ORIGINAL PAPER

H.-T. Mun · W.G. Whitford

Changes in mass and chemistry of plant roots during long-term decomposition on a Chihuahuan Desert watershed

Abstract We studied the spatial and temporal patterns of decomposition of roots of a desert sub-shrub, a herbaceous annual, and four species of perennial grasses at several locations on nitrogen fertilized and unfertilized transects on a Chihuahuan Desert watershed for 3.5 years. There were few significant differences between the decomposition rates of roots on the NH_4NO_3 fertilized and unfertilized transects. Decomposition of all roots followed a two-phase pattern: early rapid mass loss followed by a long period of low mass loss. Rates of decomposition were negatively correlated with the initial lignin content of the roots ($r = 0.90$). Mass loss rates of the roots of the herbaceous annual, *Baileya multiradiata*, were significantly higher than those of the grasses and the shrub, probably as a result of subterranean termites feeding on *B. multiradiata* root material. The only location where mass loss rates were significantly different was the dry lake bed, where mass loss rates were lower than those recorded on the upper watershed. The spatial differences in mass loss rates in the dry lake were attributable to the high clay content of the soils, which reduced water availability, and to the absence of termites. Non-polar substances in decomposing roots decreased rapidly during the first year, then decreased at a low but fairly constant rate. Water-soluble compounds decreased rapidly (50–60% of initial concentration) during the first 3–6 months. Lignin concentrations of roots of perennial grasses were higher than those of herbaceous annual plants and woody shrubs. Lignin concentrations increased in all species during decomposition. The chemical changes in decomposing roots followed the patterns described for decomposing litter in mesic environments.

H.-T. Mun [1] · W.G. Whitford [2] (✉)
Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

Present addresses:
[1] Department of Biology, Kongju National University, Kongju, Chungnam 314-701, Korea
[2] U.S. Environmental Protection Agency, Office of Research and Development, National Exposure Research Laboratory, Characterization Research Division, PO Box 93478, Las Vegas, NV 89196, USA

Introduction

Decomposition of plant litter on the soil surface in deserts appears to be primarily an abiotic process due to leaching of solubles and breakdown by high temperature and ultraviolet radiation (Moorhead and Reynolds 1989). Variables that have an effect on biological activity, such as rainfall and evapotranspiration, have no direct effect on the rates of decomposition of surface litter (Elkins et al. 1982; Schaefer et al. 1985; Whitford et al. 1986). However, decomposition rates of buried litter and dead roots to vary with soil moisture and temperature, as expected for processes of biological decay (Santos and Whitford 1981; Urbaniak and Whitford 1983; Parker et al. 1984; Whitford et al. 1988a). The changes in carbon chemistry of buried litter are also consistent with biologically mediated decomposition (Moorhead and Reynolds 1993). In mesic systems, decomposition of plant litter results in a series of predictable chemical changes in the decomposing material (McClaugherty et al. 1982; Berg et al. 1984). In arid systems, dead roots are the most reliable source of recalcitrant compounds that contribute to the soil organic matter pool (Parker et al. 1984). Although decomposition rates and soil microarthropods associated with decomposing roots have been measured (Whitford et al. 1988a, b), chemical changes in decomposing roots have not been examined in desert environments.

Spatial and temporal patterns of decomposition are central to the dynamics of desert ecosystems because they are related to the spatial and temporal patterns of nutrient availability. In several types of desert ecosystems, the relationship between decomposition, nutrient availability, and rainfall may be altered and thus lead to a level of primary productivity from the available soil moisture which is less than the potential maximum (Whitford et al. 1987; Fisher et al. 1988; Fisher and Whitford 1995). The spatial distri-

bution soil organic matter in the Chihuahuan Desert has been shown to vary inversely with the abundance of subterranean termites (Nash and Whitford 1995). Rates of surface litter decomposition on a Chihuahuan Desert watershed were highest on parts of the watershed where termites were most abundant (Cepeda-Pizarro and Whitford 1990). Decomposition rates of litter located on the soil surface were not correlated with initial lignin or nitrogen content (Cepeda-Pizarro and Whitford 1990). Because of variation in water run-off and run-on patterns on desert watersheds, and because of the spatial variation and patchiness in the distribution of soil fauna (Santos et al. 1978; Wallwork et al. 1985; Freckman and Mankau 1986; Cepeda-Pizarro and Whitford 1989), we hypothesized that rates of decomposition of roots should vary with their location in the watershed. We also hypothesized that the patterns of carbon chemistry of decomposing roots would vary with their position in the watershed and with nitrogen availability in the transects.

