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CARBON AND NITROGEN DYNAMICS DURING THE DECOMPOSITION OF LITTER AND ROOTS OF A CHIHUAHUAN DESERT ANNUAL, *LEPIDIUM LASIOCARPUM*[1]

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Abstract. Carbon and nitrogen dynamics were analyzed during the decomposition of litter and roots of the desert ephemeral pepperweed (*Lepidium lasiocarpum*). We treated litter bags with the insecticide chlordane and the fungicides benomyl and captan to eliminate or restrict groups of soil biota.

The mass losses of buried litter (51, 39, and 25% for untreated, insecticide-treated, and fungicide-insecticide-treated material, respectively) were higher than those of the respective root treatments (35, 18, and 15%) at 96 d. The mass loss of untreated material was correlated with numbers of detritivorous-fungivorous microarthropods, and only a small percentage of this loss was as CO_2: 27 and 42% for litter and roots, respectively. In the absence of microarthropods a higher percentage of mass-loss carbon could be accounted for as CO_2: 33 and 76% for litter and roots, respectively, indicating that mass loss was due primarily to litter removal by microarthropod activity and not to mineralization. Litter removal by microarthropods was less dependent on abiotic constraints such as soil moisture ($r = 0.65$, $P < .001$) than was mass loss when microarthropods were absent ($r = 0.79$, $P < .001$). In the absence of microarthropods, mass loss was more closely coupled with biomass of grazers, such as nematodes, which require free water for activity ($r = 0.99$, $P < .0001$).

Unlike mass loss, carbon mineralization was highest in untreated roots, suggesting a stimulation of microbial activity by microarthropods, while in untreated litter no stimulation was observed when compared to insecticide treatments. This difference was primarily a function of fungivorous microarthropod density, with overgrazing occurring in the untreated litter.

Nitrogen budgets indicated the importance of microarthropods in the turnover of root nitrogen. In the presence of microarthropods 132% of the initial root nitrogen could be accounted for after 96 d, while in the absence of microarthropods 270% could be accounted for. This net immobilization of nitrogen was primarily in the soil organic fraction around the roots and was associated with fungal development.

Data from this study re-emphasize the importance of microarthropods as regulators of decomposition in deserts and suggest that predation by nematodes or protozoa on bacteria and fungi contributes to rate regulation. Nitrogen flux data suggest that when spring ephemeral plant production is high, decomposition of ephemeral roots with attendant nitrogen immobilization can reduce the nitrogen available to creosotebush, *Larrea tridentata,* thus reducing shrub production. Higher taxa of soil biota, i.e., nematodes and microarthropods, may thus be important regulators of nitrogen fluxes and of mass loss in decomposition.

Key words: abiotic; Acari; annual plant; bacteria; carbon; decomposition; desert; fungi; immobilization; microarthropods; mineralization; nematodes; nitrogen; protozoans.

INTRODUCTION

The importance of ephemeral plants in nutrient cycling in North American deserts has been overlooked because of the dominance of perennial plants. Since ephemeral plants die after maturing and setting seed, it is possible to estimate the nutrient pools at one point in time and then to follow the release of these materials as the roots and aboveground parts decompose. It is therefore easier to investigate decomposition in ephemeral plants than in perennial plants as one avoids the difficulty of measuring the growth and death of both above- and belowground parts of perennial plants. For these reasons we chose an important desert ephemeral plant, *Lepidium lasiocarpum,* for studies of decomposition and nitrogen fluxes.

In deserts, wind and water not only produce the mechanical fragmentation of dead plants but also redistribute these organic materials in patches, usually at the bases of shrubs. A significant fraction of this material is physically buried in excavations made by rodents (Steinberger and Whitford 1982). Micro- and macroarthropods and nematodes are only active for short periods of time in surface litter (Whitford et al. 1981*a*) but can be active in buried organic matter all of the time (Santos and Whitford 1981). Examination of buried litter provides insight into the trophic relationships of soil biota living in and on dead organic material and allows measurement of decomposition rates of buried plant material.

Many interesting factors affect decomposition rates, i.e., chemistry of the material (lignin content, carbon-to-nitrogen ratio, phenolic compounds), soil moisture, soil temperature, etc. (Swift et al. 1978). Meentemeyer

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(1978) proposed a simple model that predicted decomposition rates in forest ecosystems as a function of actual evapotranspiration (AET) and lignin content. Whitford et al. (1981*b*) and Elkins et al. (1982) demonstrated that this model fails in arid ecosystems in situations where the activity of desert soil animals is relatively independent of AET. Santos and Whitford (1981) found that decomposition of buried litter was greatly reduced in the absence of soil animals, and they suggested that soil microarthropods uncoupled decomposition from environmental constraints. With data on virtually all groups of soil biota, it may be possible to refine our understanding of how the physical environment interacts with the soil biota in regulating the rate of this important process.

There is an increasing number of papers that suggest that above some threshold amount of water (200–250 mm/yr) other factors limit productivity in arid and semiarid ecosystems (Floret et al. 1982, Penning de Vries and Djiteye 1982). Ludwig and Flavill (1979) found primary productivity reduced in the second of two successive wet years, suggesting nutrient limitation in the second year. The nutrient most often cited as potentially limiting productivity is nitrogen (West and Skujins 1978). In the Chihuahuan desert, Ettershank et al. (1978) found that nitrogen addition stimulated productivity of shrubs and grasses. However, nitrogen deficiency may only be the manifestation of other system limitations. For example, we have evidence that rates of decomposition vary with substrate (carbon) quantity (Whitford et al. 1982*a*), and it has been suggested that in deserts, nitrogen fixation, mineralization, and immobilization may be dependent on carbon as an energy source (West and Skujins 1978).

The death of ephemeral plants introduces a large pulse of carbon and then nutrients into the system. In North American hot deserts ephemeral plant biomass is considerably higher under shrub canopies than in intershrub spaces (Muller 1953, Patton 1978, Parker et al. 1982). The highest concentration of rodent excavations in which litter is accumulated and buried is also under shrub canopies (Steinberger and Whitford 1983). The distribution and abundance of the soil biota reflect this distribution of organic matter: nematode density (Freckman and Mankau 1977), microarthropod density (Santos et al. 1978, Franco et al. 1979), and microbial activity (Ryder-White 1980).

This study was designed to examine the relationships between organic matter inputs from dead *Lepidium lasiocarpum*, the organisms responsible for the decomposition and mineralization of that organic matter, and factors affecting the rates of these processes. We hypothesized that the same taxa of soil biota would be involved in processing of roots and aboveground parts. Finally, we constructed carbon and nitrogen budgets in order to examine the relationship between ephemeral plants and the nitrogen economy of a Chihuahuan desert ecosystem.

The Study Site

This study was conducted on the Jornada Long Term Ecological Research Site on the New Mexico State University Experimental Ranch 40 km north-northeast of Las Cruces, Dona Ana County, New Mexico. The Jornada Site is a desert watershed varying in elevation from 2000 to 1000 m and draining into a small, dry, lake (playa). The mean 100-yr average annual rainfall ± 1 SD at the New Mexico State University Station, Las Cruces, New Mexico, is 211 ± 77 mm (Houghton 1972). Most of that rainfall occurs during late summer from convectional storms. Summer maximum temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Site Weather Station).

The site is a bajada (alluvial piedmont sloping from Mt. Summerford on the west to the Jornada basin on the east and north). The bajada is drained by a large ephemeral wash (arroyo) which flows south to north. The soil is an Alladin complex, an Aridic Entic Haplustoll coarse loam with a bulk density of 1.62 g/cm^3 and a pH of 7.6. Creosotebushes average 1 m or more in height and a caliche layer is >1.2 m below the surface.

The differentiation in soils and drainages produces distinct assemblages of perennial vegetation. Non-arroyo areas have an essentially monotypic cover of creosotebush (*Larrea tridentata* Cov.). The arroyos on the east side are lined with mesquite (*Prosopis glandulosa* Torr.), tarbush (*Flourensia cernau* D.C.), desert willow (*Chilopsis linearis* Cav.) Sweet, soaptree yucca (*Yucca elata* Engelm.), and banana yucca (*Yucca baccata* Torr.).

Materials and Methods

A variety of techniques have been used to examine the relative importance of various groups of soil biota in decomposition and nutrient cycling processes, i.e., chemical exclusion, mechanical exclusion, and combinations of these (Witkamp and Crossley 1966, Malone and Reichle 1973, Macauley 1975). All these methods are subject to limitations. Mechanical exclusion generally results in marked changes in the physical environment, while chemical agents have effects on nontarget organisms. We chose the insecticide chlordane and fungicides benomyl and captan because in laboratory studies we found these to have minimal effects on nontarget organisms isolated from our desert soils (L. W. Parker et al., *personal observation*). In addition these chemicals are sufficiently persistent to allow an experiment to span most of the growing season.

The densities of ephemeral plants were estimated in April 1979. *Lepidium lasiocarpum* was the most abundant annual on our study site (Parker et al. 1982). On 1 May, soon after the death of *Lepidium* and before substantial decomposition had occurred, above- and belowground plant parts of *Lepidium* sp. were harvested, separated, and oven dried at 40°C. Ten grams

of oven-dried litter or roots were placed in separate 100-cm^2 square fiberglass mesh litter bags with mesh openings of 1.3 × 1.1 mm. The litter bags were then soaked for 2 h in either: (1) surfactant (Tween 20) as a control, (2) the insecticide chlordane plus surfactant, (3) benomyl, captan, and chlordane as fungicide plus insecticide and surfactant. The litter bags were then air dried. Three litter bags of each treatment were used to measure the initial mass. Litter bags were buried under the canopy of creosotebushes at a depth of 10 cm.

Twenty-eight bags of each treatment containing roots and 28 of each treatment containing litter were buried in the field in May 1979. Six bags of each treatment of litter and roots were removed from the field 10, 32, 56, and 96 d after initial placement. These bags were then subdivided with three bags per treatment being used for microarthropod extraction and mass loss and three bags per treatment for estimation of the remaining soil biota populations and measurements of carbon and nitrogen. The remaining four litter bags per treatment were used to measure carbon mineralization.

Loss of mass and carbon determination

Carbon mineralization or CO_2 evolution was measured by placing 12.7 cm diameter by 17 cm high coffee cans (open at each end) on top of the four litter bags of each treatment just prior to burial. The bags and cans were then buried, insuring that the soil level inside the cans was the same as outside. The tops of the cans were sealed with plastic lids and the cans were covered with aluminum foil to reduce thermal loading. Carbon dioxide was trapped in 1 mol/L NaOH in glass jars in which the surface area of the absorbent was 25% of the surface area of the soil inside the can. No greater than 30% base neutralization occurred (Coleman 1973). One set of cans was buried in soil without litter bags as controls to obtain a measure of soil respiration. Soil respiration was subtracted from total CO_2 evolution in all treatments to calculate carbon mineralization from the decomposing plant material. Blanks were maintained in the laboratory. For carbon budgets all data were converted to a CO_2–C basis.

First-order rate constants (k_m) for carbon mineralization were calculated as follows:

$$\ln C = mt + a \quad (1)$$

$$k_m = -m \quad (2)$$

where m is the slope (grams per day), a is the intercept (grams) and C is the mass of plant carbon (grams) remaining at time t. All mass loss was assumed to be through mineralization for this calculation.

