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Changing Carbon Chemistry of Buried Creosote Bush Litter during Decomposition in the Northern Chihuahuan Desert

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ABSTRACT.—In a previous study, creosote bush (*Larrea tridentata*) fine litter that was buried 5 cm beneath the soil surface in the northern Chihuahuan Desert lost about 20% of the original mass during the following three month summer-autumn period. A mathematical model was devised to elucidate the interactions between litter decay and decomposer microorganisms, using soil moisture and temperature as primary driving variables and litter quality as a controlling factor. Chemical analyses of the litter remaining at various stages of decay now provide additional insight to the decomposition process and another assessment of model behavior. As litter decayed, quantities of soluble and holocellulosic materials decreased by 41% and 22% (respectively), and acid-insolubles increased by 34%. This is consistent with microbially mediated decay processes in which recalcitrant microbial products (*e.g.*, cell wall materials) accumulate as total litter mass decreases. Simulation results were comparable to observed patterns of changing litter chemistry, corroborating a microbial based explanation for decay in desert soils that is very similar to decomposition processes in more mesic temperate ecosystems.

INTRODUCTION

A substantial fraction of surface litter in the northern Chihuahuan Desert is buried by wind, water and small mammals (Steinberger and Whitford, 1983; Whitford *et al.*, 1983). Decomposition of buried materials is more rapid than surface litter (Santos and Whitford, 1981; Elkins and Whitford, 1982) and more strongly influenced by biotic factors (Santos *et al.*, 1981; Elkins and Whitford, 1982; Parker *et al.*, 1984). In a study examining both mass loss and nitrogen concentrations in decomposing desert litter, Moorhead and Reynolds (1989) found that about 20% of the mass of creosote bush fine litter was lost in three months. During this period, the total nitrogen concentration of the litter increased 25%, but the absolute amount of nitrogen present in decaying litter remained essentially constant (26 to 28 mg). This pattern of nitrogen conservation in conjunction with carbon losses was interpreted as evidence of microbial mediated decomposition.

Moorhead and Reynolds (1991) used a general model of decomposition (GENDEC) to explore the relationships between buried litter, decomposer microorganisms, and C and N pools in this system. This approach integrated microbial physiology and population dynamics with empirical observations of C and N pool dynamics, litter mass loss and changing system C:N ratios. Good agreement was achieved between simulations and observations, suggesting that short-term nutrient availabilities in the northern Chihuahuan Desert may be controlled by litter carbon dynamics mediated by microflora activities. However, the details of changing carbon chemistry of decaying litter were not available for comparisons with model predictions.

Additional chemical analyses were performed on litter samples from the study of Moor-

head and Reynolds (1989). The objectives of this study were to: (1) evaluate changes in the carbon chemistry of decaying materials and (2) compare these data to predicted patterns of change obtained from model simulations. These data provide additional insight into mechanisms underlying litter decomposition in this ecosystem and factors controlling patterns of nitrogen availability.

METHODS

Study site.—The field study of buried creosote bush fine litter decomposition was conducted on the Jornada Long Term Ecological Research (LTER) site in the northern Chihuahuan Desert, 40 km NNE of Las Cruces, New Mexico. Detailed site information and experimental procedures are provided by Moorhead and Reynolds (1989), but a brief synopsis follows.

Senescent litter was collected from litter traps placed beneath creosote bush plants, dried and placed in small polyethylene petri dishes. Nylon screen was used to cover large holes cut in the lids, and the lids were attached to the dishes with cellophane tape. The screen side of the dishes was oriented downward when buried, in contact with the soil. This permits exposure to prevailing soil climate while excluding gravitational soil and water movement through the litter. Dishes were buried at a depth of 5 cm beneath selected creosote bush plants on July 1, 1986. Samples were collected approximately monthly (to October 18), placed in polyethylene bags and returned to the lab for determinations of litter dry weights and total Kjeldahl nitrogen concentrations.