We designed a study to examine the long-term spatial and temporal patterns of mass loss, changes in nitrogen contant and chemical composition during decomposition of roots on a desert watershed. Because nitrogen availability has been hypothesized to affect the decomposition rates of buried litter in deserts (Parker et al. 1984), we studied decomposition of roots along a transect on a desert watershed that had been fertilized with ammonium nitrate and compared these results with the decomposition of roots along a transect that had not been fertilized.

Materials and methods

This study was conducted from October 1986 through April 1990 on a watershed in the Chihuahuan Desert Rangeland Research Center, approximately 40 km northeast of Las Cruces, N.M. The watershed is an east-facing alluvial piedmont, ranging in elevation from 1400 m at the base of the mountain to 1300 m in the small dry lake basin at the terminus of the watershed. The watershed vegetation is arranged in five distinct vegetation zones from the top of the watershed to the dry lake: black grama (*Bouteloua eriopoda*) grassland, mixed bunch grass-shrub mosaic, creosotebush (*Larrea tridentata*) shrubland, lower basin slope mosaic grassland with scattered shrubs, and dry lake bottom with a cover of grass (*Panicum obtusum*) (Wondzell et al. 1987). The long-term average precipitation is 225 mm year^{-1} with 60% falling between and September during convectional storms. Temperature maxima regularly exceed 40°C in summer and winter minima are frequently below 0°C. Two transects (3 km long × 30 m wide) extending from the dry lake to the base of the mountain were established in 1981. The transects were separated by a 50 m buffer zone. One of the transects was fertilized with ammonium nitrate NH_4NO_3 by aerial application of approximately 30 g·m^{-2} of fertilizer each year in early summer from 1983 to 1990.

Roots were collected from areas on the watershed adjacent to the study transects. The roots were gently washed to remove adhering soil particles, then dried to a constant mass at 50°C. Roots were collected from species that comprise more than 10% of the vegetative cover. Between one and three root segments of the woody sub-shrub, *Gutierrezia sarothrae*, and the most common summer herbaceous annual, *Baileya multiradiata*, were tethered with fine wire attached to an aluminium tag labeled with an identity code and initial mass. Approximately 1 g of roots of each species: black grama grass (*Bouteloua eriopoda*) fluff grass (*Erioneuron pulchellum*) and the grass from the dry lake basin (*Panicum obtusum*), were placed in each 12 cm ×

12 cm fiberglass mesh bag (mesh size = 1 mm). We made 960 bundles of *G. sarothrae* roots and 960 bags of *E. pulchellum* roots. There were 160 bags or root bundles of the other species. Each bundle or bag was attached to a unique number tag connected to a 30 cm wire. The study was designed for the retrieval of 8 units of each species from each watershed location and each transect on ten sample dates. Roots were buried in short trenches (3 m long) separated by approximately 3 m between trenches. Each bag or root bundle was separated from others in a trench by a minimum of 50 cm. The trenches were located at the approximate mid-point of the vegetation zones on each of the transects. For example, 80 bundles of *Baileya multiradiata* roots were buried in the mid-section of the fertilized transect of the basin slope and 80 bundles were buried in the mid-section of the unfertilized transect of the basin slope.

The roots of *P. obtusum* were placed in the dry lake basin, the roots of *Bouteloua eriopoda* were placed in the black grass grass zone at the top of the watershed, and the roots of *Baileya multiradiata* were placed in the basin slope. Roots of *G. sarothrae* and *E. pulchellum* were placed in all vegetation zones because these species occur in all the zones on the watershed. The other species are restricted to one zone, and although *Baileya multiradiata* occurs in four zones, its highest abundance is in the basin slope zone. At all sites, roots and root bags were buried at 5–10 cm soil depth. Eight samples of each species were retrieved after 1, 3, 6, 12, 18, 24, 30, and 36 months in the field. The sequence of removal was determined by drawing numbers from the remaining bags at random. Although this study was designed for a 48 months duration, parts of the study had to be terminated early. At 42 months the trenches were completely and carefully excavated and the remaining material recovered. We were unable to retrieve complete samples of roots except for *G. sarothrae*. The small number of root samples that were collected in month 42 were pooled by site and treatment in order to obtain sufficient material for the chemical analyses. After retrieval, roots were removed from the bags, gently washed in distilled water to remove adhering soil particles and dried to a constant mass at 50°C. After the final dry mass measurement, the roots were ground in a laboratory mill equipped with a 1 mm screen. An exponential decay model was used to estimate the mass loss rate:

