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The relative contributions of termites and microarthropods to fluff grass litter disappearance in the Chihuahuan Desert

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Summary. We tested the hypotheses that both subterranean termites and soil microarthropods are important in the disappearance of fluff grass (*Erioneuron pulchellum*) litter on the soil surface by an experiment designed to separate termite and microarthropod effects. Subterranean termites (*Gnathamitermes tubiformans*) removed more than 50% of the fluff grass litter in one year.

Since there was no difference in mass loss of fluff grass with microarthropods present or excluded, they had no effect on decomposition of fluff grass litter. Microarthropod densities increased during the first 3 months then slowly decreased. The densities of microarthropods in fluff grass litter were too low to have a measurable effect on decomposition even if we assumed that the microarthropods consumed litter equivalent to their body weight each day.

Litter decomposition in terrestrial ecosystems involves interaction between microflora, microfauna and the environment (MacFayden 1963; Crossley 1970; Douce and Webb 1978). Some workers (Chew 1974; Lee and Inman 1975; Mattson and Addy 1975) have suggested that consumers can affect ecosystem structure and function indirectly by regulating decomposition rates, nutrient cycling and primary productivity. In desert ecosystems, the processing of litter is poorly understood (Noy-Meir 1974). Soil-inhabiting termites and microarthropods are the major consumers of litter in the northern Chihuahuan Desert (Johnson and Whitford 1975; Santos and Whitford 1981; Elkins and Whitford 1982; Whitford et al. 1982b). Termites are involved in the breakdown of the organic material, the recycling of nutrients, organic matter turnover, and soil-water properties.

Gnathamitermes tubiformans is the most abundant termite species in the region. In the northern Chihuahuan Desert, it has been estimated that subterranean termites (*G. tubiformans*) consume at least 50% of the net productivity (Johnson and Whitford 1975; Whitford et al. 1982b) feeding on several kinds of plant material (wood, grasses and herbs). Whitford et al. (1982b) found that *G. tubiformans* exhibited preferences for certain types of dead plant material including dead fluff grass (*Erioneuron pulchellum*).

Several investigators reported that microarthropods increase the rate of decomposition of plant litter (Edwards and Heath 1963; MacFayden 1963; Witkamp and Crossley 1966; Crossley 1970; Edwards et al. 1970; Wallwork 1970) by increasing the surface area for microbial activity, grazing on microfloral populations and inoculating litter with microflora. Santos and Whitford (1981) found that elimination of microarthropods resulted in lower rates of decomposition of buried *Larrea tridentata*. There are no data on the contributions of microarthropods to decomposition of surface fluff grass litter in deserts.

Based on the generalizations in the literature, we hypothesized that both microarthropods and subterranean termites would contribute to the disappearance of fluff grass, *E. pulchellum* litter. We designed an experiment to measure the relative contributions of these two groups of soil animals on the decomposition rate of *E. pulchellum*.

Methods and materials

Study area

The study area is located on the Jornada Long Term Ecological Research Site 40 km NNE of Las Cruces, Dona Ana County, New Mexico. The elevation of the site varies from 1200 to 2000 m. Summer maximum air temperatures reach 40° C while freezing temperatures have been recorded from October to mid-April (data from the Jornada Site Weather Station). The 100-year annual average precipitation is 211 mm (Houghton 1972), most of which is late summer rainfall from convectional storms.

The site is an alluvial piedmont (bajada) sloping from the west to the east and north. The soils are either Hawkeye or Alladin series (Sandy Aridic Haplustolls) with intrusions of sandy clay loams (calciorthids) high in carbonates. A caliche layer generally exists 0.8 to 1.0 m below the surface.

The differentiation between soils and drainages produces distinct assembleges of vegetation (Ludwig and Whitford 1981; Whitford and Bryant 1979). The arroyos are lined with several species of large shrubs and trees. Non-arroyo areas have an essentially monotypic cover of creosotebush (*Larrea tridentata*) (Ludwig and Whitford 1981) and support a variety of annuals and the small perennial grass *Erioneuron pulchellum* (H.B.K.) (Tateoka). Our studies were conducted on non-arroyo areas of the upper bajada.

Selective termite removal procedure

In 1977, a factorial designed experiment was initiated to assess the effects of termite removal on nutrient cycling

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and plant productivity (Elkins 1983). The experimental design consisted of 4 blocks with 5 completely randomized treatment plots, 30 m × 40 m. Two plots of each block were treated with 10.3 kg/ha of the insecticide, chlordane, to eliminate termites. No active arthropods were found in treated soils to a depth of 20 cm through the spring of 1978, but by mid-fall arthropods had re-established the soil surface and upper few centimeters (Whitford and Freckman unpublished data). By the spring of 1979, essentially all known species of arthropods and nematodes common in the watershed soil were present in the treated soil, with the exception of subterranean termites (Elkins 1983). Treated soils on the Jornada have been constantly devoid of termites through the period of this study.

