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PARTITIONING THE BIOTIC AND ABIOTIC EFFECTS ON DECOMPOSITION AND MINERALIZATION

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TABLE OF CONTENTS

ABSTRACT

A litter bag study was conducted on the Pawnee grasslands using chemicals ($HgCl_2 + CuSO_4$) to exclude microbes (abiotic treatment), 53 μm nylon mesh to exclude mesofauna (microbial treatment), and 1 mm nylon mesh to allow the access of mesofauna while containing the blue grama grass. After 9 months, 15.24% of the blue grama grass litter was decomposed from the microbial treatment and 29.43% of the litter was decomposed from the mesofaunal treatment. After seven months 7.18% of the litter was gone from the abiotic treatment. Chemical analysis showed a general decrease in carbon-to-nitrogen ratios; the microbial treatment showed the lowest carbon-to-nitrogen ratio at the end of the experiment. Total available carbohydrates showed a decrease with time, but no effect due to treatment was found. Population analysis showed seasonal fluctuations in mite populations according to family. Among the mite populations, the Tydeids were shown to be a winter family whereas tetranychids showed strong evidence of being a summer family. Mite families were correlated to abiotic factors.

CHAPTER 1. INTRODUCTION

The Pawnee Site is a native shortgrass prairie on which ecological studies are being conducted. It is the field research facility of the Natural Resource Ecology Laboratory, Colorado State University and is located on the USDA Agricultural Research Service Central Plains Experimental Range in northeastern Colorado. This study was done on a plot approximately 20 × 20 m on the Central Plains Experimental Range, located about 19 km northeast of Nunn, Colorado.

The common soil series are Ascalon, Bona, Renohill, and Shingle. The soil series for the plots used in this experiment was Ascalon, which is formed mostly by fluvial outwash.

The predominant vegetation on the plot consisted of blue grama grass (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), fringed sagewort (*Artemisia frigida*), and plains pricklypear (*Opuntia polyacantha*).

Rainfall on the Pawnee Site is variable. The average annual precipitation ranges from 25-38 cm, about 80% of which falls during the growing season between May and September. High amounts of wind and radiation along with the low annual precipitation account for the dryness of the Pawnee Site.

The primary aim of this study was to examine the effects of three factors or components on decomposition of blue grama grass on the Central Plains site. The factors considered in this study were classified as abiotic (weather), microbial (bacteria, fungi, and actinomycetes), and mesofauna (mites, nematodes, and insects). Access of the biotic and mesofaunal components to the decomposition of the grass was controlled through the use of litter bags and chemical sterilants.

The second aim of this study was to examine changes in mite populations in the mesofaunal treatment with time. This was done to try to determine whether changes in mite populations were seasonal or successional.

A third aim of this study was to observe changes in relative amounts of carbon, nitrogen, and total available carbohydrates both with respect to treatment and time.

CHAPTER 2. REVIEW OF LITERATURE

Litter bag studies can be used to compare the contributions of various soil organisms to the disappearance of leaf litter through exclusion. Exclusion is controlled by the mesh size of the bags. To understand these experiments and to properly interpret the data, one must look carefully at all the parameters involved in each experiment. These parameters include the chemical and structural characteristics of the soil and leaves, as well as the experimental effects which alter conditions naturally present in decomposition. One must also take into consideration climatic factors such as rainfall, temperature, and radiation.

Early studies were aimed at using a mesh to simulate field conditions while containing the leaves and were not used for the exclusion principle (Falconer et al. 1933). Falconer used 5 mesh galvanized wire to make baskets and covered the bottom of each basket with cheesecloth. His purpose was to measure decomposition rates of litter of white, red, and jack pine in the field and to measure the losses of various constituents of the litter including cellulose and lignin. Falconer concluded that weight losses were related to temperature, precipitation, and lignin content. Decomposition was measured using weight loss on a dry weight basis.

One aim of litter experiments has been to measure decomposition under the most natural conditions possible. Bocock and Gilbert (1957) used nylon hair netting to contain leaves on the basis that the litter would become incorporated into the litter layer rather than staying above ground as was the case with the metal baskets. The openings in the netting were approximately 1 cm^2. The experimental design involved five deciduous leaf types in three soil types. Bocock found that leaves which decomposed easily, such as birch and lime, did so much more rapidly on a mull site than on moder and peat sites. Leaves such as oak, which decompose slowly, showed no significant differences between sites. Again, disappearance was measured by weight loss on a dry weight basis. It was also suggested by Bocock at this time that the vast difference in rates of disappearance across soil types was dependent on the soil fauna. The mull site contained many earthworms and the peat and moder sites did not. This idea agrees with the opinion of Satchell and Lowe (1966), that *Lumbricus terrestris* selects litter with the highest nitrogen and soluble carbohydrate content and the lowest tannin content.

The first use of litter bags of varying mesh size for exclusion purposes is found in a study done by Edwards and Heath (1963). They used two types of leaves in bags of four mesh sizes. The leaves were cut into discs, placed in bags and buried 2.5 cm deep in freshly plowed soil. Decomposition was measured visually by placing the leaves on a grid and estimating the percent of the leaf remaining. This estimation was checked photometrically. The experimentors concluded that earthworms were the single most important factor in decomposition because the litter within the 7 mm mesh bags (accessible to earthworms), disappeared three times as rapidly as that in the .003 mm mesh. It was also concluded that oak leaves decompose much more rapidly than beech leaves in the field. The importance of polyphenols was also mentioned.

Experiments of this type give us insight into what may be happening in the field. At the same time many questions arise about the validity of the experiment in simulated field conditions. As a result much discussion has arisen about the Edwards and Heath article (1963). Dickinson and Pugh (1974) suggested that earthworms may only be using easily digested portions of the leaves such as soluble nitrogenous compounds and carbohydrates. The soil fauna may also be pulling the leaves out of the bags as do earthworms for lining burrows, in which case the leaves are not necessarily decomposed when measurements are taken.

Dickinson and Pugh (1974), also pointed out many problems with the Edwards and Heath experiment. Litter buried 2.5 cm into newly plowed soil is subject to a much different environment than that in a natural litter layer. Also, tannins inhibit the growth of fungi. These tannins are easily leached on the soil surface and may be slow to leach when buried. Carbon to nitrogen ratios are also important in the speed of decomposition, and the available nitrogen in the plowed soil may be considerably lower than in a natural litter layer. Burges (1963) criticized the experiment on the basis that 60% of the leaf could be lost before actual pieces of the leaf were gone.

A more recent litter bag study (Anderson 1975) on the decomposition of chestnut and beech leaves also lends evidence to a large role of soil animals in decomposition. Anderson compared weight loss in fine, medium, and coarse mesh bags using the two leaf types on two types of litter. The results showed a 45% increase in decomposition due to the effect of larger soil animals such as *Lumbricus terrestris*. Two important points were made by him. First the leaves must be palatable as was shown in a faster rate of decomposition of chestnut leaves than of beech. Observations were made and a feeding preference was shown by the earthworms for chestnut leaves over beech. The second point is that the animals must be present in the leaf litter. The bags placed on the chestnut litter site decomposed more rapidly than those placed on the beech litter. In part II of Anderson's (1975) paper, an inverse relationship is shown between rate of decomposition and polyphenol content of the leaf litter. This relationship exists only across species types and not among leaves of the same species. King and Heath (1967) suggest that it may be important to look at gallic and protocatechuic acids rather than overall polyphenol content.

Both Anderson (1975) and Edwards and Heath (1963) showed a tremendous increase in decomposition when the leaves were palatable and soil animals, such as earthworms and isopods, could get to the leaves. Anderson also showed that the presence of mesofauna such as Acari, Collembola, and Dipteran larvae made a less significant contribution to the decomposition of the chestnut leaves than did the earthworms, yet the effect was still statistically significant.

Chemicals can also be used to exclude certain fractions of soil organisms. Kurcheva (1960) used napthalene to kill the invertebrates in oak leaves without appreciably effecting the microbial populations. Piles of oak leaves were used, covered with wooden frames. During the course of the experiment, 2.5 kg of naphthalene per meter square was poured over the leaves to exclude the invertebrates and counts were taken periodically to test the effectiveness of the napthalene. On the naphthalene-treated plots with no invertebrates, 9% of the litter decayed in 140 days, whereas 55% of the litter was gone in the untreated plots.

As part of the same experiment Kurcheva tried to determine the direct role animals play in humus formation. This was done by measuring the amount of humus in the animal excrement by determining the quantities of acetyl bromide - soluble organic matter in fresh leaves and in the animal excrement. Humic substances are thought to be soluble in acetyl bromide. Kurcheva found only a small increase in humic substances. She also implies that animals produce less humic substances when eating leaves which are less digestible such as oak and beech.

Crossley and Witkamp (1964) tried using naphthalene to selectively reduce arthropod populations without killing the microorganisms. They found that naphthalene actually increased the numbers of microorganisms so that the effect of soil animals on decomposition was actually underestimated. They found that untreated litter lost 60% of its weight, whereas naphthalene treated litter lost 45% of its weight in one year. Again a greatly increased rate of decomposition was attributed to soil animals.

Zlotin (1970) also used naphthalene to exclude soil animals as well as toluene to exclude microbes. This technique was in combination with the use of varying mesh sizes of nylon bags. Zlotin compared percent decomposition for four exclusion factors in grass on the steppes of the central Chernozyomony Reservation and in an oak forest. The exclusion results for oak litter were abiological decomposition 8%, abiological plus microbial decomposition 12%, decomposition with mesofauna admitted 25% and decomposition with macrofauna admitted 35%. In steppe grassland, abiological decomposition was 21%, abiological plus microbial decomposition 24%, decomposition with mesofauna admitted 28%, and decomposition with macrofauna admitted 32%.

Zlotin concluded that the overall decomposition rates of 35% for the oak leaves and 32% for the steppe grass were equal but the rates were attributable to different factors. In the oak forest the most important factors were the meso- and macrofauna. The steppes were too dry in the summer to support much trophic activity of these organisms, and as a result, the most important factors in decomposition on the steppes were the abiotic ones such as wind and sun. It should be kept in mind that different leaf types were used at the two different sites.

In addition to the naphthalene, Zlotin used toluene to maintain sterile conditions inside the abiotic treatment. No quantitative indication was given by Zlotin as to the effectiveness of these chemicals in excluding soil organisms or to the ability of these in leaching organic compounds.

Curry (1969) also studied the decomposition of grassland herbage. Fine, medium, and large mesh bags were placed on the surface and also buried 7.5-10 cm below the surface. Curry found, as did Zlotin, a small but significant difference in the rates of decomposition between the medium mesh bags which prevented the entrance of macrofauna and the large mesh bags which permitted the macrofauna to enter. Curry's data show decomposition rates of 59.8% for fine, 62.4% for medium, and 63.4% for course mesh bags for a 9½ month period. A 3.6% increase in decomposition falls far short of the three fold increase that Edwards and Heath (1963) showed in oak leaves, yet it agrees with the findings of Zlotin (1970), which was also conducted on a grassland herbage. In an effort to explain the discrepancies with Edwards and Heath, Curry suggests that the grass was packed too densely in the bags which decreased the ability of the macrofauna to feed on the entire surface area of the litter.

Litter bags have also been used to look at feeding behavior (Wallwork 1958), arthropod succession (Crossley and Hoglund 1962; Anderson 1973; Howard and Howard 1974), and the effects of one or two dominant species (van der Drift and Witkamp 1960; Bocock and Gilbert 1957).

