

Decomposition of roots in a Chihuahuan Desert ecosystem

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Summary. Mass losses of tethered buried roots of two woody shrubs and two herbaceous annuals buried in plots irrigated at $25 \text{ mm} \cdot \text{month}^{-1}$, $6 \text{ mm} \cdot \text{week}^{-1}$ and no irrigation were measured. At the end of 1 year, 10–15% of the mass of the herbaceous annual roots remained and 60% of the mass of woody shrub roots remained. There were no differences in mass loss attributable to added water. Rates of mass losses of roots in the Chihuahuan Desert were equal to or higher than those reported from mesic ecosystems. Roots of woody shrubs had relatively constant C:N ratios through the experiment. There was significant N immobilization in *Baileya multiradiata* roots. Percent mass loss of grass roots, *Erioneuron pulchellum*, and herbaceous annual roots, *B. multiradiata*, in plots with termites was 62% and in plots without termites was 15%. These data suggest that subterranean termites are responsible for most of the mass loss and mineralization of carbon and nitrogen in dead grass and herbaceous roots in the northern Chihuahuan Desert.

Key words: Decomposition – Desert – Nitrogen immobilization – Roots – Termites

There have been few studies of decomposition of roots in any ecosystem (Berg 1984) and there are numerous difficulties in following the decomposition of roots in the soil under natural or near natural conditions (Jenkinson 1965). However, as Berg (1984) pointed out, not only is quantification of root decomposition necessary, but of equal importance, is an understanding of factors regulating that process. Studies of decomposition of leaf litter in arid ecosystems have shown that the rates of mass loss are high and relatively independent of rainfall, C:N ratio and lignin content (Whitford et al. 1985; Schaefer et al. 1985). Other studies have shown that subterranean termites account for much of the mass loss from certain types of litter (Silva et al. 1985). Buried leaf litter in the Chihuahuan Desert decomposed at a constant rate in contrast to surface litter which disappeared at low rates in the cold months and high rates in the warm months (Schaefer et al. 1985). We hypothesized that mass losses from roots would be similar to those measured in buried litter. Ettershank et al. (1980) concluded that subterranean termites do not feed on buried litter or roots based on studies using buried baits. If termites do

not feed on roots, then mass losses would be due to the activity of soil microflora and microfauna, hence, would vary with soil moisture and soil temperature. Therefore, we hypothesized that mass losses and nitrogen immobilization/mineralization in roots would vary directly with moisture availability. In this study we tested the hypothesis that decomposition of herbaceous and woody roots is affected by moisture availability and we experimentally examined the contribution of termites, if any, to mass loss in roots.

Methods

Supplemental rainfall. These studies were conducted in the northern Chihuahuan Desert on the Jornada Long Term Ecological Research Site 40 km NNE of Las Cruces, N.M. The average annual precipitation is 230 mm; average annual evaporation is 2290 mm and 60% of the annual precipitation occurs between July and October. Maximum temperatures in summer range from 36°C to 40°C and winter minimum temperatures regularly drop below 0°C . We collected roots of a common sub-shrub, *Zinnia acerosa*, an evergreen shrub, *Larrea tridentata*, and two herbaceous species, *Dithyrea wislizenii*, a spring annual and, *Baileya multiradiata*, a spring summer annual. The roots were washed and air dried. Groups of 2–3 roots were weighed and tied with aluminum wire to an aluminum tag. These tethered roots were buried in the soil with the tops at 2 cm below the surface. The roots were buried in soil at the edge of shrub canopies in $5 \times 15 \text{ m}$ plots that received varying patterns of rainfall. Three plots received $6 \text{ mm} \cdot \text{week}^{-1}$, 3 plots received $25 \text{ mm} \cdot \text{month}^{-1}$ and 3 plots received no supplemental moisture. Three sets of roots were removed from each plot at 30 day intervals for the first 4 months, at 9 months and 12 months. The root material remaining was brushed to remove adhering soil particles, oven dried and weighed to obtain mass loss.

Chemical analyses. The cleaned, dried roots were ground in a Wiley Mill for chemical analysis. The ground roots were prepared for nitrogen analysis by a micro Kjeldahl digestion using an aluminum block digester (Keeney and Nelson 1982). Plant nitrogen analyses were performed on the digest using automated procedures (Keeney and Nelson 1982) on a Scientific Instruments Continuous Flow Analyser. Sub-samples of the ground roots were analysed for carbon in a split furnace carbon analyser (Nelson and Sommers 1982).

