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THE ROLE OF MITES AND NEMATODES IN EARLY STAGES OF BURIED LITTER DECOMPOSITION IN A DESERT[1]

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Abstract. We studied changes in populations of mites, nematodes, bacteria, and fungi in buried creosote bush litter treated with selected inhibitors. Elimination of microarthropods (primarily tydeid mites) resulted in increased numbers of bacteriophagic nematodes and reduction in numbers of bacteria; elimination of both nematodes and microarthropods resulted in increased numbers of bacteria compared to untreated controls. Fungal grazing mites, Pyemotidae, and fungivorous nematodes, *Aphelenchus* sp., increased in numbers between days 25 and 30, reducing the fungi on untreated leaves but not on stems and petioles, while mean length of fungal hyphae increased in insecticide-treated leaves. Elimination of mites resulted in a 40% reduction in decomposition suggesting that in a desert, tydeid mites affect decomposition of buried litter by regulating the population size of the bacterial grazers, cephalobid nematodes.

Key words: bacteria; bacteriophagic nematodes; buried litter; decomposition; desert; fungi; predation; tydeid mites.

In our previous study (Santos and Whitford 1981), we found that tydeid mites were the initial arthropod colonizers of buried creosote bush litter and that organic matter loss was significantly reduced in the absence of these mites. We hypothesized that the tydeid mites were predators on free-living nematodes, and regulated decomposition by regulating the population size of microbial grazers (the nematodes).

Based on microcosm studies several authors have suggested that bacterial grazers stimulate mineralization, bacterial activity, and the decomposition rates (Barsdate et al. 1974, Fenchel and Harrison 1976). Stout (1974) proposed that grazers speed decomposition by releasing nutrients tied up in microbial biomass. However, since Chlordane does not affect microorganisms (Bollen et al. 1954, Eno 1958, Martin et al. 1959, Pathak et al. 1961, Eno and Everett 1968) but eliminates tydeid mites with subsequent increase of bacterial grazers, we should expect insecticide-treated bags to have greater decomposition than control bags, and not the opposite as shown in our previous study (Santos and Whitford 1981). Anderson et al. (1978) reported that bacterial grazers (nematodes) reduced bacterial populations but increased mineralization of N and P in microcosms. However, in the absence of predators, high population numbers of grazers may be detrimental to decomposition (Hanlon and Anderson 1979). In N-limited media, grazers may decrease both biomass and the rate of N uptake (Hunt et al. 1977). In Chihuahuan desert ecosystems nitrogen may limit productivity when water is available (Ettershank et al. 1978).

This study was designed to examine the relationships between mites and bacteriophagous nematodes and changes in population numbers and/or biomass of the groups of organisms we hypothesized to be involved in the early stages of buried litter decomposition in the Chihuahuan desert.

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MATERIALS AND METHODS

Experiments were performed at the Jornada Experimental Range 40 km north–northeast of Las Cruces, New Mexico on the site described in Santos and Whitford (1981). Leaf litter and small stems were picked fresh and oven dried. Preweighed 30-g samples of litter were placed in 2-dm^2 fiberglass mesh bags (mesh = 1.5 mm). To prevent loss of material and escape of microarthropods due to transportation during the time of collection, the fiberglass bags containing litter were placed individually in plastic Ziploc® bags in an insulated container for transport.

Macauley (1979) demonstrated the efficiency of using selective inhibitors to examine the effects of insects and fungi in leaf litter decomposition. We modified his method for our study. We used the following treatments: (1) Control (C), water containing Tween®, a wetting agent; (2) Insecticide treatment (I), 1% (by volume) of Chlordane® plus wetting agent in water to eliminate microarthropods; (3) Fungicide-insecticide treatment (FI), a combination of the Chlordane (1% by volume), benomyl, and captan (.1% and .2%, respectively, by mass) plus wetting agent in water; and (4) Nematicide-fungicide-insecticide treatment (NFI), a combination of the fungicide-insecticide in the concentrations of the FI treatment, Nemagon® (1% by volume), plus wetting agent in water. Litter bags were soaked for 2 h, then oven dried for 24 h.