Observations on the specific feeding behavior of mites as given by Wallwork (1958), Woolley (1960), and Baker and Wharton (1952), inspired Crossley and Hoglund (1962) to study succession in litter bags. It was thought that if characteristics such as particle size, chemical composition, and microbial populations of litter changed with time then so would the arthropod populations. Crossley and Hoglund (1962) also compared arthropod numbers between pine, oak, and dogwood. They concluded that moisture was the most important factor influencing the numbers of arthropods present in the bags and that the numbers were also highest in dogwood litter, which decomposed most rapidly.

Numbers were given for the genus *Tydeus* as a function of time. Populations were extremely high in winter months and sharply decreased to summer. Core samples of natural litter were taken for comparison with the numbers in the bags. It was found that numbers were unusually high in the bags and that a "bag" effect existed.

Three arthropod groups were measured by Stevanovic (1968), in relationship to the decomposition of three litter types, oak, hornbeam, and mixed litter. Collembola, Oribatei, and other microarthropods were examined. The study was conducted for an eleven month period after which the bags were retrieved, the arthropods extracted, the bags dried, weighed, and placed back in the field. Unfortunately it is difficult to tell whether the arthropod groups changed numbers because of season or succession, as the study ran for only eleven months. Stevanovic concluded that the groups showed seasonal phases in their colonization.

Wiegert (1974) measured arthropod populations in litter bags in three South Carolina old fields. Percent moisture content of the grass was measured as a function of mite populations. Wiegert classified the soil arthropods as mites, Collembola, and other arthropods. A direct relationship was found between the number of mites and the log of the percent moisture content of the bags. Wiegert concluded that the hot dry litter prevents a permanent establishment of soil arthropods and that the arthropods are moving into the bags during periods of high moisture and low temperatures.

Wiegert (1974), Stevanovic (1968), and Crossley and Hoglund (1962) all found seasonal changes in arthropod populations. None of these studies gave any indication of successional changes. The hypothesis that microbial succession was taking place and therefore faunal succession should follow had not been proven. Because none of these studies ran for over a year it seems that the hypothesis had not even been tested.

Anderson (1975) studied succession in litter bags containing beech and chestnut leaves over a 20 month period. Oribatid mites were identified to the species level and the other arthropods were identified to the family level. In addition, the gut contents of the mites were analyzed to observe changes in feeding patterns with time. From the data collected concerning fluctuations in numbers, a successional change was seen most clearly in the enchytraeids and a seasonal change was seen in the Harpacticoidea. Analysis of gut contents showed changes in feeding preferences over time. Chironomids fed almost exclusively on fungal material during the winter of 1968-1969 and extensively on plant material later on in the study. Oribatid mites showed slight feeding preferences. These individual preferences also changed during the course of the study. Whether these changes were seasonal or successional is not clear from the data presented. The changes in populations of soil animals for beech and chestnut leaves closely followed each other and as Anderson shows, the population fluctuations appeared to be synchronous.

The significance of soil animals in the decomposition of leaf litter may also be approached by measuring the effects of a single family or species. Van der Drift and Witkamp (1960) measured the consumption of leaf litter by the caddis fly larva of *Enoicyla pusilla*. Measurements of the leaf consumption on an air dry weight per day basis were made from March till June. The average percent of food retained was measured to determine a food assimilation rate of 7%. The larvae consumed 4.2 mg of leaves per day on a dry weight basis. The total consumption of leaves for the entire period of March to June was 100 times the daily figure. Growth of the larvae was also measured to obtain a growth/assimilation ratio of 29%. Van der Drift and Witkamp emphasized that although a loss of only 7% of the leaf material took place due to larval digestion the fecal pellets formed are subject to much more rapid decomposition than the leaf material.

Earthworms and their effect on soil fertility has been studied to a large extent. B. M. Gerard (1963) described what is known about Lumbricidae and how they were responsible for increased yields due to aeration of soil, breakdown of leaf material, and effects on crumb size.

J. A. van Rhee (1963) discussed visual observations made on the effect earthworms have on soil. Van Rhee characterizes mull and mor soils and explained the layer differences by saying that mor soils have no animals such as earthworms which turn over the soil by feeding on the surface and burrowing deep into the soil. He also pointed out instances where earthworms were killed off and a litter layer subsequently built up. It is interesting to note that van Rhee feels that grassland litter in moist regions is quickly decomposed by earthworms. Curry (1969) found only a small increase in decomposition due to the availability of grass herbage to soil animals.

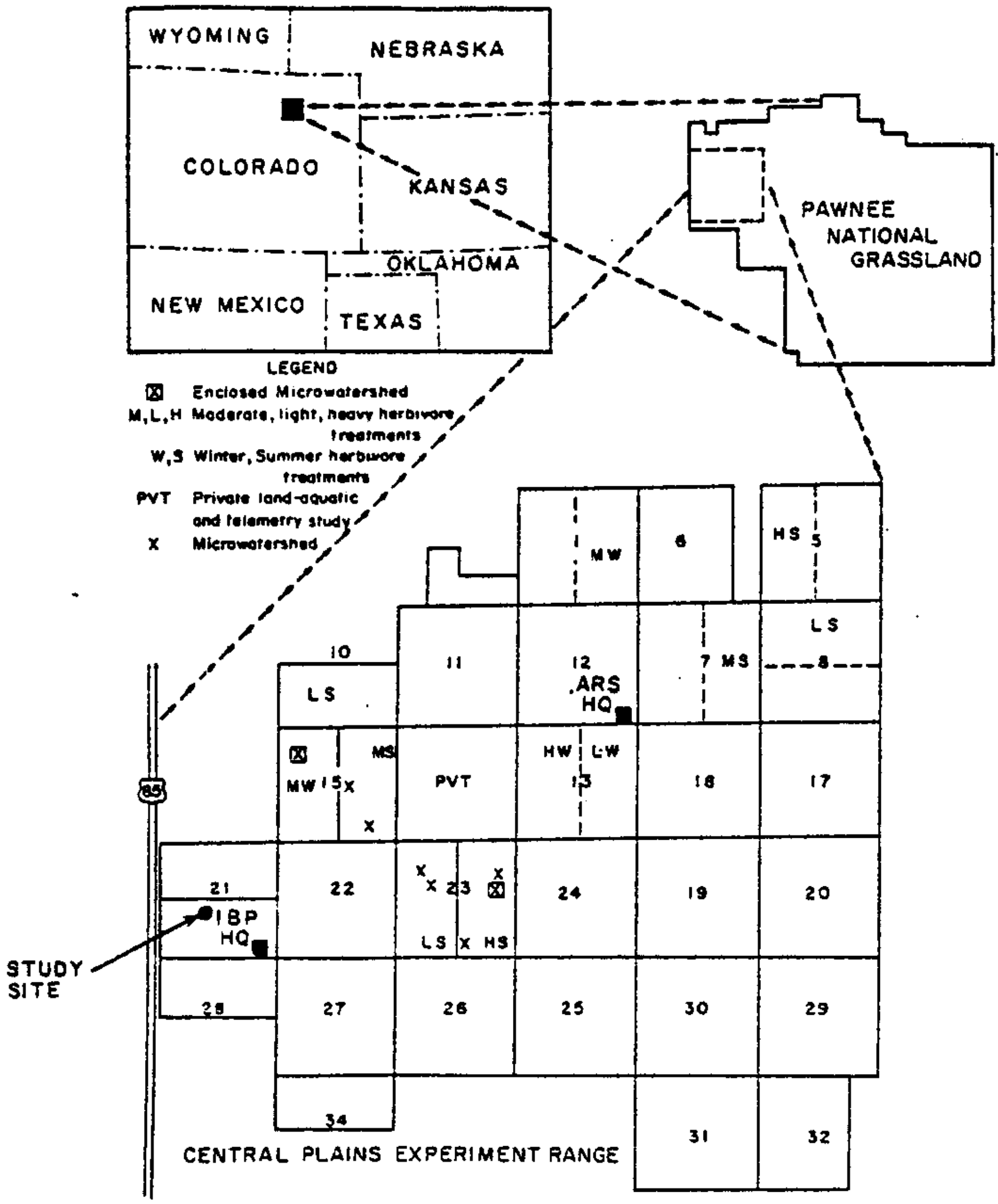
CHAPTER 3. MATERIALS AND METHODS

Litter bags of two mesh sizes were used to partition the effects of three factors, abiotic, microbial, and mesofaunal, on the decomposition of blue grama grass (*Bouteloua gracilis* H.B.K. Lag.). The larger mesh was made of nylon illusion veil purchased from a local fabric store. This mesh size was approximately 1 mm square, and was the largest mesh used so that the fragments of the blue grama leaves and the straw-like stems could be contained. To exclude the mesofauna (mites, insects, and nematodes), a 53 μm mesh nylon plankton netting was used (Wildo Supplies, Saginaw, Michigan).

Weighed samples of an average of 3 grams of grass were placed inside each 10 × 10 cm bag and sewn closed. A border was sewn around each bag so that it could be nailed to the ground without perforating the inside of the bag. All bags were then numbered using #1005 size 1-Monel metal numbered fish tags. The bags were weighed on a Mettler top-loading balance (± 5 mg) and the weights and numbers were recorded.

All bags were placed on a non-irrigated plot at the Pawnee Site on May 15, 1975 (see map for study site, p. 14). All bags were nailed directly to the soil surface in areas between patches of vegetation. In all, 350 bags were placed on the site. This provided enough bags so that once a bag was retrieved from the field, it was not necessary to use it again. This was done because it was felt that drying and reusing the bags would alter the characteristics of the grass.

Upon placing the bags in the field, half of the 53 μm mesh bags were treated with saturated solutions of copper sulfate and mercuric chloride. Each bag received about 50 ml of solution to maintain sterile conditions inside the bags. This was the abiotic treatment. Each month


WYOMING
NEBRASKA
COLORADO
KANSAS
OKLAHOMA
NEW MEXICO
TEXAS
PAWNEE
NATIONAL
GRASSLAND
LEGEND
Enclosed Microwatershed
M,L,H Moderate, light, heavy herbivore treatments
W,S Winter, Summer herbivore treatments
PVT Private land-aquatic and telemetry study
X Microwatershed
STUDY SITE
IBP HQ
ARS HQ
85
CENTRAL PLAINS EXPERIMENT RANGE

an additional 50 ml of each solution was added to each bag of the abiotic treatment to maintain sterile conditions.

Measurements of Weight Loss

At the beginning of the experiment a sample of grass was ashed at 650°C for two hours. This gave a beginning value of 6.4% ash content for the grass. At the same time another sample was dried in a drying oven at 90°C for two days to determine the percent moisture content.

On the 15th of each month, eight bags of each treatment type were retrieved from the field, dried and weighed. The samples were then ashed to determine how much inorganic matter such as sand, had blown into each bag. The percent decomposition of the retrieved bags was determined each month from knowing the initial weight of the samples, their equivalent dry weights, the dry weights of the samples after a given period of time, and the amount of inorganic matter which had blown into the bags.

Microarthropod Populations

Each month five bags of the 1 mm mesh size were processed through modified Tullgren funnels for an estimate of the microarthropods in the bags at the time of collection. The microarthropods were then identified to the family level.

Chemical Analysis

Chemical analyses were done by Range Science laboratories. Analysis for carbon was accomplished volumetrically by combustion with oxygen in an induction furnace (Leco), with absorbtion of CO_2 in alkali.

Total available carbohydrates was determined by acid hydrolysis followed by determination of reducing capacity against copper (II) in alkaline solution.

Nitrogen was done by a semi-micro Kjeldahl procedure. For a reference on the chemical analyses see Jackson (1958).

