | .254 | .022 | .384 | .001 | .822 |

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[1] ns = non-significant

[2] df = category degrees of freedom/error degrees of freedom

Only in the case of Diptera did the main effect associated with litter site approach significance at P (05).

Nevertheless, seasonal and vertical distributions were different at cob sites than at stalk sites, giving rise to significant first order interactions for several groups and second order interactions for two (Hymenoptera, Psocoptera). Seasonal changes in numbers were usually parallel in litter and soil. However, except for the May sampling, numbers of most groups were greater in soil, and seasonal variation in soil was also greater. As a result, means for the soil tratum were more often statistically different than were means for the litter populations.

Even where statistical significance was not attained, the relationship of specific groups to litter site and/or stratum varied uniquely through the season, and these differences will be pointed out.

Acarina, Araneida and Hemiptera increased in numbers as the season progressed, reaching maxima in September. This maximum for Acarina was five-fold greater in soil under corn stalks than under cobs.

Chilopoda in the litter layer decreased sharply in the second sampling but increased in the soil. There were significant first order interactions of stratum with site and date: centipedes in the litter layer were more numerous at cob sites than stalk sites, but soil populations were greater under stalks, significantly so in September.

Population patterns for Coleoptera and Diptera were similar to those for Chilopoda, except that much larger numbers were encountered in both soils and litter in May. Fewer numbers of Diptera remained in the litter after May, but all three groups were recovered in much greater numbers from soil than from litter in July and September.

Hymenoptera were found mainly in soil and in sporadic seasonal numbers under both litter types.

Diplopods were found only in May but more frequently at cob sites. Isopods were found in both litter types in May but appear to have moved later into soil only under corn stalks. The data for these two groups may have behavioral significance, but the plot layout and statistical design were inappropriate for a critical evaluation of these sparse and irregularly distributed groups.

Psocoptera showed a marked preference for corn stalks early in the season, although they appeared in the soil stratum earlier and in higher numbers under cobs. None at all were encountered in September.

Annelids were recovered from both litter types and from soil at cob sites in May but seem to have moved later into lower (unsampled) soil strata in July. They appeared in the upper 0-5 cm soil stratum at both sites in September.

Collembola were the most numerous group in the May sampling--both in litter and in soil. In litter, their numbers decreased in each successive sampling. The soil population, however, reached a peak in July.

## Collembola--Acarina Populations

The dominant animal groups encountered, numerically, were Acarina and Collembola. There was an inverse seasonal distribution in their numbers (Fig. 8), but these two groups together comprised 90 to 99 percent of the

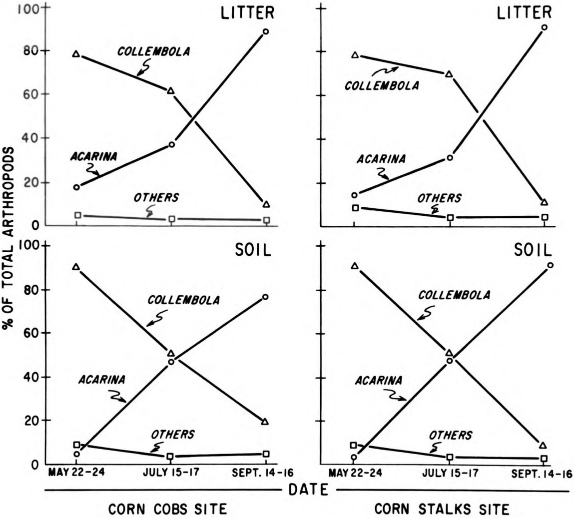

FIG. 8. DISTRIBUTION OF COLLEMBOLA, ACARINA AND OTHER ARTHROPODS AS PERCENT OF TOTAL ARTHROPOD NUMBERS.

total arthropod numbers in each sampling. The biomass represented by other arthropod groups would have been relatively of greater magnitude (Edwards, et al., 1970). Nevertheless, since respiration rates per unit mass are inversely related to body size, Acarina and Collembola must contribute significantly to the faunal component of energy turnover. They certainly play unique roles in reworking of feces from other animals, disintegration of litter, redistribution of organic matter and interaction with the microflora (Jongerius, 1963; Ghilarov, 1968; Atlavinyte, 1971).

The data in Table 1 indicate that Collembola were prepared to move from the litter into the soil underneath much earlier in the season than Acarina. It is significant that Chilopoda, Coleoptera and Diptera were already present in the soil in large numbers in May. These larger animals would have opened up passageways and deposited substrates to support downward migration of the mesofauna.

Many species of mites are phoretic or pass through inactive hypopial stages attached to larger animals, notably Coleoptera and Diptera (Wallwork, 1970; Kevan, 1962). Physical transport on larger animals may have been an additional factor in the very large increases in numbers of Acarina in the soil which occurred between the May and July samplings. These increases coincided with disappearance from the litter of several groups of larger animals in substantial numbers: Chilopoda, Coleoptera, Diptera, Isopoda (Table 1-A). At the same time there were substantial increases in the soil populations of larger animals. Araneida, Chilopoda, Isopoda (Table 1-B).

The very dramatic September increase in Acarina in soil under corn stalks was also accompanied by increased soil numbers of Chilopoda and Coleoptera. Fairly large numbers of Hymenoptera were also recovered, where none had been found in July.

## Collembola Species

Separation of Acarina to lower taxa proved impractical. It is possible that increased numbers in successive samplings reflect increases in species diversity as well as numbers of individuals.

In the case of Collembola, however, three species comprised 78 to 98 percent of the populations in litter and in soils: Isotoma eunotabilis (Folsom), Isotoma viridis (Bourlet) and Entomobrya griseoolivata (Packard). Juvenile-to-adult ratios in Table 2 indicate that a single generative population was involved in each case.

Reproduction and recruitment appear to have taken place primarily in the litter early in the season. In the May samples, juveniles represented half or more of the litter population but were relatively much less numerous in the soil.

At the time of maximum numbers in July, juveniles were distributed in a rather uniform proportion (.4 to .6) to adults in both litter and soils, except for I. eunotabilis. This species appears to have developed somewhat more slowly than the other two: the litter population retained a larger proportion of juveniles and was associated with a larger soil population.

The large decrease in numbers of all three species in September was accompanied by a marked decrease in average age of the population (juvenile/adult ratios of .2 or smaller).

