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DECOMPOSITION AND SOIL NITROGEN AVAILABILITY IN CHIHUAHUAN DESERT FIELD MICROCOSMS

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Summary—We examined the relationships between the decomposition of seven litter and root substrates, soil N availability, and populations of soil biota in field microcosm for 13 months. Most of the variation of N loss from the substrates was a function of initial substrate N concentration. Small portions of the variation of substrate mass loss and soil inorganic N were explained by initial substrate N concentration. Most of the variation of substrate mass loss, soil inorganic N, and soil biota populations was explained by differences between the decomposition of roots vs litter and of annual roots vs perennial roots. N loss from roots was more rapid than from litter. Mass of bacteria plus yeast in root microcosms was lower, nematode populations were higher, and the potential N mineralization rate at 9 months was higher than in litter microcosms. These results suggest that organic matter turnover in root microcosms was more rapid than in litter microcosms. Mass loss from annual roots was higher but N loss was lower than from perennial roots. Bacteria plus yeast mass in annual-root microcosms was lower, nematode populations were higher, and soil inorganic N was less than in perennial-root microcosms. The addition of annual roots reduced inorganic N concentrations below that of the unamended controls and the other substrate treatments in month 6 and 9 samples indicating that annual-root decomposition led to N immobilization or denitrification. The addition of litter or perennial-roots increased soil inorganic N concentrations above the unamended control in the month 9 samples. The decomposition of N-poor annual plant roots may significantly reduce N availability in desert ecosystems.

INTRODUCTION

Primary production in the northern Chihuahuan Desert is controlled by interactions between the availability of water and N (Fisher *et al.*, 1987, 1988; Gutierrez and Whitford, 1987; Gutierrez *et al.*, 1988). Water and N are temporally and spatially variable resources and high availabilities of both do not always coincide (Charley, 1972; Fisher *et al.*, 1987; Moorhead *et al.*, 1988). High moisture and N availabilities are most likely to coincide when precipitation resumes after a drought because of increased N turnover of native soil organic matter and microbial biomass (Charley, 1972; Fisher *et al.*, 1987). Increased growth of annual plants then results, followed by nearly simultaneous death and decomposition. The decomposition of such a pulse of organic matter may significantly affect subsequent N availability (Parker *et al.*, 1984; Whitford *et al.*, 1988). Predicting the effects of variations in precipitation on desert ecosystem productivity requires a detailed understanding of the immobilization and mineralization of N during the decomposition of a variety of substrates.

N release from decomposing litter and roots has often been studied using litter bags (Schlesinger, 1985). However, much nutrient loss from litter bags probably occurs as soluble or particulate organic matter. Most of this organic matter will eventually be catabolized to inorganic forms available to plants but some will remain in organic form, becoming incorporated into the soil humus (Swift *et al.*, 1979). Therefore, only an indirect linkage exists between the disappearance of a litter or root substrate and the availability of soil N.

This problem may be especially severe for litter in the Chihuahuan Desert. Rates of mass loss from litter bags on the soil surface are insensitive to water and N availability (Whitford *et al.*, 1986; Mackay *et al.*, 1987). There is little or no immobilization of N by surface litter during the decomposition process, even with litter C-to-N ratios as high as 60:1 (Schaefer *et al.*, 1985; Montaña *et al.*, 1988). Despite this, rates of litter disappearance are far more rapid than predicted by models based on AET and lignin content and rival those of tropical and mesic deciduous forests (Whitford *et al.*, 1981, 1986; Elkins *et al.*, 1982). The lack of N immobilization in substrates with high C-to-N ratios, and the lack of response to water and N amendments suggest that the microflora populations are small or inactive and that there is little catabolism of litter on the soil surface. Thus, litter is probably lost from the soil surface mainly by fragmentation with the litter being catabolized below ground [see Moorhead and Reynolds (1989) for a more detailed review].

Our goal was to develop a technique which could be used to study the relationship between decomposition and soil N availability. This was attempted by using field microcosms to expose selected substrates to as many factors affecting decomposition and mineralization as possible while minimizing N addition and loss to and from the soil system. Root

and litter substrates were selected to represent two important plant groups, the perennial shrubs and the annual forbs. Based on field observations and experience, we hypothesized that decomposition and mineralization of a substrate are often dependent upon readily-observable characteristics of the substrate such as the plant organ (root vs shoot), life cycle (annual vs perennial), or the surface-to-volume ratio of the substrate (fine roots vs coarse roots). Hypotheses were posed as a set of comparisons between paired groups of substrates in which one group was predicted to have a larger and more rapid effect on N availability than the other (">" indicates "larger and more rapid effect on N availability").

(1) Roots > surface litter, because surface litter fragments must first be transported below ground.

(2) Fine roots > coarse roots, because fine roots have less structural material and a higher surface-to-volume ratio.

(3) Annual plant roots > perennial shrub roots, because annual plant roots consist of less structural material.

Additionally, we predicted that substrates with high N content will result in increased N availability compared to those of low N content.

We tested these predictions by following changes in available soil N associated with the decomposition of seven types of litter and root substrates. Populations of several groups of microorganisms and soil fauna were estimated to aid interpretation of results.

MATERIALS AND METHODS

The study was made at the Jornada Long-Term Ecological Research (LTER) site located 40 km NNE of Las Cruces, N.M. on a northeast facing piedmont in a shrubland dominated by creosotebush (*Larrea tridentata* [DC.] Cov.). The creosotebush zone is located at mid-slope (3% gradient) on loamy sand soils with a calcium carbonate deposition layer (caliche) at *ca* 40 cm. The soil is classified as a Typic Haplargid of the Dona Ana series (Wierenga *et al.*, 1987). Total N at 0–10 cm averages 400–500 mg kg^{-1} under shrubs and 200–400 mg kg^{-1} between shrubs. Annual precipitation averages 213 mm, 55% falling during July–September as convectional thundershowers. Temperatures regularly > 40°C in summer and regularly fall below 0 C during winter nights.

