The effects of nitrogen, water and sulfur amendments on surface litter decomposition in the Chihuahuan Desert

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The effects of nitrogen, water and sulfur amendments on the decomposition rates of three types of surface litter in the northern Chihuahuan Desert were evaluated. The amendments had no effects on the decomposition rates of leaf litter from black grama (Bouteloua eriopoda) and creosote bush (Larrea tridentata). The rate of fluff grass (Erioneuron pulchellum) litter decomposition was increased by water and decreased by sulfur. Water affected fluff grass decomposition by increasing termite (Gnathamitermes tubiformans) above-ground activity. Sulfur decreased termite activity. These data suggest that the decomposer microflora and microfauna of the northern Chihuahuan Desert are more limited by quantity of organic matter than by water and nitrogen. Hence they do not respond opportunistically to increased availability of such resources.

Introduction

Rates of litter decomposition in deserts have been found to be surprisingly high, often equalling or exceeding rates obtained from mesic forests (Schaefer, Steinberger et al., 1985). Decomposition rates in deserts are also significantly higher than those predicted by models based on actual evapotranspiration (AET). For example, the rates in the northern Chihuahuan Desert are about four times greater than expected when actual precipitation is used and almost two times greater than expected when using average precipitation (Whitford, Meentemeyer et al., 1981; Santos, Elkins et al., 1984).

Santos, Elkins et al. (1984) found that decomposition rates of creosote bush litter in several warm deserts were relatively independent of actual rainfall but were correlated with long-term average precipitation. They hypothesized that the organisms responsible for decomposition were well adapted to low and unpredictable moisture availability. If organisms are adapted to ambient moisture conditions, then it is logical to suppose that other factors are limiting decomposition rates. Two possible controlling factors are soil nitrogen and pH. Nitrogen has been shown to be important in limiting primary production in other experiments in the northern Chihuahuan Desert (Ettershank, Ettershank et al., 1978; Whitford, unpublished data). Soil micro-organisms have a relatively high requirement for nitrogen, and nitrogenous compounds are often limiting in decomposer habitats (Park, 1976). The addition of nitrogenous substances to accelerate decay of organic matter has been used for years (Findlay, 1934). We hypothesized that addition of nitrogen should increase the rate of decomposition of plant materials.

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Soil pH influences the availability of several important nutrients, including phosphorus, iron, manganese and zinc. Soil pH of the study area ranges from 7 to 8, conditions under which the availability of the aforementioned elements is restricted (Brady, 1974). Since the growth of microflora is affected by the availability of mineral nutrients, especially phosphorus, we hypothesized that a lower soil pH would accelerate the rates of decomposition of plant materials. We further hypothesized that additional water would accelerate the decomposition rates of all plant materials. As part of a general investigation of factors limiting ecosystem processes in the northern Chihuahuan Desert, we tested factors limiting litter decomposition by amending field plots with water, nitrogen and sulfur (to lower pH). Experiments were performed in three vegetation types using leaf litter of a dominant plant of each vegetation type.

Materials and methods

Study site

The study was conducted on the Jornada Long-Term Ecological Research Site located 40 km north-northeast of Las Cruces, Dona Ana County, New Mexico. The focus of the Jornada site is a 3-km long transect that passes through seven vegetation types along an elevational gradient. Three vegetation types, making up 77% of the transect, were chosen for intensive study of ecosystem processes. These assemblages, from highest to lowest elevation, are as follows: (1) black grama—upper piedmont, dominated by black grama grass (Bouteloua eriopoda (Torr.) Torr.); (2) creosote bush (Larrea tridentata (DC) Cov.); and (3) mixed-basin slopes, consisting of a variety of perennials and annuals, including soap-tree yucca (Yucca elata Engelm.), morman tea (Ephedra trifurcata Torr.), snakeweed (Xanthocephalum sarothrae (Pursh) Shinners) and fluff grass (Erioneuron pulchellum (HBK) Takeoka).