Carbon chemistry.—Moorhead and Reynolds (1989) dried, ground and stored remaining litter at room temperature. A modification of standard methods was used to determine the fraction of each sample that was: (1) soluble in water and ethanol, (2) removed by sulfuric acid digestion, and (3) acid insoluble. Although not precisely accurate, for convenience we will herein refer to these chemical fractions as solubles, holocellulose and lignins, respectively.

Solubles.—About 0.5 g oven-dried sample was placed into a preweighed 50-ml centrifuge tube. About 25 ml distilled water was added and the tube placed in a sonicating water bath at 60 C for 30 min. The tube was then spun at 10,000 rpm for 15 min in a high-speed centrifuge. The supernate was suctioned and the procedure repeated five times. Following water extraction, the process was repeated five times with ethanol. The samples were then oven dried at 60 C for 24 h and the residue was weighed. The soluble content of the litter was estimated as the difference between original and extracted sample weights.

Holocellulose and lignin.—About 0.20 g of the dried sample remaining after solubles were extracted was placed into a 15-ml glass test tube and 2 ml 72% sulfuric acid added. The sample was incubated for 1 h at 30 C and 56 ml of distilled water used to transfer the material to a 125 ml flask. Flasks were autoclaved for 1 h at 120 C, the sample was suctioned onto a preweighed millipore filter and oven dried at 60 C for 24 h. The holocellulose content of the sample was estimated as the difference between pre- and postacid digested dry sample weight. The residue was assumed to consist primarily of lignins.

Ash masses.—Residue following acid digestion was put in a preweighed, dry crucible and placed in a muffle furnace at 500 C for 24 h. Crucibles were then weighed and ash mass recorded.

MODELING APPROACH

GENDEC is described in detail by Moorhead and Reynolds (1991), but a brief outline of the modeling rationale follows. GENDEC recognizes six pools of carbon (C) and nitrogen (N), including: (1) labile plant compounds, (2) holocellulose (cellulose + hemicellulose), (3) resistant plant compounds (*e.g.*, lignins), (4) live microbial biomass, (5) dead microbial

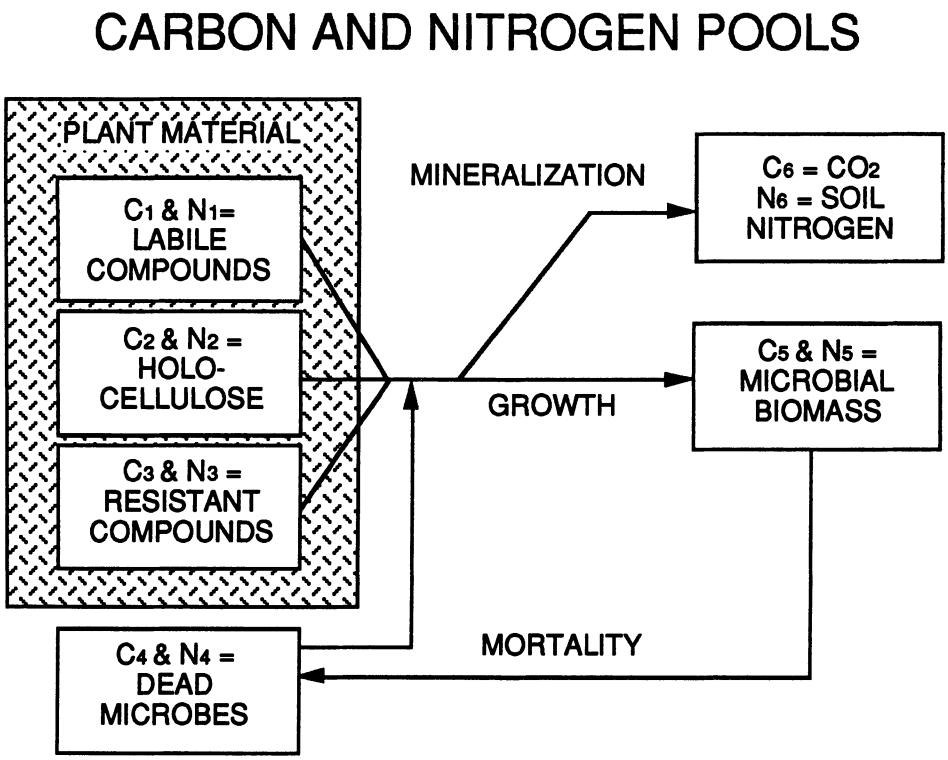

FIG. 1.—Model carbon and nitrogen flows

biomass, and (6) mineral N and carbon dioxide (Fig. 1). Nitrogen flows are assumed to balance calculated carbon flows.