Mass loss was measured on three samples by drying the litter bags at 60°C for 5 d and then weighing and burning at 700° for 6 h in a muffle furnace to obtain organic matter content (Santos and Whitford 1981). Since the buried bags were infiltrated with varying quantities of mineral soil, litter organic masses were corrected using the method described in Santos and Whitford (1981). First-order rate constants (k_w) for mass loss were calculated from the relationships described in Eqs. 1 and 2, where C was the plant mass remaining in the litter bag.

The use of litter bags to determine the turnover of plant debris assumes that all of the material remaining in the bag is plant debris. However, a considerable portion of the remaining mass may be living or dead decomposer biomass. By using mass loss data we may be underestimating the turnover of plant material. The method used in this study enables us to determine plant debris carbon by subtracting the microfloral and micro- and mesofauna biomass present in the litter bags from the total carbon. We were able to compare the actual turnover of plant debris with the turnover estimated by mass loss and, therefore, determine the validity of mass loss data for estimating turnovers.

Total plant carbon was measured by first removing as much soil from the litter bag as possible; the plant material was ground to pass through a number 40 mesh sieve and was then oven dried (40°). Total carbon was measured on a Coleman carbon analyzer and expressed as ash-free dry mass.

Nitrogen measurements

The ground plant material was analyzed for total-N by the micro-Kjeldahl method and steam distillation (Bremner 1965). The soils extracted from the litter bags were analyzed for total-N, excluding NO_2- + NO_3-N, by the micro-Kjeldahl method, and for 2 mol/L KCl-extractable NH_4+- and NO_2- + NO_3-N. Ammonium- and NO_2- + NO_3-N were measured by Conway microdiffusion (Stanford et al. 1973). Nitrogen values were converted to a surface area basis by using a bulk density of 1.62 g/cm^3 and a depth of 2.5 cm. To separate litter from seasonal effects on soil nitrogen compartments, soil cores were taken at a distance of 0.5 m from the litter bags. These soil samples were used as controls to determine the net increases or decreases in various nitrogen compartments in soils associated with litter bags.

Soil biota

Litter bags returned from the field were immediately emptied into modified Tullgren funnels to extract microarthropods (Santos et al. 1978). Three bags of each treatment were extracted into water-filled containers. The funnels produced a gradient from 38° at the top of the sample to ≈25° at the bottom of the funnel. All microarthropods were counted and representatives of the different microarthropods were mounted on slides in Hoyers medium and identified to family using Krantz (1975). Microarthropod numbers were converted to biomass using the data of Franco et al. (1979).

Nematodes were extracted from three litter bags of each treatment by a combination of the Cobb sieving method and the Oostenbrinck cotton-wool filter (Nicholas 1975). Only one-half of the litter bag contents was

TABLE 1. The highest order of interaction, overall model F, probability of a greater F value, error degrees of freedom, and total sample size from the analyses of variance. BIOL is roots and litter, and TR is treatment.

Variable	Highest order of interaction	F	P	df	n
Percent mass loss	BIOL × TR × DATE	53.58	.0001	47	72
CO_2	BIOL × TR BIOL × DATE TR × DATE	23.67	.0001	26	360
Fungivorous microarthropods	BIOL × TR × DATE	51.67	.0001	47	72
Detritivore-fungivore microarthropods	BIOL × TR × DATE	156.48	.0001	47	72
Nematode-predatory microarthropods	BIOL × TR × DATE	40.84	.0001	47	72
General predator microarthropods	BIOL × TR × DATE	114.76	.0001	47	72
Bacteriophagous nematodes	BIOL × TR × DATE	59.16	.0001	40	65
Fungiphagous nematodes	BIOL × TR × DATE	13.34	.0001	40	65
Protozoa	BIOL × TR BIOL × DATE TR × DATE	8.74	.0001	42	67
Bacteria	BIOL × TR × DATE	7.18	.0001	43	68
Fungi	BIOL × TR × DATE	23.57	.0001	43	68
Plant-N	BIOL × TR	15.58	.0001	41	66
Soil-N	BIOL × TR × DATE	11.25	.0001	31	56
Ammonium	BIOL × TR BIOL × DATE TR × DATE	7.12	.0001	41	66
Nitrite + Nitrate	BIOL × DATE	2.98	.0011	41	66

extracted; the other half was used for bacterial, protozoan, fungal, and chemical analysis. To convert nematode numbers to biomass, we used the mass of 0.36 μg per nematode (McKercher et al. 1979). We estimated that each nematode was 50% carbon with a C:N ratio of 10:1 (Meyers and Krusberg 1965).

Bacteria were counted by the FITC method (van Veen and Paul 1979). We blended the 1 g of litter and 100 mL water in a water-cooled blender for 5 min, removed four 10-mL aliquots and spread them evenly over four 1-cm² areas of a microscope slide and placed the slide on a hot plate (≈40°). After the slides had dried, they were heat-fixed for 3 s. Cell volume was estimated by the mean length and diameter per field. The cell volume was multiplied by 0.33 to esimate biomass-C (van Veen and Paul 1979). Biomass-N was estimated by assuming a C:N ratio of 5:1.

Fungal biomass was estimated using the same slides as for bacteria, but counting 30 fields per 1-cm² area. Fungal lengths were measured by the method described by Olson (1950). Biovolumes were estimated by measuring the mean diameter per field. The biovolume was multiplied by 0.33 to estimate biomass-C (van Veen and Paul 1979) and biomass-N by assuming a C:N ratio of 10:1.

Protozoan numbers were estimated using the most-probable-number method (Cutler 1920 and Singh 1946). Each protozoan was assumed to have a dry mass of 1.2 ng (Coleman et al. 1978) and to contain 50% carbon and have a C:N ratio of 10:1.

Abiotic parameters

Soil moisture of triplicate samples collected at 10 cm depth under creosotebush in study areas was measured gravimetrically (after drying at 105°) at 45-day intervals. Soil temperatures at 15 cm were measured continuously at a weather station 600 m from the study area. Rainfall was measured at that station by a weighing bucket rain gauge.

Statistical analysis

All data were subjected to analysis of variance. When significance was observed at the $P = .05$ level, Tukey's Q values were calculated for separation of means (Sokal and Rohlf 1969:237). Table 1 gives the results of the analyses of variance. Differences between k_w or k_m were determined by t tests (Barr et al. 1979). Correlation matrices were constructed to examine the potential relationships between parameters. The data were also subjected to stepwise regression to examine possible interactions between the litter biota and weight loss and mineralization, and relationships between taxa of the soil biota.

RESULTS

Mass loss and carbon mineralization.

The removal of microarthropods by insecticide treatment resulted in reduction in the rate of mass loss of both roots and litter that was apparent on all sample dates (Fig. 1). The addition of the fungicide further reduced mass loss in litter, but not in roots. There was no difference between respective litter and root treatments on day 10. However, by day 32 all litter treatments had lost more mass than the corresponding root treatments (Fig. 1).

First-order rate constants for the untreated and insecticide-treated litter were larger than those for corresponding root treatments; there was no difference between substrates in the fungicide-insecticide treatments (Table 2). The k_w values were used to estimate half-lives ($0.693/k_w$) and turnover times ($3/k_w$) (Table

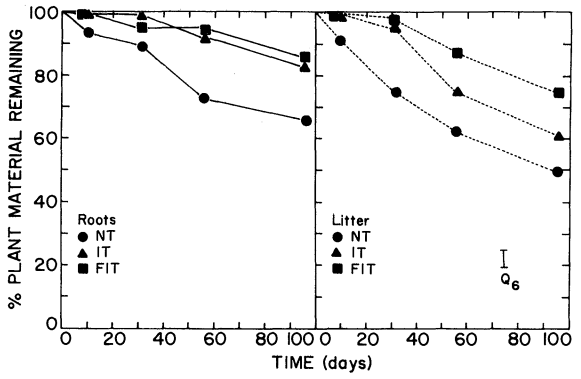

FIG. 1. Mass loss of buried litter and roots of the desert ephemeral *Lepidium lasiocarpum,* expressed as percent plant material remaining. NT is untreated; IT is insecticide-treated; FIT is fungicide-insecticide treated. Each point represents the mean of six litter bags. Q_6 is provided for examination of significant differences at $P = .05$.

2). The turnover times for roots were 1.89, 4.44, and 5.17 yr for untreated, insecticide, and fungicide-insecticide treatments, respectively, and 1.11, 1.49, and 2.63 yr for the respective litter treatments.

There were no differences in percent plant carbon ($\bar{x} = 59\%$) between treatments or across time; therefore, mass loss dynamics were indicative of total carbon dynamics. Furthermore, the correction of mass loss values for conversion into microbial and faunal biomass did not significantly alter turnover times ($F = 0.14$, $P > .56$).

Carbon mineralization occurred in pulses following rain events (Fig. 2). The rate of CO_2 evolution was higher in the litter treatments for the 1st 32 d than in the root treatments (Fig. 2). However, after day 60 untreated roots and fungicide-insecticide treated roots exhibited higher rates of CO_2 evolution than the corresponding litter treatments (Fig. 2).

The presence of microarthropods resulted in a higher overall respiration in decomposing roots but not in the litter, a response which was different from mass loss (Table 2). Further differences between mass loss and carbon mineralization dynamics with respect to pesticide additions were a depression in root carbon mineralization by the addition of the fungicide and no difference between the untreated and insecticide-treated litter carbon mineralization.

The proportion of mass loss that was accounted for as CO_2-C was higher in the absence of microarthropods (insecticide and fungicide-insecticide treatments) than in the untreated litter and roots at day 10 (Tables 5 and 6). This same pattern was observed on day 32 except in the fungicide-insecticide roots, which had a very low rate of CO_2-C evolution (Fig. 2). More plant carbon was accounted for as CO_2-C in the insecticide-treated roots than litter on days 56 and 96.

Percent mass remaining of both below- and aboveground parts of *Lepidium* was correlated with soil moisture and rainfall. The correlation coefficients for these parameters increased with the removal of microarthropods, from $r = 0.65$ and 0.70 to 0.79 and 0.84 ($P < .001$), respectively. Only the mass remaining in untreated *Lepidium* was correlated with soil temperature ($r = 0.41$, $P < .05$), but soil temperature provided the best correlation with carbon dioxide release ($r = -0.76$, $P < .001$). Carbon dioxide production correlated with soil moisture and rainfall (0.69 and 0.61, respectively) only in the absence of microarthropods.

Examination of the stepwise regression models ($P < .5$ to enter) showed that carbon dynamics of untreated *Lepidium* was primarily attributable to various groups of microarthropods. Mass loss was primarily attributed to collembola and psocopterans that we included as detritivore-fungivores ($r = 0.65$, $P < .02$). Variation in carbon dioxide production was related to numbers and biomass of fungiphagous and nematode-predator microarthropods: pyemotids and tydeids ($r = 0.39$, $P < .01$). In the insecticide treatments, fungi and the fungiphagous nematodes accounted for most of the loss of mass in the stepwise regression analysis ($r = 0.99$, $P < .001$) but only the nematode populations were entered into the regression with CO_2 evolution. For the fungicide-insecticide treatments, only nematodes entered the regression for loss of mass ($r = 0.72$, $P < .002$) and fungi for CO_2 evolution ($r = 0.27$, $P < .01$).

TABLE 2. The effect of biocidal treatments on first-order rate constants (k_w) and half lives ($t_{½}$) for loss of mass, plant carbon, and carbon mineralization (k_m) of *Lepidium* roots and litter. Values followed by the same letter for roots or litter are not significantly different at the $P = .05$ level. NT = untreated, IT = insecticide treated, and FIT = fungicide-insecticide treated.