$$X/X_0 = \ln^{-kt}$$

where X = mass remaining at time t (months), X_0 = original weight, ln is the natural logarithm and k is the decomposition constant (Olson 1963).

For the analysis of total nitrogen, sub-samples of ground roots were treated by Kjeldahl digestion in a block digestor. Ammonium nitrogen was analyzed by an automated salicylate procedure in a Scientific Instruments autoanalyzer (Fisher et al. 1987). Three organic matter fractions (water and non-polar solubles, acid solubles, and acid insolubles) were analyzed in the remaining root material. Non-polar and water soluble substances were extracted using dichloromethane followed by hot (100°C) water (McClaugherty et al. 1984). Acid soluble fiber, which was largely holocellulose, was separated from acid-insoluble fiber (largely lignin and suberin) using a two-stage digestion in sulfuric acid (Effland 1977).

Comparisons of the root mass remaining in different locations on the unfertilized and fertilized transects were analyzed using a paired *t*-test. All other comparisons were made by ANOVA.

Results

Decomposition

The decomposition rates of the roots varied inversely with initial lignin concentration and directly with initial nitrogen content (Tables 1, 2). There was a high negative correlation ($r = -0.90$, $P < 0.05$) between initial lignin content and rates of mass loss. Rates of mass loss of the roots of the herbaceous annual, *B. multiradiata*, were highest dur-

Table 1 Initial concentrations of nitrogen (mg · g⁻¹)±standard deviation and organic fractions (%)±standard deviation in the sample roots

| Species	Nitrogen	Non-polar	Water solubles	Acid solubles	Lignin
Baileya multiradiata	7.2±2.9	5.2±1.1	12.0±4.2	66.1±3.9	16.7±5.9
Gutierrezia sarothrae	7.3±1.0	5.3±2.5	13.3±2.8	57.8±4.2	23.6±4.2
Erioneuron pulchellum	6.5±0.3	4.8±1.8	9.7±3.7	58.5±2.7	27.0±2.7
Bouteloua eriopoda	5.9±0.7	4.9±0.7	9.3±0.7	54.3±1.4	29.5±1.4
Panicum obtusum	6.9±0.7	4.7±0.7	11.0±2.7	55.9±9.9	28.7±0.1

Table 2 Decomposition rates (*k*) calculated for roots of plant species after 36 months. Data are for the combined decomposition rates of roots in the fertilized and unfertilized transects

Species	*k*
Baileya multiradiata	0.60
Gutierrezia sarothrae	0.30
Erioneuron pulchellum	0.28
Bouteloua eriopoda	0.24
Panicum obtusum	0.13

Fig. 1 Comparison of average mass losses from roots of several species of Chihuahuan Desert plants

ing the first month (mass loss of 25%), while roots of the other species lost approximately 10% of their initial mass during this period (Fig. 1). After 36 months, only 20% of the original mass of the roots of *B. multiradiata* remained. Mass loss rates for the grasses, except for *P. obtusum*, were not significantly different from the mass loss rates of roots of the woody shrub, *G. sarothrae*, over the course of the study (*P*>0.05). There was no measurable mass loss from the roots of *P. obtusum* in the dry lake bed from month 18–36, which resulted in the low *k* calculated for this species (Fig. 1, Table 2).

Subterranean termites began to remove a substantial fraction of the *G. sarothrae* and *B. multiradiata* roots during the first 2 years. Termite activity was apparent on the tethered roots in all of the vegetation zones except for the dry lake basin. During the first year, between 6.3% and 31% of *B. multiradiata* roots and between 0.6% and 3.8% of *G. sarothrae* roots exhibited substantial mass removal by termites (estimated to be between 11% and 16% of the original mass). This is a conservative estimate based on those roots exhibiting physical evidence of termite feeding. In the second year, 25% of *B. multiradiata* roots were totally consumed (probably by termites).