Experimental procedures

Microcosms were constructed from 0.5 l. glass canning jars with threaded openings. A conical top of nylon mesh (1.5 mm) was secured to the jars which allowed gas transfer while excluding most litter inputs from the creosotebush canopy.

Each microcosm contained *ca* 450 g sieved soil (2 mm mesh) removed from the location where the jar was to be exposed. All microcosms except controls received 1 g of one of the following substrates: fine roots (< 2 mm dia) from a common summer annual (*Baileya multiradiata*), fine roots from a common perennial (*Zinnia grandiflora*), coarse roots (> 2 mm dia) from an annual (*B. multiradiata*), coarse roots from either of two common perennials (*L. tridentata*, *Z. grandiflora*), or litter from an annual (*B. multiradiata*) or a perennial (*L. tridentata*). The 1 g amount of the substrates approximated the amounts found in canopy soil. Litter was placed on the soil surface of the microcosms and roots were buried *ca* 5 cm below the surface. Litter and roots were placed in different position because our objective was to simulate as many of the factors affecting decomposition and mineralization as possible.

Eight microcosms, each containing one of the 7 substrates plus soil or containing soil only, were buried under each of 20 shrubs chosen for their similar appearance. Microcosms were randomly assigned to locations under the N side of each shrub, a location of high litter accumulation, moisture availability, and N availability. The microcosms were buried with the top of the jar within 1 cm of the soil surface at 0.5 canopy radius.

Subsamples for determination of initial values were collected during the filling of the jars on 5 January 1984. All jars from five randomly-selected shrubs were destructively sampled after 3, 6, 9 and 13 months (respectively, 4 April 1984, 17 July 1984, 10 October 1984 and 5 February 1985). After precipitation events, excess water was carefully poured from all microcosms into plastic bottles and returned to the laboratory for inorganic N analysis. Water samples were preserved with 1.0 mg l^{-1} phenylmercuric acetate (PMA) and stored at 2–7°C until analysis of $NO_3^- + NO_2^-$-N and NH_4^+-N, usually in < 2 weeks. Water accumulated after larger precipitation events but does not seem to have had a major effect on the use of the data for comparisons between substrates until after month 9.

Litter and roots were separated with forceps and then subsamples of soil were used for determination of soil moisture, KCl extractable $NO_3^- + NO_2^-$-N, NH_4^+-N, total N and populations of bacteria, nematodes and microarthropods. Month 13 samples had well-developed algal crusts which were carefully removed and analyzed for total N.

Soil moisture content of the microcosms was determined by oven-drying. Soil moisture content outside the microcosms was estimated from soil psychrometer measurements made at a site < 1 km away (Fisher *et al.*, 1987). Moisture tension measurements (MPa) were converted to moisture content (g g^{-1}) using the relationship given by Schlesinger *et al.* (1987).

NH_4^+-N and $NO_3^- + NO_2^-$-N were determined in 2.0 M KCl extracts with a 10:1 ratio of soil to KCl (Keeney and Nelson, 1982) and in water samples collected from the microcosms. NH_4^+-N was measured in the extracts by an automated salicylate procedure (Wall and Gehrke, 1975; Nelson, 1983) and $NO_3^- + NO_2^-$-N was measured by an automated cadmium reduction procedure (Henriksen and Selmer-Olsen, 1970). Total N (Nelson and Sommers, 1980) was determined after air drying and grinding samples with a motorized mortar and pestle (< 0.15 mm). Micro Kjeldahl digestions were performed using an aluminum block digestor (Nelson and Sommers, 1980). NH_4^+-N in the digest was measured using an automated salicylate procedure (Wall and Gehrke, 1975).

Potential N mineralization was estimated after 9 months using the leaching incubation technique (Stanford and Smith, 1972; Fisher *et al.*, 1987). The month 9 samples were selected to estimate the final response of potential N mineralization because later samples were frequently water-logged. Soils were held for 37 weeks at 35°C at 0.03 MPa and were periodically leached with $CaCl_2$ and a minus-N nutrient solution.

Bacterial numbers were estimated by direct counts using FITC staining (Parker *et al.*, 1984). Fungal hyphae length was not determined on the FITC slides because the hyphae deteriorated before the measurements were completed. Nematodes were extracted using modified sugar flotation and were identified and placed in one of four trophic groups: fungivores, bacterivores, omnivore–predators or phytophages (Freckman *et al.*, 1975). Nematode numbers were not corrected for extraction afficiency or soil moisture. Microarthropod populations were extracted from the initial soils and from month 3 collections using modified Tullgren funnels (Santos *et al.*, 1978). Microarthropod population estimates were very low, probably because of soil disturbance in microcosm construction, and these measurements were discontinued after month 3.

Throughfall was collected beneath the canopy of 6 shrubs using a 10.3 cm dia funnel for 5 rain events during August–October, 1985. The throughfall was collected within 24 h, preserved with PMA, and refrigerated. Samples were analyzed for $NO_3^- + NO_2^-$–N, NH_4^+–N and total N.

Calculations and statistical analysis

Mass loss was calculated as the difference between initial mass and the mass of identifiable substrate recovered at each sampling. N loss was calculated as the difference in initial mass of N and the mass of N of the identifiable substrate recovered at sampling. Soil inorganic N and total N values for added substrates were adjusted for the contribution of native soil organic matter by subtracting the controls (no added substrate). N loss and soil inorganic N were transformed to the natural log for statistical analysis.