Plant material	Treatment	Mass loss			Carbon mineralization		
		k_w (d^{-1})	$T_{½}$ (d)	r^2	k_m (d^{-1})	$T_{½}$ (d)	r^2
Roots	NT	0.00434[b]	160	0.86	0.00048[d]	1444	0.89
	IT	0.00185[a]	375	0.71	0.00036[c]	1925	0.96
	FIT	0.00159[a]	436	0.83	0.00016[a]	4331	0.63
Litter	NT	0.00739[c]	94	0.98	0.00041[c]	1690	0.98
	IT	0.00550[b]	126	0.96	0.00040[c]	1733	0.94
	FIT	0.00312[a]	222	0.93	0.00025[b]	2772	0.95

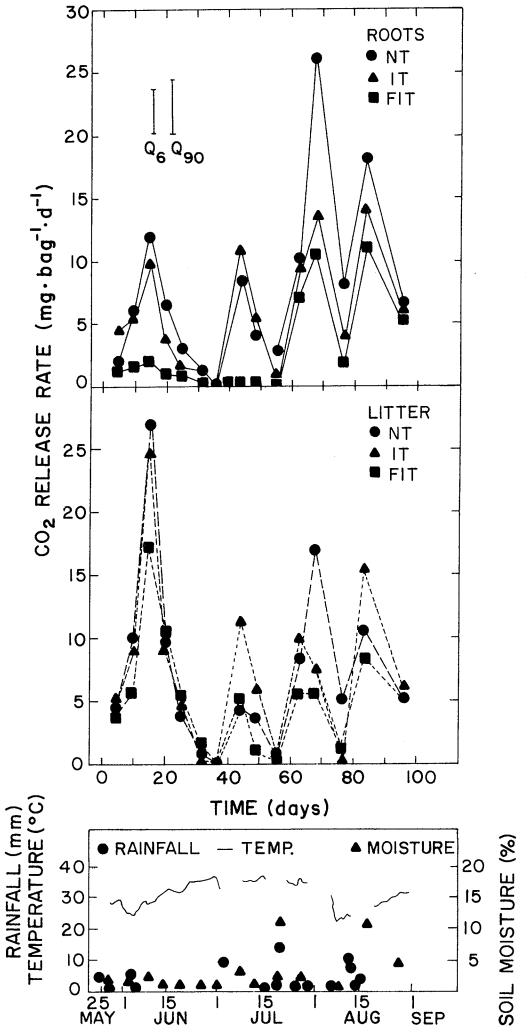

FIG. 2. The relationship between soil temperature at 10 cm, soil moisture and rainfall, and respiration of soil and litter bags containing roots or litter of the desert ephemeral *Lepidium lasiocarpum*. See Fig. 1 for treatment descriptions.

Microfloral and faunal dynamics

The only difference in bacterial biomass on untreated plant material was on day 96 when bacterial biomass on litter was twice that on roots (Fig. 3). The removal of microarthropods resulted in a five-fold greater biomass of bacteria in roots at day 10 and only a nonsignificant trend for higher bacterial biomass in litter for the first three sample dates. The dynamics of bacteria when fungi were inhibited differed between roots and litter (Fig. 3). There was no difference in bacterial biomass between the fungicide-insecticide and untreated roots, while for litter these treatments were always different.

In the presence of microarthropods, fungal biomass was higher on roots than litter on all dates except day 56 (Fig. 3). There was no difference between fungal biomass on the two plant materials in the absence of microarthropods except on day 96, when the fungal biomass on insecticide-treated roots was higher than on litter.

The microbial turnover in litter was different from that in roots (Table 3). The presence of microarthropods in litter stimulated microbial turnover, while in roots they had no effect on days 10 and 32. The turnover of untreated-litter microbial biomass was higher than that of untreated roots on these dates.

Protozoan biomass on the litter was not affected by microarthropod removal, while on roots protozoan biomass was increased (Fig. 3). The protozoan biomass on the fungicide-insecticide treatments was the lowest for both types of plant material (Fig. 3). However, by the end of the experiment there were no differences in protozoan biomass among the treatments (Fig. 3).

Microarthropod removal resulted in an increase in nematode numbers in roots but had no effect in litter

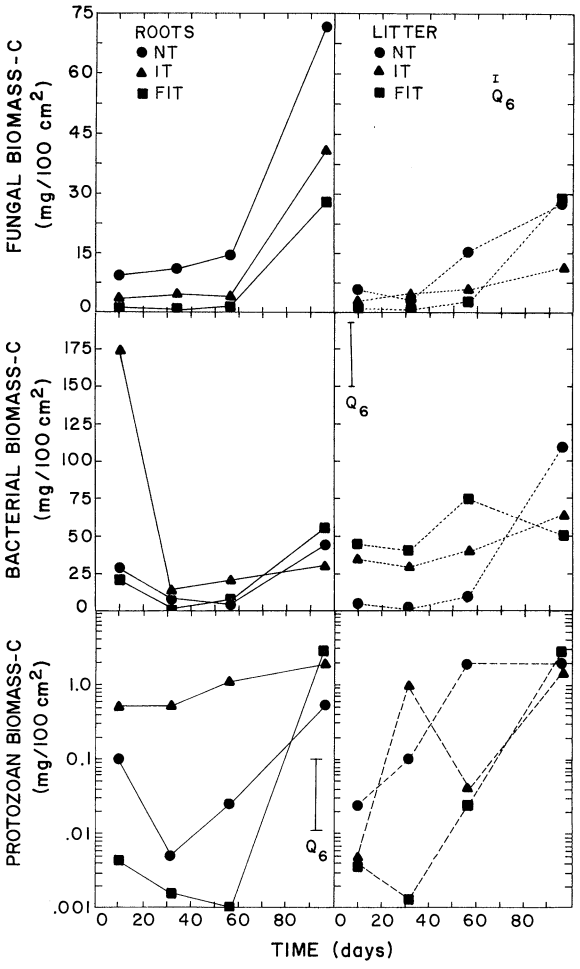

FIG. 3. Changes in biomass of bacteria, fungi, and protozoa (expressed as mass of carbon per 100-cm^2 litter bag) on roots and litter of the desert ephemeral *Lepidium lasiocarpum*. See Fig. 1 for treatment descriptions.

TABLE 3. The effect of biocidal treatments on the estimated total microbial biomass (as mass of carbon) and on turnover, per unit litter bag area, during the decomposition of *Lepidium* roots and litter. Values in a column followed by the same superscript letter are not significantly different at the $P = .05$ level.

		Day							
		10		32		56		96	
Plant material	Treatment	Biomass-C (g/m^2)	Turnover	Biomass-C (g/m^2)	Turnover	Biomass-C (g/m^2)	Turnover	Biomass-C (g/m^2)	Turnover
Roots	NT	1.9^{a}	0.7^{abc}	7.0^{b}	6.0^{a}	11.4^{b}	7.7^{b}	32.5^{d}	2.6^{ab}
	IT	2.2^{a}	0.2^{a}	6.2^{b}	4.7^{a}	11.8^{b}	10.3^{b}	27.8^{c}	3.4^{ab}
	FIT	0.6^{a}	0.3^{ab}	1.8^{a}	8.1^{a}	1.9^{a}	3.2^{ab}	13.5^{a}	1.3^{a}
Litter	NT	3.2^{a}	3.0^{d}	12.3^{c}	35.1^{b}	15.3^{c}	6.0^{ab}	29.3^{c}	2.4^{ab}
	IT	3.0^{a}	1.7^{cd}	11.2^{c}	4.7^{a}	17.4^{c}	6.2^{ab}	29.4^{c}	5.6^{b}
	FIT	2.3^{a}	0.4^{abc}	10.2^{c}	2.6^{a}	11.8^{c}	1.7^{a}	22.2^{b}	3.6^{ab}

(Fig. 4). Nematode biomass around the fungicide-insecticide-treated roots increased by four orders of magnitude by day 56 (Fig. 4). At the end of the experiment, nematode biomass associated with roots was higher than in the litter.

Fungiphagous nematode biomass, like bacteriophagous nematode biomass, was higher in the roots than litter in all treatments except the insecticide treatment by day 96 (Fig. 4). In the fungicide-insecticide-treated litter there was a drop in fungiphagous nematode biomass between days 56 and 96, at which time fungiphagous nematode biomass continued to increase in the roots. There was a surprisingly higher nematode biomass on the fungicide-insecticide-treated roots than in the other treatments.

The most abundant microarthropods on roots and litter during the early stages of decomposition (0–32 d), were tydeid mites (Table 4). Tydeid populations declined rapidly and were insignificant by day 96 (Table 4, Fig. 4). By day 32 the fungus-feeding tarsonemid mites appeared, and they maintained relatively high densities for the duration of the experiment. The major differences in microarthropod populations between roots and litter were that mesostigmatid mites and psocopterans appeared sooner in the litter than the roots (Table 4). The other difference was that on day 56, tarsonemid mite numbers were an order of magnitude higher in the litter than the roots (Table 4, Fig. 4).

Carbon budgets

A higher percentage of the root carbon could be accounted for when microarthropods were eliminated (Table 5). The insecticide and fungicide-insecticide roots were not different. More carbon was tied up in bacterial biomass than fungal biomass on day 10 in untreated roots, but the reverse was observed on days 32 and 56 (Table 5). By day 96, there were no differences in fungal vs. bacterial biomass in untreated roots. The insecticide-treated roots had a higher bacterial, protozoan, and bacteriophagous-nematode biomass than the untreated roots, but fungal biomass was nearly three times higher on untreated roots on days 10-56 (Table 5). Bacterial and protozoan biomass decreased between days 10 and 56 on the fungicide-insecticide-treated roots, while bacgeriophagous-nematode biomass increased over this time (Table 5); the CO_2 evolution in this treatment was considerably lower than any other treatment.

In litter, as in roots, a higher percentage of the carbon was accounted for in the insecticide and fungicide-insecticide treatments than in the untreated material (Table 6). All of the litter treatments were different from each other ($P > .05$).

Fungal biomass was generally higher in untreated litter than in treated litter except for day 96, when bacterial biomass was four times as large as fungal biomass (Table 6). This shift in relative dominance of fungi was measured after the highest estimates of fungivorous microarthropod biomass. In insecticide- and fungicide-insecticide-treated litter, fungal biomass was generally lower than bacterial biomass.