There were no significant differences in rates of mass loss of roots on the untreated and fertilized transects until the end of the second year (Figs. 2, 3). The differences in mass losses from roots on the fertilized and untreated transects were not related to their location on the watershed nor time. For example, after 24 months the mass losses of *G. sarothrae* roots were higher in the fertilized transect except in the basin slope locations. After 36 months, the mass loss of the roots of *G. sarothrae* was significantly higher in the untreated transect in the basin slope locations and in the fertilized transect of only two zones: the dry lake and black grama grassland of the watershed (*t* values>2.6, *P*<0.05). There were no differences in the rates of mass loss of the roots of *P. obtusum* in the
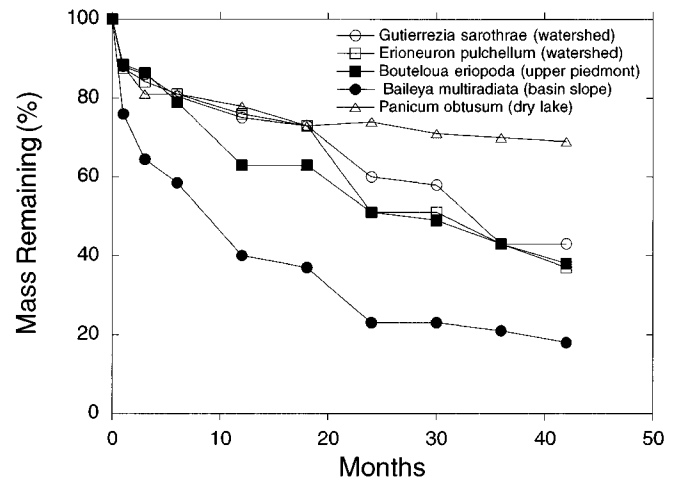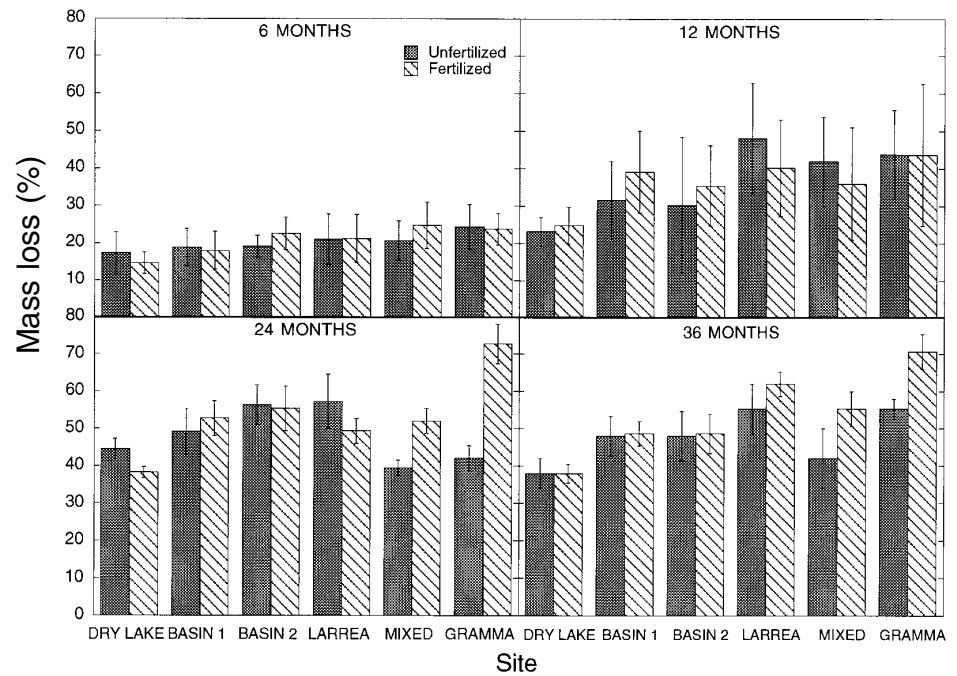
fertilized and unfertilized transects (*t*=0.91, *P*<0.05) in the dry lake bed. There were also no differences in mass losses from roots of *B. multiradiata* in the fertilized and untreated transects at the basin slope locations (*t* values <1.0, *P*>0.05).