Experimental design and application of amendments

Study plots were located in each of the three selected vegetation types. The experiments were set up as a complete factorial design including water, nitrogen, sulfur, water + nitrogen, water + sulfur, nitrogen + sulfur, water + nitrogen + sulfur and a control. Each plot was 8×8 m. Each watered plot received 12 mm at 2-week intervals delivered from eight 'Rain Bird' sprinkler heads, in addition to any natural precipitation. The water was obtained from a well near the area. Fertilizer was applied on 20 April 1983 at rates of 40 g/m² ammonium nitrate and 40 g/m² of 90% elemental sulfur after the litter bags were placed on the plots.

Litter bags

Leaf material was collected from a dominant species of each vegetation type (black grama grass, creosote bush and fluff grass, respectively) during February and March of 1983. Standing leaf material was collected from the two grasses and creosote bush leaves were stripped from branches. The material from black grama was largely senescent, but approximately half of the fluff grass leaf material and most of the creosote bush leaves were still green.

We used standard, fibreglass mesh litter bags (Santos, Elkins et al., 1984) containing 5 g of air-dried plant material. The bags were placed in the field on 20 April 1983 and retrieved at 40, 91, 121, 181 and 306 days after placement. Ten litter bags were collected from each

treatment on each date at 08:00 MST. Micro-arthropods were extracted into water for 3 days using modified Tullgren funnels (Santos, Depree et al., 1978). Soil and water samples were collected on day 181 and pH, electrical conductivity, SO_4^{2-} concentration and CaCO₃ concentration were determined on bulked samples by the New Mexico State University soil and water testing laboratory. Termite activity was estimated from the percentage of bags containing entry holes, gallery carton or termites.

Calculation of percentage organic mass remaining

The litter was oven dried (60°C for 72 hours), weighed and burned in a muffle furnace at 600°C for 8 hours to obtain organic matter content by mass loss. Since the bags were infiltrated with mineral soil, it was necessary to correct the dry masses of litter. The following equation, modified from Santos & Whitford (1981), was used to calculate the percentage of organic mass remaining:

$$r(\%) = \frac{F - ((A - CI)/S_i)}{I} \times 100$$

where r = percentage organic mass remaining, F = final dry weight of the sample after field collection, A = ash weight of final sample, C = inorganic (ash) content of initial litter samples as a proportion of 1, based on 10 samples, I = initial litter dry weight corrected by subtracting a handling loss based on 10 samples, and $S_i =$ inorganic (ash) content of mineral soil under a litter bag.

Statistical analysis

Statistically significant treatment effects were identified using the general linear modelling procedure (PROC GLM) of SAS (Helwig & Council, 1979). The decomposition data were analyzed as an incomplete factorial design (nitrogen \times water \times sulfur \times time) where the fourth-order and third-order interactions with time were assumed to result from experimental error. Plotting of error versus means indicated that the variance increased with time. The data were therefore transformed from percentage remaining to ln (percentage loss + 20) (error associated with the dry-ashing procedure used to estimate weight remaining can cause the calculation of negative weight-loss values). These transformations successfully homogenized the variances, and the error distributions were not significantly different from a normal distribution according to the Shapiro-Wilk W-test used by PROC UNIVARIATE of SAS. Exponential loss equations were fitted simultaneously to significantly different treatments using analysis of covariance as performed by PROC GLM (Helwig & Council, 1979). In the absence of significant treatment effects, this procedure simplified to a linear regression of ln (percentage remaining) versus time. The y-intercepts of the fitted curves were treated for significant deviations from ln (100%) using a t-test (Sokal & Rohlf, 1969). The soil-test data were analyzed as a three-factor analysis of variance. Since each chemical analysis was performed on a single bulked sample, interactions between treatments were assumed to be absent and were used as the error term.

Results

Mean decomposition rates of the three kinds of litter were similar, with 60-70% of the initial weight remaining after 306 days (Figs 1-3, Table 1). The treatments had no effect on the decomposition of litter from creosote bush and black grama. In contrast, the calculated decomposition of fluff grass was increased by water amendments and decreased by sulfur amendments (Table 1, Fig. 3).