Exclusion effectiveness

Since the purpose of the 53 µm mesh size bags was to exclude all soil fauna, grass samples from the 53 µm mesh treatment were processed through modified Tullgren and Baermann funnels to check for microarthropods, nematodes, and tardigrades.

Abiotic Sterility

To check the effectiveness of the mercuric chloride and copper sulfate solutions as sterilants, dilution plate counts were done monthly for the abiotic and 53 µm mesh treatments. Dilution was accomplished by placing 2 g of the grass into a sterile flask containing 200 ml of sterile distilled water and shaking the flask for 15 minutes. This was considered to be a dilution of 10^{-2}. Subsequent dilutions (10^{-3}, 10^{-4}, 10^{-5}, and 10^{-6}) were achieved stepwise by taking 10 ml of the dilution using sterile pipetes, and placing it in 90 ml of sterile distilled water. The plate counts were done on Difco Bacto-Plate Count Agar. One milliliter aliquots were then placed in each plate when the agar was cool but not yet hard and the plates were gently mixed. The plates were then incubated at room temperature (20°C). The differentiation of colonies into the groups, bacteria, fungi, and actinomycetes was done visually on agar plates but not checked microscopically.

Abiotic Factors

Weather information concerning precipitation, wind velocity, and radiation was obtained from the IBP Weather Station, CPER, Nunn, Colorado.

CHAPTER 4. RESULTS AND DISCUSSION

Weight Loss

Weight loss was measured as percent loss with time on an ash free dry weight basis. The analysis of variance shows significant effects of treatment (α = .0000) and of time (α = .0000). Figure 1 shows the treatment effect for the pooled data of 9 months showing mean values of $\pm \frac{1}{2}Q$ (as per Snedecor and Cochran 1969). The mean weight loss for the abiotic treatment is much lower than that for the 1 mm and 53 μm mesh treatments. Although the means for the 53 μm and 1 mm mesh treatments are closer than the abiotic treatment, they still show significant difference. Figure 2 shows the combined data for treatment measured over time. A distinct weight loss with time can be observed. The sharpest weight loss took place in the winter months between November and January. The abiotic group shows a very irregular weight loss pattern with time. This pattern is hard to account for except to say that the abiotic group differed from the 53 μm mesh group only in that chemical sterilants were added to the abiotic group and that these chemicals are responsible for the fluctuations. Figure 3 shows that weight loss in the 1 mm and 53 μm mesh treatments is similar until the seventh month when the weight loss in the 1 mm mesh treatment increases much more rapidly than in the 53 μm mesh treatment. Figure 3 also shows that the abiotic treatment is significantly lower somewhat earlier in the experiment, about the sixth month. The Q value is indicated on the graph and shows a significant difference in mean values by treatment at the 95% level if the $\frac{1}{2}Q$ values are non-overlapping.

Measurements for abiotic decomposition are erratic, but show a significantly lower decomposition rate than the 53 μm and 1 mm mesh

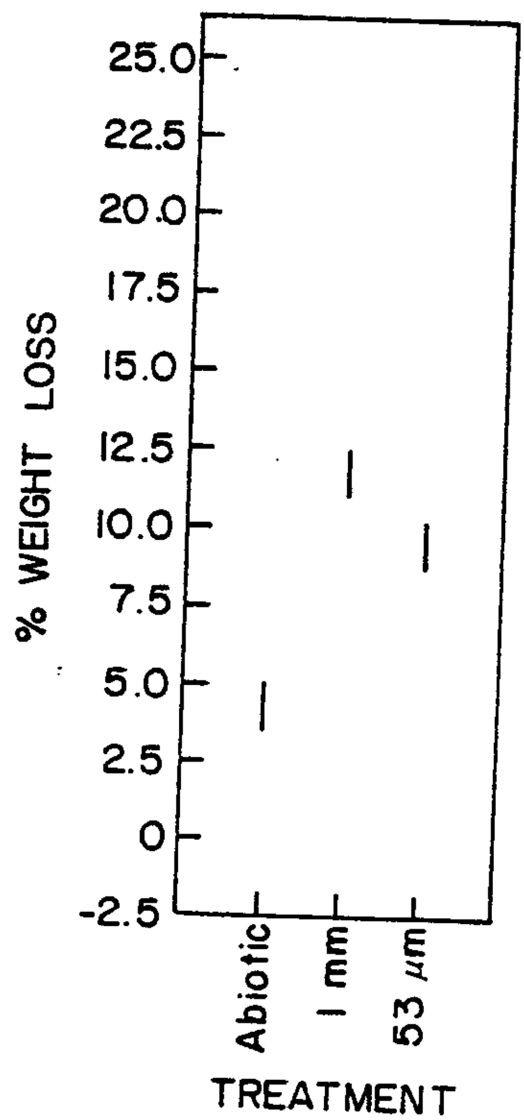


Fig. 1. Percent weight loss for each treatment averaged for the 9 months of the experiments ± ½Q.

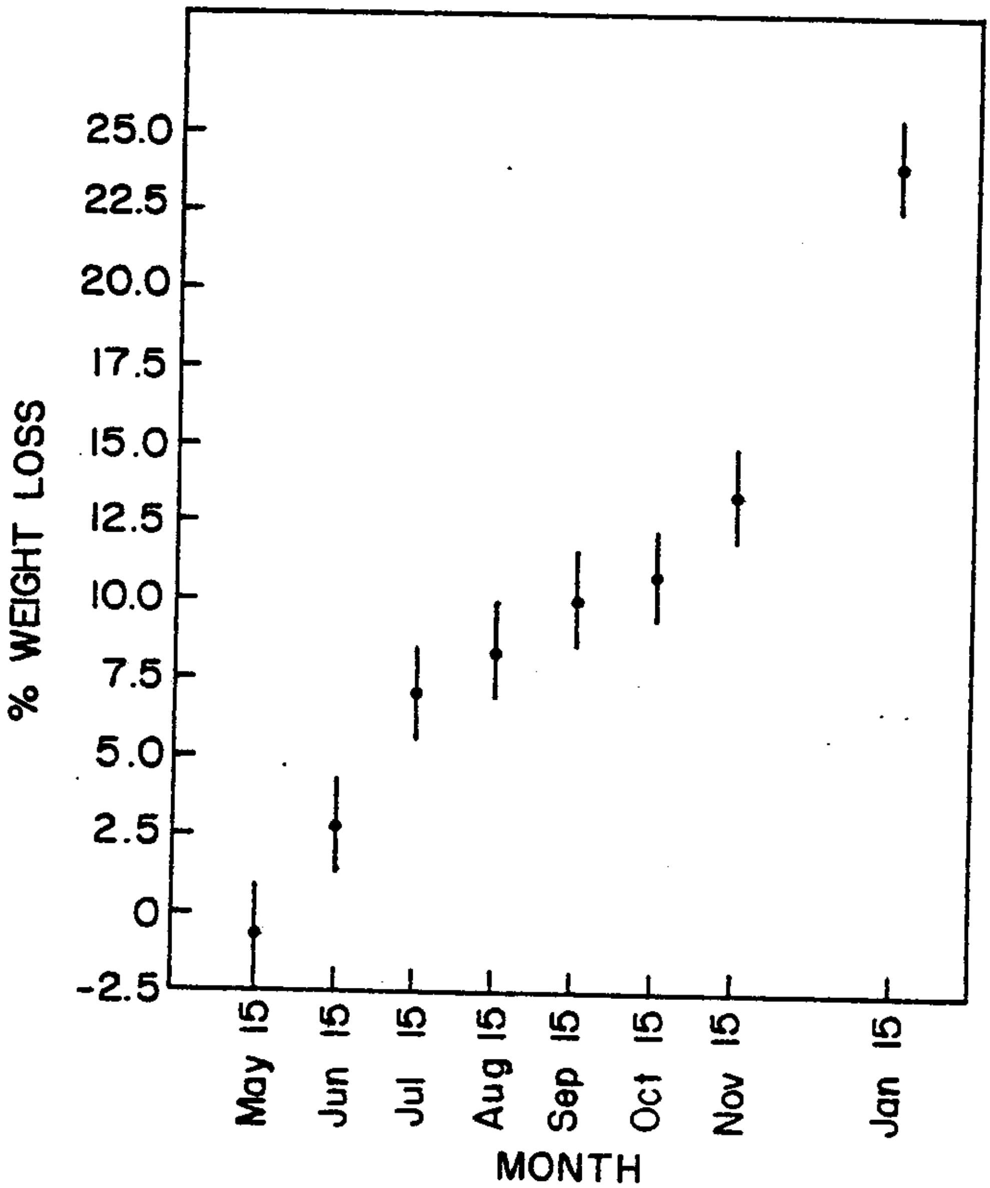


Fig. 2. Percent weight loss for combined treatments with time $\pm \frac{1}{2}Q$.

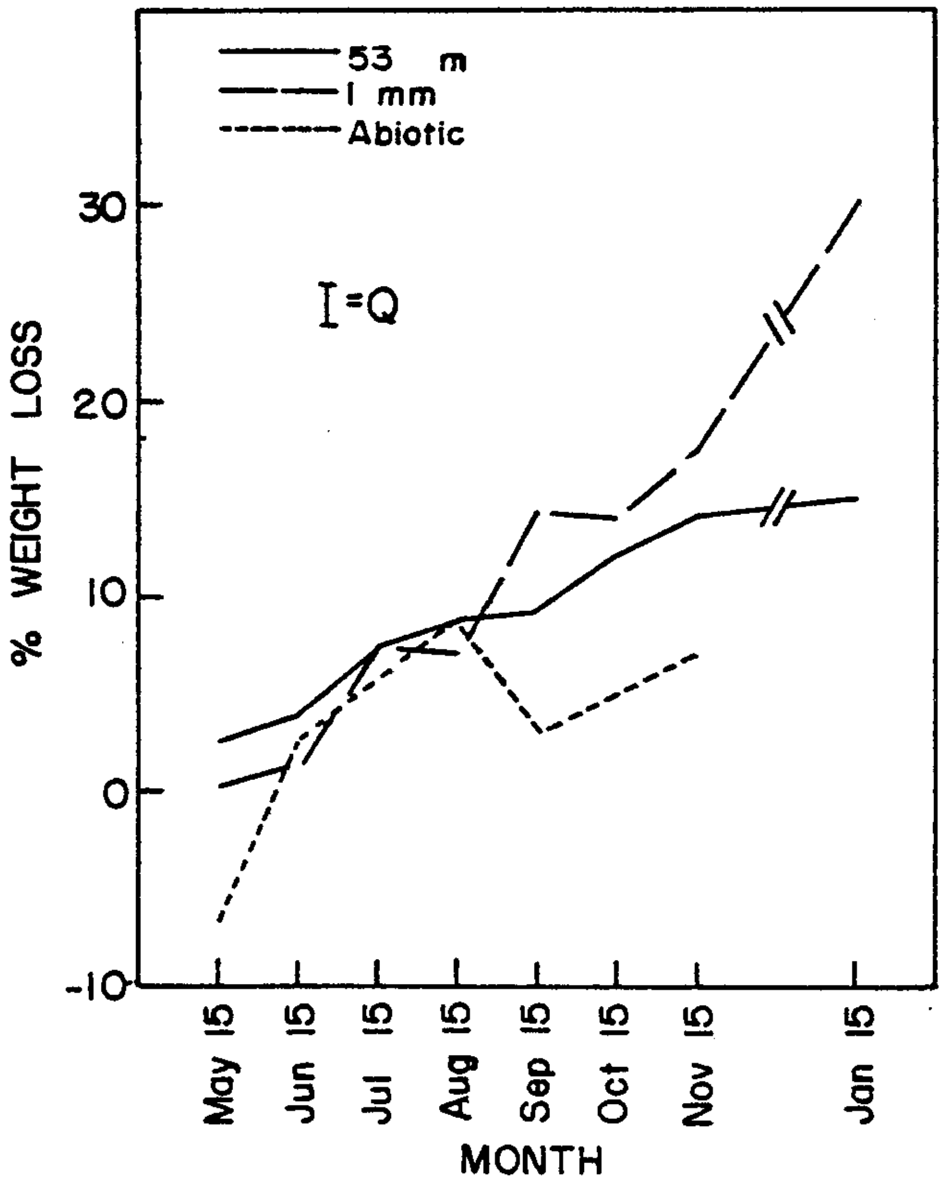


Fig. 3. Average percent weight loss with time showing all three treatments.

treatments. Data for the carbon-to-nitrogen ratios corroborate the evidence that the rate of decomposition for the abiotic treatment is by far the slowest.