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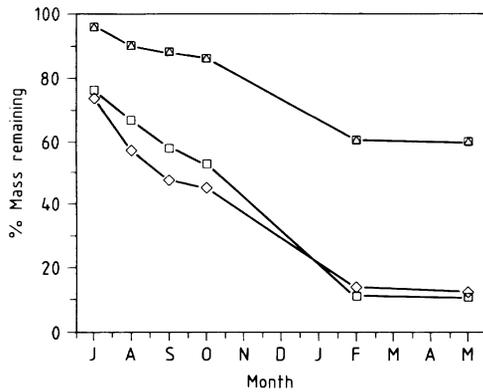


Fig. 1. The effects of supplemental rainfall on the decomposition of woody roots; *Zinnia acerosa* (Δ) and *Larrea tridentata* (\square) and annual plant roots *Baileya multiradiata* (\square) and *Dithyrea wislizenii* (\diamond) in the northern Chihuahuan desert

Termite consumption. Roots of the grass, *Erioneuron pulchellum*, and the herbaceous annual, *Baileya multiradiata*, were excavated, washed and air dried. Sub-samples were oven dried to correct air dried values. Two grams of root were enclosed in fiberglass mesh bags with a mesh size of 1.5 mm, which is sufficiently large to allow movement in and out by Chihuahuan Desert subterranean termites. There were 120 bags of each species buried in plots in which termites had been eliminated in 1977 and which have intact soil biota except for termites (see Silva et al. 1985; Whitford et al. 1982; Parker et al. 1982 for details). Ten bags of each species in each treatment were retrieved at monthly intervals for six months and at the end of one year. Litter bag contents were oven dried, weighed and burned in a muffle furnace for 12 h at 350° C. Organic matter loss was calculated using the correction equation of Santos and Whitford (1981). Data were analysed by ANOVA and where significant differences were indicated least significant difference (LSD) was calculated to estimate significance among means.

Results

Supplemental rainfall. Supplemental rainfall had no effect on rates of mass loss of any of the root species (Fig. 1). There were no significant differences in rates of mass loss of the two species of herbaceous roots. There were no significant differences in the rates of mass loss of the two species of woody roots but the rates of mass loss of woody roots were significantly lower than those of herbaceous roots ($p < 0.001$). There were numerous rainfall events in August but the other months were relatively dry. Total rainfall for the year of the supplemental rainfall experiment was 229.7 mm, with 27.8 mm in July and 30.8 mm August. Soil water potentials on the unwatered plots were -1 to -2 MPa higher than the irrigated plots during most of the year (Gutierrez and Whitford 1987).

The C:N ratios of the roots were: *B. multiradiata*, 70; *D. wislizenii*, 65; *L. tridentata*, 21; and *Z. acerosa*, 52. Supplemental water had some effects on nitrogen immobilization patterns in the decomposing roots (Table 1). For example, there was rapid nitrogen immobilization in *B. multiradiata* roots by day 30 followed by slight mineralization through

Table 1. Nitrogen concentrations ($\text{mg} \cdot \text{g}^{-1}$ dry mass) of roots in plots receiving supplemental water of $6 \text{ mm} \cdot \text{wk}^{-1}$, $25 \text{ mm} \cdot \text{mo}^{-1}$ or 0 mm after field exposures between one and four months

	30 days $\times (\text{mg/g}) \pm \text{sd}$	60 days $\times (\text{mg/g}) \pm \text{s}$	90 days $\times (\text{mg/g}) \pm \text{s}$	120 days $\times (\text{mg/g}) \pm \text{s}$
<i>Baileya multiradiata</i>				
0 mm	4.96 ± 2.28	8.18 ± 1.91	8.70 ± 2.57	7.25 ± 1.72
6 mm	4.96 ± 1.28	7.25 ± 1.29	8.93 ± 0.97	9.07 ± 1.80
25 mm	8.05 ± 1.03	5.98 ± 1.37	7.65 ± 1.32	8.38 ± 2.53
<i>Dithyrea wislizenii</i>				
0 mm	7.59 ± 1.24	9.29 ± 1.30	8.40 ± 0.97	11.74 ± 1.32
6 mm	7.91 ± 1.45	7.87 ± 2.69	9.40 ± 2.34	10.62 ± 2.17
25 mm	8.00 ± 1.23	6.95 ± 1.63	8.28 ± 1.63	8.18 ± 1.56
<i>Larrea tridentata</i>				
0 mm	17.95 ± 4.15	16.93 ± 2.37	17.35 ± 2.54	14.11 ± 1.93
6 mm	17.80 ± 3.32	15.68 ± 1.90	14.47 ± 3.60	15.61 ± 1.44
25 mm	18.06 ± 1.40	17.64 ± 1.61	13.17 ± 1.37	15.87 ± 1.80
<i>Zinnia acerosa</i>				
0 mm	7.61 ± 1.26	7.92 ± 0.83	7.36 ± 1.09	8.17 ± 1.32
6 mm	8.51 ± 0.53	6.91 ± 0.75	6.68 ± 0.94	8.48 ± 1.10
25 mm	9.58 ± 1.08	6.48 ± 0.67	6.97 ± 0.69	8.62 ± 0.87