To estimate flows of carbon (grams per square metre per day), we made a number of assumptions from cumulative CO_2 data. Assuming a growth efficiency of 30%, we estimated how much carbon flowed into the microbial biomass (Table 3). (At a growth efficiency of 25%, there was not enough carbon flowing into the bacteriophagous nematodes to support the observed biomass. A growth efficiency of 35% allowed too much carbon to flow into the predatory mites, by almost two orders of magnitude. We therefore think that 30% is a valid estimate for the growth efficiency of the microbial population.) The proportions of microbial carbon flowing into the bacteria and fungi were assumed to be 90 and 10%, respectively, for both roots and litter on day 10 (Figs. 5 and 6). This may overestimate the carbon flow into fungal biomass, since there was lack of fungal predators and no change in fungal biomass at this time. By day 96, we assumed that 46% of root and 15% of litter carbon flowed into microbial biomass. The low carbon flux from litter resulted from a depression of fungal activity by the tarsonemid mites between days 56 and 96. The carbon flows shifted from bacteria to a fungal-based system. However, after 3 mo, more car-

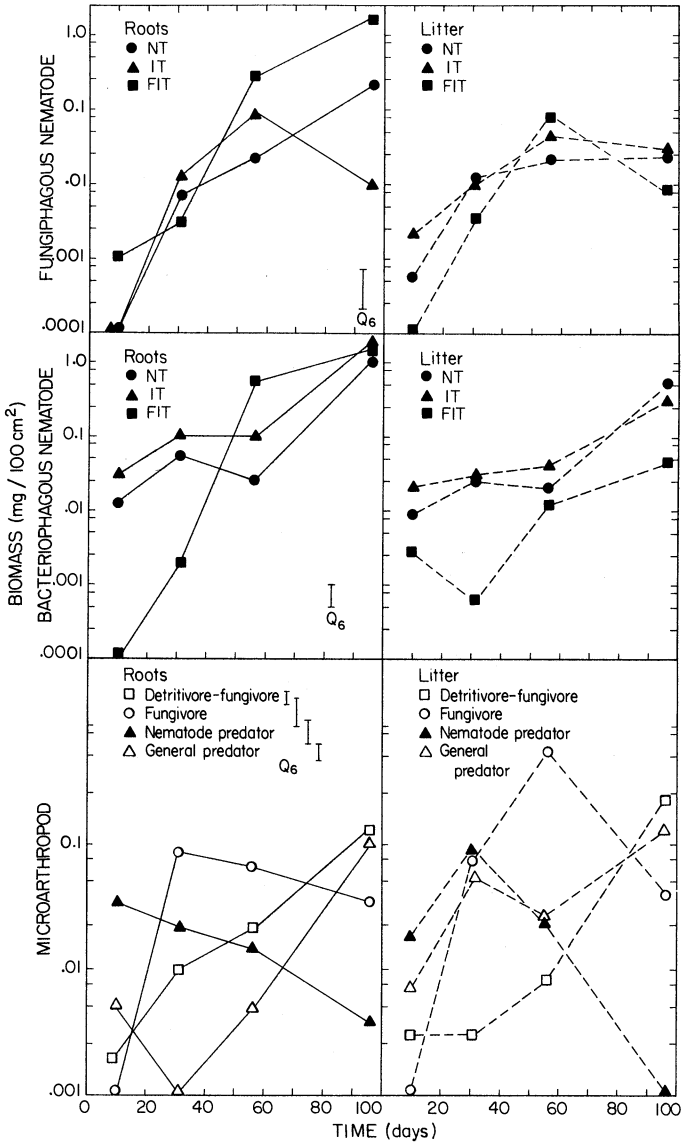

FIG. 4. Changes in biomass of bacteriophagous and fungiphagous nematodes and microarthropods (expressed as mass of carbon per 100-cm² litter bag) on roots and litter of the desert ephemeral *Lepidium lasiocarpum*. See Fig. 1 for treatment descriptions.

bon was going to bacteria than fungi. Fungal biomass was undoubtedly underestimated because fungal mycelium extended into the surrounding soil. Fungal grazers may also have been active outside the litter bag, feeding on this hyphal mass. Microbial death was assumed to be through predation. A portion of the population will no doubt die by other causes, but we think that these were insignificant compared to predation.

Nematode production (P), respiration (R), and excretion (E) values were 11, 39, and 50%, respectively (Sohlenius 1980). Protozoan values for P (37%), R (21%), and E (42%) were from Heal (1967). The percent intake of bacterial biomass directly by nematodes was 23%, while the intake of bacteria by protozoa was 77% (data of Elliott et al. 1980).

Microarthropod production, excretion, and respiration were 18, 44, and 38%, respectively (Berthet 1971). The feeding rate of detritivorous microarthropods was assumed to be 8.4 $\mu g \cdot individual^{-1} \cdot d^{-1}$ (Berthet 1971). On day 10 there was no flow between tydeid mites and general predators because gamasine mites were absent at that time (Figs. 5 and 6).

Nitrogen

The initial C:N ratio of *Lepidium* roots was 64:1. There was no change in total root nitrogen between

TABLE 4. Abundance of various taxa of microarthropods extracted from 100-cm² litter bags containing roots or litter of *Lepidium lasiocarpum*.

Order / Taxon	Trophic group	Day 10 Roots	Day 10 Litter	Day 32 Roots	Day 32 Litter	Day 56 Roots	Day 56 Litter	Day 96 Roots	Day 96 Litter
		No. microarthropods per 100 cm² ± 1 SD							
Prostigmata									
Tydeidae	Nematode predator	36 ± 32	18 ± 11	22 ± 6	93 ± 10	15 ± 5	24 ± 13	4 ± 2	1 ± 1
Tarsonemidae	Fungivore	0	0	87 ± 37	76 ± 12	67 ± 36	546 ± 230	32 ± 47	35 ± 6
Nanorchestidae	Detritivore-fungivore	0	0	0	0	13 ± 3	0	0	0
Bdellidae	General predator	0	0	0	0	2 ± 1	0	0	0
Pyemotidae	Fungivore	0	0	0	0	0	0	3 ± 1	2 ± 2
Cunaxidae	Predator	0	0	0	0	0	0	0	1 ± 1
Mesostigmata	General predator	0	0	0	29 ± 5	0	16 ± 6	47 ± 8	56 ± 37
Astigmata									
Acaridae	Detritivore-fungivore	0	0	6 ± 5	2 ± 1	0	0	0	0
Anoetidae	Parasite on Staphylinidae	28 ± 12	19 ± 14	0	0	0	0	0	0
Collembola									
Onchyrcibols sp.	Detritivore-fungivore	0	0	0	0	0	0	18 ± 22	22 ± 16
Lepidocertes sp.	Detritivore-fungivore	0	0	0	0	0	0	5 ± 2	2 ± 1
Isotoma sp.	Detritivore-fungivore	0	0	0	0	0	0	4 ± 3	8 ± 8
Coleoptera									
Staphylinidae	Predator	3 ± 1	5 ± 1	0	0	0	0	0	0
Thysanoptera									
Thripidae	Detritivore	2 ± 0	3 ± 1	0	0	0	0	0	0
Psocoptera									
Liposcelidae	Detritivore-fungivore	0	0	0	0	0	4 ± 1	1 ± 7	42 ± 29

days 0 and 10 in any treatment (Fig. 7). However, by day 32 a net loss of nitrogen was observed for all treatments and no net immobilization of N was observed. Soil NH_4^+-N levels in untreated and fungicide-insecticide-treated root soil were generally not different from soils not associated with litter bags (control) while the soil from around insecticide-treated roots had higher NH_4^+-N than control soils on days 10, 32, and 56 (Fig. 8). Total soil nitrogen from around roots was not different from control soils until day 96 (Fig. 7). There was insufficient soil in the untreated root bags for analysis until day 32. On day 96 soil from the untreated and insecticide-treated root bags had higher soil-N than the fungicide-insecticide treatment.

The initial C:N ratio of *Lepidium* litter was 30:1, and it was 10:1 in fungicide-insecticide-treated litter as a result of the addition of Benomyl nitrogen. There was no change in total litter nitrogen between days 0 and 10 in any treatment (Fig. 7). For all treatments a net loss of nitrogen was observed between days 0 and 32, and continued to day 56 in fungicide-insecticide-treated litter. Net immobilization occurred in only the fungicide-insecticide and untreated litter by day 96. However, when total plant nitrogen was compared on a dry mass basis, net immobilization had occurred in all litter treatments, with the untreated litter greater than the insecticide treatment by day 96. By day 96, the untreated and fungicide-insecticide treatments were not different ($P > .05$) (Fig. 5).

Mineralization of NH_4^+-N was higher in soil taken from around litter than in soils not associated with litter bags (control) (Fig. 8). Ammonium levels peaked and decreased sooner in untreated litter than in insecticide-treated litter. Soil from the fungicide-insecticide litter treatment had higher soil NH_4^+-N levels than control soil by day 96.

There was more total soil nitrogen in soil from the fungicide-insecticide-treated litter than in control soils on all sample dates (Fig. 7). Total soil-N was higher in soils from insecticide-treated litter than in control soils only on the last two dates (Fig. 7). Soil-N from the insecticide-treated litter differed from the soil nitrogen in the untreated litter only on day 56.

Mineralization of NH_4^+-N was generally higher in soil taken from around litter than from around roots (Fig. 8). The correlations of nitrogen mineralization with soil moisture and rainfall were higher in the biocide treatments ($r = -0.66$ and -0.67, respectively, $P < .05$) than in the untreated soils ($r = -0.3$ and -0.03, respectively). Stepwise regression analysis of the biomass of the trophic groups of soil biota affecting nitrogen fluxes showed that in untreated soil NH_4^+-N was related to numbers of various groups of microarthropods ($r = 0.53$, $P < .0001$) and that in biocide treatments NH_4^+-N varied with nematode and protozoan populations ($r = 0.86$, $P < .0009$).

The only differences in total soil-N between the two types of plant material were that the fungicide-insec-

TABLE 5. Effect of biocidal treatments on carbon budgets for *Lepidium* root decomposition. Mean initial plant-carbon values for the untreated, insecticide-treated and fungicide- + insecticide-treated bags were 5180, 5404, and 5517 mg/100 cm² litter bag, respectively. MA denotes microarthropods.

Treatment	Budget compartment	Day			
		10	32	56	96
		Percent of initial plant-carbon			
Untreated	Plant	91.45	89.55	68.89	63.71
	Bacteria	0.52	0.06	0.03	1.27
	Fungi	0.17	0.21	0.29	1.09
	Protozoa	0.002	0.0001	0.0005	0.01
	Bacteriophagous nematodes	0.0005	0.002	0.0009	0.04
	Fungiphagous nematodes	0.00	0.0003	0.0008	0.008
	Nematode-predatory MA	0.0007	0.0004	0.0003	0.00007
	Fungivorous MA	0.00	0.002	0.001	0.0007
	Detritivore-fungivore MA	0.0004	0.0002	0.0004	0.002
	General predatory MA	0.0009	0.00	0.0001	0.002
	CO_2-C	0.83	3.04	4.92	14.00
	C unaccounted for	7.02	7.14	21.68	19.77
	C accounted for	92.98	92.86	78.32	80.23
	Mass loss-C as CO_2-C (%)	12	14	14	42
Insecticide	Plant	95.88	99.36	93.41	87.08
	Bacteria	3.67	0.23	0.35	0.56
	Fungi	0.07	0.07	0.07	0.72
	Protozoa	0.01	0.01	0.02	0.04
	Bacteriophagous nematodes	0.001	0.004	0.004	0.07
	Fungiphagous nematodes	0.00001	0.0005	0.003	0.0003
	Nematode predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	CO_2-C	0.90	2.49	4.76	11.28
	C unaccounted for	−0.85	−1.57	1.38	4.71
	C accounted for	100.85	101.57	98.62	95.29
	Mass loss-C as CO_2-C (%)	100	100	78	76
Fungicide + insecticide	Plant	99.61	95.54	95.13	85.63
	Bacteria	0.36	0.03	0.10	1.35
	Fungi	0.02	0.005	0.02	0.48
	Protozoa	0.00008	0.00003	0.00	0.05
	Bacteriophagous nematodes	0.00	0.00008	0.02	0.06
	Fungiphagous nematodes	0.00004	0.0001	0.01	0.06
	Nematode predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	CO_2-C	0.22	0.69	0.75	5.35
	C unaccounted for	−0.21	3.74	4.71	8.82
	C accounted for	100.21	96.26	95.29	91.18
	Mass loss-C as CO_2-C (%)	100	20	21	38

ticide-treated litter had higher nitrogen levels due to fungicide for the first three sample dates than did the same root treatment, and the insecticide-treated litter had higher soil-N than the same root treatment on day 56 (Fig. 7). The correlations between abiotic parameters and changes in total soil nitrogen were higher in the biocide treatments than in the untreated samples. Correlation coefficients for soil temperature, soil moisture, and rainfall in untreated plant material were: $r = 0.66$, 0.71, and 0.72, respectively. The respective coefficients for the combined biocide treatments were 0.35, 0.95, and 0.96. Biomass of detritrivorous-fungivorous microarthropods accounted for 53% ($P < .0013$) of the variation in total soil nitrogen; no other biotic groups entered the regression. In the biocide treatments bacteriophagous nematodes were the only biotic group whose biomass entered the total soil nitrogen regression ($r = 0.94$, $P < .0001$).