After seven months only 7.18% of the material was decomposed, whereas the 53 μm and 1 mm mesh treatments had lost 14.28 and 17.8% of the litter from their bags, respectively. At seven months the mean values for the 53 μm and 1 mm mesh treatments are not statistically different. After 9 months the 53 μm mesh treatment showed a loss of 15.24% and the 1 mm mesh treatment showed a loss of 29.43%. The last two months of the experiment, December and January, indicate that microbial decomposition was slow while the effect due to mesofauna was actually enhanced. The decrease in decomposition rate of the 53 μm mesh treatment can be explained by a decrease in the growth and activity of microbes in cold conditions. The increase in decomposition rate of the 1 mm mesh treatment may be due to the large increase of mites, especially the Tydeids, during the cold months.

In this study on the Pawnee grasslands, a small but statistically significant increase in decomposition rate can be seen with mesofauna admitted into the bags. This was also the case in experiments conducted previously by Anderson (1973), Zlotin (1970), Edwards and Heath (1963), and Curry (1969). I think that the mesofauna are feeding on the microbes and small particulates of the decaying leaves. As a result of the grazing of mesofauna and the availability of the feces for microbial decomposition, a small but significant increase in decomposition occurs. The mesofaunal action is thus related to the microbial rate of decomposition.

Population Analysis

Table 1 shows the families of mites found in the bags at the times of extraction. A seasonal change is apparent when examining the populations of Tetranychidae in the spring and summer and Tydeidae in the fall and winter. High winter population of Tydeidae have already been noted by Crossley and Hoglund (1962). A correlation matrix (Fig. 4 and 5) reveals two groupings. The first group consists of the Nanorchestidae, Tetranychidae, Acaridae, Stigmaeidae, Scheloribatidae, Tectocepheidae, Oribatulidae, and Trombidiidae from May to September. The second group consists of the Tydeidae, Bdellidae, Raphignathidae, Passalozedidae, and Phytoseiidae. Each family in these two groups is directly correlated to another family within its group, at least at the 95% level of significance and has no correlation to any family outside its group. In addition, both groups contain families which show correlations to abiotic factors at the 99% level of significance.

Population analysis reveals changes in mite families with time (Table 1). The correlation matrix (Fig. 4 and 5) does not reveal whether the changes in mite families are due to succession or to changes in season, except to say that in certain instances there is a high correlation between mite families and abiotic factors. Both Nanorchestidae and Tetranychidae have a high correlation with precipitation at the 99% level of significance. Crossley and Hoglund (1962) found that Tydeids were an abundant winter group. They also found that high mite populations were related to the moisture content of the material in the bags. Anderson (1975) also showed that the mite populations were heavily dependent on moisture. Anderson (1975) examined successional changes by examining the gut contents of the mites. He

Table 1. Population data of mite families showing the numbers of individuals extracted from litter bags at the time of collection. A change in families with time can be observed.

	Family														
	Nano	Tetr	Acar	Stig	Sche	Tect	Orib	Trom	Tyde	Anys	Bdel	Raph	Pass	Phyt	Noth
May 15	10	51	1	1	1										
June 15	1	4		2											
July 15	12	18	22	1	5	3	4								
August 15		4				5	8	5	5						
September 15		2				2	3	2	4	1					
October 15							1	3	215		5	1	5	3	
November 15				1			2	1	115		2		5		
January 15							1		128		1		4		1

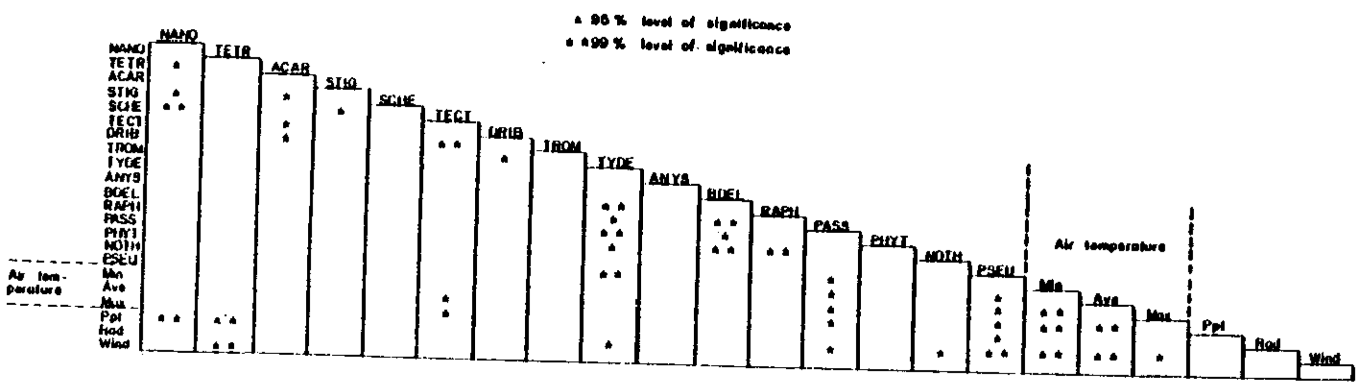


Fig. 4. Correlation matrix showing the relationships between families and the insect family Pseudoccidae of mites and their relationship to abiotic factors.

* = 95% level of significance
** = 99% level of significance

	NANO	TETR	ACAR	STIG	SCHE	TECT	ORIB	TROM	TYDE	ANGS	BOEL	RAPH	PASS	PHTY	NOTH	PSEU	Air temperature MIN	Air temperature AVE	Air temperature MAX	PPT	RAD	WIND
NANO	1.000																					
TETR	.804	1.000																				
ACAR	.605	.399	1.000																			
STIG	.745	.448	.812	1.000																		
SCHE	.851	.376	.645	.794	1.000																	
TECT	.187	-.094	.797	.478	.320	1.000																
ORIB	-.070	-.241	.708	.441	.176	.960	1.000															
TROM	-.484	-.379	.264	-.091	-.364	.618	.721	1.000														
TYDE	-.455	-.440	-.527	-.396	-.143	-.495	-.311	.140	1.000													
ANGS	-.230	-.184	-.276	-.339	-.173	.159	.095	.137	-.264	1.000												
BOEL	-.367	-.362	-.440	-.325	-.276	-.422	-.272	.262	.934	-.228	1.000											
RAPH	-.230	-.230	-.276	-.339	-.173	-.265	-.208	.356	.759	-.143	.912	1.000										
PASS	-.467	-.454	-.560	-.296	-.352	-.538	-.313	.024	.947	-.290	.827	.539	1.000									
PHTY	-.230	-.230	-.276	-.339	-.173	-.265	-.208	.356	.759	-.143	.912	1.000	.539	1.000								
NOTH	-.230	-.207	-.276	-.339	-.173	-.265	-.208	-.301	.338	-.143	.000	-.143	.373	-.143	1.000							
PSEU	-.529	-.493	-.635	-.589	-.398	-.459	-.318	.005	.841	.076	.646	.481	.801	.481	.683	1.000						
Air temperature MIN	.410	.208	.687	.426	.478	.695	.514	.281	-.691	.116	-.446	-.130	-.813	-.130	-.657	-.798	1.000					
Air temperature AVE	.369	.168	.671	.396	.451	.708	.535	.334	-.654	.140	-.401	-.081	-.787	-.081	-.667	-.765	.998	1.000				
Air temperature MAX	.305	.123	.642	.345	.392	.717	.554	.401	-.615	.172	-.356	-.031	-.761	-.031	-.678	-.730	.989	.996	1.000			
PPT	.924	.894	.540	.608	.651	.099	-.108	-.463	-.682	-.088	-.568	-.389	-.684	-.389	-.343	-.709	.500	.453	.393	1.000		
RAD	.512	.374	.590	.599	.458	.422	.277	-.016	-.764	-.102	-.516	-.353	-.834	-.353	-.780	-.970	.922	.894	.858	.659	1.000	
WIND	.508	.902	.064	.132	-.010	-.375	-.452	-.398	-.232	-.199	-.231	-.195	-.209	-.195	-.003	-.244	-.147	-.184	-.216	.652	.088	1.000

Fig. 5. Correlation matrix showing the relationships between families of mites and the insect family Pseudoccidae and their relationship to abiotic factors with all r values included.

found evidence for successional changes in Enchytraeids and seasonal changes in Harpacticoidea. Anderson (1975) showed also that the fluctuations in mesofaunal groups were the same in both chestnut and beech litter. This indicates that most changes in populations are due to climatic changes and not successional. The analysis of gut content shows that the mesofauna are generalized feeders, changing their diet with season. It appears that niche separation is spatial with time and that some trophic separation exists according to the size of the animal.

Chemical Analysis for Decomposing Litter

Analysis of carbon and nitrogen was done for all three treatments. Analysis of total available carbohydrates (TAC) was only done for the 1 mm and 53 μm mesh treatments and could not be done for the abiotic treatment because the copper sulfate interfered with the Fehling's reduction test. Data could only be collected for seven months for the abiotic treatments because the chemical sterilants caused the bags to weather and disintegrate before completion of the experiment.

The statistical design involved a two-way factorial analysis of variance under the following model: $Y_{ij} = \mu t_i + m_j + \varepsilon_{ij}$ where t equals the treatment and i represents the treatments 53 μm, abiotic, and 1 mm mesh. m = month with j running from 1-8 and ε is the error factor.

Carbon

The analysis for carbon shows a decreasing trend in the percent carbon present in the bags for all three treatments. This result is to be expected because of aerobic respiration on the part of the microbes. I believe that there was little aerobic respiration in the abiotic bags, and that one would not expect a decrease in the percent carbon in the bags. Data for the chemical analysis of carbon are plotted in Fig. 6 and 7. Figure 6 represents the percent carbon content for each of the three treatments with time. Tests cannot be made on the significance of each treatment by month interaction but the trends of the treatments across time are similar for the 1 mm and 53 µm mesh treatments and that the abiotic treatment shows no clear effect with time which was previously stated as being expected. Figure 6 shows extreme fluctuations in percent carbon when looking at the months of August and September. Again this graph is not statistically valid because only one sample was analyzed per month. An extreme fluctuation as seen on Figure 6 seem highly unlikely and can be explained by the sample size and variations in chemical analysis. Figure 7 is a graph of the time effect (α = .0089) as averaged across the three treatments. The carbon values are plotted plus and minus $\frac{1}{2}Q$ and the means are considered to be significantly different if the Q values are non-overlapping. Figure 7 shows a decreasing trend of carbon with time and month 1 is significantly different from months 5 and 7. There was no significant effect of treatment on the percent carbon content (α = .3416). The partitioning of the sums of squares due to months into orthogonal polynomials in the analysis of variance shows the time trend to be most significant linearly.