Bags were randomly buried in the soil at depths between 10 and 20 cm on 16 June 1978. A set of 40 bags (10 bags per treatment) was randomly retrieved at each sampling date: 5, 10, 20, 25, and 30 d after burial. Five

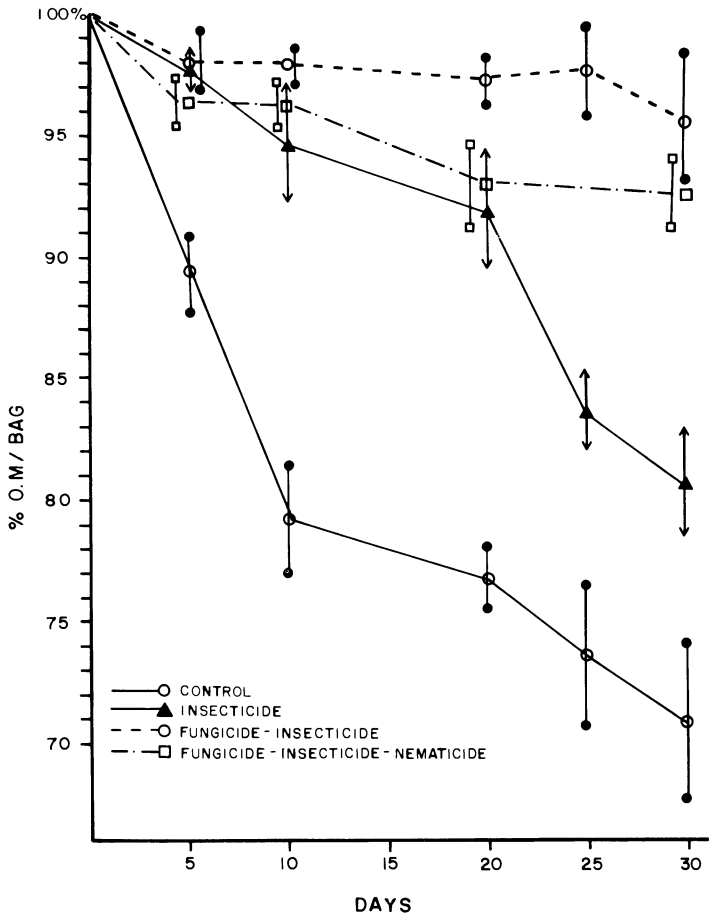

FIG. 1. Percent organic matter (% O.M.) remaining in buried litter bags removed from the field at the intervals indicated. Each vertical line equals ±1 SD.

bags of each set were used in microarthropod extractions (into modified Tullgren funnels) and to estimate organic matter loss, three bags were used to estimate nematodes and bacterial populations, and one bag for fungal biomass.

Nematodes were extracted from litter bags by a combination of the Cobb sieving method and the Oostenbrinck cotton-wool filter (Nicholas 1975). Nematodes were assigned to trophic groups based on esophageal structures (Yeates 1973).

Length of fungal hyphae per unit area of leaves and stems was estimated by a modification of the method used to estimate length of filamentous algae (Olson 1950). Leaves and stems were plated on carrot agar for identification of fungal taxa (Gilman 1957) (three plates with one leaf, three plates with one stem, and one plate with hyphae for each treatment).

Bacterial numbers were estimated by direct count using 10 leaves and 10 stems from each of the three bags per treatment. Smears of the leaf homogenates were treated before staining with 1 mL Traganos I solution for 1 min. After air drying, the smears were stained with 1 mL Traganos II (Acridine orange) solution for 20 min (pH = 3.8). The smears were counted with an ultraviolet microscope immediately after staining.

Soil moisture was determined gravimetrically and weather data collected from the Jornada Validation Site Weather Station. Five soil samples (from on and around the bags) and five soil samples taken 30 cm away from the bags were used to estimate microarthropod numbers.