Soils extracted from root and litter bags contained higher NO_2- + NO_3-N than soils not associated with litter bags when concentrations were averaged across time (Fig. 8). Soils from untreated roots had greater NO_2- + NO_3-N than soils from biocide-treated roots when values were averaged across time. In litter treatments the only difference observed was higher NO_2- + NO_3-N in untreated soils in comparison with biocide-treated soils.

TABLE 6. The effect of biocidal treatments on carbon budgets for *Lepidium* litter decomposition. Mean initial plant-carbon values for the untreated, insecticide-treated, and fungicide- + insecticide-treated bags were 4968, 4791, and 5419 mg/100 cm^2, respectively. MA denotes microarthropods.

Treatment	Budget compartment	Day 10	Day 32	Day 56	Day 96
		Percent of initial plant-carbon			
Untreated	Plant	90.92	76.09	63.19	46.42
	Bacteria	0.11	0.01	0.23	2.16
	Fungi	0.11	0.06	0.31	0.54
	Protozoa	0.0005	0.002	0.04	0.04
	Bacteriophagous nematodes	0.0004	0.001	0.00009	0.02
	Fungiphagous nematodes	0.00003	0.0005	0.00009	0.0009
	Nematode-predatory MA	0.0004	0.002	0.0005	0.00002
	Fungivorous MA	0.00	0.001	0.010	0.0007
	Detritivore-fungivore MA	0.00006	0.00006	0.0002	0.004
	General predatory MA	0.00013	0.001	0.0005	0.003
	CO_2-C	1.44	5.50	6.91	13.20
	C unaccounted for	7.42	18.33	29.32	37.61
	C accounted for	92.58	70.69	70.68	62.39
	Mass loss-C as CO_2-C (%)	20	23	19	27
Insecticide	Plant	99.24	94.28	75.02	59.64
	Bacteria	0.69	0.55	0.79	1.24
	Fungi	0.06	0.09	0.12	0.22
	Protozoa	0.0001	0.02	0.0009	0.03
	Bacteriophagous nematodes	0.0008	0.001	0.002	0.014
	Fungiphagous nematodes	0.00009	0.0004	0.002	0.001
	Nematode-predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore-fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	CO_2-C	1.37	5.12	7.94	13.43
	C unaccounted for	−1.35	−0.07	16.13	25.65
	C accounted for	101.35	100.07	83.87	74.35
	Mass loss-C as CO_2-C (%)	100	83	33	34
Fungicide + insecticide	Plant	99.07	96.44	86.83	73.16
	Bacteria	0.81	0.68	1.29	0.90
	Fungi	0.01	0.05	0.05	0.50
	Protozoa	0.00006	0.00003	0.0005	0.05
	Bacteriophagous nematodes	0.0001	0.00003	0.0005	0.002
	Fungiphagous nematodes	0.00	0.0001	0.003	0.0003
	Nematode-predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore-fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	CO_2-C	0.95	4.17	4.82	9.04
	C unaccounted for	−0.85	−1.35	7.01	16.34
	C accounted for	100.85	101.35	92.99	83.66
	Mass loss-C as CO_2-C (%)	100	100	43	36

Nitrogen budgets

Nitrogen budgets for root and litter decomposition are presented in Tables 7 and 8, respectively. The percent nitrogen accounted for increased for all treatments from day 56 to 96, and closely corresponded with an increase in soil organic N. The most striking difference between roots and litter was in the insecticide treatment, where we could account for 270% of the nitrogen originally added as plant material in the roots and 137% in the litter. Total nitrogen accounted for was generally lower at days 32 and 56 than at days 10 or 96.

The flows of plant-N to bacteria and fungi were estimated by the total biomass-C divided by 5 for bacteria (C:N = 5) and by 10 for fungi (C:N = 10) (Figs. 9 and 10). As for carbon, it was assumed that 73% of bacterial-N flowed into protozoa and 27% directly to nematodes. The flow from bacteria to protozoa was thus 73% of the total bacterial-N minus the standing bacterial-N. Since bacteria have a C:N ratio of 5:1 and protozoa 10:1, protozoa production measured as N would be half that calculated for carbon or 18.5% of the available bacterial N, with 81.5% being excreted. This excreted N was assumed to be ammonia.

Nematodes, like protozoa, have a C:N ratio of 10; therefore, nematode assimilation of N would be half that of carbon, or 5.5%, with 94.5% excreted. The excreted N was assumed to be 62% as ammonia and 38% as particulate-N (Lee and Atkinson 1977). The assimilation of protozoa-N by nematodes was assumed to be the same as for C, or 11%, with 89% being excreted.

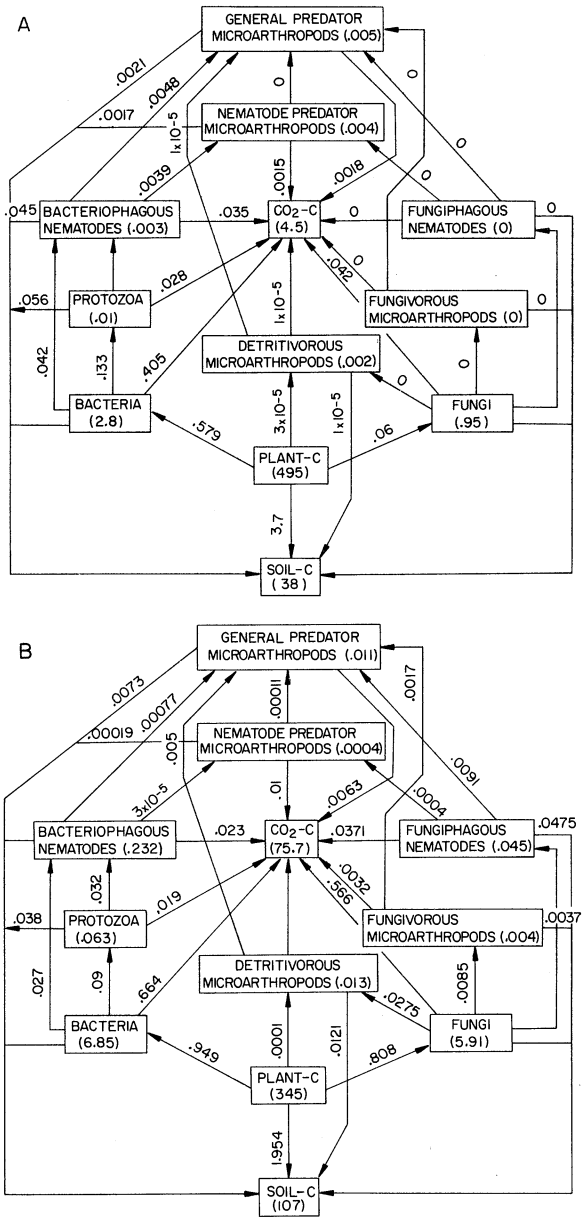

FIG. 5. Carbon budgets per unit litter bag area for the decomposition of *Lepidium lasiocarpum* roots at days (A) 10 and (B) 96. Carbon flows are $g \cdot m^{-2} \cdot d^{-1}$; compartments are g/m^2.

In estimates of microarthropod flows, 18% of the N went for production and 82% as feces. The N in mite feces was assumed to be composed of 91.2% particulate-N and 8.8% ammonium (Bocock 1963).

We assumed that all ammonium was converted to nitrite and nitrate and the excess nitrate was leached out of the system (litter bag). The estimated net loss from the litter bags on day 10 was 8.2 and 5.4% for litter and roots, respectively. The observed loss was 6.8 and 4.6%, respectively, indicating we are closely approximating the system at day 10. However, on day 96 the assumption was erroneous. Due to the high nitrogen demand a large portion of the ammonium never entered the nitrate pool, and what nitrate was formed was probably immobilized in the soil fungal biomass. Since we did not measure the soil fungal biomass this pool is included in the soil organic-N.

DISCUSSION

Mass loss is a result of a number of physical and biological processes: mineralization, leaching, volatil-

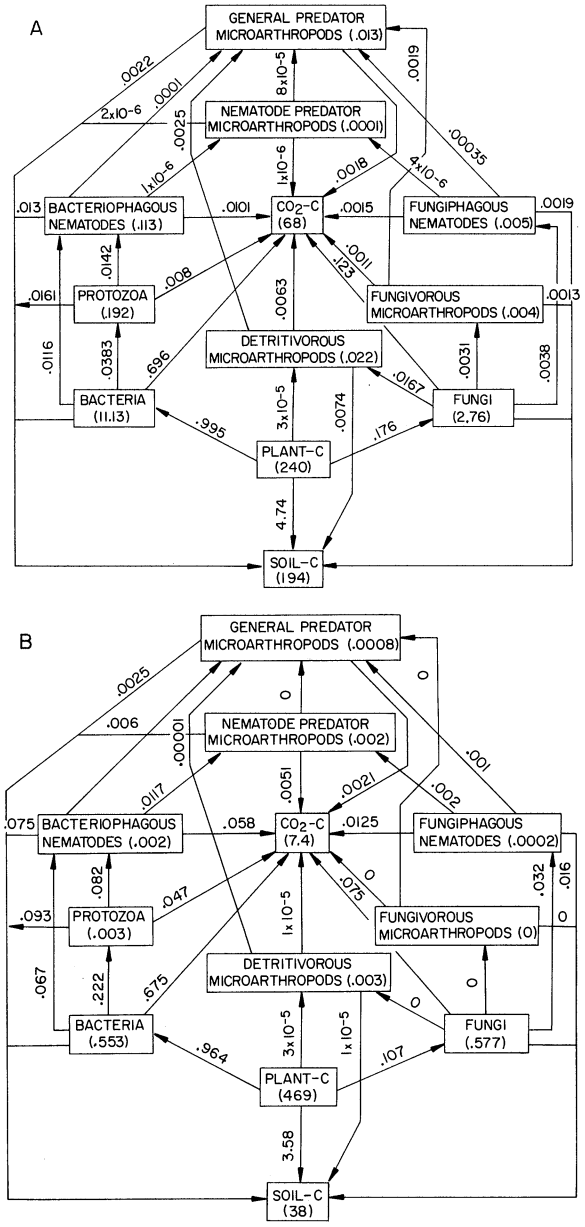

FIG. 6. Carbon budgets per unit litter bag area for the decomposition of *Lepidium lasiocarpum* litter at days (A) 10 and (B) 96. Carbon flows are g/m^2; compartments are $g \cdot m^{-2} \cdot d^{-1}$.