TABLE 2.--Numbers of adults and juveniles, and juvenile/adult ratios for the three principal species of Collembola.

| Litter Site | Date | <u>Isotoma eunotabilis</u> (Folsom) |  |  |  | <u>Isotoma viridis</u> (Bourlet) |  |  |  | <u>Entomobrya griseoolivata</u> (Packard) |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | Total | Adults | Juveniles | Juv./Ad. | Total | Adults | Juveniles | Juv./Ad. | Total | Adults | Juveniles | Juv./Ad. |
|  |  | Individuals $m^{-2}$ |  |  |  | Individuals $m^{-2}$ |  |  |  | Individuals $m^{-2}$ |  |  |  |
| A. In litter (12-plot means) |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Corn cobs* | May 22-24 | 4302 | 1717 | 2581 | 1.33 | 2126 | 937 | 1189 | 1.32 | 685 | 326 | 369 | 1.15 |
|  | Jul 15-17 | 818 | 544 | 273 | .51 | 763 | 517 | 247 | .52 | 309 | 257 | 132 | .52 |
|  | Sep 14-16 | 257 | 218 | 39 | .18 | 223 | 185 | 36 | .21 | 135 | 119 | 16 | .15 |
| *Corn stalks* | May 22-24 | 1656 | 957 | 699 | 1.05 | 1517 | 662 | 855 | 1.23 | 622 | 302 | 320 | .93 |
|  | Jul 15-17 | 916 | 588 | 327 | 1.02 | 777 | 509 | 268 | .57 | 480 | 314 | 166 | .57 |
|  | Sep 14-16 | 156 | 137 | 19 | .14 | 137 | 123 | 14 | .12 | 97 | 84 | 13 | .16 |
| *LSD (05) dates within sites* |  | 2105 | 1162 | 1055 | .47 | 1109 | 609 | 547 | .21 | ns | ns | 310 | .22 |
| *LSD (05) sites within dates* |  | 1912 | ns[1] | ns | .43 | ns | ns | ns | ns | ns | ns | ns | .20 |
| B. In soil to 5 cm under litter (12-plot means) |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Soil under cobs* | May 22-24 | 1718 | 1275 | 444 | .29 | 1275 | 831 | 444 | .43 | 1178 | 799 | 379 | .37 |
|  | Jul 15-17 | 3347 | 2162 | 1186 | .52 | 2364 | 1500 | 863 | .53 | 2049 | 1323 | 726 | .50 |
|  | Sep 14-16 | 718 | 637 | 81 | .15 | 4356 | 495 | 40 | .09 | 678 | 605 | 73 | .14 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Soil under stalks* | May 22-24 | 1508 | 1113 | 395 | .27 | 1339 | 920 | 419 | .29 | 1250 | 952 | 298 | .23 |
| | Jul 15-17 | 4025 | 2783 | 1242 | .40 | 2428 | 1638 | 791 | .41 | 2646 | 1815 | 831 | .41 |
| | Sep 14-16 | 1065 | 952 | 113 | .18 | 912 | 831 | 81 | .10 | 1129 | 1016 | 113 | .12 |
| *LSD (05) dates within sites* | | 2105 | 1162 | 1055 | ns | 1109 | 609 | 547 | .21 | 722 | 438 | 310 | .22 |
| *LSD (05) sites within dates* | | ns | ns | ns | ns | ns | ns | ns | ns | ns | 400 | ns | ns |

C. Probabilities (P) for significance of F associated with replications, dates, sites, and strata

| Category | df[2] | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Reps (R)* | 11/22 | .753 | .674 | .759 | .184 | .558 | .449 | .642 | .489 | .375 | .253 | .579 | .439 |
| *Dates (D)* | 2/22 | .014 | .026 | .010 | <.0005 | .001 | .005 | <.0005 | <.0005 | .001 | .002 | <.0005 | <.0005 |
| *Sites (S)* | 1/11 | .349 | .983 | .095 | .894 | .943 | .579 | .472 | .080 | .194 | .064 | .870 | .146 |
| *S x D* | 2/11 | .076 | .195 | .048 | .325 | .546 | .487 | .662 | .561 | .597 | .616 | .640 | .226 |
| *Strata (s)* | 1/88 | .071 | <.0005 | .689 | <.0005 | .017 | <.0005 | .970 | <.0005 | <.0005 | <.0005 | <.0005 | <.0005 |
| *s x D* | 2/88 | <.0005 | .001 | <.0005 | <.0005 | .001 | .004 | <.0005 | <.0005 | <.0005 | .001 | <.0005 | <.0005 |
| *s x S* | 1/88 | .143 | .224 | .119 | .556 | .334 | .157 | .680 | .667 | .157 | .027 | .837 | .306 |
| *s x S x D* | 2/88 | .511 | .978 | .109 | .084 | .828 | .826 | .764 | .482 | .811 | .729 | .922 | .547 |

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[1] ns = non-significant

[2] df = category degrees of freedom/error degrees of freedom

## Vertical Distribution of Animal Groups and Collembola Species

The numbers of most animal groups in soil relative to their numbers in litter increased sharply between May and July (Table 3). The soil/litter ratios in July for a number of groups at cob sites were similar to those at stalk sites. In the September sampling, however, vertical distributions were very different. A substantially larger proportion of the animals associated with corn stalks were recovered from soil than at cob sites.

Changes in vertical distribution of the Collembolan species (Table 4) tended to parallel each other and the changes for major arthropod groups.

## Environmental Parameters in Relation to Population Distribution

The vertical distribution of litter-soil populations is frequently associated with temperature and/or moisture gradients (Kevan, 1962; Wallwork, 1970).

TABLE 3.--Ratios of numbers in soil to numbers in litter for principal animal groups.

| Litter site | Date | Animal Groups | | | | | | | | | Total Arthropods |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Acarina | Araneida | Chilopoda | Coleoptera | Collembola | Diptera | Hymenoptera | Psocoptera | Annelida | |
| Corn cobs | May 22-24 | .1 | 3.4 | .4 | 1.6 | .6 | .7 | $S_o$ | 3.2 | 1.6 | .5 |
| | Jul 15-17 | 6.5 | 4.1 | 9.6 | 2.6 | 3.9 | 11.7 | 65.0 | 10.1 | $L_oS_o$ | 4.9 |
| | Sep 14-16 | 1.4 | 1.9 | 3.1 | 4.2 | 3.3 | 4.3 | 1.7 | $L_oS_o$[1] | $L_o$ | 1.7 |
| Corn stalks | May 22-24 | .1 | 4.0 | 2.1 | 1.9 | 1.1 | .5 | 16.0 | $S_o$ | $S_o$ | 1.0 |
| | Jul 15-17 | 8.3 | 4.9 | 19.8 | 2.1 | 3.8 | $L_o$ | $S_o$ | 5.0 | $L_oS_o$ | 5.2 |
| | Sep 14-16 | 11.4 | 3.6 | 11.1 | 9.0 | 9.1 | 13.0 | 9.6 | $L_oS_o$ | $L_o$ | 11.1 |

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[1] No animals recovered from litter ($L_o$) or from soil ($S_o$).

**TABLE 4.**--Ratios of numbers in soil to numbers in litter for Collembola species.

| Litter Site | Date | *Isotoma eunotabilis* | *Isotoma viridis* | *Entomobrya griseoolivata* | Other species |
|---|---|---|---|---|---|
| Corn cobs | May 22-24 | .4 | .6 | 1.7 | .6 |
| | Jul 15-17 | 4.1 | 3.1 | 5.3 | 3.8 |
| | Sep 14-16 | 2.8 | 1.9 | 5.0 | 9.4 |
| Corn stalks | May 22-24 | .9 | .9 | 2.0 | 1.4 |
| | Jul 15-17 | 4.4 | 3.1 | 5.5 | 1.8 |
| | Sep 14-16 | 6.8 | 6.7 | 11.6 | 5.5 |

Seasonal changes in composition, size and distribution of populations are further influenced by the changing nature of available substrates as decomposition proceeds.