The loss of carbon from each dead organic matter pool (C_s, s = 1, 2, 3, 5) (Fig. 1) is a function of moisture availability (S_M), temperature (S_T), N limitation (N_S) and a maximum intrinsic decay rate (k_s):

$$dC_s/dt = C_s \cdot -k_s \cdot S_M \cdot S_T \cdot N_S \quad [1]$$

where S_M, S_T and N_S are scalar multipliers. The total quantities of C and N available for microbial use consist of the sum of all losses from the dead organic matter pools, whereas available N includes mineral forms.

The decay rate coefficients and functions used to express temperature, moisture and nitrogen limitations are reported by Moorhead and Reynolds (1991). We slightly simplified the moisture function in GENDEC to achieve maximum decomposition at -0.3 MPa and preclude decay at ≤ -1.5 MPa, since xeric tolerant saprophytic fungi are not common in northern Chihuahuan Desert ecosystems (Anders, 1992). Microbial growth and respiration are driven by total C losses from the various pools, assuming an assimilation efficiency of 60% (Paul and Juma, 1981). Microbial death consists of a minimum daily mortality of 0.1% of the standing biomass and 20% of incremental growth (Parnas, 1975).

Simulations.—Plant litter characteristics on the July 27 sampling date of the field study (*see* below) were used to provide initial values for simulation (Table 1). The simulation period was July 27 through October 18, corresponding to the period of time during which

TABLE 1.—Characteristics of carbon pools used in model simulations

Carbon pool	k[a]	[N:C][b]	Percent[b]
C_1	0.20	1:10	25
C_2	0.08	∞	53
C_3	0.01	1:34.4	22
C_4	0.30	9:1	0
C_5	na	9:1	0

[a] Fraction day^{-1} at 25 C (Paul and Juma, 1981)
[b] Based on litter characteristics of 27 July (*see* text)

litter was in the field. Soil moisture and temperature regimes at 5-cm depth (the depth of litter burial) were provided by J. Cornelius (pers. comm.) and used to drive the model. Estimated mass losses and carbon chemistry of the decomposing litter were compared to the results of the field experiment at subsequent sampling dates to evaluate model performance. The pool of mineral N was considered zero at the start of simulations.

RESULTS

Between 27 July and 18 October, the soluble content of the litter decreased from 25 to 17% of the total remaining mass, holocellulose content decreased from 53 to 49%, and lignin content increased from 22 to 34% (Fig. 2A). Separate linear regression analyses of litter carbon fractions over time consistently indicated highly significant differences in soluble, holocellulose and lignin content between dates ($n = 66$, $P = 0.0001$). Although ash mass increased slightly during the study (1.2 to 1.8% of the total mass), regression analysis failed to detect significant differences between dates ($n = 49$, $P = 0.4204$).

The absolute quantities of soluble, holocellulose and lignin materials present through time can be estimated by multiplying the litter mass remaining on each date by the fraction represented by each chemical component (Fig. 2A). Moorhead and Reynolds (1989) reported ca. 15% reduction in the mass of litter between 27 July and 18 October. This represents a reduction in the absolute quantities of solubles and holocellulose of 41% and 22% (respectively), concurrent with a 34% increase in lignin (Fig. 2B).