Chemical constituents

There were no significant differences among species, watershed locations or between fertilized and untreated transects in the changes in concentrations of the chemical constituents of the roots. Therefore the data from all locations and both transects were averaged for presentation. Between 40% and 60% of the water solubles were lost during the first 30–90 days (Fig. 4). After that the loss of water solubles was lower but dropped to less than 20% of the original concentration by month 42 (Fig. 4). The concentration of non-polar substances fell dramatically during the first year, after which the concentrations remained essentially unchanged (Fig. 5). There were low rates of loss of acid soluble compounds during the entire experimental period (Fig. 6). After 24 months the remaining root mass contained approximately 80% of the original concentration of acid soluble compounds (Fig. 6). The lignin concentration increased to approximately 140% of the original concentration in all species except for *B. multiradiata*. In this species the lignin concentration increased to approximately 200% of its original level (Fig. 7). The changes in the

Fig. 2 Comparison of average mass losses from roots of the sub-shrub, *Gutierrezia sarothrae,* at various locations on nitrogen fertilized and unfertilized transects on a watershed in the northern Chihuahuan Desert. Playa is the dry-lake location

Fig. 3 Comparison of average mass losses from roots of the perennial grass, *Erioneuron pulchellum,* at various locations on nitrogen fertilized and unfertilized transects on a watershed in the northern Chihuahuan Desert. Playa is the dry-lake location
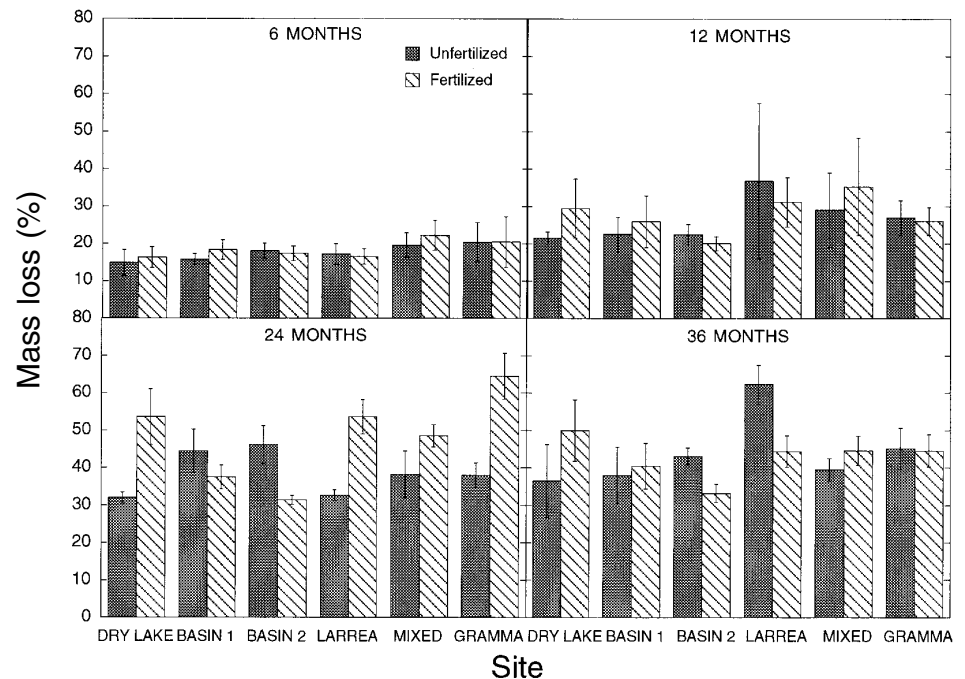

nitrogen concentration of the decomposing roots exhibited a pattern of nitrogen immobilization, with an increase in nitrogen concentration between 12 and 18 months and some decline in nitrogen concentration after 36 months (Fig. 8).