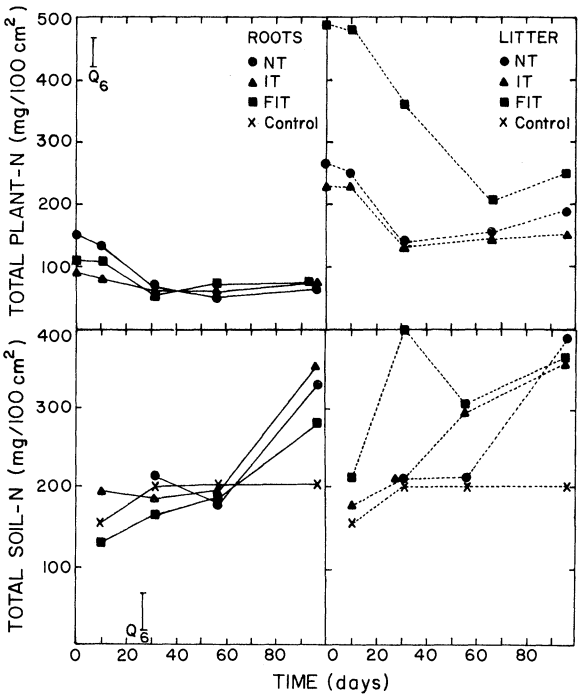

FIG. 7. Changes in total plant and soil nitrogen from buried roots and litter of the desert ephemeral *Lepidium lasiocarpum*. See Fig. 1 for treatment descriptions.

ization, and litter removal. All of these processes can be regulated by one or more of the following microarthropod activities: comminution; maintaining microflora in exponential growth by grazing; inoculation of litter with microflora (Edwards and Heath 1963, Witkamp and Crossley 1966, Wallwork 1970); and predation on other soil biota (Santos et al. 1981). When insecticides are applied to litter a reduction in mass loss of that litter is observed (Witkamp and Crossley 1966, Malone and Reichle 1973, Santos et al. 1981). This reduction may be in part due to pesticide effects on nontarget organisms; however, in laboratory studies chlordane had no effect on mass loss by nontarget organisms (L. W. Parker et al., *personal observation*). Therefore any effect of chlordane on mass loss in this study was probably a result of microarthropod removal.

Further insight into the importance of microarthropods in the early stages of *Lepidium* decomposition (<32 d) can be obtained from an analysis of the reduction in mass loss caused by the addition of the insecticide and the increased proportion of mass loss as carbon mineralization in these treatments. Mass loss at days 10 and 32 was by biological rather than by abiotic mechanisms, as most of the mass loss in the insecticide-fungicide- and insecticide-treated bags was CO_2-C. Mass loss in the untreated bags during this time was not a result of microarthropod stimulation of microbial activity, because only a small portion of the mass loss was CO_2, and there was no difference between the untreated and insecticide treatments in the rates of CO_2 evolution. Mass loss in the untreated bags was primarily due to litter removal by microarthropods. There was probably a portion of the microarthropod population in the soil around the litter at all times; however, we have no estimate of the size of that population. If we assume that the mass loss was a result of the microarthropod biomass present in the bags at day 10, then this biomass was insufficient to account for the observed mass loss. We determined this by assuming that the microarthropod biomass is turning over once a day (an overestimate) and has an efficiency of plant material use of 10% (90% being removed from bags as feces and respiration). Microarthropods could then account for at most a 2% mass loss in the 10-d bags. This is far less than the mass actually lost (7–8%). Either the microarthropod biomass outside the litter bags was four times greater than inside, and/or the microarthropods mechanically caused the loss of small plant particles from the bag, a process commonly observed when extracting mites from litter bags.

Microarthropods play a major role in root decomposition by both removing plant material and stimulating microfloral activity. The high percentage of mass-loss carbon accounted for as CO_2-C for the insecticide-treated roots in comparison to the low percentage from

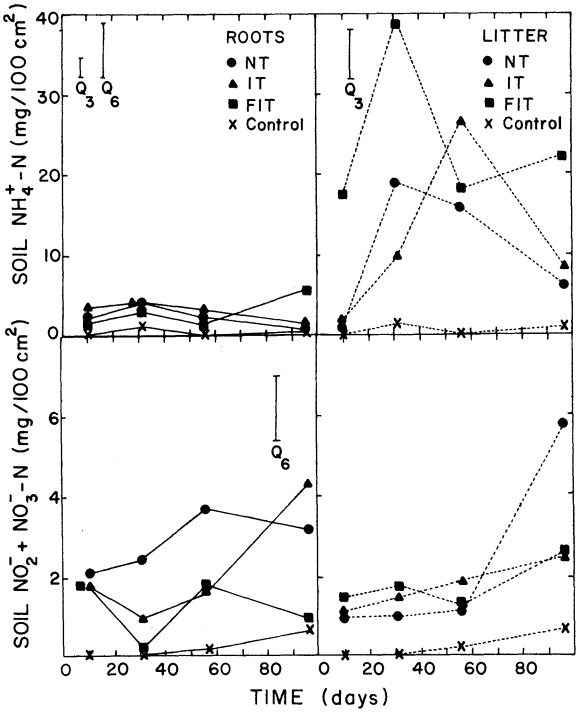

FIG. 8. Changes in soil ammonium- and nitrite- + nitrate-nitrogen in soil around buried roots and litter of the desert ephemeral *Lepidium lasiocarpum*. See Fig. 1 for treatment descriptions.

TABLE 7. Effect of biocidal treatments on nitrogen budgets for *Lepidium* root decomposition. Mean initial plant-N values for the untreated, insecticide-treated, and fungicide- + insecticide-treated bags were 80.2, 81.6, and 81.2 mg/100 cm², respectively. MA denotes microarthropods.

Treatment	Budget compartment	Day			
		10	32	56	96
		Percent of initial plant-N			
Untreated	Plant	87.67	43.13	33.92	30.34
	Bacteria	3.81	0.45	0.21	9.37
	Fungi	0.64	0.75	0.99	4.02
	Protozoa	0.006	0.0004	0.002	0.04
	Bacteriophagous nematodes	0.002	0.008	0.003	0.16
	Fungiphagous nematodes	0.00002	0.001	0.003	0.03
	Nematode-predatory MA	0.002	0.001	0.001	0.003
	Fungivorous MA	0.00	0.006	0.005	0.002
	Detritivore-fungivore MA	0.0002	0.0007	0.001	0.009
	General predatory MA	0.0003	0.00	0.0004	0.007
	Soil organic-N		20.81	3.12	85.92
	Soil ammonia-N	1.40	2.73	1.67	0.53
	Soil nitrate- + nitrite-N	1.90	1.67	2.53	2.01
	N unaccounted for	4.57	50.05	57.53	−32.43
	N accounted for	95.43	49.95	42.47	132.43
Insecticide	Plant	49.36	74.57	63.41	77.40
	Bacteria	41.78	3.05	4.77	7.59
	Fungi	0.45	0.50	0.44	4.88
	Protozoa	0.07	0.09	0.12	0.28
	Bacteriophagous nematodes	0.007	0.03	0.02	0.48
	Fungiphagous nematodes	0.00004	0.003	0.02	0.002
	Nematode-predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore-fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	Soil organic-N	47.65	−15.16	−11.60	172.28
	Soil ammonia-N	4.60	4.92	3.92	1.75
	Soil nitrate- + nitrite-N	2.22	1.13	1.89	5.19
	N unaccounted for	−46.13	40.35	37.01	−169.85
	N accounted for	146.13	69.16	62.99	269.85
Fungicide + insecticide	Plant	95.76	55.88	67.11	56.80
	Bacteria	4.18	0.39	1.14	15.55
	Fungi	0.09	0.03	0.13	2.73
	Protozoa	0.0005	0.0002	0.00002	0.31
	Bacteriophagous nematodes	0.00	0.0005	0.10	0.33
	Fungiphagous nematodes	0.0002	0.0007	0.05	0.35
	Nematode-predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore-fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	Soil organic-N	−16.56	−37.39	−17.07	91.76
	Soil ammonia-N	1.70	3.03	1.40	5.35
	Soil nitrate- + nitrite-N	1.85	0.24	2.67	0.98
	N unaccounted for	12.98	77.80	44.47	−74.11
	N accounted for	87.02	22.20	55.53	174.11

untreated roots was probably a reflection of the fibrous nature of the roots. Therefore, comminution may be very important in mass loss other than mineralization during root decomposition. For the 1st 32 d there was no difference in community respiration between untreated and insecticide-treated roots, indicating that microarthropods were not stimulating microbial activity at this time and mass loss might result merely from the sifting of fine roots out of the bags. However, between day 56 and 96 microbial activity was higher on the untreated roots than on insecticide-treated roots, suggesting stimulation of the microflora by comminution and/or moderate grazing of the microflora by microarthropods. This stimulation in microbial activity occurred after the appearance of the fungiphagous tarsonemid mites.

Tarsonemid mites appeared to control microbial activity by grazing on fungi in untreated bags between the 3rd and 4th mo of the decomposition process. Their density stimulated microbial activity in the roots and either had no effect or depressed microbial activity in the litter. Overgrazing of fungi by mites or collembola has been observed in the laboratory studies when collembola populations are too high (Hanlon and Ander-

TABLE 8. Effect of biocidal treatments on nitrogen budgets during *Lepidium* litter decomposition. Values are reported as percent of initial plant-N (untreated, insecticide, and fungicide + insecticide were 174, 178, and 500 mg/100 cm^2, respectively). MA denotes microarthropods.

Treatment	Budget compartment	Day			
		10	32	56	96
Untreated	Plant	91.79	50.15	54.99	59.93
	Bacteria	0.41	0.04	0.87	8.19
	Fungi	0.21	0.12	0.58	1.02
	Protozoa	0.001	0.003	0.07	0.07
	Bacteriophagous nematodes	0.0007	0.002	0.002	0.04
	Fungiphagous nematodes	0.00005	0.0009	0.002	0.002
	Fungivorous MA	0.00	0.003	0.02	0.001
	Detritivore-fungivore MA	0.0001	0.0001	0.0003	0.008
	General predatory MA	0.0002	0.002	0.0009	0.005
	Soil organic-N		−4.76	−1.85	67.07
	Soil ammonia-N	0.45	7.12	5.89	2.24
	Soil nitrate- + nitrite-N	0.36	0.35	0.40	2.24
	N unaccounted for	6.78	46.97	39.02	−40.84
	N accounted for	93.22	53.03	60.98	140.84
Insecticide	Plant	96.76	53.82	59.86	60.17
	Bacteria	3.09	2.48	3.52	5.54
	Fungi	0.13	0.19	0.26	0.50
	Protozoa	0.0002	0.05	0.002	0.06
	Bacteriophagous nematodes	0.002	0.003	0.004	0.03
	Fungiphagous nematodes	0.0002	0.001	0.004	0.003
	Nematode-predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore-fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	Soil organic-N	11.01	−2.35	29.94	66.71
	Soil ammonia-N	0.80	4.41	11.96	2.67
	Soil Nitrate- + nitrite-N	0.49	0.67	0.82	1.45
	N unaccounted for	−12.32	39.69	−3.37	−37.13
	N accounted for	112.32	60.31	103.37	137.13
Fungicide + insecticide	Plant	97.37	72.96	39.49	69.78
	Bacteria	1.90	1.62	3.04	2.13
	Fungi	0.02	0.06	0.06	0.58
	Protozoa	0.00007	0.00004	0.0006	0.06
	Bacteriophagous nematodes	0.0001	0.00003	0.0005	0.002
	Fungiphagous nematodes	0.00001	0.0001	0.003	0.0004
	Nematode predatory MA	0.00	0.00	0.00	0.00
	Fungivorous MA	0.00	0.00	0.00	0.00
	Detritivore-fungivore MA	0.00	0.00	0.00	0.00
	General predatory MA	0.00	0.00	0.00	0.00
	Soil organic-N	12.60	36.62	17.31	29.40
	Soil ammonia-N	3.65	8.15	3.82	4.53
	Soil nitrate- + nitrite-N	0.33	0.36	0.26	0.54
	N unaccounted for	−15.77	−19.77	36.02	−7.03
	N accounted for	115.77	119.77	63.98	107.03

son 1978). The rate of CO_2 evolution between these dates was greater in the roots. These data suggest that the tarsonemoid mite biomass may have surpassed the level at which a stimulation of fungal activity could occur, resulting in depression of fungal activity in the litter.