### 1. Moisture

Rainfall from March through the July 15-17 sampling totaled 36 cm (Fig. 9). This is normal for this 4-1/2 month period. The September sampling came near the end of a long drought period which included most of August.

Soil moisture in the May sampling was much higher than moisture capacity at 1/3 atmosphere tension (Table 5). This was due to the imperfect drainage at this site and the fact that free water was still present in the subsoil at a relatively shallow depth. By the time of the July sampling, drainage had lowered this free water surface and moisture content in the soil at 0 to 5 cm approximated that at 1/3 atmosphere tension. In spite of the long drought period which preceded the September sampling, the soil under litter at that time was still perceptibly moist, well above the wilting point for plants.

Moisture in the litter itself was not determined. The stalks and leaves are less dense tissues than corn cobs and they were more loosely distributed in the litter

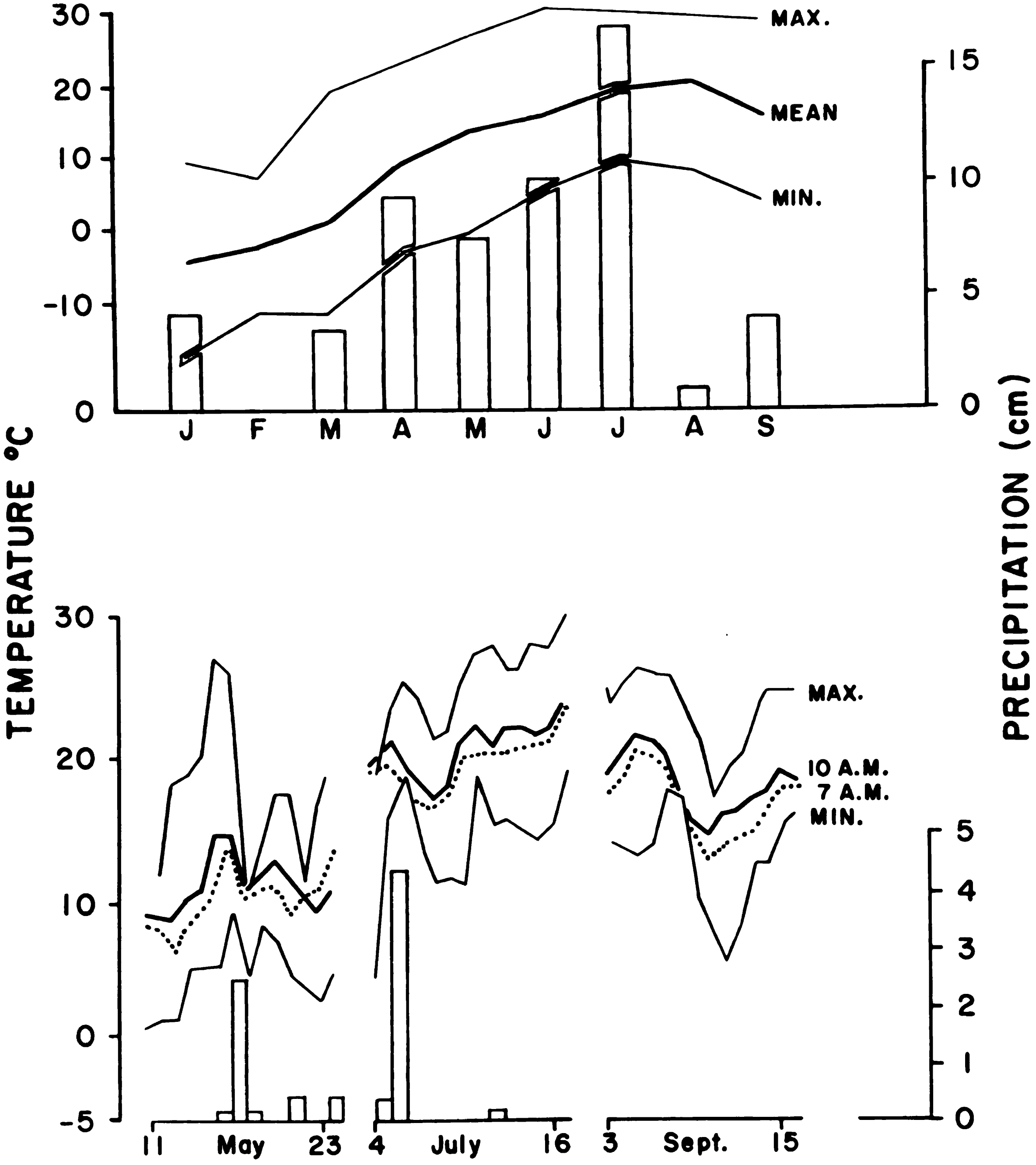

Fig. 9. U. S. Weather Bureau records (M. S. U. South Farm Station). Upper figure: monthly rainfall and average cardinal air temperatures. Lower figure: daily rainfall, maximum and minimum air temperatures, and soil temperatures (7 a.m. and 10 a.m.) at 5 cm under grass sward.

TABLE 5.--Numbers of Collembola, Acarina, and other arthropods in soil under litter in relation to total carbon and Kjeldahl nitrogen in the soil.

| Litter site | Date | Soil (0-5 cm) | | | | Soil Moisture[2] | Soil Temperature | Individuals $m^{-2}$ in soil (0-5 cm) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Observed | | | Per g C in soil | | |
| | | Soil Weight[1] | C | N | C/N | | | Acarina | Collembola | Other Arthropods | Acarina | Collembola | Other Arthropods |
| | | Kg x $m^{-2}$ | % | % | | % | °C | | | | | | |
| Corn cobs | May 22-24 | 67.5 | 1.09 | .090 | 11.2 | 18.1 | 72.0 | 186 | 4,558 | 493 | .25 | 6.2 | .67 |
| | Jul 15-17 | 67.5 | 1.09 | .093 | 11.7 | 13.5 | 22.0 | 8,179 | 8,631 | 550 | 11.1 | 11.7 | .75 |
| | Sep 14-16 | 67.5 | 1.13 | .096 | 11.6 | 10.9 | 18.0 | 8,373 | 2,178 | 420 | 11.0 | 2.9 | .55 |
| Corn stalks | May 22-24 | 67.5 | 1.04 | .085 | 12.6 | 17.8 | 12.5 | 113 | 5,235 | 419 | .16 | 7.5 | .60 |
| | Jul 15-17 | 67.5 | 1.11 | .093 | 11.9 | 13.1 | 23.0 | 9,236 | 9,793 | 444 | 12.3 | 13.1 | .59 |
| | Sep 14-16 | 67.5 | 1.16 | .096 | 11.3 | 10.5 | 18.5 | 45,592 | 3,654 | 581 | 61.4 | 4.9 | .78 |
| LSD (05) dates within sites | | -- | .07 | ns[3] | ns | .9 | -- | 8,904 | 4,279 | -- | -- | -- | -- |
| LSD (05) sites within dates | | -- | ns | .07 | ns | ns | -- | 26,748 | ns | -- | -- | -- | -- |

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[1] Assuming volume weight = 1.33 gm $cm^{-3}$

[2] Moisture content at 1/3 atm tension = 12.3 percent

[3] ns = non-significant

TABLE 5.--Numbers of Collembola, Acarina, and other arthropods in soil under litter in relation to soil carbon, Kjeldahl nitrogen, moisture and temperature.

layer. Consequently, they lost moisture more rapidly after wetting. The generally more moist condition of the cobs observed in the field is reflected in the slight but consistently higher moisture content of the soil under the corn cobs.