The data were analyzed using the two-way factorial analysis of variance (ANOVA) across all months and, in the event of significant interactions, a one-way ANOVA for each month. Different shrubs were destructively sampled for each collection so that a repeated-measures analysis was unnecessary for examining all months. Planned contrasts were used to partition the variance due to the substrate treatments into seven components (Steel and Torrie, 1980; Freund and Littell, 1981) that tested the hypotheses relating decomposition to plant organs (roots or litter) or life cycle (annual or perennial; Table 1). Residuals were plotted against predicted values and tested for normality. Transformations were used as necessary to produce homogeneous variances and normal distributions.

The proportion of substrate N covered as soil inorganic N was calculated from the mean values of soil inorganic N by dividing by substrate N loss if N loss was >0. Negative values of recovery of substrate N could result if the soil inorganic N value for a particular treatment was less than the soil inorganic N value for the control. Negative values indicate the occurrence of N immobilization in the soil, gaseous N losses, or organic N losses in water compared to the control microcosms. Negative values of substrate N loss indicated net immobilization of N in the substrate so that no N was recoverable. No statistical analysis could be performed on N recovery data because means were used for the calculations. The calculations were attempted for the individual data points but small values of N loss in the denominator produced very erratic distributions which did not appear to give meaningful results in statistical testing.

The importance of initial substrate N concentration vs other factors affecting decomposability was examined using analysis of covariance (ANCOVA) to adjust treatment means for the contribution of initial substrate N concentration (Freund and Littell, 1981). Slope and intercept values for the regression of initial substrate N concentration vs N loss, mass loss, soil inorganic N, soil total N and soil biota populations resulted from this analysis. Both the initial substrate N concentration regression parameters and the treatment-effect contrasts were tested over the adjusted error term resulting from ANCOVA.

The soil biota population data were also examined by multivariate analysis of variance. This analysis can identify responses of groups of populations that may not be apparent from the individual ANOVA's. The data were transformed to units of standard deviations so that the coefficients of the characteristic vector indicate the relative importance and direction of response of each of the population measurements (Harris, 1975).

The potential N mineralization data were used to estimate the size and decomposition rate constants of two pools of organic N; a small, fast pool that turns over in less than a month under laboratory incubation conditions, and a larger, slower pool (Jones, 1984; Fisher *et al.*, 1987). Pool-size and rate coefficients were estimated by fitting the data to an

Table 1. Coefficients of planned treatment contrasts (Steel and Torrie, 1980) used to test hypotheses concerning substrate treatments

	Treatments							
Contrast	Control	Annual fine roots	*Zinnea* fine roots	Annual coarse roots	*Zinnea* coarse roots	*Larrea* coarse roots	Annual litter	*Larrea* litter
Treatments vs control	12	−2	−2	−2	−1	−1	−2	−2
Roots vs litter	0	2	2	2	1	1	−4	−4
Fine roots vs coarse roots	0	2	2	−2	−1	−1	0	0
Annual roots vs perennial roots	0	2	−2	2	−1	−1	0	0
Zinnea coarse roots vs *Larrea* coarse roots	0	0	0	0	1	−1	0	0
Baileya litter vs *Larrea* litter	0	0	0	0	0	0	1	−1

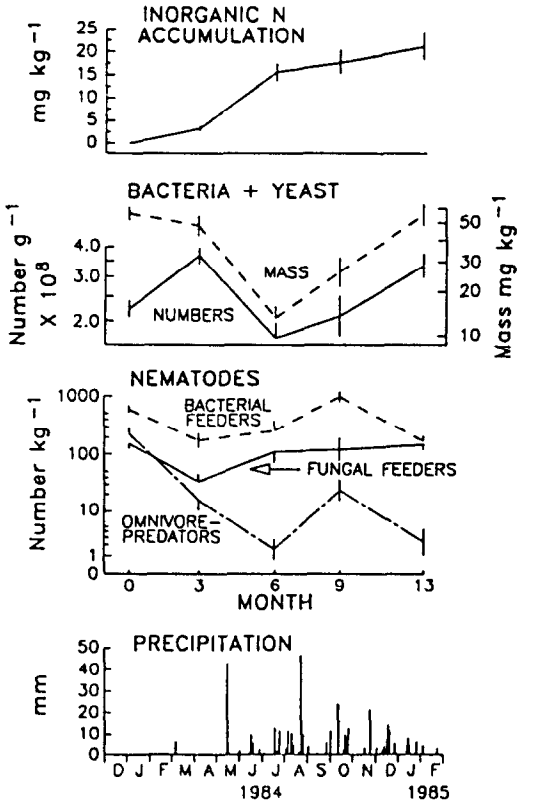

Fig. 1. Mean soil inorganic N accumulation, soil biota populations and precipitation during the field incubation. Error bars indicate ± 2 SE.

exponential equation of the form

$$N_t = N_1 + N_2 - N_2 e^{-k_2 t}$$

where N_t is cumulative N mineralized (mg kg^{-1}) at time t (days), N_1 is the pool size (mg kg^{-1}) of the small, fast pool, and N_2 and k_2 are the pool size and rate coefficient of the large, slow pool. In this formulation of the model, the small, fast pool is assumed to decompose completely during the first incubation period and therefore no rate coefficient is necessary.

Two estimates of throughfall inputs of total N were calculated for comparison with observed treatment effects on soil inorganic N. One estimate was calculated simply as the mean of the 1985 throughfall samples times the total precipitation for the periods of field exposure (months 0–3, 3–6, 6–9, 9–13). The second method used a regression between precipitation volume and throughfall total N concentration to estimate the contribution of each precipitation event.