Further evidence that overgrazing of fungi had occurred in the untreated litter was the increased dominance of bacteria on day 96. This suggests that the microarthropods overgrazing the fungi gave bacteria a competitive advantage in litter. Thus, microarthropods may indirectly control bacterial biomass by altering competitive balances of the microflora. Stimulation of bacterial numbers and depression of fungal hyphae has been observed in the laboratory for macroarthropods feeding on litter (Hanlon and Anderson 1980).

Santos et al. (1981) suggested that the reduction in mass loss for insecticide-treated *Larrea* litter was a result of nematodes overgrazing bacteria because the nematode predator tydeid mites were removed. In *Lepidium* litter decomposition we did not observe higher nematode numbers in the insecticide-treated litter, and bacterial numbers were higher in the insecticide treatment than in the untreated litter. However, the higher turnover of microbial carbon in untreated litter compared to the insecticide-treated litter may have compensated for the differences in bacterial biomass be-

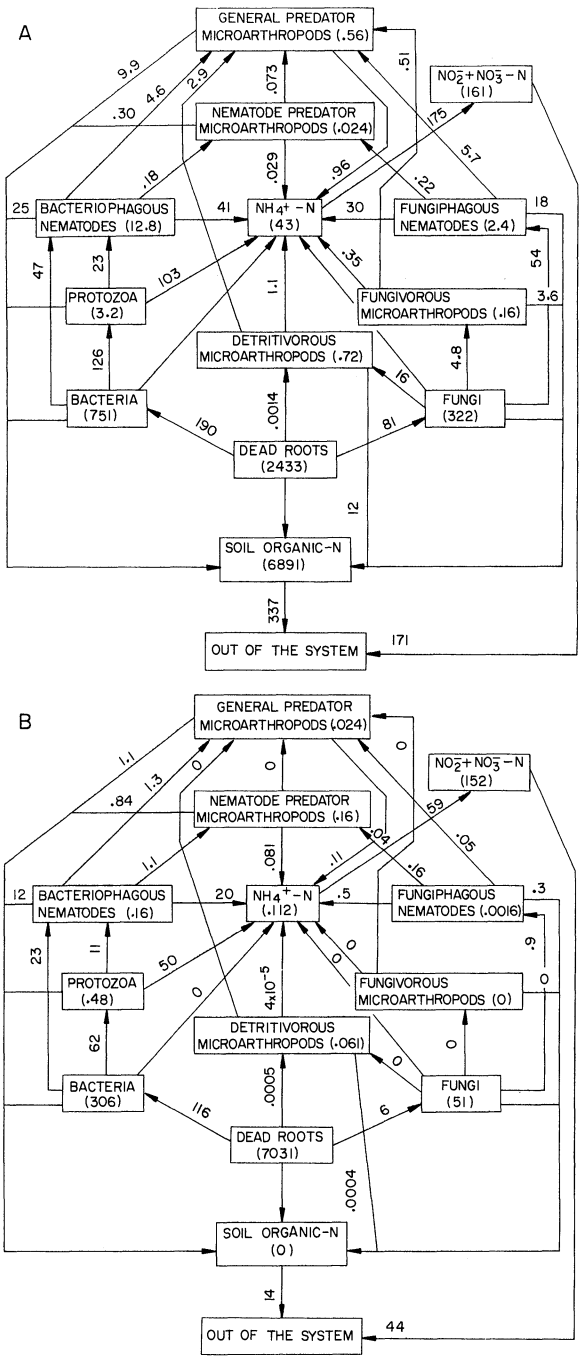

FIG. 9. Nitrogen budgets for the decomposition of *Lepidium lasiocarpum* roots at days (A) 10 and (B) 96. Nitrogen flows are $mg \cdot m^{-2} \cdot d^{-1}$; compartments are mg/m^2.

tween these two treatments (Table 3). A possible reason for this difference in response to insecticide treatment between *Lepidium* and *Larrea* could be inhibition of bacterial growth by toxic compounds present in nonsenescent *Larrea* (Fowler and Whitford 1980). A decrease in litter decomposition rates by the addition of insecticides has been observed for a number of forest ecosystems (Macauley 1975, Weary and Merriam 1978), and for roots in grasslands (Malone and Reichle 1973).

The addition of the insecticide increased nematode biomass on roots, a response similar to that reported by Santos et al. (1981). We observed an initial stimulation in bacterial biomass with the addition of chlordane, a response not reported by Santos et al. (1981). This stimulation was a result of fungal inhibition by the pesticide (Wilde and Persidsky 1956; L. W. Parker et al., *personal observation*). The net result was greater prey availability and thus the development of high protozoa and nematode biomasses. After the first sample date, untreated and insecticide-treated root bacteriophagous nematode biomasses were essentially parallel. This suggests that their prey were supplied at the same rate in both treatments, which corresponds to the lack of difference in microbial turnover between untreated and insecticide-treated roots. The lack of tydeid mites that prey on nematodes in the insecticide treatment probably enabled the nematode numbers to remain high.

The addition of the fungicides in conjunction with the insecticide enabled us to investigate the bacterial food web and how it operates under field conditions. Microbial activity and percent mass loss accounted for as CO_2-C were extremely low in the fungicide-insecticide root treatment. This was coupled with a decrease in bacterial and protozoan biomass at the same time that bacteriophagous nematode biomass was increasing by four orders of magnitude (days 10–56). This indicates that nematodes were feeding on bacteria and protozoa. If nematode biomass is not regulated (by predatory mites), overgrazing can depress microbial activity and nutrient turnover.

The fungicide-insecticide-treated litter did not have the same response. Bacterial and protozoan numbers did not decrease and nematode biomass was generally considerably lower. We do not know why nematodes did not develop in this treatment. There may have been chemical inhibition by organics in the litter that reduced nematode growth or migration into the litter bags, since nematode biomass was always lower in litter than roots. This suggests that the chemical makeup of the litter may affect predator-prey relationships at the nematode trophic level.

The low correlation between decomposition and abiotic factors when microarthropods were present and high correlation when they were absent suggests that the microarthropods uncouple mass loss and respiration from abiotic factors. Microarthropods can be active even in very dry soil, while the other soil biota (nematodes, protozoa, bacteria, and fungi) depend on soil moisture (Whitford et al. 1981*a*). Thus, microarthropods either directly or indirectly affect decomposition of buried plant materials relatively independently of soil moisture and other microclimatic factors. Because of this, the rate of decomposition of buried

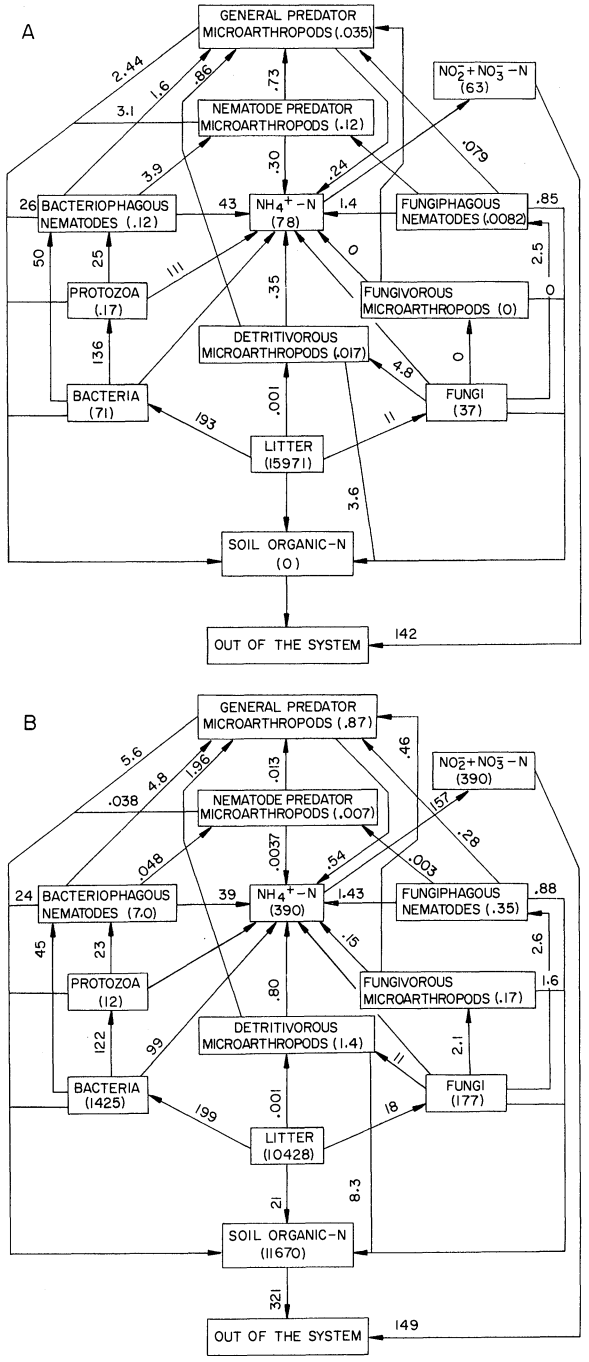

FIG. 10. Nitrogen budgets per unit litter bag area for the decomposition of *Lepidium lasiocarpum* litter at days (A) 10 and (B) 96. Nitrogen flows are $mg \cdot m^{-2} \cdot d^{-1}$; compartments are mg/m^2.

Lepidium litter (0.718%/d) was considerably higher than such rates for leaf material on the surface in most temperate ecosystems and was similar to that observed for tropical ecosystems (Singh and Gupta 1977). The decomposition rates comparable to tropical ecosystems suggest that temperature may be more important than water in regulating microarthropod activity and plant litter turnover. Even though the decomposition rates for buried *Lepidium* litter observed in this study were high, they were slower than that observed for buried *Larrea* litter in the Chihuahuan desert (Santos et al. 1981).

Like *Lepidium* litter, the decomposition rate of *Lepidium* roots (0.414%/d) was considerably faster than some plant species (*Phleum pratense* L. [Stenina 1964] and *Festuca arundinacea* [Malone and Reichle 1978] ≒0.06 and 0.23%/d, respectively) and the turnover time for *Lepidium* roots (1.89 yr) is approximately half that for tall-grass prairie (3–4 yr) (Dahlman and Kucera 1965). However *Lepidium* roots decomposed slower than red clover (*Trifolium pratense* L.) roots (1.17%/d) over the same time period (Stenina 1964), and maximum decomposition rates for suberized roots of a short-grass prairie (3.0%/d) were considerably higher (Ares and Singh 1974).

Lepidium litter decomposed faster than roots. This same trend has been observed for *Fescue* decomposition (Malone and Reichle 1973) and holds true when the plant material is ground (Jenkinson 1965). The C:N ratio of litter (30:1) was approximately half that of roots (64:1) in our study. However, nitrogen limitation was probably not the only reason for the lower degradation rate in roots (Smith 1966). Sinha (1972) proposed that the higher lignin content and the presence of inhibitory substances in the roots were responsible for the slower degradation rate and these factors may have contributed to the slow decomposition rate of *Lepidium* roots.