The generally more moist conditions in the corn cobs may have contributed to the larger numbers of most arthropods encountered in litter at cob sites than at stalk sites in all samplings (Table 1) and the much smaller proportion in soil at cob sites in the September sampling (Table 3).

The litter structure at cob sites would have included extensive interconnected spaces between the corn cobs, facilitating movement within the litter layer. This and the more equable moisture regime in cob litter would have encouraged mobile animals to spend more time in the litter. Longer residence times for larger animals would favor increased numbers of less mobile populations dependent upon them for substrates (excreta, comminuted litter fragments).

Acarina numbers in soil (Table 5) and their total site numbers (Table 6) were inversely related to seasonal

TABLE 6.--Total site numbers (litter plus soil) of Collembola, Acarina and other arthropods in relation to dry matter, carbon and nitrogen retained in surface litter.

| Litter Site | Date | Surface Litter | | | | | Individuals $m^{-2}$ in Litter plus Soil | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Observed | | | Per g C in Litter | | |
| | | Dry Matter | C | N | C/N | Temper-ature | Acarina | Collembola | Other Arthropods | Acarina | Collembola | Other Arthropods |
| | | $g \times m^{-2}$ | % | % | | °C | | | | | | |
| Corn cobs | May 22-24 | 4315 | 32.7 | .93 | 35.9 | 10.5 | 1,871 | 12,297 | 990 | 1.3 | 8.7 | .8 |
| | Jul 15-17 | 2841 | 32.8 | 1.04 | 31.5 | 26.0 | 9,442 | 10,831 | 635 | 10.1 | 11.6 | .7 |
| | Sep 14-16 | 1775 | 30.4 | 1.09 | 27.9 | 22.0 | 14,219 | 2,831 | 564 | 26.4 | 5.4 | 1.0 |
| Corn stalks | May 22-24 | 1765 | 39.2 | .76 | 52.0 | 11.0 | 899 | 9,853 | 946 | 1.3 | 14.3 | 1.4 |
| | Jul 15-17 | 1345 | 38.9 | .82 | 47.7 | 25.0 | 10,348 | 12,243 | 521 | 19.8 | 23.6 | 1.0 |
| | Sep 14-16 | 1141 | 37.8 | .89 | 42.5 | 23.5 | 49,589 | 4,054 | 660 | 114.5 | 9.4 | 1.5 |
| LSD (05) dates within sites | | 330.3 | ns | .05 | 4.3 | -- | -- | -- | -- | -- | -- | -- |
| LSD (05) sites within dates | | 271.2 | 2.43 | .06 | 5.7 | -- | -- | -- | -- | -- | -- | -- |

TABLE 7.--Probabilities (P) for significance of F associated with replications, dates and litter site, for data in Tables 5 and 6.

| Category | df[1] | Kjeldahl N | Total C | C/N | Dry Matter |
|---|---|---|---|---|---|
| A. Litter materials | | | | | |
| Replications | 11/22 | .032 | .943 | .465 | .083 |
| Dates (D) | 2/22 | < .0005 | .418 | < .0005 | < .0005 |
| Materials (M) | 1/33 | < .0005 | < .0005 | < .0005 | < .0005 |
| D X M | 2/33 | < .0005 | .114 | .002 | < .0005 |
| B. Soil samples | | | | | |
| Replications | 11/22 | .596 | .661 | .379 | |
| Dates (D) | 2/22 | .182 | .030 | .647 | |
| Site (S) | 1/33 | .088 | .442 | .178 | |
| D X S | 2/33 | .029 | .671 | .113 | |

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[1] df = category degrees of freedom/error degrees of freedom

changes in moisture status as reflected in soil moisture content (Table 5). However, there was no consistent relationship to seasonal changes in moisture status with numbers of Collembola or other arthropods. The data in Fig.8 suggest that Acarina simply increased to fill a trophic niche made vacant as numbers of Collembola declined in relation to the total animal population.

### 2. Temperature

Litter and soil temperatures were recorded at the experimental site only at the time of sampling. Samples were taken routinely between 7:00 A.M. and 10:00 A.M. One replication (Fig. 3) was sampled each day, 3 days being required for complete sampling of the study area.

Soil temperatures encountered at 5 cm under the litter (Table 8) were very similar to those recorded during the same morning period at 5 cm under grass sward at the M.S.U. South Farm Weather Station (cf. lower half of Fig. 9). The 7:00 A.M. reading frequently coincides with the daily minimum soil temperature at this depth.

The May sampling had been preceded by 6 to 8 weeks of mean air temperatures above freezing. Soil temperatures during the previous 2 weeks would have averaged

TABLE 8.--Soil and air temperature (°F) at and near (1 km) study area.

| Time | | Sampling Periods | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | May | | | July | | | Sept. | | |
| | | 22 | 23 | 24 | 15 | 16 | 17 | 14 | 15 | 16 |
| | | °C | | | | | | | | |
| U.S. Weather Bureau Records | | | | | | | | | | |
| Air Temp | 7 AM | 4.5 | 6.1 | 8.1 | 17.2 | 26.6 | 23.8 | 15.0 | 17.2 | 17.8 |
| | 8 AM | 5.0 | 9.0 | 10.5 | 21.1 | 22.8 | 24.7 | 16.6 | 17.8 | 17.8 |
| | 9 AM | 5.6 | 10.6 | 13.6 | 23.3 | 24.4 | 26.0 | 19.4 | 21.1 | 17.8 |
| | 10 AM | 6.1 | 11.7 | 15.5 | 25.0 | 26.1 | 27.2 | 22.2 | 21.6 | 17.8 |
| Soil Temp[1] | 7 AM | 10.6 | 9.2 | 10.7 | 22.2 | 22.4 | 25.0 | 17.2 | 18.9 | 18.9 |
| | 8 AM | 10.6 | 9.2 | 11.7 | 21.9 | 22.7 | 25.0 | 16.6 | 19.2 | 19.2 |
| | 9 AM | 10.6 | 10.6 | 12.8 | 22.2 | 23.3 | 24.7 | 18.3 | 18.9 | 19.2 |
| | 10 AM | 10.7 | 10.6 | 13.9 | 23.0 | 23.3 | 24.7 | 18.3 | 20.0 | 19.2 |
| Experimental Area | | | | | | | | | | |
| Air Temp (mean) | 7-10 | 6.1 | 12.2 | 14.4 | 23.3 | 25.0 | 26.1 | 21.1 | 20.5 | 17.8 |
| Soil Temp[2] (mean) | 7-10 | 10.6 | 10.6 | 13.3 | 22.2 | 23.0 | 24.7 | 18.3 | 18.6 | 18.6 |

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[1] Soil temperature at 5 cm depth under grass sod.