RESULTS

Precipitation during the 13 month field exposure was negligible during January–April, 1984 (months 0–4), but was quite high after that (Fig. 1). Mean soil moisture contents of the microcosms when sampled at months 3, 6, 9 and 13, respectively, were 0.02, 0.02, 0.07 and 0.16 g g^{-1}. The month 13 moisture content exceeded the soil field capacity (−0.01 MPa = 0.12 g g^{-1}; Schlesinger *et al.*, 1987). Soil moisture contents outside of the plots at months 3, 6, 9 and 13, respectively, were 0.02, 0.01, 0.04 and 0.12 g g^{-1}.

During months 0–3, the driest period during the experiment, bacteria populations increased, nematode populations decreased, and soil inorganic N increased slightly (Fig. 1). Bacteria populations fell during months 3–6, bacterivorous and fungivorous nematode populations increased, omnivore–predator nematodes continued to decline, and inorganic N increased rapidly. During months 6–9, bacteria populations, fungivorous nematode populations, and soil inorganic N changed little. Standing water occasionally accumulated during months 3–9. The mass of inorganic N lost pouring off the water was <0.5% of that in the soil except for one replicate where the loss was 3.1%. During months 9–13, standing water frequently accumulated in the microcosms due to the high precipitation and low evaporation caused by cool temperatures. Inorganic N losses from pouring off the water were variable but ranged as high as 22% of the soil inorganic N. Thick algal crusts formed in the microcosms at this time, a rare condition in this normally well-drained, sandy soil.

Initial substrate N concentration was significantly correlated with N loss, mass loss and soil inorganic N, but only the relationship between initial substrate N concentrations and substrate N loss was important (Table 2). Differences between the seven substrate treatments other than N concentration explain a larger proportion of the variation of substrate mass loss and soil inorganic N (Table 3).

Relatively few differences resulted from the substrate treatments in month 3 because of the dry conditions and the short time elapsed since the beginning of the experiment. Conditions for months 9–13 were not representative of this well-drained desert soil because of frequent waterlogging. Therefore, the results of the ANOVA's of the seven substrate treatments will be presented for only months 6 and 9.

Mass loss from the substrates was significantly different for most of the substrate contrasts. The most

Table 2. Correlations between initial substrate N concentration and microcosm litter and soil measurements

	Sample collection (month)				
Measurements	All	3	6	9	13
Ln substrate N loss	+0.70*	+0.59*	+0.85*	+0.90*	+0.90*
Substrate mass loss	+0.26*	+0.16	−0.05	+0.34*	+0.48*
Ln soil inorganic N	+0.10*	+0.06	+0.14	+0.20	+0.23*
Soil total N	+0.06	ND	−0.02	+0.01	+0.20*

Values are correlation coefficients (r).
*$P < 0.05$.

Table 3. Importance of the effects of the 7 substrate treatments relative to the total amount of variation explained by the substrate treatments plus the initial substrate N concentration

Measurements	Sample collection (month)				
	All	3	6	9	13
Ln substrate N loss	0.18*	0.58*	0.18*	0.10*	0.05
Substrate mass loss	0.79*	0.92*	1.00*	0.82*	0.65*
Ln soil inorganic N	0.65*	0.91*	0.92*	0.82*	0.66*
Soil total N	0.79	ND	0.99	1.00*	0.23

Values are proportion of explained variance = $SS_{Substrate\ treatments}/(SS_{Initial\ substrate\ N\ concn} + SS_{Substrate\ treatments})$, where SS is sum of squares.
Significance tests of the substrate treatments were made after removing the covariance due to the initial substrate N concentration.
*$P < 0.05$.

consistent differences in mass loss occurred between fine roots and course roots (Table 4, Fig. 2). N loss from the substrates differed for all contrasts but this is mostly due to differences in N content (Table 5, Figs 2 and 3). Soil inorganic N mainly different between annual and perennial roots: inorganic N was significantly lower in annual-root microcosms than in perennial-root microcosms (Table 6, Fig. 3). (The apparent difference between roots and litter in month 9 largely resulted from the low inorganic N values associated with annual roots.) Although perennial roots and litter had similar effects on soil inorganic N, mean recovery of substrate N loss was higher for litter in month 9, and appears to be essentially complete (Table 6, Fig. 3). Mineralizable soil organic N showed only one important difference: soil from root microcosms had significantly more labile organic N than did soil from litter microcosms (Table 7). Soil biota populations differed mainly for roots vs litter and for annual roots vs perennial roots. Root microcosms had lower bacteria plus yeast biomass and higher populations of bacterivorous and fungivorous nematodes than did litter microcosms. Annual-root microcosms had lower bacteria plus yeast biomass and higher fungivorous nematode populations than did perennial-root microcosms (Table 8).

Generally higher throughfall estimates resulted from the regression between precipitation volume and throughfall total N concentration (regression $r^2 = 0.71$) than from the use of a single mean total N concentration. Using the highest of the values estimated by the two methods for each time periods the estimated throughfall inputs for months 0–3, 3–6, 6–9 and 9–13 were 0.02, 0.32, 1.23 and 0.69 mg kg^{-1} soil. These values were much lower than the significant differences in soil inorganic N (Table 6) or in mineralizable soil organic N (Table 7).

DISCUSSION

Table 9 summarizes important results of the experiment in terms of the predictions and the associated statistical contrasts. It illustrates that differences in mass loss or N loss are often not reflected by soil N measurements or soil biota populations. The only important treatment contrasts for soil N measurements and soil biota populations were roots vs litter and annual roots vs perennial roots. In addition, we observed that despite the similar effects of perennial-roots and litter on soil inorganic N, the estimated net recovery of substrate N from litter was much higher than for perennial roots, implying differences in organic matter processing.