Nitrogen

Although one would expect a change in percent nitrogen with time, a significant effect could not be seen (α = .3416). Figure 8 shows the changes in percent nitrogen with time for each of the three treatments. The graph shows that the 53 µm and abiotic treatments closely follow each other.

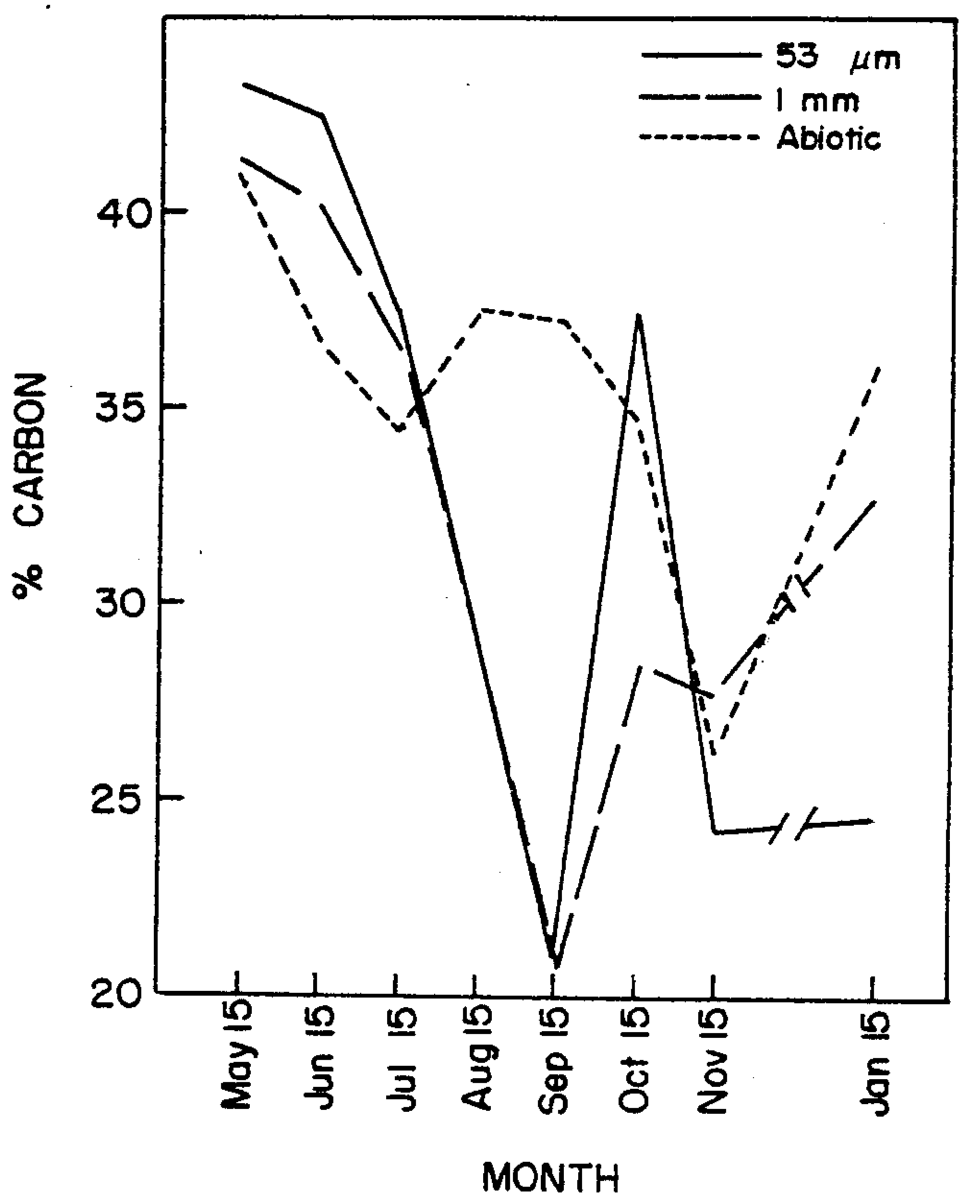


Fig. 6. Change in percent carbon content for each treatment with time.

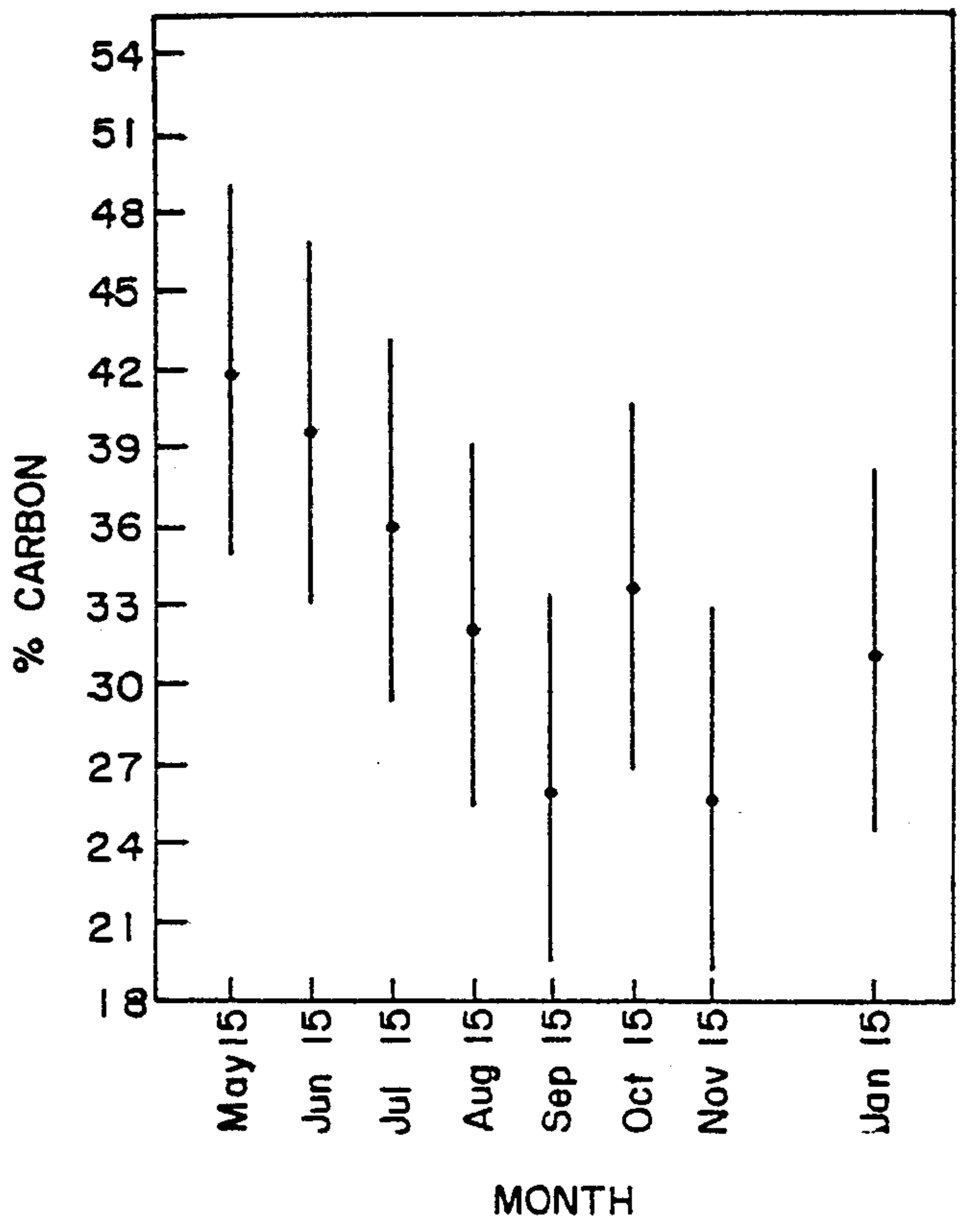


Fig. 7. Percent carbon for combined treatments with time ± ½Q.

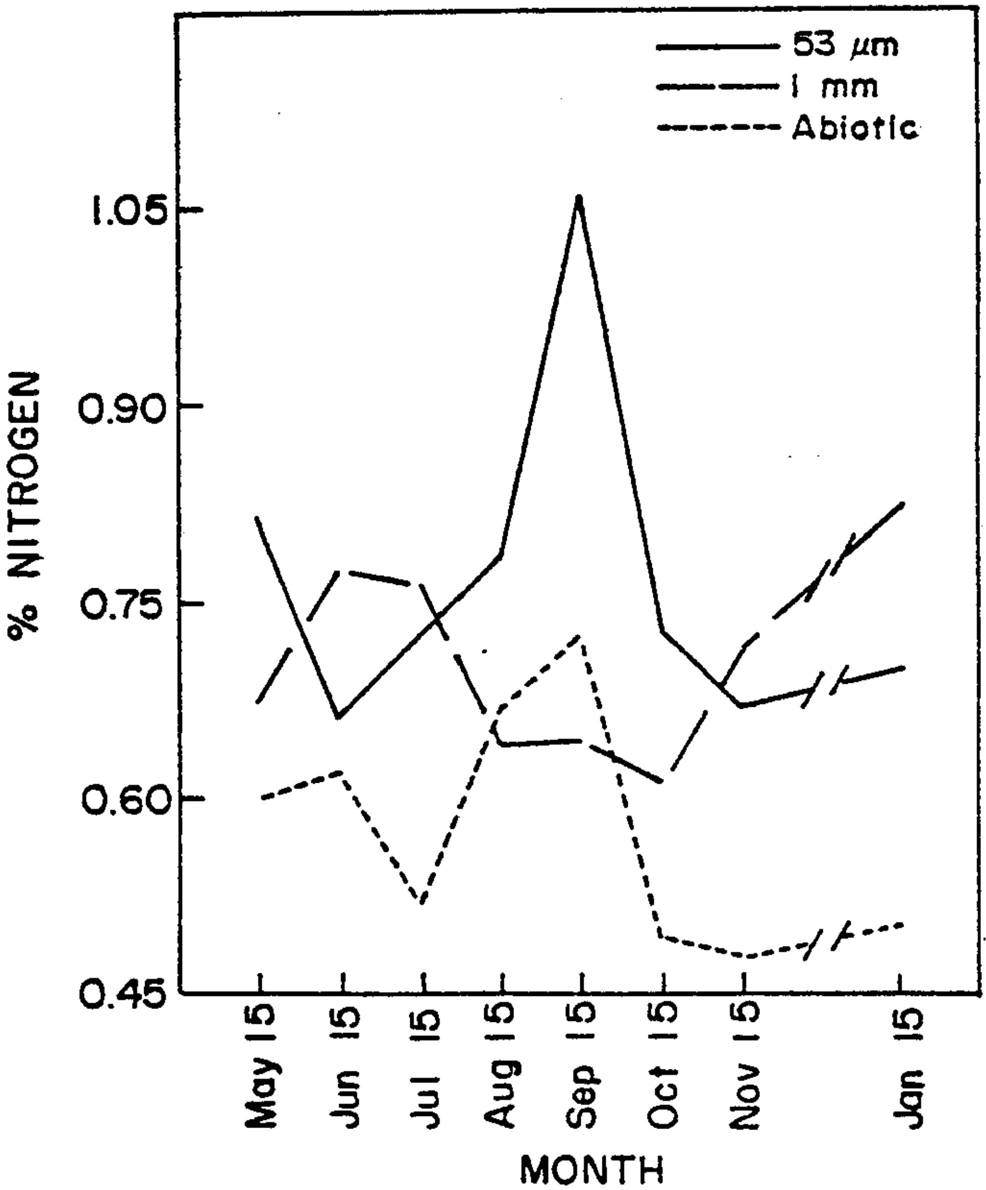


Fig. 8. Change in percent nitrogen with time showing all three treatments.