Table 2. Carbon concentrations ($\text{mg} \cdot \text{g}^{-1}$ dry mass \pm SD) in roots buried in plots receiving supplemental water of $6 \text{ mm} \cdot \text{wk}^{-1}$, $25 \text{ mm} \cdot \text{mo}^{-1}$ or 0 mm after field exposure of the roots of 1 and 4 months. Numbers in parenthesis are C:N ratios

<i>Baileya multiradiata</i>			
0 mm	(96) 478.8 ± 10.2	(60) $433.0 \pm 9.6^*$	
6 mm	(97) 483.2 ± 6.8	(50) $452.9 \pm 2.5^*$	
25 mm	(61) 488.5 ± 9.5	(49) 410.9 ± 4.3	
<i>Dithyrea wislizenii</i>			
0 mm	(58) 441.8 ± 28.7	(38) 449.2 ± 4.8	
6 mm	(61) 480.9 ± 7.8	(37) $387.6 \pm 5.8^*$	
25 mm	(59) 474.8 ± 18.2	(52) $429.0 \pm 3.5^*$	
<i>Larrea tridentata</i>			
0 mm	(28) 494.8 ± 11.6	(32) $449.6 \pm 5.5^*$	
6 mm	(27) 486.2 ± 10.2	(29) 449.3 ± 7.0	
25 mm	(27) 486.7 ± 7.9	(28) $448.3 \pm 8.3^*$	
<i>Zinnia acerosa</i>			
0 mm	(65) 493.5 ± 6.2	(56) $456.2 \pm 2.8^*$	
6 mm	(59) 503.6 ± 6.7	(56) $477.3 \pm 7.2^*$	
25 mm	(52) 502.8 ± 9.8	(54) $462.1 \pm 0.3^*$	

day 60. However, the general pattern was nitrogen immobilization by decomposing herbaceous roots during the growing season and little change in nitrogen in decomposing roots of woody perennials (Tables 1 and 2).

Termite consumption: There were no differences in decomposition rates between *E. pulchellum* and *B. multiradiata* ($F_{3,66} = 0.02$, $p > 0.9$) but mass losses of these roots in plots with termites were significantly higher than in plots where termites were absent (Fig. 2) ($F_{3,66} = 5.42$, $p < 0.02$ and 4.30 , $p < 0.04$) for *E. pulchellum* and *B. multiradiata* respectively. Roots in plots with termites present lost an average of 57%

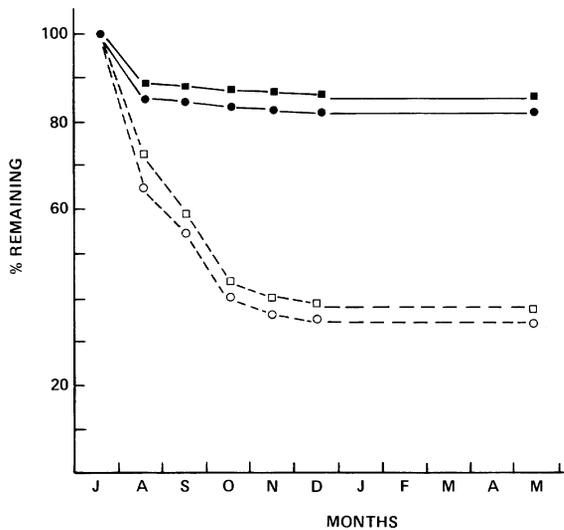


Fig. 2. The decomposition of grass *Erioneuron pulchellum* (□ with and ■ without termites) and herbaceous annual *Baileya multiradiata* (○ with and ● without termites) roots

of their initial mass in comparison to an average of 16% in plots where termites were absent (Fig. 2).