Initial substrate N concentration had surprisingly little effect on soil inorganic N. One reason for the absence of an initial substrate N effect was that the high N concentration of the *Larrea* roots did not lead to high soil inorganic N concentrations. The low net recovery of substrate N suggests that much of the N in the *Larrea* roots was difficult to mineralize.

Comparisons of roots and litter showed that roots had lower bacteria plus yeast populations, higher nematode populations, and higher potential rates of N mineralization after 9 months. These characteristics are consistent with the occurrence of faster N turnover in root microcosms. Nematodes are thought to increase turnover of primary decomposer biomass through grazing and predation (Ingham *et al.*, 1985; Freckman, 1988). These activities could have contributed to the higher potential N mineralization

Table 4. Treatment contrasts of mean substrate mass loss

Contrast	Mean mass loss (mg kg^{-1} soil)			
A vs *B*	*A*	*B*	F^1	*P*
Month 6				
Roots vs litter	507	449	3.01	0.095
Fine roots vs coarse roots	601	413	26.4	<0.0001
Annual roots vs perennial roots	517	497	0.31	0.58
Zinnea coarse roots vs *Larrea* coarse roots	418	431	0.06	0.81
Baileya litter vs *Larrea* litter	482	417	1.37	0.25
Month 9				
Roots vs litter	854	717	4.09	0.055
Fine roots vs coarse roots	999	709	15.7	0.0007
Annual roots vs perennial roots	1002	706	16.4	0.0005
Zinnea coarse roots vs *Larrea* coarse roots	557	537	0.03	0.86
Baileya litter vs *Larrea* litter	574	860	6.33	0.020

[1]Degrees of freedom *F* statistics: month 6 = 1, 24; month 9 = 1, 22.

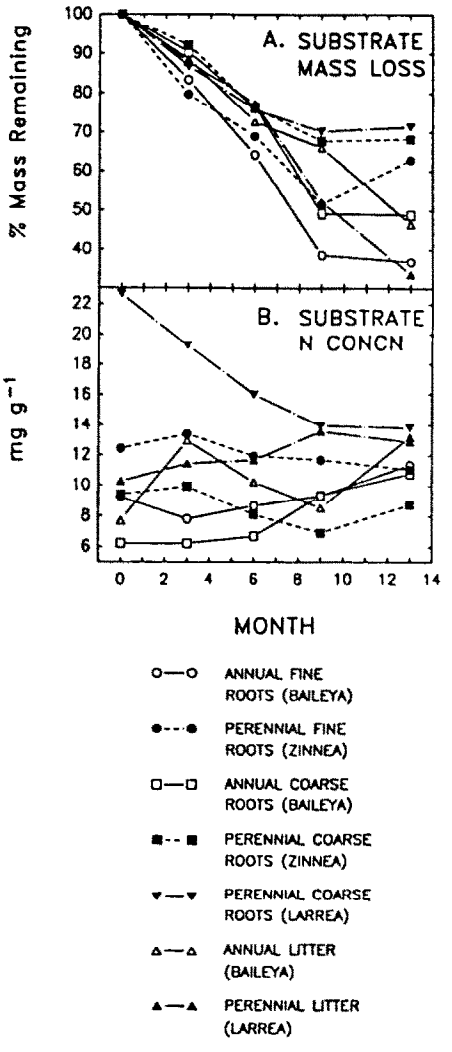

Fig. 2. (A) Mass loss from the 7 experimental substrates. (B) N concentration of the substrates.

rates. The higher nematode populations associated with roots could result because all of the root substrate was located in the more favorable physical environment found belowground.

Annual roots had lower bacteria plus yeast populations and higher nematode populations than did perennial roots, also implying faster organic matter turnover. Annual roots had higher C-to-N ratios and fragmented during handling much more than the perennial roots, indicating the presence of less structural material. These differences suggest that carbon (energy) availability of annual roots was higher than for perennial roots. High carbon availability and low N availability combined to significantly reduce inorganic N concentrations compared to the control by month 6 and to maintain significantly lower inorganic N concentrations in month 9. Perennial roots did not produce a significant change in soil inorganic N until month 9 when they increased inorganic N compared to the no-substrate control, in agreement with our prediction that annual roots would have a more rapid effect on N availability than would perennial roots.

The lower inorganic N concentrations and recoveries associated with annual roots could have resulted either from immobilization or denitrification. Both are enhanced by increased carbon availability. It is not possible to determine from the data whether the increased soil biota populations in the annual-root microcosms served as an N sink by immobilizing N or whether they enhanced losses of N by dentrification. However, decomposing roots of *Baileya* and other annual plants have been shown to immobilize N (Parker *et al.*, 1984; Whitford *et al.*, 1988). The higher populations of fungivorous nematodes observed in our work suggest that fungi might be more important in the decomposition of annual roots compared to perennial roots or litter (Sohlenius and Wasilewska, 1984; Sohlenius and Bostrom, 1986). The ability of fungi to extend hyphae out into the surrounding soil makes them more effective at immobilizing N than are bacteria. These considerations and the low N concentrations of the *Baileya* roots suggest that immobilization would be most important in well-drained, undisturbed soil.

The effects of perennial roots on soil inorganic N concentrations were similar to litter, despite appearing to have produced more rapid organic matter turnover than did litter. Therefore, our prediction that roots would have a more immediate effect on N availability was not fully supported. As discussed above, only part of the organic matter in perennial-roots appears to be readily available to decomposers and this seems to have a lower N content than do the roots as whole.