Decomposition data (in percentages) were normalized by arc sine transformation using the SAS 79 procedure (Barr et al., 1979). Duncan's multiple range test was used to compare treatment means (Kirk 1968).

RESULTS

The loss of organic matter from the bags was consistently higher in the controls than in any of the other treatments for all sampling dates (F between 39.8 and 142.9, $P > .01$). By the end of the 30-d experiment, control bags had lost 29.3 ± 2.82% ($\bar{x}$ ± SD) of the initial organic matter with 20.74 ± 2.37% having disappeared by the 10th d after burial (Fig. 1). There were no differences in organic matter loss in the 1st 10 d

TABLE 1. Changes in length of fungal hyphae ($\bar{x} \pm$ SD beneath) per unit area of creosote bush leaf and stem for the experimental period from control (C), insecticide (I), fungicide-insecticide (FI), and nematicide-fungicide-insecticide (NFI) treated bags (N = 30 fields each for stems and leaves). Units are millimetres per square millimetre.

	5 d		10 d		20 d		25 d		30 d	
	Leaf	Stem	Leaf	Stem	Leaf	Stem	Leaf	Stem	Leaf	Stem
C	2.24 ± 0.92	0	2.76 ± 1.34	3.27 ± 1.62	3.82 ± 1.73	4.40 ± 2.29	3.59 ± 2.26	6.83 ± 2.93	2.83 ± 1.60	6.24 ± 2.46
I	2.47 ± 0.99	0	2.20 ± 1.10	2.71 ± 1.03	3.84 ± 1.79	4.51 ± 2.59	5.88 ± 2.30	6.42 ± 2.62	6.36 ± 2.16	6.85 ± 2.34
FI	0	0	0	0	0.60 ± 0.79	0.74 ± 0.76	0.80 ± 0.82	0.23 ± 0.37	0.76 ± 0.95	0.50 ± 0.48
NFI	0	0	0	0	0.59 ± 0.75	0.34 ± 0.41	0.59 ± 0.70	0.33 ± 0.52	0.65 ± 0.62	0.78 ± 0.69

between nematicide-fungicide-insecticide (NFI) and insecticide (I) or fungicide-insecticide treated (FI) bags ($P > .05$). Organic matter loss in these treatments was <5% in the 1st 10 d after burial. There were no significant differences in organic matter loss between I and NFI at day 20, or between NFI and FI by day 30 (Fig. 1).

Changes in mite, nematode, and bacterial populations for C and I treatments are shown in Fig. 2. All changes in numbers between dates were significant ($P < .05$, t test). There was no significant difference between control and insecticide-treated bags in length of fungal hyphae per unit area of leaf up to day 20 and per unit area of stem up to day 30 (Table 1). After day 20, leaves of the I bags had significantly more fungal hyphae than NT bags. The failure of the fungi to increase in leaves of the C bags corresponds to the period of colonization of pyemotid mites and the increase in fungivorous nematodes (*Aphelenchus* spp.) (Fig. 2).

The carrot agar plates showed that *Rhizopus* spp., *Penicillium* spp., *Aspergillus* spp., and *Mycellium sterillia* were the most abundant fungi cultured from leaves and stems or mycelia of insecticide-treated or untreated controls. No fungi were collected from FI and NFI leaves or stems for the 1st 10 d. *Fusarium roseum* was found on plates of leaves and stems from these treatments after 20 d.

Changes in population sizes of mites, nematodes, and bacteria for the different treatments are summarized in Fig. 2.

In the absence of tydeid mites there were significantly higher numbers of cephalobid nematodes and reduced numbers of bacteria in the insecticide-treated litter when compared to controls during 0–20 d (Fig. 2). At the beginning of the experiment, density of bacteria was $\approx 10^3$ individuals/g litter.