Discussion

The initial rates of mass loss of grass roots in our study were lower than those reported for perennial grass roots in Sweden (Larsson and Steen 1988) and in the mesic prairie in Kansas (Seastedt et al. 1992). However, the initial rates of mass loss from the roots of the annual herbaceous species *B. multiradiata*, were higher than the rates reported for the roots of perennial grasses by these authors, and the overall rates of mass loss of roots of *B. multiradiata* were equal to those of perennial prairie grasses (Seastedt et al. 1992). These differences in initial mass loss rates appear to be a function of the initial lignin content of the roots. The initial lignin contents of the roots of the desert grasses in this study (average=28.4%) was 6% higher than the
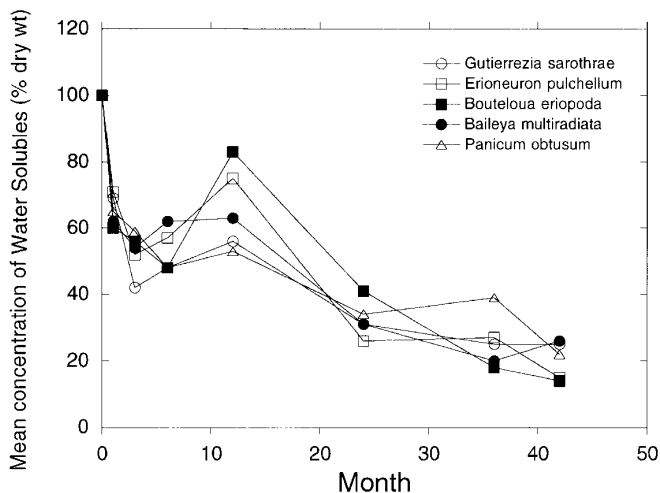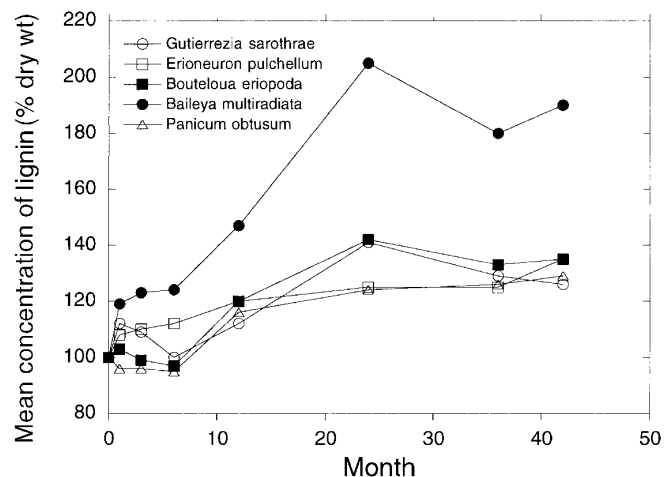
Fig. 4 Changes in the mean concentration (% dry wt.) of water soluble compounds in roots of several species of Chihuahuan Desert plants during decomposition
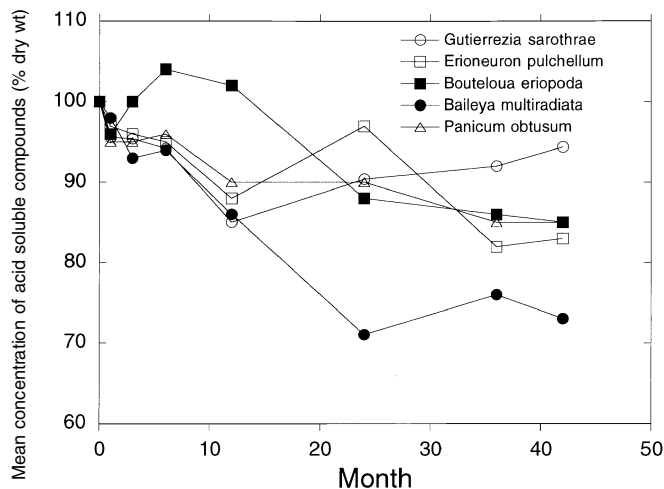
Fig. 6 Changes in the mean concentration (% dry wt.) of acid soluble compounds in roots of several species of Chihuahuan Desert plants during decomposition
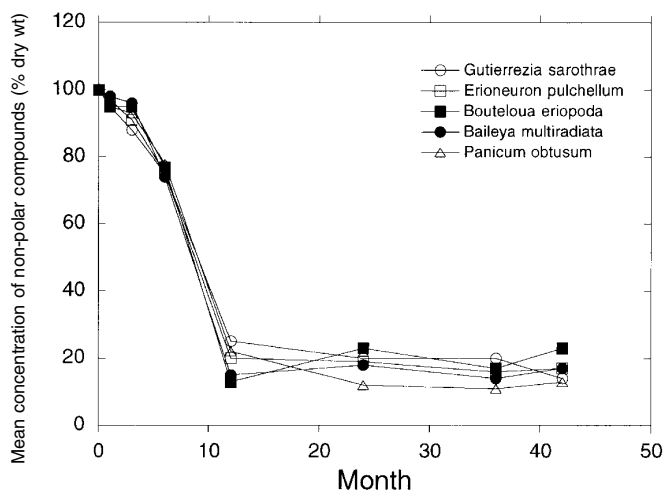
Fig. 5 Changes in the mean concentration (% dry wt.) of non-polar compounds in roots of several species of Chihuahuan Desert plants during decomposition
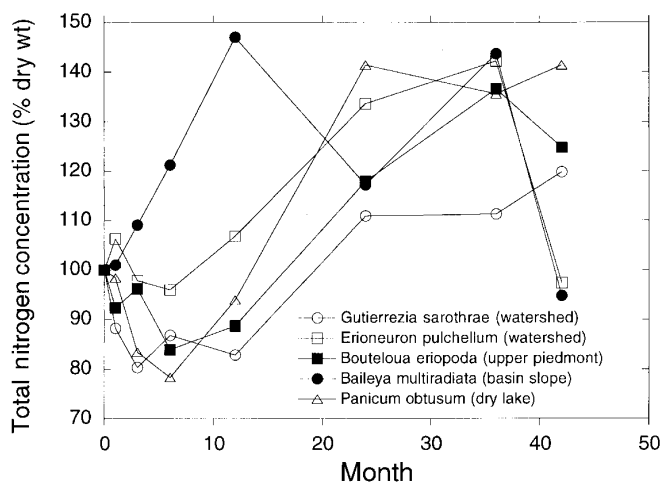