Table 5. Treatment contrasts of mean substrate N loss

Contrast	Mean mass loss (mg kg^{-1} soil)			
A vs *B*	*A*	*B*	F^1	*P*
Month 6				
Roots vs litter	6.6	1.3	72.8	<0.0001
Fine roots vs coarse roots	7.1	6.0	1.77	0.20
Annual roots vs perennial roots	4.1	9.4	44.9	<0.0001
Zinnea coarse roots vs *Larrea* coarse roots	5.6	18.1	73.4	<0.0001
Baileya litter vs *Larrea* litter	0.3	2.3	4.67	0.041
Month 9				
Roots vs litter	9.5	4.8	33.8	<0.0001
Fine roots vs coarse roots	11.1	8.0	10.6	0.0037
Annual roots vs perennial roots	6.2	13.3	53.9	<0.0001
Zinnea coarse roots vs *Larrea* coarse roots	8.3	23.3	74.7	<0.0001
Baileya litter vs *Larrea* litter	4.1	5.6	1.66	0.21

[1]Degrees of freedom *F* statistics: month 6 = 1, 24; month 9 = 1, 22.

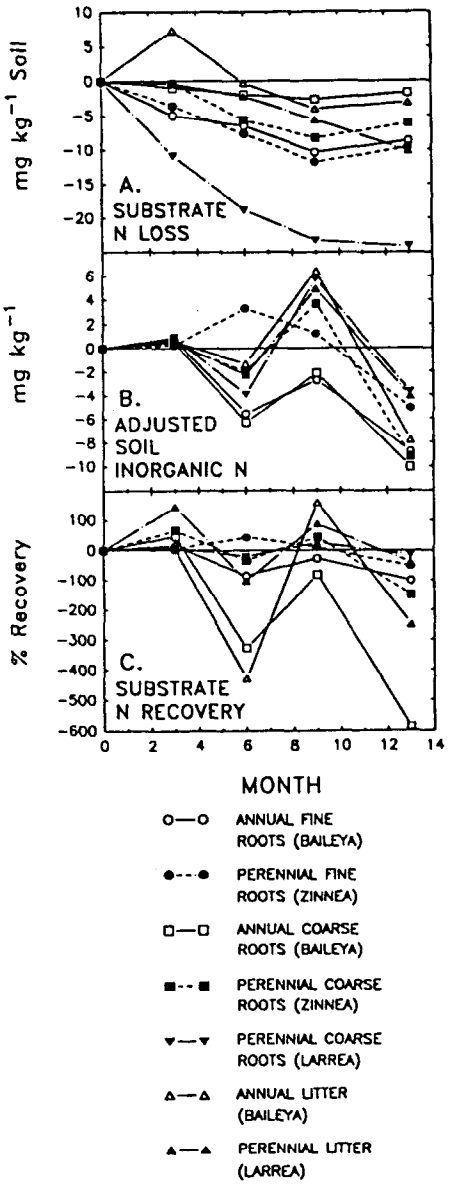

Fig. 3. (A) Net N loss from the 7 experimental substrates. (B) Soil inorganic N as the difference between substrate treatments and the non-substrate control. (C) Recovery of substrate N loss as soil inorganic N.

Comparison of fine and coarse roots explained surprisingly little of the variation between treatments; only mass loss was affected. The lack of effect on other processes could have resulted because the structural composition of the fine (<2 mm) and coarse (>2 mm) roots was similar. Nearly all the roots had diameters from 1–5 mm, which are considered fine roots in some classification systems (Fogel, 1983). We have observed many very fine fibrous roots (<0.5 mm dia) in these soils but these were not used in the experiment because it is nearly impossible to identify the source plants.

The litter data are probably the least generalizable to field conditions of all the substrates because the microcosms were shaded by the conical nylon mesh caps. Litter bags and unconfined litter are not shaded in this manner because the nylon mesh contacts the litter surface. If fragmentation of litter is driven by intense sunlight, its intensity would be reduced by shading. Additionally, the litter moisture content was maintained unrealistically high by the wet microcosm soils. The patterns of mass and N loss reflected a period of immobilization similar to roots and to litter in mesic environments. This pattern was quite different from the pattern observed in litter bags by Schaefer *et al.* (1985) and Montaña *et al.* (1988). This suggests that differences in processing of litter and roots are underestimated by this experiment.

Rates of mass loss observed in this experiment are difficult to compare with previous studies for several reasons. Probably most importantly, the wet conditions in the microcosms do not occur in the field. Other aspects of experimental techniques, such as the season of the experiment or the methods for selecting roots also differ (see Whitford *et al.*, 1986, 1988). Qualitatively, however, the results are similar to previous experiments. For example, rates of mass loss from coarse roots of *Larrea* and *Zinnea* were very similar to each other in this experiment and in a previous experiment (Whitford *et al.*, 1988). Mass loss from *Baileya* roots was much faster than *Larrea* and *Zinnea* roots in both experiments. *Baileya* roots lowered soil inorganic N concentrations in this experiment and immobilized N in the previous experiment (Whitford *et al.*, 1988), as did roots of another annual, *Lepidium lasiocarpum*, in a different experiment (Parker *et al.*, 1984). Therefore, the field

Table 6. Treatment contrasts of mean soil inorganic N and estimated net recovery of substrate N

Contrast	Mean inorganic N (mg N kg^{-1} soil)				Recovery of substrate N	
A vs *B*	*A*	*B*	*F*[1]	*P*	*A*	*B*
Month 6						
Treatments vs control	−2.6	0.00	1.38	0.25	−57%	
Roots vs litter	−3.0	−1.8	0.49	0.49	−46%	−146%
Fine roots vs coarse roots	−1.6	−4.3	2.26	0.14	−23%	−72%
Annual roots vs perennial roots	−6.0	+0.5	12.4	0.0016	−146%	+5%
Zinnea coarse roots vs *Larrea* coarse roots	−2.0	−2.2	0.01	0.94	−35%	−12%
Baileya litter vs *Larrea* litter	−1.3	−2.3	0.11	0.74	−432%	−103%
Month 9						
Treatments vs control	+1.4	0.00	0.43	0.52	+23%	
Roots vs litter	0.0	+5.7	5.94	0.021	0%	+117%
Fine roots vs coarse roots	−0.9	+2.2	0.69	0.41	−8%	+22%
Annual roots vs perennial roots	−2.5	+3.5	5.59	0.025	−40%	+22%
Zinnea coarse roots vs *Larrea* coarse roots	+3.7	+5.8	0.25	0.62	+44%	+25%
Baileya litter vs *Larrea* litter	+6.4	+4.9	0.12	0.73	+158%	+87%

Values are differences between substrate treatments and the no-substrate control.
[1]Degrees of freedom for *F* statistics: month 6 = 1, 27; month 9 = 1, 28.