Although we extracted no tydeid mites at day 5 from the C bags, we found large numbers of tydeids in the soil around the bags, i.e., 71.4 ± 22.9 mites/200 cm^3 soil around the bags vs. 4.6 ± 4.3 mites/ 200 cm^3 soil in soil not near bags. Between days 10 and 30 there was a gradual increase in predatory mesostigmatid mites in the soil around the bags (25.2 ± 12 mites/200 cm^3 soil vs. 5.0 ± 3.1 mites/200 cm^3 soil not near bags). No mites were extracted from the soil around I, FI, or NFI bags.

In the untreated litter, tydeids peaked at day 20 then declined rapidly by day 25. With the drop in tydeid populations during days 25–30 there was a large increase in bacteriophagous nematodes (Fig. 2). In the insecticide treatment bacteriophagic nematodes peaked by day 10 and had decreased to relatively low numbers by day 30 (Fig. 2).

Suppression of nematodes, fungi, and microarthropods in the NFI bags resulted in increases in bacteria density several orders of magnitude higher than controls in insecticide treatments (10^7 cells/g on day 5 to 10^9 cells/g on day 30). Density of bacteria in the fungicide-insecticide treatment stabilized at 10^7 cells/g. Nematodes in the FI bags increased to 200 individuals/bag by day 10 and increased to 300 individuals/bag by day 30.

DISCUSSION

A large number of studies have addressed the problem of the role of microarthropods in decomposition of plant litter (Edwards and Heath 1963, Macfadyen 1963, Witkamp and Crossley 1966, Crossley 1970, Edwards et al. 1970, Wallwork 1970). These investigators list the following as contributions of microarthropods to decomposition: (1) litter fragmentation (comminution) which increases surface area for microbial activity; (2) grazing microfloral population to levels of exponential growth, and (3) inoculation of litter with microflora. In this study we demonstrated a heretofore undescribed role for microarthropods in decomposition, that of preying on grazers of primary decomposers.

The dominant mites associated with early stages of decomposition of buried litter in North American hot deserts belong to the family Tydeidae. Elimination of tydeids by the insecticide Chlordane resulted in an increase in free-living nematodes. Approximately 80% of the nematodes associated with early stages of de-