Decomposition rates of roots in the plots with termites present were modeled using negative exponential regression analysis. Correlation coefficients (r) for *B. multiradiata* and *E. pulchellum* were 0.92 and 0.83 respectively. Regression equations were *B. multiradiata*: $y = 38.52 + 61.48 e^{-0.029x}$ and *E. pulchellum*: $y = 44 \times 52 + 55.48 e^{-0.028x}$. Virtually all of the measurable mass loss occurred within the first 120 days during the warm growing season.

Discussion

The absence of measurable effect of soil moisture on the rates of mass loss of roots may be due to the feeding termites since roots in termite free soils exhibited no further loss of organic matter after one month. These data suggest that mass losses from roots via microbes and soil microfauna are insignificant. Thus both the direct and indirect evidence from this study confirms that termites are as important in the decomposition and mineralization of grass and herbaceous plant roots as in the removal of above ground dead plant material (Whitford et al. 1982).

The rates of mass loss recorded for herbaceous plant roots in this study are approximately equal to those recorded for *Trifolium* roots and considerably higher than those reported for grass roots in a mesic environment (Malone and Reichle 1973). The rates of mass loss of the woody perennial plant roots were 40% yr^{-1} higher than those reported for Scots pine roots by Berg (1984) who reported mass losses between 9 and 25% for coarse, 7–11 mm diameter, roots and fine, 2–3 mm diameter, roots respectively. The woody roots used in our studies ranged between 5 mm and 10 mm in diameter. The high rates of mass loss recorded between October and February, independent of soil moisture, suggests that termites may have been responsible for most of that mass loss.

The absence of an effect of varying soil moisture on rates of decomposition of dead roots in a desert soil is consistent with the hypothesis that most of the mass loss

is due to termites. Subterranean termites remain active in dry soils (Johnson and Whitford 1975) but construction of surface galleries and extensive surface feeding requires that soil be moist (Whitford et al. 1982). Termites could continue to feed on roots in the upper 10 cm of soil until soil temperatures at that depth became too cold (late December to early January) and then resume activity when soil temperatures return to suitable levels (late March or April) (Whitford 1974).

The rates of mass loss for roots of herbaceous species were higher than those reported for buried litter and the rates of mass loss of woody roots was within the range reported for buried litter in the Chihuahuan Desert (Schaefer et al. 1985). The high rates of organic matter loss from decomposing roots and the consumption of roots by subterranean termites are undoubtedly important contributions to the low organic matter content of desert soils. If the plant litter and dead roots is being mineralized in the guts of termites that live at depths below the root zone of most plant, there is virtually no residual or recalcitrant fraction to add to the soil organic matter pool. The low organic matter content of Chihuahuan desert soils contributes to the low productivity of many of the component ecosystems. This study adds further evidence in support of the contention that termites are “key” species in Chihuahuan desert ecosystems.

In arid and semi-arid ecosystems, primary productivity varies temporally as a function of water and nitrogen availability (Whitford 1986). In these ecosystems herbaceous plants (largely annuals or short-lived perennials) may constitute a large proportion of the net primary productivity (Ludwig and Whitford 1981). Such herbaceous plant roots introduce a pulse of high C:N. It has been suggested that decomposition of annual plant roots immobilizes nitrogen thus affecting growth of annuals and perennials in subsequent wet periods (Parker et al. 1984; Gutierrez and Whitford 1987). One important result of these studies is the documentation of nitrogen immobilization by annual plant roots. The changes in nitrogen content of the annual plant roots nearly balances mass loss from the roots. Thus the total quantity of nitrogen immobilized in decaying roots of annuals remains relatively constant over the year despite the loss of mass to termites. Considering these data it is clear that much of the available nitrogen would be immobilized in decaying annual plant roots in October and November which is the time of germination and establishment of spring annual plants in the northern Chihuahuan Desert. These data provide support for the hypothesis of Gutierrez and Whitford (1987) who proposed that the marked reduction in annual plant abundance and biomass on plots during the second year of 300 $\text{mm} \cdot \text{yr}^{-1}$ water addition when compared to the first year was due to lack of available nitrogen.

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