Using *Lepidium* decomposition data as a representative of the total ephemeral biomass, a rough estimate of ephemeral turnover can be made in relation to that

TABLE 9. The effects of a wet year in which rainfall in autumn, winter, and spring is added to the typical summer rainfall, and a dry year with summer rainfall only, on the biomass production of creosotebush *Larrea tridentata* and spring forbs. Turnover is the quantity of the plant materials produced that is estimated to decompose during the year. Primary production values are derived from Ludwig and Flavill (1979) and *L. tridentata* decomposition rate of 0.54%/d is derived from Santos and Whitford (1981).

	Aboveground			Belowground		
Vegetation	Biomass (kg/ha)	Turnover ($kg \cdot ha^{-1} \cdot yr^{-1}$)	% turnover in 1 yr	Biomass (kg/ha)	Turnover ($kg \cdot ha^{-1} \cdot yr^{-1}$)	% turnover in 1 yr
Larrea						
Wet year	636	533	87	347	?	?
Dry year	2226	1936	87	1213	?	?
Forbs						
Wet year	63	59.2	94	63	48.5	77
Dry year	2	1.9	94	2	1.5	77

TABLE 10. Estimated rate of biomass-C production and turnover for *Lepidium* litter and root fauna after 10 and 96 d of decomposition. MA denotes microarthropods.

	10 d				96 d			
	Litter		Roots		Litter		Roots	
Budget compartment	Production ($g \cdot m^{-2} \cdot d^{-1}$)	Turnover (d)	Production ($g \cdot m^{-2} \cdot d^{-1}$)	Turnover (d)	Production ($g \cdot m^{-2} \cdot d^{-1}$)	Turnover (d)	Production ($g \cdot m^{-2} \cdot d^{-1}$)	Turnover (d)
Protozoa	0.082	0.036	0.049	0.203	0.014	13.56	0.034	1.87
Bacteriophagous nematodes	0.016	0.122	0.010	0.306	0.003	0.030	0.065	35.71
Fungiphagous nematodes	0.004	0.057	...	...	0.0004	11.76	0.011	4.30
Nematode-predatory MA	0.033	0.830	0.0007	5.68	0.000001	111.11	0.00008	5.17
Fungivorous MA	...	...	...	...	0.0006	7.27	0.002	2.61
Detrivorous-fungivorous MA	0.000005	55	0.000005	333	0.003	7.31	0.005	2.62
General predatory MA	0.001	0.778	0.00087	5.73	0.0009	14.65	0.003	3.66

of *Larrea* (Table 9). The turnover values for both *Larrea* and forbs may be overestimates because they are based on short-duration studies in the growing season and on buried litter. However, they may underestimate surface litter removal because of high termite activity in the fall. Termites select forbs over *Larrea* (Whitford et al. 1982*a*) but will feed on *Larrea* litter (Elkins et al. 1982). These yearly turnover values (Table 9) are considerably higher than those measured by isotopic dilution in cold deserts (21–32% aboveground and 2–23% belowground; Caldwell et al. 1977).

Carbon budgets

The direct role of microarthropods in decomposition processes (e.g., ingestion of dead plant material) was insignificant, even when these populations peaked. Very little carbon flowed through microarthropods compared to the microflora, and the total animal respiration was always <10% of the total CO_2 output (Figs. 5 and 6). Excretion by detritivorous-fungivorous microarthropods was high only because of the high flow into them from fungi. The role of microarthropods in decomposition appears to be primarily as population regulators, either directly by feeding on fungi, or indirectly by feeding on other biota (Santos et al. 1981). One of the most striking differences between root and litter decomposition was that nematodes were important rate regulators of the root process, while detritivorous-fungivorous microarthropods were the most important regulators in litter.

Flows to the general predators were generally higher than expected for the biomass of predatory mites present. Mesostigmatid mite biomass may be underestimated since they are the largest microarthropods in our system and the values used to convert these numbers to biomass (Franco et al. 1979) are underestimated for our system. One of the highest flows into predatory mites on day 96 was from detritivorous-fungivorous microarthropods. These two compartments were highly correlated ($r = 0.98$, $P < .00001$) throughout the study.

By using the flows between carbon compartments it was possible to estimate faunal production and turnover. Faunal production was the sum of the flows into a compartment multiplied by the production efficiency. Turnover was the observed mass divided by the production. The turnover times of all faunal groups were lower for the litter than roots at day 10. At day 96, the opposite was true for all biota except bacteriophagous nematodes (Table 10). Carbon budgets indicated that elimination of microarthropods increased the percent of initial plant carbon that could be accounted for. The carbon unaccounted for could have been transported into the soil by various processes. In litter, fungi appeared to be important in this loss, probably as a result of fungal growth into the soil. Total fungal biomass was probably far greater than that measured, especially at day 96, since fungal hyphae extended from the litter bag into the soil.

Nitrogen

Microarthropods were important in regulating the loss of plant nitrogen and the mineralization and immobilization of nitrogen. Microarthropods, by being the major mechanism for mass loss, also regulated the initial loss of plant-N through litter removal. Though microarthropods are the major mechanism in this loss, they are not the sole mechanism. Ammonia volatilization, denitrification, and leaching may also contribute to nitrogen loss.

Microarthropods reduced the immobilization of nitrogen around roots by stimulating mineralization as indicated by a higher microbial activity in untreated than in insecticide-treated roots. The reduction in N-immobilization when fungi are inhibited indicates that they may be the major mechanism for this immobilization. Tarsonemoid mites would thus be very important in regulating the turnover of nitrogen immobilized by the fungal flora.

The mineralization product of plant nitrogen, unlike carbon, is not a sink; therefore calculation of mineralization constants is impossible, since NH_4^+-N can be converted to NO_2^- and NO_3^-. For the same reason interpretation of nitrogen dynamics is difficult. Min-

eralization of plant nitrogen depended on the initial C:N ratio of the plant material. Greater soil ammonium concentrations occurred in litter (C:N = 30:1) than in roots (C:N = 64:1). Plant materials with carbon-to-nitrogen ratios of 30:1 or less generally exhibit nitrogen mineralization, while those with greater C:N ratios have net immobilization during the initial stages of decomposition (Alexander 1977). However, significant immobilization of nitrogen did not occur until the last sample date.

Correlation analysis showed that total soil-N and NH_4^+-N dynamics became more closely associated with the abiotic parameters of soil moisture and rainfall when biocides were used. This in conjunction with stepwise regression analysis suggested that microarthropods are important in uncoupling the system from abiotic parameters and are important regulators. In biocide treatments, nematodes and protozoa best explain the nitrogen dynamics. Coleman et al. (1978) have shown that protozoa and nematodes are important regulators of nitrogen mineralization in the absence of fungi and higher trophic groups. Further, Elliott et al. (1980) showed that protozoa form an important trophic link between bacteria and nematodes by increasing the substrate available for nematode growth. As with mass loss, this suggests that the process rates are regulated by microbial-feeding arthropods. The negative correlations with soil moisture and rainfall indicate N-immobilization by the microflora when the soil is wet.

Nitrification occurred in all treatments. However, higher concentrations of NO_2^-- + NO_3^--N were usually in the untreated material. Since nitrifiers are relatively sensitive to pesticides, this was expected. No appreciable buildup of nitrite plus nitrate was observed, as has been observed in other desert systems (Charley and West 1977, Wallace et al. 1978). A number of processes could account for this: denitrification, fungal immobilization, and leaching. Nitrification inhibition could have resulted from a soil pH of 7.8 (Martin et al. 1942), ammonium inhibition in the litter treatments (Broadbent et al. 1957), and/or allelopathy as a result of bags being buried under *Larrea* bushes (Skujins and Trujillo Fullgham 1978).

Nitrogen budgets

Between days 56 and 96 (July and August), there was an increase in the total nitrogen. This corresponded to an increase in plant-N and soil-N in the litter and generally in the soil-N in the root treatments. The greatest increase in fungal biomass occurred during this time. We observed fungal hyphae extended from the litter bag into the surrounding soil. This uptake of nitrogen into the bag probably resulted from immobilization outside the litter bag by fungi. Fungal immobilization of nitrogen during the decomposition of plant material has been hypothesized for a number of systems (Macauley 1975, Swift 1977, Staaf 1980). Plant-N could increase in litter from the absorption of mineral-N, since litter moisture content increased from 6 to 80% between days 56 and 96.

Net nitrogen movement to decomposing ephemeral roots during August could have a dramatic effect on the productivity of *Larrea.* In years of wet falls and winters, spring N-mineralization and ephemeral production is high. Only the shallow-rooted grasses and ephemerals respond to low rates of nitrogen fertilization (Ettershank et al. 1978). Ephemerals therefore would absorb most nutrients mineralized from plant material decomposing in the spring. Most ephemerals die during the hot dry summer months (May–July). Nutrients remain in the ephemerals as standing dead, litter, and roots. The soils are hot and dry and the potential for N-mineralization is low during these summer droughts. When the droughts break in late July and early August, the potential mineralization is high. The first rain event in late summer will carry nutrients from the surface horizons into the rooting zone of *Larrea.* This first rain will also stimulate the microflora that decompose the roots of ephemerals, as observed on day 96 of our study. Fungi will develop a network of hyphae around the roots that could act as a sieve, removing nutrients from the downward-moving water of subsequent rain events. The greater the ephemeral production (and thus carbon input), the greater the density of the microbial sieve and the greater the stress for nutrients other than carbon. This microbial sieve could absorb nutrients being leached during subsequent rains, decreasing the nutrients available for *Larrea* production. Newbery (1979) observed that production by grassland plants grown in pots containing decomposing roots was reduced, and attributed this reduction to phosphorus deficiency. The majority of the root biomass of ephemerals is above the rooting zone of *Larrea.* However, with abundant winter moisture, ephemeral roots can penetrate the rooting zone of *Larrea.* The decomposer biomass would, therefore, be in direct competition with *Larrea* roots.

Ephemeral production in spring is low compared to *Larrea* production in the autumn. However, whenever spring ephemeral production is high, fall *Larrea* production is dramatically reduced (Table 9). Consequently, in desert ecosystems there is less increase in net primary production with respect to actual evapotranspiration (Webb et al. 1978). Webb et al. (1978) hypothesized that desert species have evolved a "conservative strategy" for water use. We hypothesize that net primary production is limited not only by water but also by nitrogen, and nitrogen availability is dependent on production of ephemerals. The greater the ephemeral production, the greater the immobilization of nutrients into their biomass, and the greater the carbon input to the soil as root exudates, sloughing, and death. This carbon input places a nitrogen stress on the microflora, since the C:N ratio of the microflora is considerably lower than that of the plant material.

We would therefore expect maximum *Larrea* production the summer after a dry fall and winter, a phenomenon observed by Ludwig and Flavill (1979). These conditions would not allow for the development of a large ephemeral biomass either in fall or spring. A wet fall could result in a high ephemeral biomass at that time, and if the winter and spring are dry, substantial ephemeral root biomass would be present in the late summer to reduce *Larrea* production. Winter moisture is necessary for spring ephemeral production.

Conclusions

We hypothesize that a relationship exists between the timing of rain events, ephemeral plant production and decomposition, and perennial production. An increase in ephemeral plant biomass places a nitrogen stress on perennial plant production as a result of its decomposition and the subsequent fungal immobilization of nitrogen. We have shown that microarthropods are important decomposition regulators and increase the turnover of this immobilized nitrogen. In the absence of microarthropods, nematodes become the system regulators, and thus the decomposition process becomes closely associated with soil water content.

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