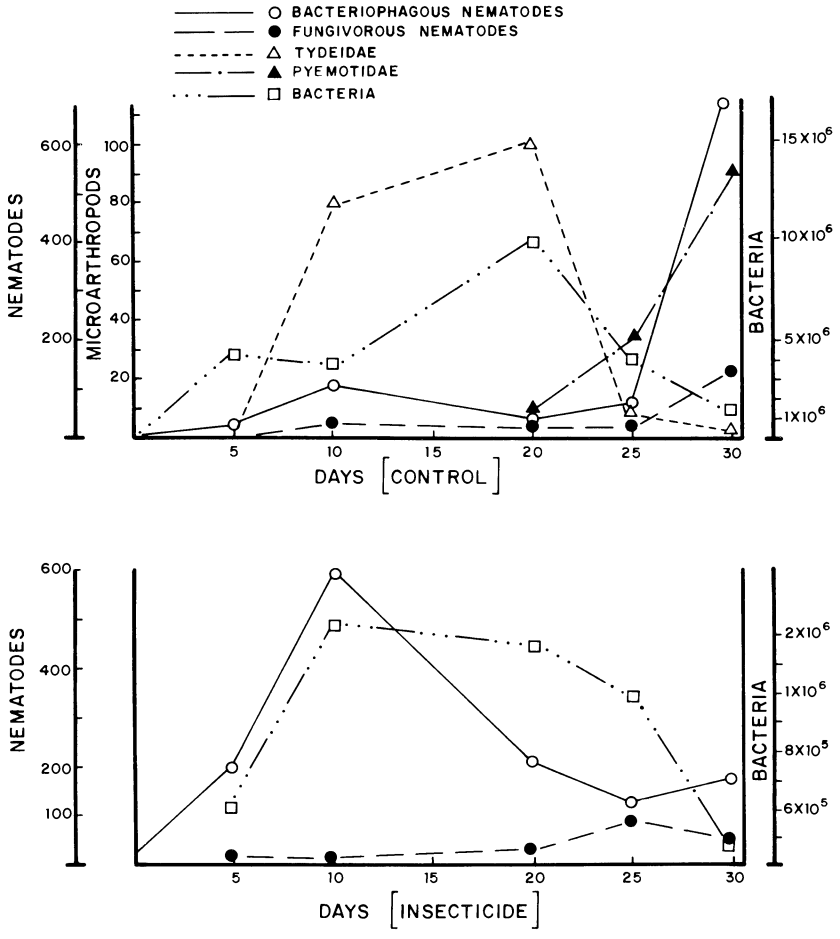

FIG. 2. Mean numbers of bacteria and nematodes per gram of litter and mean number of microarthropods per litter bag from untreated and insecticide-treated buried litter removed at the intervals indicated.

composition of buried creosote bush litter in a Chihuahuan desert were bacteriophagic nematodes (Cephalobidae). This increase of bacterial grazers markedly reduced the bacterial population resulting in 40% less decomposition compared with bags where only tydeid mites were present. This relationship suggests that predation of nematodes by mites reduces the nematode population and effectively prevents nematodes from overgrazing the bacteria. Some grazing on bacteria apparently stimulates decomposition because in the absence of nematodes bacterial cells increased 1000 times but organic matter loss was very small.

It is generally accepted that the microflora associated with decomposition of plant material provide a large energy source for the major components of the nematode community (Stolzy and Van Gundy 1968). Microbial feeders are the most abundant trophic group of nematodes in the Chihuahuan and Sonoran desert soils, representing 50–55% of the nematode community (Mankau 1975, Freckman 1978). Only 8% of the nematode populations in a desert soil are fungivorous (Freckman et al. 1975). Nematodes, because of their small size, high density in soils, short generation time, and anhydrobiotic capabilities are one of the first groups of invertebrates to begin grazing on bacteria in desert soils (Popovici 1972, Freckman 1978).

Tydeid mites not only affected changes in nematode numbers inside bags but also affected the nematode colonization rate. Before litter entered the soil, bacterial numbers were $\approx 10^3$ individuals/g litter and increased to 10^6 individuals/g litter by the 5th d, which apparently attracted bacteriophagic nematodes from the soil to the buried litter. The high density of tydeid mites in the soil around the bags appears to have reduced the movement of nematodes from the soil to the litter because the I bags at day 5 had 20 nematodes/g in comparison to 3 nematodes/g in the C bags.

Fungal biomass was virtually the same in C and I bags for the 1st 20 d. Elimination of tydeid mites and fungi had the same effect of reducing decomposition as did eliminating tydeid mites alone.

Disrupting the mite-nematode interrelationship resulted in a decrease in organic matter loss. This indi-

cates that the early stages of decomposition of buried creosote bush litter occur primarily via the bacteria-nematode-mite food chain, and therefore are controlled by predators.

Fungal grazers were present in significant numbers only after day 20. After colonization by pyemotid mites there was a reduction in the fungal biomass, as measured by hyphal length, on leaves. The absence of pyemotid mites in I bags resulted in high fungal biomass on leaves for the period 20–30 d. This may have been the cause of the higher rate of organic matter loss present by day 20 observed in I bags when compared with C bags. In the same period (20–30 d) fungal biomass was not different on stems from C or I bags. The presence of fungi only on leaves by day 5 and the reduction of biomass on leaves by grazers after day 20 indicates that most of the organic matter loss in the 1st 30 d was due to leaf not stem decomposition.

Fungal grazers are hypothesized to increase decomposition rates by browsing on senescent hyphae and thus increasing fungal activity (Macfadyen 1963, Wallwork 1967). However, by the same time fungal grazer populations increased in the litter bags the most rapid decomposition had already occurred. In this experiment the rate of organic matter loss did not change between day 25 and day 30, suggesting that fungal grazers and decomposition due to fungi were just compensating for decreases in bacterial numbers and bacterial decomposition.