Fig. 7 Changes in the mean concentration (% dry wt.) of lignins in roots of several species of Chihuahuan Desert plants during decomposition

roots used in the studies of Larsson and Steen (1988) and 15% higher than the roots used in the study of Seastedt et al. (1992). The initial lignin content of *B. multiradiata* was 5.3% lower than the grass roots in the Swedish study but 3% higher than the roots from the Kansas prairie experiment.

The root decomposition studies in Sweden and Kansas were conducted in areas that receive more than 800 mm of rainfall year^{-1} compared with the 250 mm average annual rainfall in the Chihuahuan Desert. Since microbial activity is greatly reduced in dry soils (Whitford 1989), we would expect rates of mass loss to be considerably lower for roots in desert soils than for roots in mesic grassland soils. In a study comparing the decomposition rates of roots of a perennial herb in irrigated plots and in plots exposed to induced drought by "rain-out" shelters, Whitford et al. (1995) found that irrigation had no effect on rates of de-

composition but that exposure to drought reduced the rates of decomposition to half that of the controls. The "rain-out" shelters eliminated all water inputs and as a consequence, the soils became completely dry. In this study, soil water differences resulted from run-off, run-on patterns. These patterns produce variation in soil water content more similar to the irrigation treatment than to the "drought" treatment (Whitford et al. 1995). Thus, the rates of decomposition of desert plant roots appear not to be affected by variation in soil water content. In our study, the high negative correlation between the initial lignin content of roots and their rates of mass loss support the argument of Mellilo et al. (1982) and McClaugherty et al. (1984) that initial lignin content is the best predictor of rates of mass loss from both litter and roots.

Root decomposition studies in the Chihuahuan Desert are complicated by the activities of subterranean termites.

Fig. 8 Changes in the nitrogen concentration (% dry wt.) in roots of several species of Chihuahuan Desert plants during decomposition

We have observed that termites eat only the outer layers of woody materials which have been softened by fungi (unpublished data). This may account for the differences between the small quantities large woody root mass eaten by termites and the mass of *B. multiradiata* roots eaten by termites. In addition, termites may be less efficient at locating potential food sources underground than food sources on the surface. Regardless of the quantity of root material consumed by termites, the changes in the chemical composition of roots, and activities of the soil microflora and microfauna, should proceed at rates determined by the initial chemical composition of the substrate and by soil moisture and temperature. The chemical composition of the remaining root material is a reflection of losses plus additions resulting from the growth of hyphae and/or bacterial cells within the root tissue. Therefore the decomposition and mineralization measures made during this study should accurately portray these processes and provide an estimate of the contribution of various species of dead roots to the nutrient and organic pools in desert soils.