Analysis of variance shows, however, a significant treatment effect (α = .0055). Figure 9 illustrates that the percent nitrogen for the abiotic treatment is lower than the 53 µm treatment. The 53 µm treatment may have a higher mean percent nitrogen than the 1 mm treatment because the nitrogen may have been contained better in the 53 µm mesh bags. The 1 mm mesh may be showing weight loss because of mesofauna actually carrying material out of the bags. In the 53 µm mesh treatment the loss must come from leaching or changing an element to a gaseous state such as carbohydrates to CO_2. In that case one would expect the percent nitrogen to be higher in the 53 µm treatment. That is, bacterial decomposition tends to increase the percent nitrogen whereas mesofaunal action may not.

Carbon/nitrogen ratio

A significant effect can be seen in the C/N ratios with both treatments (α = .0003) and time (α = .0086). Figure 10 shows a significantly lower C/N ratio in the abiotic treatment than in the 53 µm and 1 mm mesh treatments. This substantiates the data for the percent nitrogen being highest in the previous analysis. The reason for the C/N ratio being highest in the 53 µm mesh treatment is attributed to the effect of microbial decomposition.

Figure 11 shows the significant time effect with combined C/N data. Differences can be seen when comparing month 5 with months 12 and 6. Figure 12 shows the changes of all three treatment with time. The fluctuations with time in C/N ratio appear to closely follow each other.

A general decrease was found for the carbon-to-nitrogen ratio with time (Fig. 11). Anderson (1973) also shows a decrease in the carbon-to-nitrogen ratio of litter samples with time. This suggests that

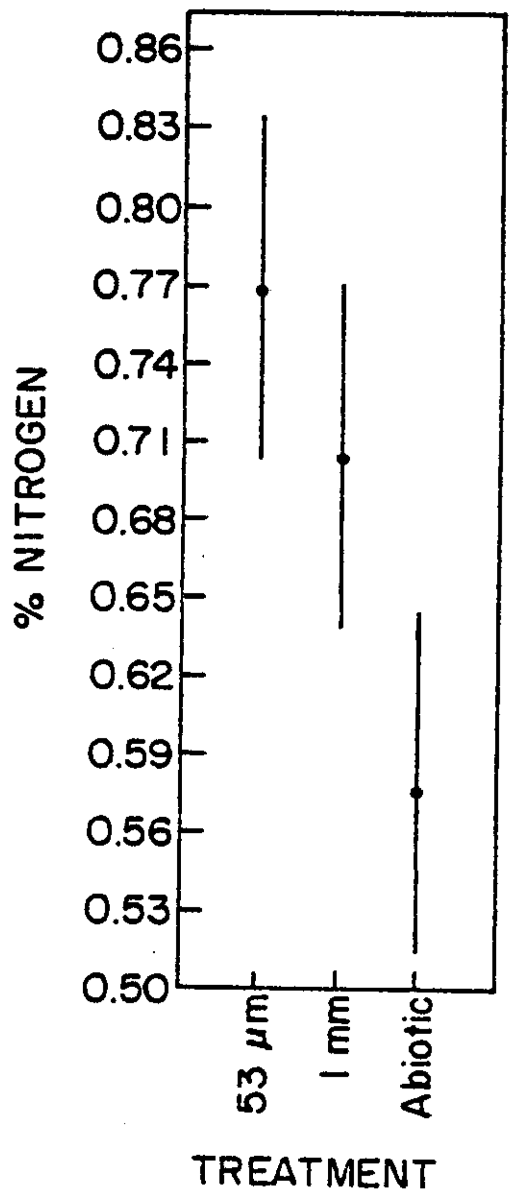


Fig. 9. Percent nitrogen for each treatment averaged for the 9 months of the experiment ± ½Q.

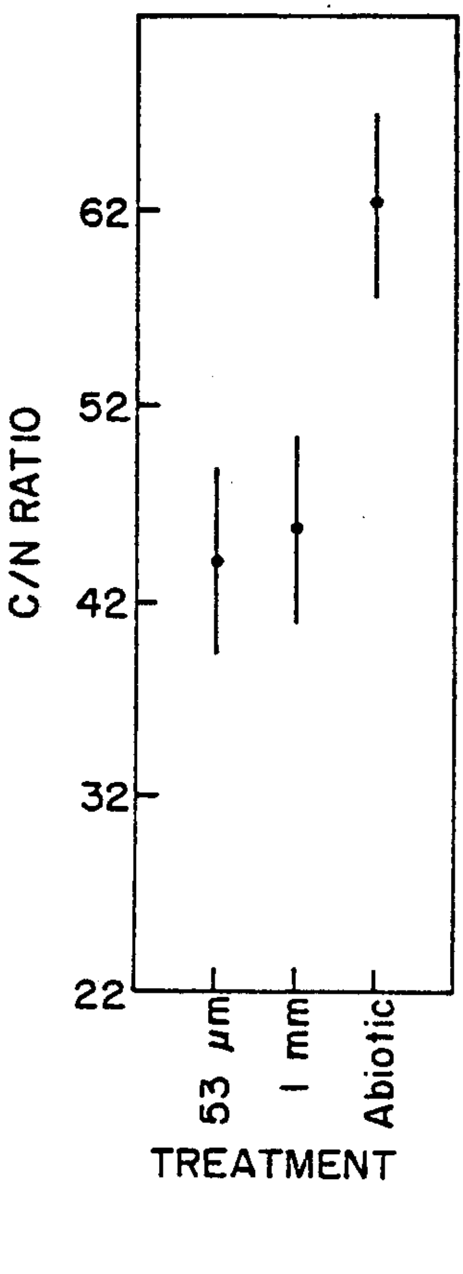


Fig. 10. C/N ratio for each treatment averaged for the 9 months of the experiment ± ½Q.

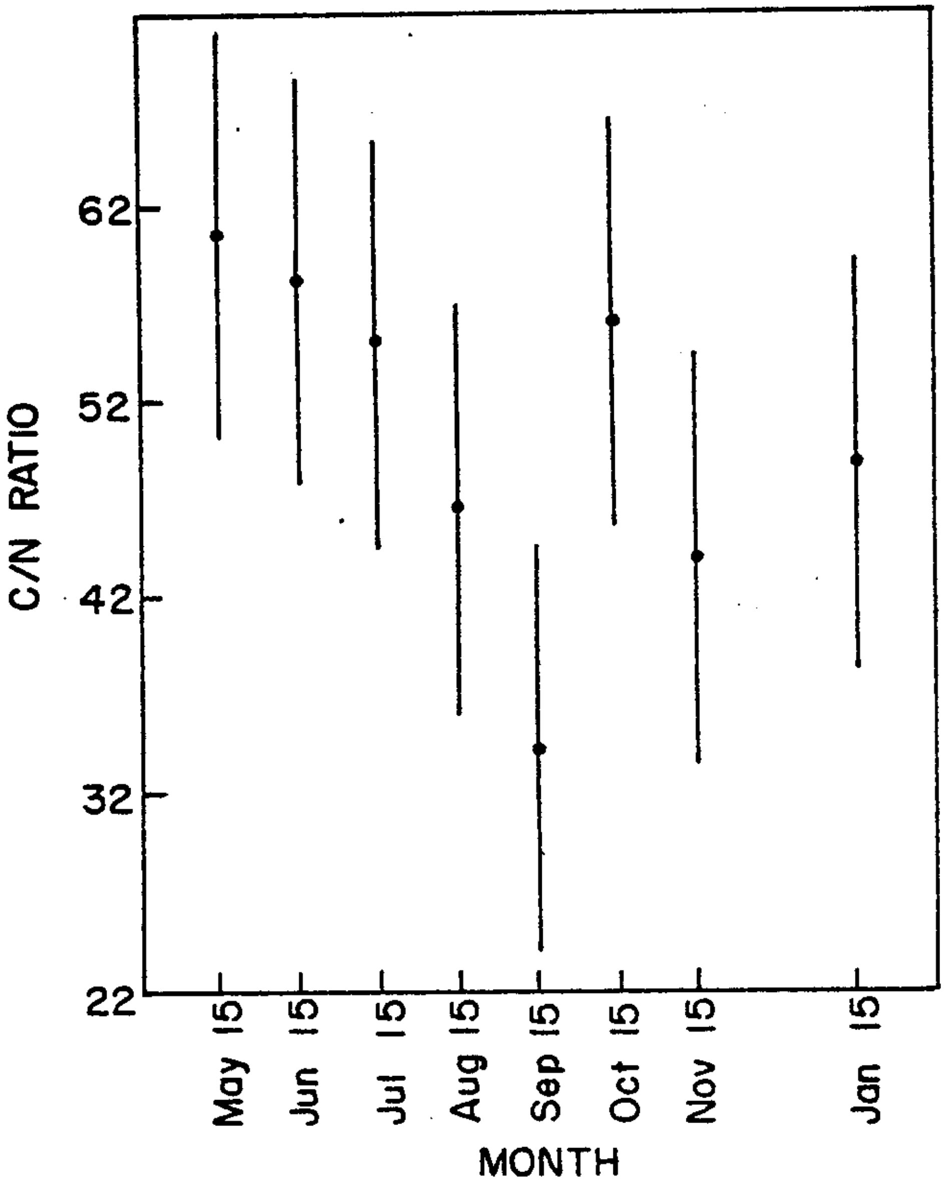


Fig. 11. C/N ratio for combined treatments with time $\pm \frac{1}{2}Q$.