An increase in the nematodes and pyemotid mites by the end of the experiment coincides with an increase in predatory Mesostigmata in soil surrounding C bags. This suggests that Mesostigmata are probably preying on pyemotid mites and nematodes in late stages of decomposition. Mesostigmata are the next group to colonize the bags (Santos and Whitford 1981). Thus, decomposition may be a predator-controlled process in the latter stages of buried litter decompositions as well.

We have no data on the protozoa populations in the litter bags. However, the bacterial population on soluble and easily decomposable derivatives of leaf litter may coexist with predaceous protozoa (Habte and Alexander 1979). Bacteria and protozoa may be preyed upon by nematodes which may in turn fall prey to microarthropods. Actinomycetes and bacteria decompose exoskeletons and tissues of mites or senescent hyphae (Novogroudsky 1948), and bacteria cause final decomposition of most biota and their decomposition products.

In order to understand the role of a particular organism in litter decomposition and subsequent material cycling, it is necessary to have information on the trophic structure of the community of which that organism is a part. Such an interdisciplinary approach has provided valuable information on the effect of grazers in bacterial populations and their implications on decomposition and nutrient cycling (Coleman et al. 1978). Bacteria appear to tie up nutrients (especially N and P) in the absence of grazers (Barsdate et al. 1974, Anderson et al. 1978). In our study, bacteriophagic nematodes only enhanced decomposition if their numbers were controlled by a predatory mite. Without the predators, grazers appear to be detrimental to decomposition. Hanlon and Anderson (1979) demonstrated that a low density of fungal grazers (Collembola) had a stimulating effect on microbial respiration but high densities of the fungal grazer inhibited respiration in the microorganisms they studied.

In our experiment the absence of fungi (FI and NFI bags) and a high population of bacteria, with or without nematode grazers, did not result in significant changes in decomposition rates. However, the bacteria in FI and NFI bags may have degraded the pesticides making it difficult to assess the effect of the nematode grazers on the organic matter loss for those treatments.

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LITERATURE CITED

Anderson, R. V., E. T. Elliot, T. F. McClellan, D. C. Coleman, C. V. Cole, and H. W. Hunt. 1978. Trophic interactions in microorganisms as they affect energy and nutrient dynamics. III. Biotic interactions of bacteria, amoeba, and nematodes. Microbial Ecology **4**:361–371.

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1979. A user's guide to SAS. SAS Institute, Raleigh, North Carolina, USA.

Barsdate, R. J., R. T. Pretki, and T. Fenchel. 1974. Phosphorous cycle of model ecosystems: significance for decomposer food chains and effect of bacterial grazers. Oikos **25**:239–251.

Bollen, W. B., H. E. Morrison, and H. H. Crowell. 1954. Effect of field treatments of insecticides on numbers of bacteria, streptomyces, and molds in the soil. Journal of Economic Entomology **47**:307–312.

Coleman, D. C., C. V. Cole, W. H. Hunt, and D. A. Klein. 1978. Trophic interactions in soils as they affect energy and nutrient dynamics. I. Introduction. Microbial Ecology **4**:345–349.

Crossley, D. A., Jr. 1970. Role of microflora and fauna in soil systems. Pages 30–35 *in* Pesticides in the soil: ecology, degradation and movement. International Symposium: Pesticides in the Soil. Michigan State University, East Lansing, Michigan, USA.

Edwards, C. A., and G. W. Heath. 1963. The role of soil organisms in the breakdown of leaf material. Pages 76–84 *in* J. Koeksen and J. Van der Drift, editors. Soil organisms. North-Holland Publishing Company, Amsterdam, The Netherlands.

Edwards, C. A., D. E. Reichle, and D. A. Crossley, Jr. 1970. Pages 147–172 *in* D. E. Reichle, editor. Analysis of temperate forest ecosystem. Springer-Verlag, New York, New York, USA.

Eno, C. F. 1958. Insecticides in the soil. Journal of Agricultural Food Chemistry **6**:348–351.

Eno, C. F., and P. H. Everett. 1968. Effect of soil appli-

cations of 10 chlorinated hydrocarbon insecticides on soil organisms. Proceedings of the Soil Science Society of America **22**:235–238.