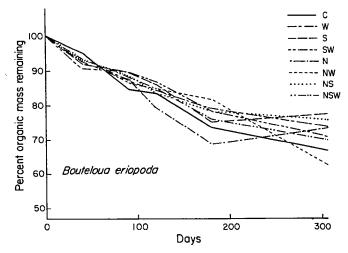


Figure 1. Effect of amendments of nitrogen, water and sulfur on the decomposition of grama grass litter (Bouteloua eriopoda). C, Control; W, + water; S, + sulfur; SW, + sulfur + water; N, + nitrogen; NW, + nitrogen + water; NS, + nitrogen + sulfur; NSW, + nitrogen + sulfur + water.

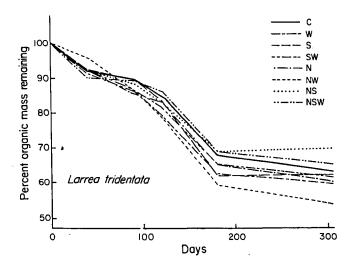


Figure 2. Effect of amendments of nitrogen, water and sulfur on the decomposition of creosote bush (*Larrea tridentata*) litter. Abbreviations as in Fig. 1.

The calculated remaining mass of fluff grass litter showed initial increases following the sulfur treatment (Fig. 3) and following the nitrogen + sulfur + water treatment (not shown); the mean percentages remaining for the nitrogen + sulfur + water treatment were nearly all greater than 100%, so these data were not included in the statistical analysis.

Exponential decay rates (K) for significantly different treatments are shown in Table 2. Including data from day 306 in the curve-fitting of the black grama and fluff grass data resulted in y-intercepts significantly lower than $\ln (100\%)$. Removing the day-306 data resulted in y-intercepts not significantly different from $\ln (100\%)$ and also improved the fit of the model as indicated by reduced standard errors of the slopes.

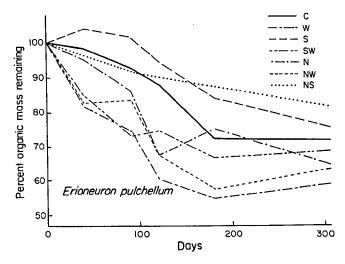


Figure 3. Effect of amendments of nitrogen, water and sulfur on the decomposition of fluff grass (*Erioneuron pulchellum*) litter. Abbreviations as in Fig. 1.

Table 1. Treatment means and results of analysis of variance for plots amended with nitrogen, water and sulfur

		Perce	ıs)	
Treatment		Black grama	Creosote bush	Fluff grass
Nitrogen	+	16.7	20.2	18.6
	_	17.2	20.0	18.9
Water	+	16.6	21.2	29·1†
	_	17·3	19.0	12.0
Sulfur	+	16.1	19-5	12.9*
	_	17.9	20.7	23.9
Time (days) 40		7·3†	7·8 †	6·7†
	91	12.5	12.3	12.7
	121	16-1	17.8	20.4
	181	23.6	35.1	28.4
	306	28.5	37.7	30.8

^{*} p < 0.001.

Termite activity was recorded in more of the fluff grass litter bags than in litter bags of black grama or creosote bush (Fig. 4). Only 1–2% of the bags containing creosote and black grama were affected by termites. Termite activity in litter bags containing fluff grass was affected by the water and sulfur amendments. Termite activity was lowest in the sulfur-amended plots and next lowest in plots that received both sulfur and water. The plots that did not receive sulfur or water had the next higher rates, and the highest rates of termite activity were in plots that did not receive sulfur but received water. Apparently, termite activity accounted for the effects of the amendments on the decomposition rates of fluff grass (Table 1). Those plots treated with sulfur had reduced termite activity and thus

[†] p < 0.0001.