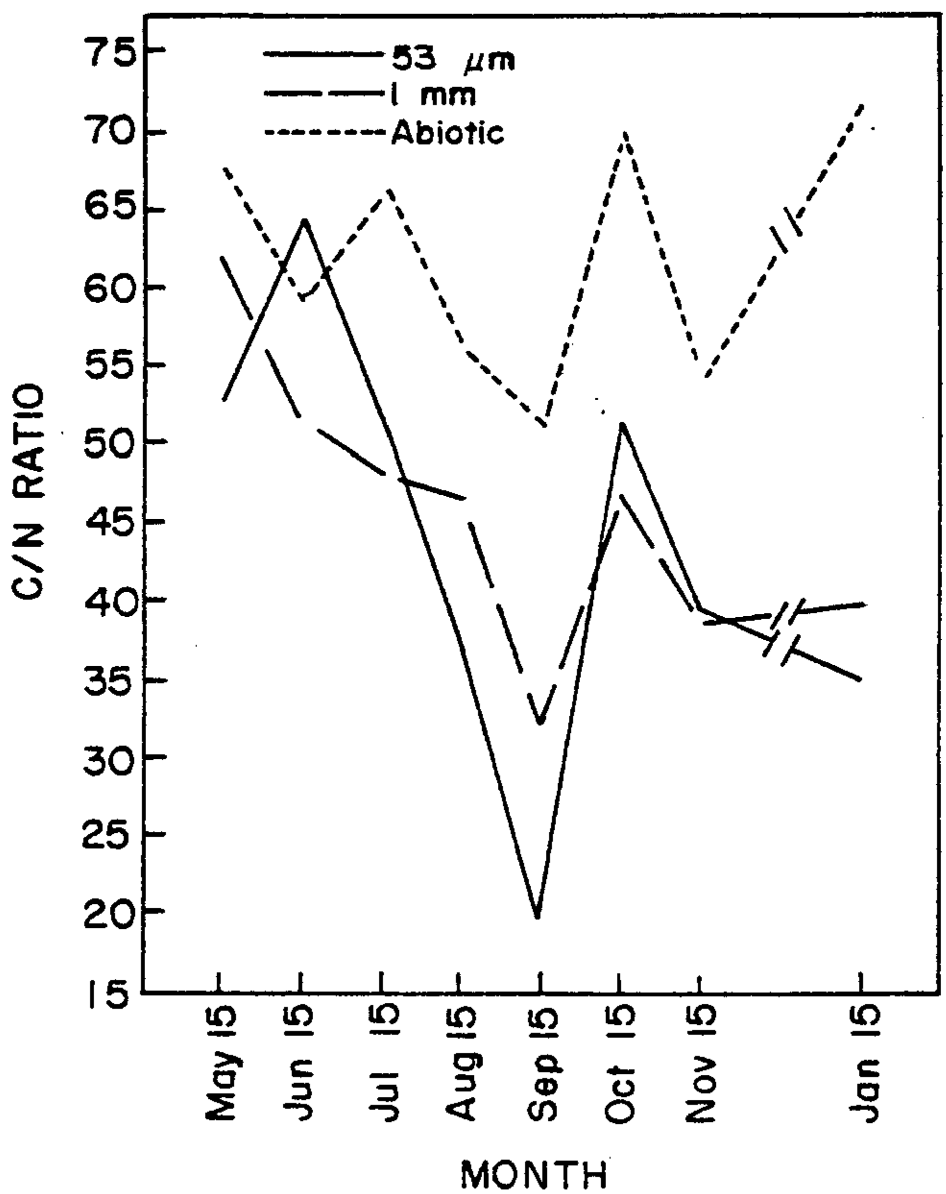


Fig. 12. Change in C/N ratio with time showing all three treatments.

carbon-to-nitrogen ratio can be an indicator of decomposition. The data from this experiment show the lowest carbon-to-nitrogen ratio for the microbial treatment (Fig. 10) while the greatest percent weight loss was observed for the 1 mm mesh treatment (Fig. 1). This suggests that the carbon-to-nitrogen ratio may not be an indicator of total decomposition, but rather an indicator of microbial decomposition. This may be because the microbes are less mobile and do not carry any of the nitrogen out of the bags, as is the case with oribatid mites. Fungal hyphae could be involved in transport of nutrients out of the bags. This is doubtful, however, in the case of this study because dry conditions prevent the buildup of hyphal masses.

Total available carbohydrates

The analysis of variance for Total Available Carbohydrates (TAC) indicates a time effect (α = .0236) but a treatment effect could not be measured. Figure 13 shows a decreasing trend of TAC with time in the combined data. A difference can be seen in the TAC content between the second and sixth months. TAC was not done for the abiotic treatments. Therefore, comparisons can only be made for the 53 μm and 1 mm mesh treatments. The loss due to time must be either because of microbial digestion or abiotic factors such as leaching.

Total available carbohydrates showed little statistical change. Figure 13 shows a general decrease in TAC, the only statistical difference being between June and September. Comparisons of Figure 2 for percent carbon with time and Figure 13 for percent TAC with time show the loss rates to be about equal. Both percent carbon and percent TAC are cut approximately in half. One would have expected the more easily decomposed available carbohydrates to disappear more rapidly, but data

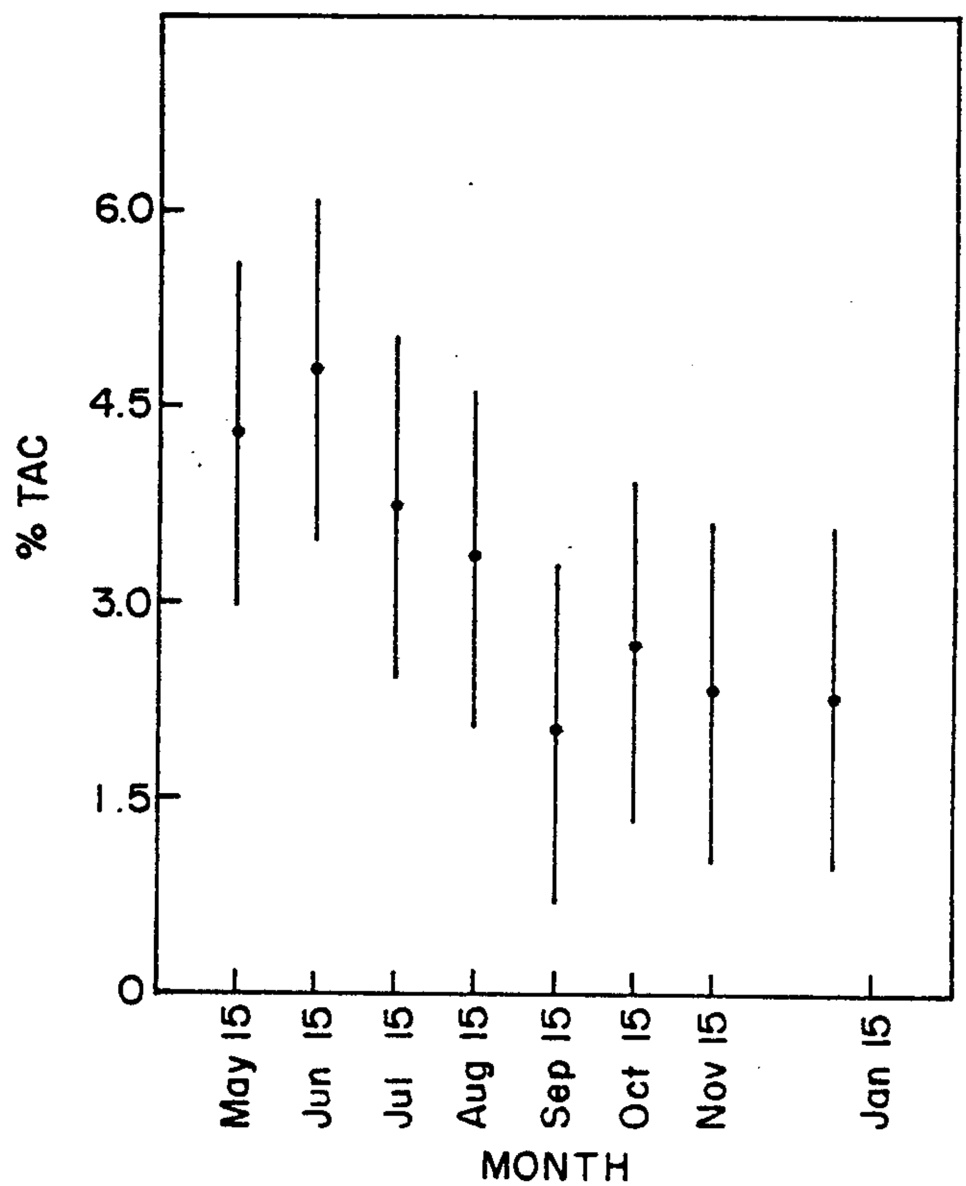


Fig. 13. Percent TAC for combined treatments with time ± ½Q.

from this experiment show no preference for either form of carbon in an energy source.

Correlations of Chemical Analysis to Abiotic Factors

Figures 14 and 15 are correlation matrices representing the interactions between chemical analysis of treatments and the abiotic factors. In comparing abiotic factors with treatment effects, TAC in the 53 µm mesh treatment forms a direct correlation to air temperature at the 95% level of significance and to radiation at the 99% level of significance. In the 1 mm mesh treatment, TAC is directly correlated to precipitation at the 95% level of significance. When making comparisons across treatments, a direct correlation can be seen between C/N ratios of the 53 µm and 1 mm mesh sizes at the 95% level of significance. In addition, a correlation in the percent nitrogen in the 53 µm and abiotic treatments is seen at the 95% level of significance. Other relationships are also seen across treatments such as TAC, carbon, and C/N in the 1 mm mesh treatments and carbon in the 53 µm mesh treatments. From this information, one can infer that the changes in carbon and nitrogen in the 1 mm and 53 µm mesh treatments closely approximate each other and that these treatments are more highly correlated to each other than to the abiotic treatment.

Effectiveness of Chemical Sterilants

The chemical ($CuSO_4$ and HgCl) exclusion factors seem to have worked well. Table 2 shows the results of the dilution plate counts. Plate counts show a lower microbial populations in the abiotic treatment than in the 53 µm mesh treatments by a factor of 10^3. Fluctuations in plate counts from the abiotic treatment can be explained by the amounts of

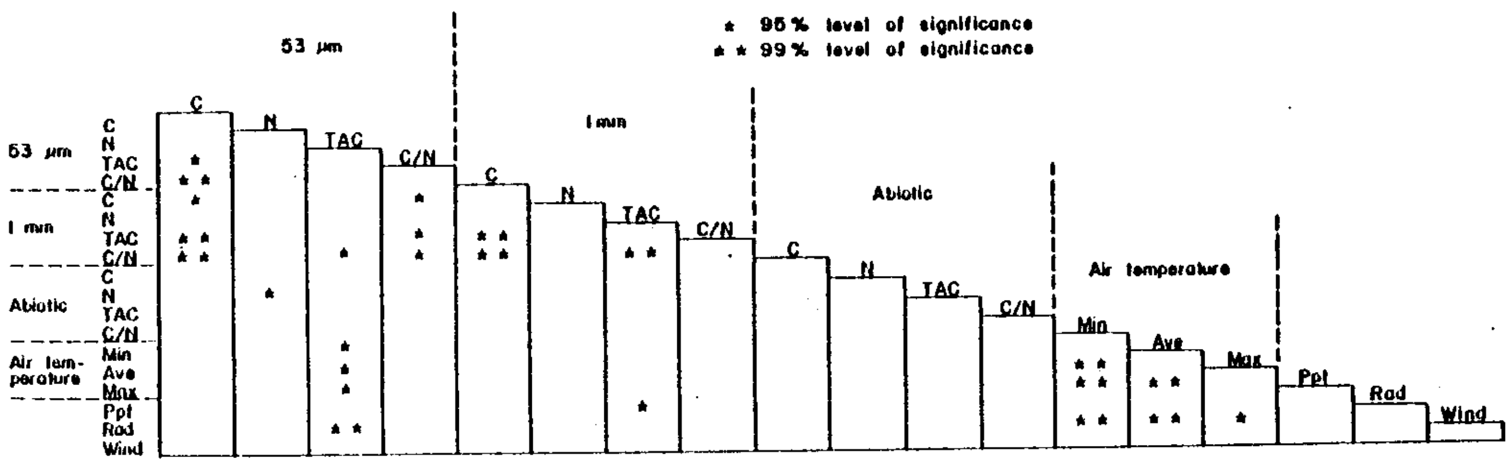


Fig. 14. Correlation matrix showing the relationships between abiotic factors and chemical analysis in treatments.

* = 95% level of significance
** = 99% level of significance

It takes an r value of .707 to be significant at α = .05.
It takes an r value of .834 to be significant at α = .01.