The initial lignin content of the root material was the only variable to have an effect on the rates of mass loss. There were no consistent differences in mass loss attributable to either topographic position on the watershed or available soil nitrogen. Studies of root decomposition on irrigated plots have shown that there were no differences in rates of mass loss from roots in soils irrigated with different patterns of supplemental water and in soils receiving only natural rainfall (Whitford et al. 1988a). The results of Whitford et al. (1988a) also demonstrated that the rates of decomposition were not related to initial nitrogen content or to the initial carbon-nitrogen ratio. The absence of differences attributable to these variables confirms the contention that materials below the surface of the soil are rapidly processed by soil microflora and microfauna and that there are some groups of soil organisms that are active even in very dry soils (Whitford 1989).

The only consistently significant differences in mass losses related to topography were observed in roots in the

soils of the dry lake when compared to roots in soils of the upper watershed. The high clay content of the ephemeral lake soils reduce water availability to soil organisms. Unless the ephemeral lake basin is flooded, very little of the rainfall infiltrates into the lake soils. We suggest that the lower rates of mass loss recorded for plant roots in the ephemeral lake are the result of moisture limitation. The soils of this emphemeral lake have the highest organic carbon and total nitrogen of any of the soils on the watershed (Wondzell et al. 1987). The low rates of mass loss may also be due in part to the absence of subterranean termites in the dry lake basin (Nash and Whitford 1995).

It has been suggested that the roots of ephemeral (annual) plants affect the availability of soil nitrogen by providing a pulse of energy for soil microflora (Fisher et al. 1987; Whitford and Herrick 1995). In order to utilize the carbon of the dead annual plant roots, the microflora immobilize nitrogen in their increasing biomass (Parker et al. 1984; Whitford et al. 1987). Our study shows that the immobilization pattern is related to the chemical composition of the root material. The low lignin content of *B. multiradiata* roots enabled rapid growth of microflora and rapid immobilization of nitrogen. The roots of the grasses and woody shrub were obviously colonized at a slower rate, and nitrogen immobilization was not apparent until 24 months after the experiment began. In a 1-year study of root decomposition, there was significant nitrogen immobilization in the roots of two annual plant species but no evidence of immobilization in the roots of shrubs (Whitford et al. 1988a). The slow rate of nitrogen immobilization in grass roots and in roots of a woody shrub suggests that this process would have little effect on nitrogen budgets in systems dominated by these species. However, the rapid rate of immobilization in the roots of *B. multiradiata* supports the contention (Parker et al. 1984) that this process may dramatically affect nitrogen availability to plants that grow in areas with high densities of annual plants.

The rapid decrease in non-polar compounds is probably the result of colonization of roots by bacteria and rapid metabolism of these compounds. Bacteria rapidly colonize buried litter (Santos et al. 1981) and their populations decline as the concentrations of readily metabolizable compounds reduce. The changes in water solubles, acid solubles and lignins followed a pattern similar to that reported by McClaugherty et al. (1984). Lignin concentration increased throughout the study period, as was expected for this recalcitrant fraction of the root material. The patterns of change in chemistry are consistent with the findings that after the initial stages of decomposition, only structural materials remain. Thus the chemical composition of the remaining material is determined by the composition of both these structural components and those of the microflora that have invaded the decaying roots.

In conclusion, the chemical changes in decomposing roots in desert soils are similar to those of roots in mesic forests. Decomposition rates of roots in desert soils are reduced in dry soils and are inversely related to initial lignin content. The results from this study support the argument that the roots of annual plants may serve to decouple pri-

mary productivity from rainfall through the mechanism of nitrogen immobilization. The slower decomposition and mineralization of roots of perennial grasses and woody plants, combined with the low concentration of these roots in the soil, suggest that they are far less important in the cycling of essential nutrients, such as nitrogen, but may be very important contributors to the (low) concentration of organic carbon in desert soils.

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