Simulation results showed a decrease in total mass, a decrease in soluble and holocellulose litter fractions to 19% and 46%, respectively, and an increase in the lignin fraction through

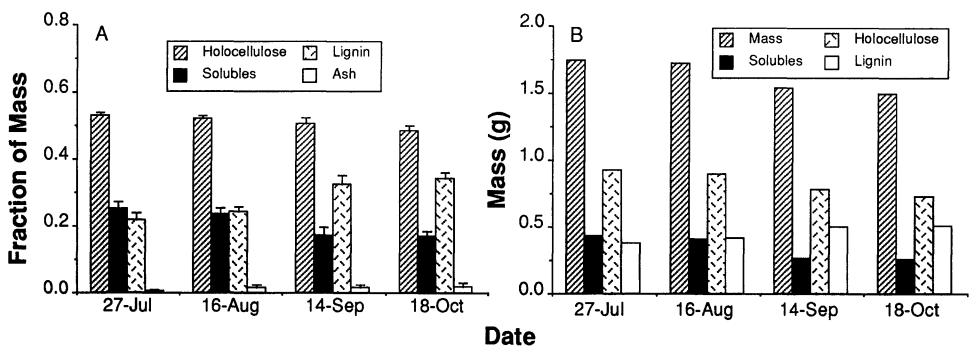

FIG. 2.—A. Litter chemistry through time (mean ± 95% CI); B. Estimated mass of litter constituents through time (based on mean values)

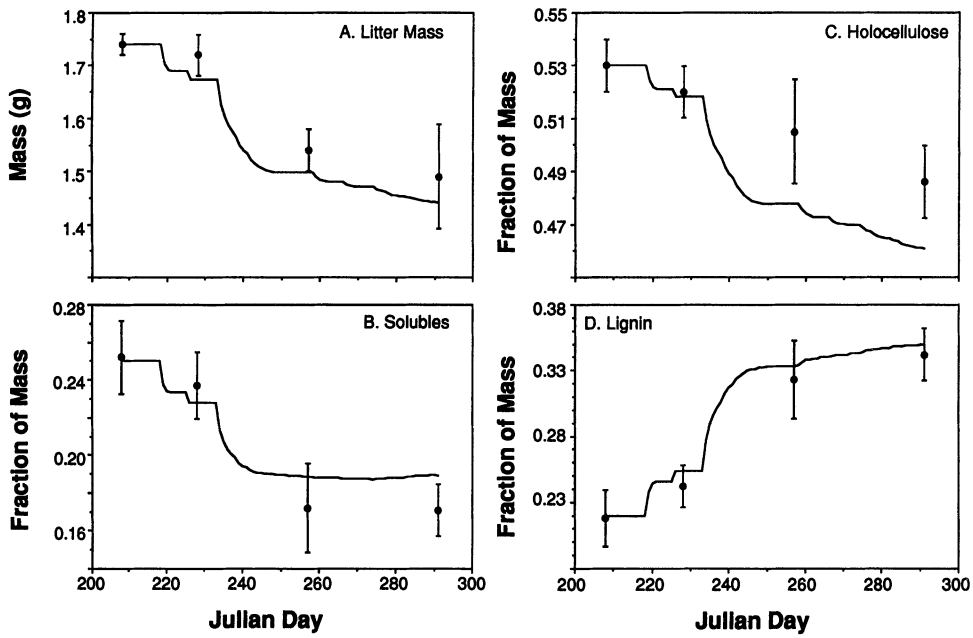

FIG. 3.—Observed (dots; means ± 95% CI) and simulated (lines) values of: A. litter mass (g), B. soluble fraction, C. holocellulose fraction, D. lignin fraction, through time

time to 35%, comparable to observations (Fig. 3). Since no attempt was made in chemical analyses to separate litter components according to plant or microbial origin, microbial pools were included in evaluations of litter chemistry. In order to similarly present simulation results, we assumed that the microflora consisted primarily of fungi (*cf.* Parker *et al.*, 1984) and that 15% of the live microbial mass consisted of cell wall material while 85% was protoplasm (*cf.* Paustian and Schnürer, 1987). Since the decay of the dead microbial pool was very rapid (Table 1), we assumed that materials remaining in this pool over time were primarily recalcitrant. Using this rationale, we added the estimated quantities of cell wall materials to the plant lignin pool (Fig. 3D), and microbial protoplasm to the plant solubles pool (Fig. 3B).