Table 7. Treatment contrasts of the estimated size of a labile pool of soil organic N for month 9

Contrast	Mean estimated N_1 (mg-N kg^{-1} soil)			
A vs *B*	*A*	*B*	$F_{1,28}$	*P*
Treatments vs control	6.4	6.9	0.07	0.79
Roots vs litter	8.0	3.0	10.9	0.0026
Fine roots vs coarse roots	8.8	7.4	0.63	0.43
Annual Roots vs perennial roots	8.2	7.9	0.00	0.97
Zinnea coarse roots vs *Larrea* coarse roots	7.8	7.0	0.09	0.77
Baileya litter vs *Larrea* litter	2.2	3.8	0.38	0.54

Values are N_1 in the equation $N_t = N_1 + N_2 - N_2 e^{-k_2 t}$ estimated from the time-course of inorganic *N* production in laboratory soil incubations at 35 C.

Table 8. Multivariate Analysis of Variance treatment contrasts for soil biota population data for months 6 and 9

Contrast	Characteristic vector[1]						
	Bacteria + Yeast		Nematodes				
A vs *B*	Counts	Mass	Bacterivores	Fungivores	Omnivore–predators	$F^2_{5,31}$	P^2
Treatments vs control	+0.04	−0.04	−0.10	−0.06	+0.17	1.37	0.25
Roots vs litter	+0.03	−0.13	+0.13	+0.09	+0.04	5.20	0.0006
Fine roots vs coarse roots	−0.02	+0.01	−0.09	+0.12	+0.00	1.27	0.29
Annual roots vs perennial roots	+0.00	−0.13	+0.02	+0.14	+0.06	4.09	0.0034
Zinnea coarse roots vs *Larrea* course roots	−0.07	−0.07	+0.15	+0.08	−0.05	0.28	0.92
Baileya litter vs *Larrea* litter	+0.04	−0.08	+0.17	+0.02	−0.00	1.29	0.28

[1]The characteristic vector indicates the relative importance and direction of response of the population means, i.e. positive coefficients indicate that population mean *A* is > *B* and negative coefficients indicate that *B* is > *A*. The magnitude of the coefficients indicates the relative importance of the difference between population means *A* and *B* (Harris, 1975).

[2]*F* and *P* indicate the overall significance of the characteristic vector (SAS Institute Inc., 1985).

Table 9. Summary of effects of initial substrate N concentration and the substrate treatments as indicated by planned contrasts (months 6 and 9)

Effects	Responses					
	Substrate mass loss	Substrate N loss	Soil inorganic N	Mineralizable organic N[1]	Bacteria + yeast mass	Nematode populations
Substrate N concentration	Small	Important	Small			
Roots vs litter	Roots high	Roots high		Roots high	Roots low	Roots high
Fine roots vs course roots	Fine high	Fine high				
Annual roots vs perennial roots	Annuals high	Annuals low	Annuals low		Annuals low	Annuals high
Zinnea coarse roots vs *Larrea* coarse roots		*Zinnea* low				
Baileya litter vs *Larrea* litter	*Baileya* low	*Baileya* low				

[1]Mineralizable organic N only determined for month 9.

microcosm technique appears to be useful for comparative examination of organic-matter processing of various substrates. Modification of the technique to allow removal of excess water and nutrients will eliminate many of the problems encountered in the present experiment. Isolation of various organic-matter fractions that link the initial decomposition stages to the final mineralization stages should improve the ability of the technique to resolve differences between substrates.

These results support previous studies showing that immobilization of N associated with the decomposition of the roots of annual plants may be a significant ecosystem process in the northern Chihuahuan Desert (Parker *et al.*, 1984; Whitford *et al.*, 1988). The results illustrate how this may occur during the decomposition of one species, *Baileya multiradiata*. The high carbon availability, low N availability and the tendency towards fungal decomposition can lead to considerable N immobilization, thereby reducing N availability for subsequent plant growth.

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REFERENCES

Charley J. L. (1972) The role of shrubs in nutrient cycling. In *Wildland Shrubs—Their Biology and Utilization* (C. M. McKell, J. P. Blaisdell and J. R. Goodwin, Eds), pp. 182–203. U.S. Department of Agriculture Forest Service General Technical Report INT-1, Washington, D.C.

Elkins N. Z., Steinberger Y. and Whitford W. G. (1982) Factors affecting the applicability of the AET model for decomposition in arid environments. *Ecology* **63**, 579–580.

Fisher F. M., Parker L. W., Anderson J. P. and Whitford W. G. (1987) Nitrogen mineralization in a desert soil: interacting effects of soil moisture and N fertilizer. *Soil Science Society of America Journal* **51**, 1033–1041.

Fisher F. M., Zak J. C., Cunningham G. L. and Whitford W. G. (1988) Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *Journal of Range Management* **41**, 387–391.

Fogel R. (1983) Root turnover and productivity of coniferous forests. *Plant and Soil* **71**, 75–85.