[2] Soil temperature at 5 cm depth under litter (means for all sites sampled each day).

about 12 to 15°C (allowing for afternoon peaks higher than recorded at 10:00 A.M.).

The July samples were taken during the period of seasonally maximum temperatures. Soil temperatures during the preceding 2 weeks would have averaged well above 20°C.

The September 14 to 16 sampling was made during a period when soil temperatures were rising rapidly from a local minimum of about 12°C on September 10.

Litter temperatures (litter-soil interface) recorded at the time of sampling (Table 6) were consistently about 2°C lower at cob sites than at stalk sites. This reflects the higher moisture content and higher heat capacity due to the water in the cobs.

Soil temperatures at 5 cm (Table 5) were 1 to 2 degrees lower under cobs in the May and September samplings but slightly higher than under stalks in July. Although these differences are small, they do relate to preceding temperature sequences (Fig. 9) and illustrate the role of moisture content and heat capacity of water in litter materials in moderating temperature regimes in the litter itself and in underlying soil.

The only consistent relationship to animal numbers is the consistently lower temperature (Table 8) and higher numbers of most groups in cob litter vs. corn stalks (Table 1). The overriding influence on numbers was probably the higher moisture content of the cobs. However, extremes of high temperature may well have occurred in stalk litter, resulting in greater movement of animals into the soil stratum. Maximum numbers of Collembola in soil coincided with seasonally high air and litter temperatures in July.

### 3. Nature of Substrates

Before the May sampling, litter materials had been subject to biological decomposition, physical weathering and leaching through the fall, winter and spring. At the time of the May sampling, the corn cobs were 2 to 3-fold higher in N than reported values (Morrison, 1959). They were also higher in N and had a narrower C/N ratio than the stalks and leaves (Table 6). This would indicate that, in May, the cobs had already undergone more extensive decomposition (dissipation of carbon) than the stalks and leaves.

Conditions were more favorable for rapid decomposition of the cob litter. Because of their greater density and the more compact arrangement in small piles, the cobs were more retentive of moisture and made more intimate contact with underlying soil than the bulkier stalks and leaves. The effect of these differences in physical structure of the two litter types can be judged from differences in the rate of disappearance of dry matter during the study period (Table 6). Thus 60 percent of the dry matter present in corn cobs in May had disappeared by September, as compared with 35 percent for stalks and leaves.

The net effect of more rapid decomposition of the cob litter was that readily available energy materials were dissipated more quickly. This is reflected in the narrower C/N ratios for cobs vs. stalks (Table 6). It was also reflected in the seasonal changes in total site number of arthropods. Thus, the totals for litter plus soil of most major groups was greater at cob sites in May, whereas in September the totals for stalks sites were greater.

When total site numbers are calculated per gram of carbon in the litter, it would appear that the residual availability of energy substrates for animal populations was greater in stalks and leaves than in corn cobs at each sampling date (Table 6).

A similar calculation relating animal numbers in soil to carbon in soil indicates no difference in availability of energy to soil populations in May or July (Table 5). In September, however, it would appear that more energy was available to soil animals under stalks than under cobs.

The indicated differential in energy substrates in soil in September was not reflected in the analyses for soil C, since differences in soil C under the two litters were not significant. There is evidence that organic materials were translocated from both litter materials into the underlying soil during the season, increases in soil C after May being significant under stalks.

The average increase in soil C for the two materials, from May to September, was .05 percent. This is equivalent to 34 g C or 58 g humified organic matter per $m^2$ to a depth of 5 cm. If allowance is made for respiratory loss, actual transport into the 0-5 cm soil stratum could have been 2 or 3-fold greater. Thus, the increases in soil carbon lead readily to the estimate that as much as a ton of organic matter per hectare (litter fragments, excreta, etc.) were translocated from litter into the 9-5 cm soil layer during the 5 months of the study.

The higher carbon content in May under cobs than stalks indicates that substantially larger translocations had occurred prior to the study period, as might be expected due to the greater numbers of larger animals, notably Diptera (Table 1).

It is probable that soil populations are dependent upon surface litter for a continuing supply of energy substrates and that mobile larger animals play an important role in this transfer of energy from litter into the soil. In this connection, it may be noted that Chilopoda and Coleoptera increased in September to much larger numbers in soil under stalks than under cobs (Table 1). Diptera and Hymenoptera were also present and would have contributed to downward transport of substrates.

A unique feature of arthropod populations in September was the very large number of Acarina encountered in soil under corn stalks. It is likely that these were supported by substrates translocated from the litter by the increased numbers of larger animals with which they were associated.

## Changes in Soil Nutrient Status

Soil tests for pH and extractable nutrients are given in Table 9. Except for $NH_4$ and $NO_3$, significant to highly significant main effects and interactions were expressed.

Ammonium concentrations of 30 to 40 ppm were maintained through the season in soil under both litters. In adjoining experimental areas, concentrations in excess of 10 ppm $NH_4$ - N are rarely encountered in cultivated soil after May due to rapid conversion to $NO_3$. Here, in soil under litter and in the absence of growing vegetation to remove it, nitrate nonetheless did not accumulate and remained at low levels throughout the study period.

Exchangeable cations appeared in increasing concentrations in soil under litter as the season progressed (Table 9). Calcium and magnesium accounted for most of the increase during the study period. Since potassium in plant materials is readily leached, its major movement from the litter would have occurred during the winter and spring before the first sampling.

Exchangeable potassium was significantly higher under cobs than under stalks. This relates to the fact

TABLE 9.--Soil nutrients and acidity under corn cobs and stalks in relation to sampling date.