		53 μ				Imm				Abiotic				Air temperature					
		C	N	TAC	C/N	C	N	TAC	C/N	C	N	TAC	C/N	MIN	AVE	MAX	PPT	RAD	WIND
53 μ	C	1.0000																	
	N	-.385	1.0000																
	TAC	.762	-.215	1.0000															
	C/N	.924	-.679	.704	1.0000														
Imm	C	.827	-.544	.620	.827	1.0000													
	N	.011	-.519	-.092	.223	.473	1.0000												
	TAC	.843	-.400	.673	.804	.976	.417	1.0000											
	C/N	.918	-.352	.718	.804	.872	-.013	.865	1.0000										
Abiotic	C	.408	.429	.377	.098	.357	-.160	.415	.487	1.0000									
	N	-.105	.759	.347	-.345	-.208	-.391	-.057	-.058	.588	1.0000								
	TAC	--	--	--	--	--	--	--	--	--	--	1.0000							
	C/N	.449	-.437	-.125	.438	.507	.300	.382	.449	.269	-.614	--	1.0000						
Air temperature	MIN	.422	.243	.759	.257	.195	-.284	.279	.331	.391	.558	--	-.307	1.0000					
	AVE	.395	.266	.737	.228	.141	-.331	.224	.297	.383	.566	--	-.317	.998	1.0000				
	MAX	.364	.297	.718	.192	.080	-.392	.163	.262	.384	.590	--	-.340	.989	.996	1.0000			
	PPT	.611	.126	.492	.402	.661	.087	.745	.683	.462	.188	--	.152	.500	.453	.393	1.0000		
	RAD	.554	-.030	.873	.462	.424	-.103	.528	.501	.176	.394	--	-.461	.922	.894	.858	.659	1.0000	
	WIND	.458	.060	.164	.270	.575	-.028	.613	.688	.475	.042	--	.333	-.147	-.184	-.216	.652	.088	1.0000

Fig. 15. Correlation matrix showing the relationships between abiotic factors and chemical analysis in treatments with all r values included.

Table 2. The results of the plate counts for the abiotic and biotic treatments by month. The units given as colonies per plate and the righthand column is the dilution factor.

	Abiotic treatment				Biotic treatment			
	Bacteria	Fungi	Actinomycetes		Bacteria	Fungi	Actinomycetes	
May 15	0	0	0	$X10^2$	15	0	3	$X10^5$
June 15	34	2	6	$X10^2$	180	600	200	$X10^5$
July 15	44	0	0	$X10^2$	95	15	40	$X10^5$
August 15	0	14	28	$X10^3$	150	105	40	$X10^5$
September 15	75	5	32	$X10^3$	75	90	85	$X10^5$
October 15	0	0	0	$X10^2$	175	50	185	$X10^5$
November 15	5	8	3	$X10^2$	40	27	108	$X10^4$
January 15	84	3	18	$X10^2$	103	87	115	$X10^4$

soil blowing into the bags which contained microbes. These microbes in the soil which was blown in, probably had no effect in decomposing the grass because the grass was saturated with sterilants. The sterilants, however, started to destroy the nylon bags after about four months, and caused them to rip. As a result, such treatment could only be run for seven months at the longest. One should consider using a material other than nylon in order to be able to use the copper sulfate and mercuric chloride. This is because the sterilants did work well and are not metabolized as are toluene and naphthalene which have been used by other workers.

Effectiveness of the 53 μm Mesh in Exclusion of Fauna

Extractions from the 53 μm mesh samples were checked. From the Tullgren extractions only a couple of dipterous larvae were found. From the Baermann extractions only a few nematodes were found and a few tardigrades were seen. No attempt was made to classify these organisms further or to quantify the results. The faunal populations seemed scant and no mites were found.

The 53 μm mesh plankton netting worked well in excluding mesofauna as only a few nematodes and tardigrades were found in the bags. The nylon withstood the intense sun of the Pawnee grasslands but it is not recommended for use of more than a year. The 1 mm mesh (illusion veil) also withstood the sun but also showed signs of weakness and should not be used for more than a year.

CHAPTER 5. CONCLUSIONS

The abiotic component of decomposition is not the single most important factor in decomposition. Rather, the microbial component is more responsible than any other component for decomposition at the Pawnee Site.

This conclusion is in conflict with Zlotin (1970), when considering the steppe grasslands of the Soviet Union. Zlotin attributed the single largest decomposition rate to the abiotic treatment. This is surprising when considering the similarity of the two habitats in terms of precipitation. More studies are needed on both sites before one can account for the discrepancies. For now we can only speculate on differences in climate, plant material sterilants and methods used in the experiments to explain these differences in results.

The mesofauna did enhance decomposition which resulted in a significant increase in the rate of decomposition over the microbial treatment. I believe that the mesofauna are dependent upon microbial action to increase the rate of decomposition, i.e., whatever the rate of decomposition due to microbial action, the mesofauna will enhance this rate by their grazing action on the microbes and on the particulates which are slowly broken off. On the other hand, feeding by herbivorous macrofauna is not related at all to microbial action, but rather to leaf palatability and climatic conditions. This perhaps is the reason that most studies show a small but significant increase in decomposition due to mesofauna action, and a wide variety of results for macrofauna action. Finally, one can find many similarities when comparing the mesofauna from habitat to habitat. Crossley and Hoglund (1962), Edwards and Heath (1963), and Anderson (1963) all show populations of Oribatid mites, Collembola, and other mesofauna. Such categories of macrofauna, however, vary highly. Some habitats have many earthworms, isopods, and millipedes, where others such as the Pawnee grasslands show very few individuals of any such groups. These differences were also shown by Anderson on two neighboring sites only differing in the type of litter layer.

Data for the mite populations indicate that changes in mite families are seasonal rather than successional and that both trophic and temporal separation exists. I believe that the studies by Crossley and Hoglund (1963) and Anderson (1975) support this conclusion.

Plant material undergoing decomposition on the Pawnee Site shows a decrease in the percent carbon content, thus lowering the carbon to nitrogen ratio. The lowering of the carbon to nitrogen ratio is best seen in the microbial treatment. The carbon to nitrogen ratio then is probably an indication of microbial decomposition rather than total decomposition.

It is important to note that studies showing the effect of macrofauna on the rate of decomposition are in conflict. For example, Edwards and Heath (1963) showed a three-fold increase in decomposition while Anderson (1973) showed only a small percent increase and only in some treatments. Kurcheva showed a six-fold increase when invertebrates are present over treatments without invertebrates, whereas Zlotin (1970) found only a 4% increase in decomposition with the addition of macrofauna after 5½ months. Anderson (1973), Edwards and Heath (1963), and Zlotin (1970) have found that tremendous differences in decomposition rates can be observed in their own experiments depending on leaf type, litter base type, and location. These discrepancies occur because the factors controlling the decomposition rate due to macrofauna are agents such as leaf palatability, abiotic factors, and macrofaunal populations present in the existing litter layer.

None of the partitions considered in past studies on decomposition (abiotic, microbial, mesofauna, and macrofaunal) can be examined alone. These complex interactions must be considered together.

Abiotic factors, although they may or may not be responsible for a large percentage of the litter decomposition, set the stage for the qualities of flora and fauna which will inhabit a given area. Abiotic factors control what plants will be able to grow in a given area and thus the type of litter that will be formed. Abiotic factors such as moisture, temperature, and wind also affect the rate at which microbial decay will occur and what type of fauna can live in a given habitat.

I believe that future litter bag studies concerning decomposition should carefully record the abiotic factors present at the study site. Careful chemical analysis of the litter should be conducted. I believe that with the knowledge of these two sets of factors, one may be able to most easily predict the rates of decomposition and also predict the effect each of the partitions will have on the litter.

ACKNOWLEDGMENTS

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APPENDIX

Appendix--Table 1. Weather information obtained from the Pawnee Site weather station.

	Air temperature (°C)			Precipitation (mm)	Radiation	Wind (km/day)
	Minimum	Average	Maximum			
April	-0.9	6.9	14.9	40.3	518.8	139.7
May	4.3	12.2	20.0	81.6	543.6	428.6
June	9.3	17.7	26.0	33.9	615.1	98.0
July	13.6	22.3	30.0	66.6	619.1	61.1
August	12.5	21.9	31.3	19.6	561.3	6219.0
September	6.7	15.9	25.1	24.7	452.2	63.5
October	2.0	11.4	208.0	3.3	371.2	64.6
November	-4.4	3.5	11.4	11.1	--	99.2
December	-4.3	2.3	8.8	6.6	183.3	101.5
January	-8.1	-0.5	7.1	6.6	233.7	123.9

Appendix--Table 2. Chemical analyses showing percent carbon nitrogen and TAC by month.

	53 µm mesh treatment				1 mm mesh treatment				Abiotic treatment			
	Carbon	Nitrogen	TAC	C/N	Carbon	Nitrogen	TAC	C/N	Carbon	Nitrogen	TAC	C/N
May 15	43.3	0.818	4.06	52.93	41.4	0.674	4.60	61.42	41.0	0.604	--	67.88
June 15	42.7	0.664	5.17	64.31	40.1	0.773	4.44	51.88	36.7	0.621	--	59.10
July 15	37.5	0.725	3.83	51.72	36.7	0.764	3.63	48.04	34.4	0.519	--	66.28
August 15	29.3	0.789	4.36	37.14	29.9	0.640	2.38	46.72	37.5	0.670	--	55.97
September 15	21.0	1.06	2.54	19.81	20.8	0.643	1.50	32.35	37.3	0.728	--	51.24
October 15	37.5	0.727	3.16	51.58	28.5	0.609	2.16	46.80	34.8	0.495	--	70.30
November 15	24.2	0.671	2.58	39.22	27.8	0.718	2.15	38.72	26.2	0.481	--	54.47
January 15	24.7	0.703	1.88	35.14	32.9	0.825	2.72	39.88	36.2	0.500	--	72.40

Appendix--Table 3. Data for percent dry weight loss for each treatment by month.

May 15	June 15	July 15	August 15	September 15	October 15	November 15	January 15
			53 µm mesh treatment				
2.21	1.84	9.31	8.75	6.35	9.19	14.40	24.30
3.21	4.51	4.44	10.63	8.06	13.08	15.60	15.10
3.70	6.27	6.73	11.47	7.53	10.23	11.40	12.50
2.78	3.84	6.95	9.42	9.62	14.72	17.90	14.90
2.62	2.90	8.57	9.03	14.07	14.63	16.50	15.40
1.16	2.26	6.27	3.51	11.32	14.15	13.40	11.70
2.97	6.63	8.70	8.87	8.78	10.46	13.00	12.80
		8.38	9.89	9.24	10.88	12.10	
			Abiotic treatment				
-7.84	1.67	6.30	8.75	2.37	2.30	3.80	
-5.51	2.87	9.47	10.63	6.94	8.20	10.40	
-2.52	-0.28	6.06	11.47	2.33	5.40	7.60	
-9.90	7.95	4.44	9.42	0.06	4.20	5.20	
-6.63	-2.50	3.59	9.03	3.27	3.80	9.60	
	6.03		3.51		7.30	6.50	
			8.87				
			9.89				

Appendix--Table 3. Continued

May 15	June 15	July 15	August 15	September 15	October 15	November 15	January 15
			1 mm mesh treatment				
0.81	2.49	9.88	4.52	5.18	5.85	21.80	33.50
0.99	2.57	10.04	12.89	14.32	15.80	13.40	32.60
0.55	0.31	4.61	10.06	12.59	11.79	24.60	30.80
-0.37	2.75	4.61	7.45	14.26	13.64	17.60	28.90
-0.27	0.21	6.63	7.72	7.81	16.27	14.20	22.50
2.25	2.59	12.21	4.84	19.50	14.16	11.20	32.10
1.17	1.89	3.48	8.83	13.59	21.64	20.10	24.80
-3.69	1.78	9.27	0.70	18.93		19.40	34.90
1.09		5.88	8.97	24.02			34.80