Freckman D. W. (1988) Bacterivorous nematodes and organic matter decomposition. *Agricultural Ecosystems and Environments* (in press).

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

Freund R. J. and Littell R. C. (1981) *SAS for Linear Models*. SAS Institute Inc., Carry, N.C.

Gutierrez J. R. and Whitford W. G. (1987) Chihuahuan desert annuals: importance of water and nitrogen. *Ecology* **68**, 2032–2045.

Gutierrez J. R., Da Silva O. A., Pagani M. I., Weems D. and Whitford W. G. (1988) Effects of different patterns of supplemental water and nitrogen fertilization on productivity and composition of Chihuahuan Desert annual plants. *American Midland Naturalist* **119**, 336–343.

Harris R. J. (1975) *A Primer or Multivariate Statistics*. Academic Press, New York.

Henriksen A. and Selmer-Olsen A. R. (1970) Automatic methods for determining nitrate and nitrite in soil extracts. *Analyst (London)* **95**, 514–518.

Ingham R. E., Trofymow J. A., Ingham E. R. and Coleman D. C. (1985) Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecological Monographs* **55**, 119–140.

Jones C. A. (1984) Estimation of an active fraction of soil nitrogen. *Communications in Soil Science and Plant Analysis* **15**, 23–32.

Keeney D. R. and Nelson D. W. (1982) Nitrogen—inorganic forms. In *Methods of Soil Analysis, Part 2*, 2nd Edn, *Agronomy* Vol. 9 (A. L. Page, R. H. Miller and D. R. Keeney, Eds), pp. 643–698. American Society of Agronomy, Madison, Wis.

MacKay W. P., Fisher F. M., Silva S. and Whitford W. G. (1987) The effects of nitrogen, water and sulfur amendments on surface litter decomposition in the Chihuahuan desert. *Journal of Arid Environments* **12**, 223–232.

Montaña C., Ezcurra E., Carrillo A. and Delhoume J. P. (1988) The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments. *Journal of Arid Environments* **14**, 55–60.

Moorhead D. L. and Reynolds J. F. (1989) Mechanisms of surface litter mass loss in the northern Chihuahuan desert: a reinterpretation. *Journal of Arid Environments* **16**, 157–163.

Moorhead D. L., Fisher F. M. and Whitford W. G. (1988) Cover of spring annuals on nitrogen-rich kangaroo rat mounds in a Chihuahuan Desert grassland. *American Midland Naturalist* **120**, 443–447.

Nelson D. W. (1983) Determination of ammonium in KCl extracts of soils by the salicylate method. *Communications in Soil Science and Plant Analysis* **14**, 1051–1062.

Nelson D. W. and Sommers L. E. (1980) Total nitrogen analysis of soil and plant tissues. *Journal of the Association of Official Analytical Chemists* **63**, 770–778.

Parker L. W., Santos P. F., Phillips J. and Whitford W. G. (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan Desert annual, *Lepidium lasiocarpum*. *Ecological Monographs* **54**, 339–360.

Santos P. F., de Pree E. and Whitford W. G. (1978) Spatial distribution of litter and microarthropods in a Chihuahuan desert ecosystem. *Journal of Arid Environments* **1**, 41–48.

SAS Institute Inc. (1985) *SAS User's Guide: Statistics, Version 5 Edition*. SAS Institute Inc., Cary, N.C.

Schaefer D., Steinberger Y. and Whitford W. G. (1985) The failure of nitrogen and lignin control of decomposition in a North American desert. *Oecologia (Berlin)* **65**, 382–386.

Schlesinger W. H. (1985) Decomposition of chaparral shrub foliage. *Ecology* **66**, 1353–1359.

Schlesinger W. H., Fonteyne P. J. and Marion G. M. (1987) Soil moisture content and plant transpiration in the Chihuahuan Desert of New Mexico. *Journal of Arid Environments* **12**, 119–126.

Sohlenius B. and Bostrom S. (1986) Short-term dynamics of nematode communities in arable soil–influence of nitrogen fertilization in barley crops. *Pedobiologia* **29**, 183–191.

Sohlenius B. and Wasilewska L. (1984) Influence of irrigation and fertilization on the nematode community in a Swedish pine forest soil. *Journal of Applied Ecology* **21**, 327–342.

Stanford G. and Smith S. J. (1972) Nitrogen mineralization potentials of soils. *Soil Science Society of America Proceedings* **36**, 465–472.

Steel R. G. D. and Torrie J. H. (1980) *Principles and Procedures of Statistics, 2nd Edn*. McGraw-Hill, New York.

Swift M. J., Heal O. W. and Anderson J. M. (1979) *Decomposition in Terrestrial Ecosystems*. University of California Press, Berkeley.

Wall L. L. and Gehrke C. W. (1975) An automated total protein nitrogen method. *Journal of the Association of Official Analytical Chemists* **58**, 1221–1226.

Whitford W. G., Meentemyer V., Seastedt T. R., Cromack K. Jr, Crossley D. A. Jr, Santo P., Todd R. L. and Waide J. B. (1981) Exceptions to the AET model: deserts and clear-cut forests. *Ecology* **62**, 275–277.

Whitford W. G., Steinberger Y., MacKay W., Parker L. W., Freckman D., Wallwork J. A. and Weems D. (1986) Rainfall and decomposition in the Chihuahuan desert. *Oecologia (Berlin)* **68**, 512–515.

Whitford W. G., Stinnett K. and Anderson J. (1988) Decomposition of roots in a Chihuahuan Desert ecosystem. *Oecologia (Berlin)* **75**, 8–11.

Wierenga P. J., Hindrickx J. M. H., Nash M. H., Ludwig J. and Daugherty L. (1987) Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. *Journal of Arid Environments* **13**, 53–63.