| Litter Site | Date | Exchangeable | | | | | Available P | pH |
|---|---|---|---|---|---|---|---|---|
| | | $NH_4$-N | $NO_3$-N | K | Ca | Mg | | |
| | | ppm | | | | | | |
| A. Soil Analyses (12-plot means) | | | | | | | | |
| *Soil under cobs* | May 22-24 | 39.93 | 1.34 | 105 | 347 | 69 | 7.3 | 5.90 |
| | Jul 15-17 | 34.24 | 1.39 | 121 | 410 | 77 | 7.3 | 5.96 |
| | Sep 14-16 | 38.32 | 1.39 | 119 | 621 | 104 | 8.3 | 6.23 |
| *Soil under stalks* | May 22-24 | 32.03 | 1.39 | 87 | 410 | 72 | 5.6 | 6.03 |
| | Jul 15-17 | 34.24 | 1.39 | 87 | 440 | 80 | 7.0 | 6.00 |
| | Sep 14-16 | 30.42 | 1.39 | 89 | 694 | 128 | 8.0 | 6.23 |
| *LSD (05) dates within sites* | | ns[1] | ns | 8 | 72 | 6 | .6 | .06 |
| *LSD (05) sites within dates* | | ns | ns | 5 | 22 | 5 | .3 | .05 |
| B. Probabilities (P) for significance of F associated with replication, dates, sites and strata | | | | | | | | |
| Category | df[2] | | | | | | | |
| *Replication* | 11/22 | NS[3] | NS | <.0005 | 1.000 | <.0005 | .022 | <.0005 |
| *Dates (D)* | 2/22 | NS | NS | .065 | <.0005 | <.0005 | <.0005 | <.0005 |
| *Sites (S)* | 1/33 | .050 | NS | <.0005 | <.0005 | <.0005 | <.0005 | .001 |
| *SXD* | 2/33 | NS | NS | <.0005 | .009 | <.0005 | .002 | .031 |

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[1] ns = non-significant P (0.05)

[2] df = category degrees of freedom/error degrees of freedom

[3] NS = non-significant at P (0.10)

that the initial weight of litter at cob sites was 3-fold or more greater than at stalk sites (Table 6).

Soil pH increased between the July and September samplings (Table 9). This was due to a large net release of calcium and magnesium. The accelerated release, at this time, of basic cations suggests that marked qualitative changes were taking place in the nature of organic materials being translocated from the litter, as well as in the residual humified materials appearing in soil through continued degradation of previously translocated materials. It is to be expected that changes in concentration of mineral species and in soil pH at local sites of animal and microfloral activity would have been much greater than detected by gross soil analyses.

# DISCUSSION

The animal populations which were observed here at 2-month intervals from May to September were similar in many ways to populations which have been described in grassland, agricultural and forest soils. The numerically dominant groups were Acarina and Collembola, present in numbers well within the range reported by others (Curry, 1969a; Davis, 1963; Dhillon and Gibson, 1962; Salt *et al*., 1948; Wood, 1967a). The dominant Collembola species encountered in this study, *Isotoma eunotabilis*, *I. viridis* and *Entomobrya griseoolivata*, are commonly found in Michigan in leaf litter, grass sweepings and field soils (Snider, 1967).

Large arthropods were present in substantial numbers in all samplings. Many of these animals or their progenitors would have made their initial invasion into litter the previous fall. Although present in lower numbers than the mesofauna, the biomass of Diptera, Coleoptera, and Chilopoda would have been much greater (Edwards, *et al*., 1970). Their activities in macerating litter, translocating litter fragments and feces, and in developing subterranean passageways and living spaces would have been an important factor determining the distribution of the Collembola and Acarina (Wallwork, 1970).

The greatest numbers of Collembola were observed in the litter in May, but in the soil not until July. Many workers have reported seasonal maxima for Collembola between late autumn and early Spring, declining to minimal numbers in the summer months (Davis, 1963; Haarlov, 1960). The apparently later decline in Collembola populations in the present study may have been due to the unusually large quantities of litter present on the sampling sites (Table 6). Dry matter present in the piles of cobs in May was equivalent to 43 metric tons per hectare (19 tons English per acre). Stalks and leaves had not been chopped or spread, and dry matter on the sites sampled was equivalent to 17 tons per hectare (8 tons/acre).

The Collembola and Acarina together comprised a rather constant proportion of the total arthropod population (90-97%). Within their combined total, however, the proportion of Collembola declined (Fig. 8). It is tempting to infer that this reflects an antagonistic relationship, Acarina preying on Collembola. However, since predatory species are present in both groups, predation pressure could work to reduce numbers in either group (MacFadyen, 1952; Sheals, 1956; Poole, 1959; Sharma and Kevan, 1963a). Also, both groups have predators among the Chilopods, Araneida and Coleoptera (Kevan, 1962; Kühnelt, 1961; Wallwork, 1970). Reproductive behavior, life cycles and ecological successions must be considered, as well as effects of changing temperature, moisture and substrate availability (McMillan, 1969; Dhillon and Gibson, 1962; Weis-Fogh, 1948).

No simple explanation for the behavior of Collembola and Acarina appears when their numbers are compared with moisture and temperature in litter and soils (Fig.10).

It would appear that Collembola in the May sampling were more tolerant of cool temperatures and high moisture than the Acarina. In particular, Acarina appeared reluctant to move into very moist soil at 12 to 13°C (cf. Table 3).

Both groups had moved extensively into the soil in July. The moisture content of the soil was now down to field capacity (1/3 at m tension), and would probably have been favorable for most animals considered in this study. The negative temperature gradient from air to litter to soil during this period of high summer temperatures was probably responsible for the marked shift from litter to soil observed for most major groups in Tables 1 and 3 (Murphy, 1953; Bellinger, 1954; Poole, 1961; Dhillon and Gibson, 1962; Wallwork, 1970). The diurnal traffic of larger animals between soil and litter would have served to maintain a substrate supply for the smaller forms in the soil (Cloudsley-Thompson, 1964).

Temperatures were somewhat cooler in September, but the air-litter-soil gradient was such that a larger proportion of animals were still found in the soil than in the litter (Table 3). The temperatures were not low enough to have interfered with growth or reproduction in Collembola (Hale, 1965a, b; Sharma and Kevan, 1963 a, b). Collembola do have high moisture requirements (Mayer, 1957; Christiansen, 1964), however larger numbers of Collembola were found in the slightly drier soil under corn stalks (Table 5).

Thus it would appear that factors other than moisture and temperature were involved in this late season decline in Collembola. The low juvenile/adult ratios suggest that reproductive activity was low and that Collembola populations were declining in vigor, perhaps due to exhaustion of appropriate substrates.

It has been pointed out by McMillan (1969) that effects of temperature and soil moisture on Acarina numbers frequently cancel one another out because the two are usually highly and negatively correlated. Both Acarina and Collembola species appear to have similar requirements for high moisture (humidity) but Acarina may prefer somewhat higher temperatures. This difference in temperature response would explain the behavior of the two groups in May but not in September.

There was a marked increase in exchangeable bases, accompanied by a small but highly significant increase in soil pH in September (Table 9). These gross changes likely reflect much more drastic microenvironmental changes, perhaps directly beneficial to Acarina, but also indicative of changes in the nature of organic materials being decomposed in the litter or in the soil. In other words, degradation had proceeded to a point where net mineralization of minerals could proceed. Readjustments in microfloral populations might be expected at this time.

For example, fungi normally initiate decomposition of plant materials and are later superceded by bacteria and streptomycetes. Increasing pH would favor this succession. Many species of Collembola are grazers on fungi, whereas Acarina are incompatible with large fungal populations (Kevan, 1962; Wallwork, 1970). It has been noted by Curry (1969c) that Acarina appear in large numbers during later stages in decomposition of grass herbage.

Changes in C/N ratio during decomposition of plant materials provide a gross index of the degree of decomposition and of energy balance in relation to net immobilization or net mineralization of mineral nutrients, notably N.