DISCUSSION

The role of microorganisms in litter decomposition in North American deserts has seldom been examined. A series of studies centered in the northern Chihuahuan Desert has shown that relationships between rainfall, AET, litter lignin and nitrogen content, and mass loss rates reported for other ecosystems apparently are not consistent with those for deserts (Whitford *et al.*, 1981; Santos *et al.*, 1984; Schaefer *et al.*, 1985). Still, the application of fungicides slowed the decay of litter in this desert (Santos *et al.*, 1981), and Parker *et al.* (1984) concluded that fungi were responsible for the immobilization of nitrogen associated with decaying buried litter. A recent, extensive survey of basidiomycete community assemblages associated with wood decay in the Chihuahuan and Sonoran deserts failed to isolate species with much tolerance to desiccation or high temperatures common to these sites (Anders, 1992). This suggests that microbial-mediated decomposition in desert systems is limited to favorable periods in time and space.

Burial of litter provides a microclimate with lower temperatures and higher moisture availability than at the soil surface, so microbial activities may be enhanced. The paired field and modeling studies of Moorhead and Reynolds (1989, 1991) sought to elucidate the role of microflora in buried litter decomposition in the northern Chihuahuan Desert. The overall patterns of nitrogen immobilization in conjunction with mass losses observed by Moorhead and Reynolds (1989) were consistent with activity patterns of saprophytic microorganisms. Similarly, the model developed by Moorhead and Reynolds (1991), based on microbial-mediated decay processes, was able to simulate these patterns. Although direct observations of microbial activities were not monitored, observed and simulated decay patterns are consistent with a microbial explanation for buried litter decomposition.

The present study further examines the dynamics of buried litter decay. If mass losses were due to fragmentation and/or physical removal of litter, then the chemical characteristics of the remaining litter would not change. If leaching of soluble compounds was the major cause for mass loss, then the soluble content of the litter should disappear very rapidly. However, these explanations for mass loss are inconsistent with observed changes in litter chemistry. Apparent nitrogen immobilization during decomposition suggested changes in the relative quantities of litter constituents (Moorhead and Reynolds, 1989), but the chemical analyses presented herein more clearly illustrate the nature of these changes. Both the absolute amounts and the relative fractions of the remaining litter mass that were represented by soluble and holocellulose pools decreased over time although not at the same rate (Fig. 1). The fraction of the remaining mass in the soluble pool decreased by 32% over the study period, while the holocellulose pool decreased by 9%. At the same time, the lignin pool increased in both relative fraction of the total mass (by 57%) and absolute amount—there was more recalcitrant material at the final sample date than three months earlier although ash content did not increase.

The application of GENDEC (Moorhead and Reynolds, 1991) provides a reasonable explanation for these patterns. Overall decomposition is limited to periods of favorable temperature and moisture availability. Within these periods litter decay is mediated by microbial activities, controlled by nutrient availabilities and the intrinsic "decomposabilities" of various litter constituents (Table 1). Use of solubles, holocellulose and lignin by microbiota proceeds at rapid, moderate and slow rates, respectively. However, the microbiota produce compounds that are perceived as soluble and recalcitrant by chemical analysis. Therefore, the soluble pool remains larger than would be anticipated based on the simple negative exponential decay function used to describe decomposition of this pool (Eq. 1; Table 1). For the same reason, the recalcitrant pool increases over time because the decay rate of lignin is so slow that the production of recalcitrant compounds by microbiota is faster than decomposition.

Very similar but more complicated models have been used to examine decomposition processes in prairie and agricultural soils (*e.g.,* Paul and Juma, 1981; Van Veen *et al.,* 1984; Parton *et al.,* 1987; Jawson *et al.,* 1989; Stroo *et al.,* 1989). We used a simpler approach since our data base was very limited, but it is likely that comparable results would be obtained with any of these formulations. We believe that our results suggest functional similarities between decomposer soil microbiota in desert ecosystems and the more mesic, temperate ecosystems described by others. It seems to be the timing, location and duration of environmental conditions favorable to microbial activity that determines the overall pattern of litter decay in deserts rather than any qualitative difference in underlying mechanism.

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