Ettershank, G., J. A. Ettershank, M. Bryant, and W. G. Whitford. 1978. Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. Journal of Arid Environments **1**:135–139.

Fenchel, T., and P. Harrison. 1976. The significance of bacterial grazing on mineral cycling for the decomposition of particulate detritus. Pages 285–299 *in* J. M. Anderson and A. Macfadyen, editors. The role of terrestrial and aquatic organisms in decomposition processes. Blackwell Scientific, London, England.

Freckman, D. R. 1978. Ecology of anhydrobiotic soil nematodes. Pages 345–347 *in* J. H. Crowe and J. S. Clegg, editors. Dried biological systems. Academic Press, New York, New York, USA.

Freckman, D. R., R. Mankau, and H. Ferris. 1975. Nematode community structure in desert soils. Nematode recovery. Journal of Nematology **7**:343–346.

Gilman, J. C. 1957. A manual of soil fungi. The Iowa State University Press, Ames, Iowa, USA.

Hanlon, R. D. G., and J. M. Anderson. 1979. The effects of Collembola grazing on microbial activity in decomposing leaf litter. Oecologia **38**:93–99.

Hunt, H. W., C. V. Cole, D. A. Klein, and D. C. Coleman. 1977. A simulation model for the effect of predation on bacteria in continuous culture. Microbial Ecology **3**:259–278.

Kirk, R. E. 1968. Experimental design: procedures for the behavioral sciences. Wadsworth Publishing, Belmont, California, USA.

Macauley, B. J. 1979. Biodegradation of litter in *Eucalyptus pauciflora* communities. II. Fungal succession in fungicide and insecticide treated leaves. Soil Biology and Biochemistry **2**:175–179.

Macfadyen, A. 1963. The contribution of the microflora to total soil metabolism. Pages 3–17 *in* J. Doeksen and J. Van der Drift, editors. Soil organisms. North-Holland Publishing, Amsterdam, The Netherlands.

Mankau, R. 1975. A semiquantitative method for enumerating and observing parasites and predators of soil nematodes. Journal of Nematology **7**:119–121.

Martin, J. P., R. B. Harding, G. H. Connell, and L. D. Anderson. 1959. Influence of five annual applications of organic insecticides on soil biological and physical properties. Soil Science **87**:334–338.

Nicholas, W. L. 1975. The biology of free-living nematodes. Clarendon Press, Oxford, England.

Novogroudsky, D. M. 1948. The colonization of soil bacteria on fungal hyphae. Microbiologia **17**:28–35.

Olson, F. C. W. 1950. Quantitative estimates of filamentous algae. Transactions of the American Microscopical Society **59**:272–279.

Pathak, A. N., H. Shankae, and K. S. Awasthi. 1961. Effect of some pesticides on available nutrients and soil microflora. Journal of the Indian Society of Soil Science **9**:197–200.

Popovici, I. 1972. Studies on the biology and population development of *Cephalobus persegnis* (Nematoda, Cephalobidae) in agriculture. Pedobiologia **12**:123–127.

Santos, P. F., and W. G. Whitford. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. Ecology **62**:654–663.

Stolzy, L. H., and S. D. Van Gundy. 1968. The soil as an environment for microflora and microfauna. Phytopathology **58**:889–899.

Stout, J. D. 1974. Protozoa. Pages 385–420 *in* C. H. Dickenson and J. G. F. Pugh, editors. Biology of plant litter decomposition. Volume II. Academic Press, London, England.

Wallwork, J. A. 1967. Pages 363–395 *in* N. A. Burgess and F. Row, editors. Soil biology. Academic Press, London, England.

———. 1970. Ecology of soil animals. McGraw-Hill, London, England.

Witkamp, M., and D. A. Crossley, Jr. 1966. The role of arthropods and microflora in breakdown of white oak litter. Pedobiologia **6**:292–303.

Yeates, G. W. 1973. Nematoda of a Danish beech forest. II. Production estimates. Oikos **24**:174–185.