Net immobilization of N occurs during early stages of decomposition of plant residues containing less than 1.2% N and frequently with residues containing up to 1.8% N (Bartholomew, 1965; Harmsen and Kolenbrander, 1965).

Critical C/N ratios for different plant materials vary with the energy availability of carbonaceous constituents. Net immobilization will be associated with narrower C/N in materials containing a large proportion of carbohydrates (cellulose, hemicellulose) than in materials in which a substantial proportion of the carbon is present as lignin. The physical properties and chemical nature of lignin make it relatively much less accessible for enzymatic degradation and lead to a much lower yield of energy to the microflora. The dilution of available energy associated with increasing lignin content reduces the size of the microbial population which can develop and its requirements for N and other nutrients.

Because of these variations in the availability of energy due to varying lignin content, critical C/N ratios for net immobilization vs. net release of mineral N vary over a range of about 25 to 1 to 35 to 1.

The nature of organic components in the two litter materials was not examined. Such determinations will be necessary in more critical studies. The differences in C/N ratios of the two litters during the study period (Table 6, Fig. 10) were probably influenced both by differences in their initial composition and by the probability that the corn cobs had lost more dry matter, hence more carbon, during the fall, winter and spring prior to the May sampling. The low N content and wide C/N ratio of both litter materials (Table 6) would have led to extensive immobilization of both $NH_4$ and $NO_3$, at least in May, if they had

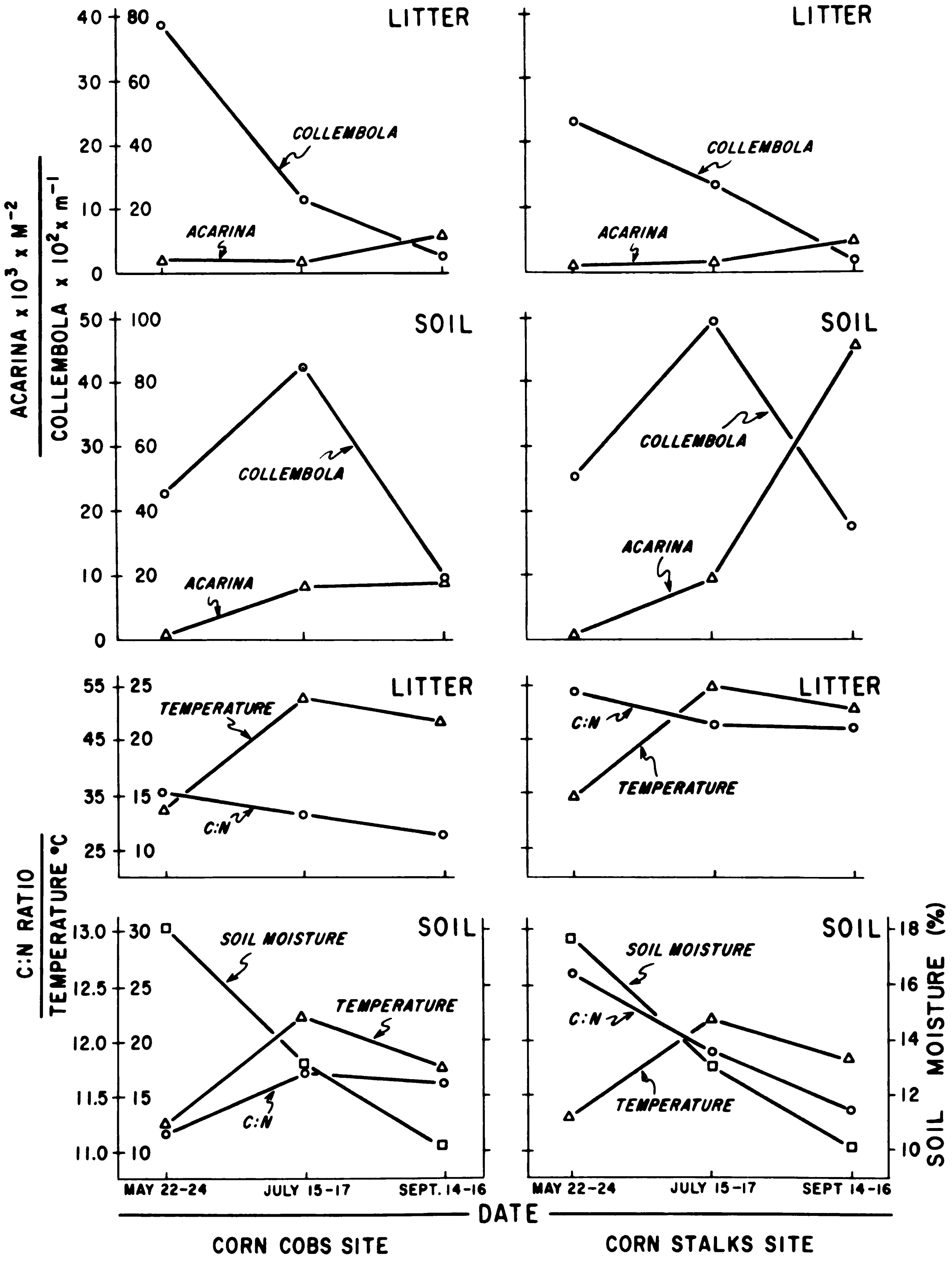

Fig. 10. Numbers of Collembola and Acarina in litter and soil under litter (above) in relation to litter and soil parameters at sites associated with corn cobs (left) and corn stalks (right).

been plowed down or otherwise incorporated into the soil. Increasing N contents and decreasing C/N ratios (Table 6) indicate that energy balances <u>within the litter layer</u> were, in fact, favorable for net immobilization of N in both litter materials.

In the soil under both litters, however, $NH_4$ accumulated and was maintained at unusually high levels through the 5-month period of the study (Table 9). This indicates that the organic materials actually being translocated into the soil were different than the bulk of the materials in the litter. Their energy content had been reduced to the point where further decomposition could proceed without net immobilization of N. It appears reasonable to infer that much of the translocated organic matter was delivered in the soil as feces and that its average energy content had been substantially reduced by earlier decomposition in the litter layer and during passage through the digestive systems of transporting animals.

The temporary isolation of surplus energy in surface litter serves to minimize direct competition between decay populations and the roots of plants. Animals in such systems play a number of roles. Among these would appear to be the translocation into the soil of organic materials substantially reduced in energy and/or enriched in minerals, so that further decomposition is accompanied by net release of minerals in the root zone.

Animals themselves contribute to the dissipation of energy from translocated organic materials. However, microbial decay populations acting directly on the litter, and gut microflora must be credited with the major release (Edwards, et al., 1970). There is also the probability that animals may feed selectively on certain components of the litter, or that they may draw upon both litter and soil, to balance their requirements for minerals and energy.

In situations where macrofauna are present, it is likely that the mesofauna play somewhat different roles than when larger animals are absent or present in small numbers. In the present study, the total of Acarina plus Collembola tended to vary with, and as a fairly constant proportion of, the total arthropod population. This suggests that the two groups occupied similar niches in relation to the total population. One important role would be as secondary decomposers, feeding on feces distributed through the litter and in the soil by more mobile larger animals.