Species	Treatment*	Period (days)	<i>m</i> –1	K (y-1)	Standard error	Significance
Black grama	All	181	-0.047	-0.56	0.055	p < 0.0001
Fluff grass	+S -W -S -W +S +W -S +W	181 181 181 181	-0.018 -0.049 -0.064 -0.093	-0·22 -0·59 -0·77 -1·11	0·124 0·120 0·139 0·119	p <0·10 p <0·0001 p <0·0001 p <0·0001
Creosote bush	All	306	-0.054	-0.65	0.041	p <0.0001

Table 2. Exponential decay rates (K) for significantly different treatments

^{*} S, sulfur; W, water.

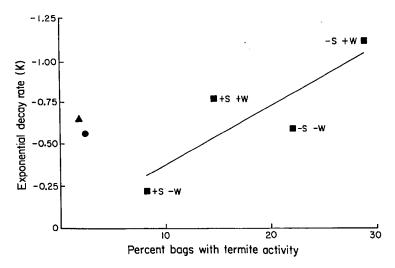


Figure 4. Effect of termite activity on the exponential decay rate of three litter types. The figure also shows the effects of sulfur and water amendments on termite activity. \triangle , Creosote bush; \bullet , grama grass; \blacksquare , fluff grass.

reduced organic mass losses. Those plots amended with water had increased termite activity and thus increased organic mass loss.

The amendments had detectable effects on the soil chemistry in all three of the vegetation types (Table 3). The nitrogen and sulfur amendments usually decreased soil pH, and there was some indication of a tendency for water to reduce pH. The amendments tended to increase conductivity, especially in the mixed-basin slope vegetation. Sulfate (SO_4^{2-}) concentration was usually increased by the sulfur amendments and, surprisingly, was also increased by moisture amendments. Changes in $CaCO_3$ were generally insignificant. Micro-arthropod abundance may have increased in response to water, but responses to nitrogen or sulfur were absent or variable.

Discussion

Our hypothesis that nitrogen addition should increase the decomposition rates because nitrogen compounds often limit decomposer activity, was not supported by the data. Allison & Cover (1960) found an increase in the decomposition rate of sawdust when they

Table 3. Soil analysis from the experimental plots 6 months after the application of nitrogen and sulfur amendments. The mean numbers of micro-arthropods (Acari, Collemobla, Pscoptera and Thysanoptera) per bag were collected on 20 February 1984. The statistical comparisons are of the sulfur-amended plots with the non-sulfur-amended plots

Treatment pH		pН	Electrical conductivity (mmhos)	SO ₄ ²⁻ (mg/l)	CaCO ₃ (%)	Micro- arthropods per litter bag
Black gran	ıa—u	pper piedn	nont			
Nitrogen	+	7·26‡ 7·62	1·91 1·22	378 433	0·33 0·25	13·4 6·6
Sulfur	+	7·27‡ 7·61	1·60 1·53	639* 172	0·30 0·28	9·0 11·0
Water	+	7·38* 7·50	1·55 1·58	566 244	0·33 0·25	10·8 9·2
Creosote bi	ısh—i	bajada				
Nitrogen	+	7·85* 7·93	1·42 0·97	386 334	1·35 2·13	4·5* 9·6
Sulfur	+	7·85† 7·93	1·33 1·06	407 313	1·90 1·58	7·7 7·2
Water	+ -	7·88 7·90	1·71* 0·68	626‡ 94	1·23* 2·25	10·2† 3·8
Fluff grass	mi:	xed basin :	slope			
Nitrogen	+	7·44* 7·71	1·89‡ 1·02	334 358	0·38 0·55	12·2 3·0
Sulfur	+	7·54 7·61	1·89‡ 1·02	559† 133	0·45 0·48	5·5 9·7
Water	+	7·53 7·62	1·66* 1·25	532† 159	0·53 0·40	12·4 2·8

^{*} p < 0.10.