In relation to immobilization-mineralization balance, coprophagous species would be important in reducing energy/mineral ratios.

Although an energy balance favoring net release of $NH_4$ was maintained in the soil, nitrate did not accumulate (Table 9). In many forest soils, nitrate does not appear because nitrifying bacteria are inhibited by certain water-soluble compounds (polyphenols in particular) which enter the soil from the canopy or from decomposing surface litter (Messenger _et al_., 1972). However, the fact that ammonium did not increase from one sampling to the next and that nitrate was present in detectable quantities suggests that an active nitrifying population was present. It then becomes necessary to postulate that nitrate and/or nitrite were removed as rapidly as formed, by re-assimilation or by chemical and/or biological denitrification (Broadbent and Stevenson, 1966; Frederick and Broadbent, 1966).

Soil organisms do not assimilate nitrate readily if ammonium is also present, since ammonium is preferred by most microflora. Thus, denitrification appears the most likely explanation for failure of nitrate to accumulate. One implication of this conclusion is that substantial quantities of nitrogen carried over in litter from the previous crop was recycled back into the atmosphere. Another implication is that a crop growing in the presence of surface litter may be maintained on ammonium rather than nitrate nutrition for substantial portions of its growth period, and this may influence its requirements for other nutrients (Thompson, 1966).

Another factor which may influence crop performance under no-till or trash mulch management derives from the fact that surface mulches decompose much less rapidly than the same materials incorporated into the soil. Slower decomposition delays the release of mineral nutrients carried over in residues from the previous crop, even when energy balances favor net mineralization.

In the present study, rapid release of Ca and Mg did not occur until September (Table 9). Phosphorus released by this time would have been of no consequence to a growing crop. Such effects on the seasonal pattern of release of recycling nutrients can influence materially the fertilizer requirements of a crop, as well as appropriate placement and time of application.

Decomposition of litter and release of nutrients take place rapidly in mull litters which supply energy materials and nutrients favorable for development of large macrofaunal populations. Organic materials are translocated in larger quantities and to greater depths in mineral strata under mull than in mor situations where animal populations are principally Acarina and other meso- or microfauna. Large animal activities are reflected by much more friable, well-aggregated structure in the upper mineral horizons of mull soils (Wood, 1967b; van der Drift, 1970).

By analogy, under conditions of no-till or trash mulch management, it can be expected that the rapid release of carryover nutrients and beneficial effects on soil structure will depend on activities of larger animals (earthworms, macro-arthropods). Mesofauna and microfauna, and their interactions with the microflora cannot be ignored, however, since these are responsible for actually dissipating much of the energy carbon. Dissipation of carbon is the essential process whereby mineral nutrients tied up in organic residues are concentrated to the point where net release of the nutrients in forms available to the succeeding crop can occur.

Minimum tillage concepts, including non-tillage, are being adopted rapidly by U.S. farmers in many areas. It becomes important to examine the roles of soil animals in such systems and to assess the effects of management practices such as chemical pest control on important animal groups. An attempt was made here to identify important groups and to point out probable functional relationships for future investigation.

# CONCLUSIONS

An important factor in successful application of no-till management concepts has been the development of chemical methods for control of weeds and of disease and insect pests. The use of chemicals to control insect pests can result also in the elimination of beneficial soil animals. Therefore, it becomes important to identify beneficial animals and evaluate their roles so that rational judgments can be made regarding probable benefits and hazards from pest control practices.

The preliminary nature of the present study does not support any generalized conclusions. The data do draw attention to several aspects of animal activity and fauna-microflora interaction which warrant critical investigation.

## 1. Relation of Macroarthropods to Soil Structure

The role of earthworms in generating soil structures favorable for development and function of plant roots in agricultural soils has been and continues to be studied intensively. Earthworms were not numerous in the study area, and this is frequently the case in cultivated soils.

Fairly large numbers of Chilopods and larvae of Coleoptera and Diptera were encountered. These animals include active burrowers. The nature of macroarthropod effects on soil structure under litter from agricultural crops and the extent to which these effects influence root distributions need to be examined and evaluated.

### 2. Material Transport by Macroarthropods

Increases in soil carbon over the 5-month period of this study indicate that as much as a ton per hectare of organic material was translocated into the top 5 cm of mineral soil. Under trash mulch systems of management, soil-litter animals are the principal agents for incorporation of crop trash into the mineral soil. The rate of translocation and the depth of incorporation will determine, very largely, the distribution of recycled mineral nutrients in the root zone and the seasonal pattern of their release.

Crops characteristically develop shallower root systems under surface trash than in plowed soil. Altered moisture and temperature relationships are involved. However, the distribution of recycled nutrients and the nature and stability of favorable soil structures are probably overriding factors determining root distribution.

It appears important to assess the material transport capabilities of important macroarthropods and to evaluate management practices which may influence this activity.

### 3. Population Structure and Dynamics in Relation to Dissipation of Carbon and Cycling of Mineral Nutrients

Together, Acarina and Collembola comprised 90 to 97% of the animals counted in this study. Changes in numbers and vertical distribution of this mesofaunal component paralleled changes in dominant groups in the macrofauna. It was inferred that the distribution of Acarina and Collembola was determined mainly by the distribution of substrates deposited as feces and litter fragments by mobile larger animals. In particular, large soil populations of Collembola and Acarina were probably maintained on substrates transported by the diurnal traffic of larger animals between litter and soil.

Thus, the mesofauna would have entered into the decomposition process as secondary decomposers. The respiratory capacity of these small animals, per unit biomass, is much greater than that of larger animals. Their activities represent an important stage in the dissipation of carbon and enrichment of residues with N and other minerals which must precede net release of mineral nutrients available to plants. Coprophagy would be among the important mechanisms for stepwise dissipation of surplus energy.

Experimental designs and modeling concepts for studying population structure and dynamics in relation to cycling of energy and nutrients are being developed, but mainly in relation to non-agricultural litter associations. Similar studies are needed in relation to agricultural crops and management practices.

### 4. Fauna-microflora Interactions

A striking feature of the mesofaunal population in the present study was the apparent progressive replacement of Collembola by Acarina as decomposition proceeded. The appearance of Acarina in increased numbers at advanced stages of decomposition has been reported by others.

An important interaction with the microflora may be involved. Thus, Collembola are known to graze on fungi, whereas Acarina are adversely affected by large fungal populations. Fungi normally initiate the decomposition process and are later superceded by bacteria and streptomycetes.

Studies of the parallel changes in fauna and flora associated with varying stages of decomposition have not been reported and were not attempted here. They should prove informative. In such studies, changes in minerals and pH should be considered. In the September sampling of this study, large decreases in Collembola and increases in Acarina were associated with a large release of basic cations and an increase in pH. Increasing pH, magnified in microhabitats, would favor a microfloral succession from fungi to bacteria and streptomycetes.

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