Table 4. Analysis of water used for amendments on the experimental plots in October 1983

Electrical conductivity (mmhos)	Concentrations of various elements and compounds (mg/litre)							
	CO ₃	HCO ₃	Na	Ca	K	Mg	Total P	TKN
0.80	36.0	80·5	302·3	34.0	9.2	21.5	0.03	1.7

added nitrogen, but Bocock (1964) found that the addition of naturally occurring nitrogen-rich material to oak litter did not increase the rate of decomposition. We intentionally added an ammonium salt because these salts have been shown to be the most readily assimilated nitrogen sources for most bacteria, actinomycetes and fungi (Alexander, 1977). Also, nitrates are often immobilized when the ammonium levels are low. A resulting increase in biological activity should be accompanied by an enhanced decomposition rate as the protoplasmic turnover increases, but no such increase was found.

[†] p < 0.05.

p < 0.01.

As the decomposition of organic matter is often dependent on moisture (Floate, 1970), we hypothesized that increased soil moisture would increase the decomposition rate. We found this to occur only in fluff grass where added soil moisture increased subterranean termite above-ground activity. In other experiments we have also found that increased soil moisture increases termite activity (MacKay, Silva et al., 1986). Apparently, desert litter decomposer guilds are adapted to low moisture levels, and increased moisture does not stimulate greater biological activity. Populations of soil biota are, therefore, probably limited by factors other than moisture (Steinberger, Freckman et al., 1984). Many taxa of soil micro-arthropods, including cryptostigmatid mites, are active in the litter layer for several hours each day even when soils are very dry (Whitford, Freckman et al., 1981).

One possible explanation for the apparent lack of an effect of moisture and nitrogen on decomposition rates is substrate limitation. Unlike forests, where there is a nearly continuous layer of organic matter available to decomposers, in deserts organic matter on the surface is limited to relatively small accumulations that vary in availability in space and time. The desert soil microflora and microfauna must be adapted to live on and utilize the energy in these materials under the usual desert conditions. We have data that show that fresh litter inputs are rapidly colonized and develop stable populations of soil biota within 60 days (Whitford, Steinberger et al., 1986). If decomposition in deserts is energy limited and the organisms are adapted to the environmental conditions at the surface, then statements like 'decomposition of litter at the soil surface-air interface is probably limited by moisture content' (Comanor & Staffeldt, 1978) will not be supported by experimental data. Our data show that the decomposition of surface litter is not affected by moisture except insofar as moisture affects the activity of a macro-arthropod detritivore, in its feeding on a preferred food (Whitford, Steinberger et al., 1982). The absence of a nitrogen fertilizer effect corresponds to the failure of decomposition rates to vary as an inverse function of initial carbon:nitrogen ratios (Schaefer, Steinberger et al., 1985).

Our third hypothesis stated that lowering the pH of the soils would increase the decomposition rate by making a number of elements available. We assumed that bacteria, actinomycetes, fungi and yeasts would oxidize inorganic sulfur compounds and the resulting sulfuric acid would react with minerals and other insoluble materials, leading to nutrient mobilization (Alexander, 1977). The small changes in soil pH resulting from the addition of sulfur may not have released sufficient nutrients to have an effect on decomposition or, as argued above, nutrient effects in a desert may be much less important than an energy source.

It is difficult to study the effect of soil pH on fauna (Hågvar & Abrahamsen, 1980). Variations in soil pH are correlated with other factors such as cation exchange capacity, nitrogen content, humus type and soil profile. Thus it is difficult to clarify the importance of soil pH from field studies. The results of culture experiments in the laboratory cannot be applied directly to field conditions. Hutson (1978), Hågvar & Abrahamsen (1980) and Hågvar & Amundsen (1981) found that pH directly affects the fecundity, longevity, developmental time and abundance of soil micro-arthropods. The absence of a significant effect of lowered soil pH on micro-arthropods in this study must be interpreted with caution, because we have data for only one sampling date and the changes in soil pH were moderate.

This study contributes another set of data that demonstrate that factors affecting rates of decomposition in more mesic environments have little or no effect on that process in a desert. Further, the data provide empirical evidence that decomposition processes in deserts are not as water dependent as has been generally thought (Noy-Meir, 1973).

This study suggests that if we are to understand why rates of decomposition are high, and relatively independent of water and nutrient content, we must look at the assemblages of organisms that break down dead plant materials and examine their growth characteristics in a variety of thermal and moisture environments.

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