Experimental design

One of the treated plots (without termites) and one of the untreated plots (with termites) were used in this study. *Erioneuron pulchellum* (fluff grass) litter was collected from the study area and brought to the laboratory. Ten grams of air-dried litter was placed in open-bottom screen cylinders on June 16, 1983 (see Whitford, 1982b for procedure). Cylinders were used to prevent litter from being scattered and to allow an unobstructed soil-litter interface. A total of two hundred and two cylinders were placed at random under creosotebushes (*Larrea tridentata*). Ninety-six cylinders were placed on the treated and 96 on the untreated plots (6 cylinders per bush). Ten cylinders were placed with fluff grass litter under creosotebushes, removed and returned to the laboratory on the same day. They were oven-dried at 60° C for 72 h and burned in a muffle furnace at 600° C for 8 h, to calculate the correction factor for handling, moisture content, and the ash content of the litter. Forty-eight of the cylinders placed in each plot were treated with 200 ml of 0.5% chlordane per cylinder by placing open-bottomed cans around each cylinder to allow the chlordane to soak in. The treatments were applied in June, August and December of 1983, and March of 1984 in order to eliminate microarthropods and termites in the untreated plots. There were two sets of treatments where termites and mites were removed: treatment 2 – termites removed in 1977, chlordane applied to eliminate microarthropods and treatment 3 – termites and microarthropods eliminated by treatment of cylinders during this study. Sixteen cylinders were collected from each plot prior to retreating one half of the remaining cylinders with chlordane. Ten samples of litter from each plot were placed in a modified Tullgren funnel (Santos et al. 1978) for 72 h to extract microarthropods. The remaining samples were placed in the oven. After microarthropod extraction, all the samples were oven dried at 60° C for 72 h, weighed and muffled at 600° C for 8 h. The percent of organic matter remaining was calculated using the following equation:

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

where %r = percent of organic mass remaining; I = initial wet weight (w) × correction factor = initial dry weight; C = inorganic (ash) content of litter as proportion of 1; S = inorganic (ash) content of soil under cylinders as proportion of 1; F = final dry weight; A = ash weight of final sample.

Means of organic mass loss were compared by analysis of variance and Duncan's multiple range test.

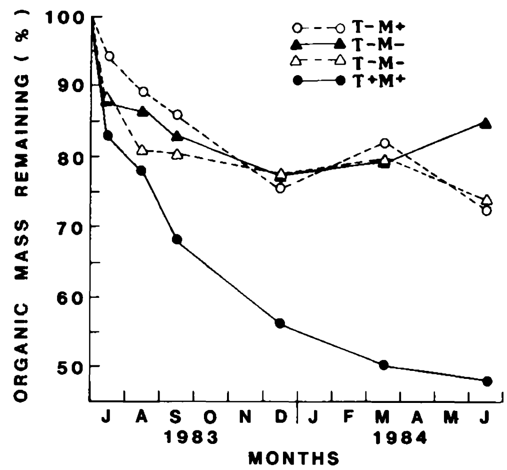

Fig. 1. Mean organic mass remaining on the experimental plots based on 8 replicates per treatment (T = termites, M = mites, + = present, − = absent). (See text for description of treatments)

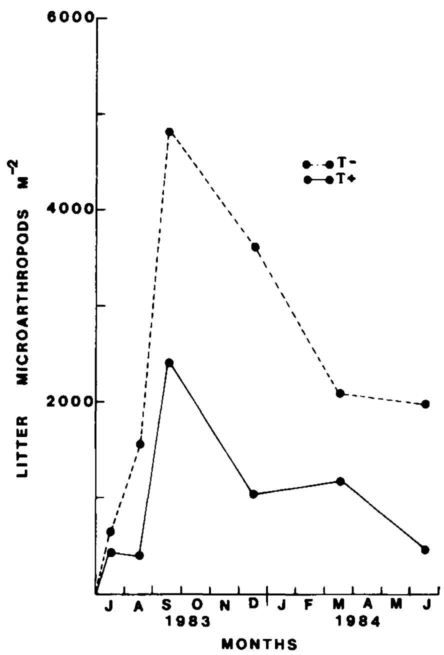

Fig. 2. Comparison of litter microarthropod densities in termites + and − plots, based on 5 replicates per treatment. Data were compared using a one-way ANOVA. Microarthropod densities in the litter on the $T-$ plots were significantly higher than on $T+$ plots ($P<0.05$)

Results

The rate of decay of surface fluff grass litter was highest in the plot with termites (Fig. 1, $P<0.05$). There were no statistically significant differences between the two treatments where both termites and microarthropods were removed (T− M−). The rate of decomposition was not significantly different ($P>0.05$) in the T− M− treatments when compared with the termite-absent, microarthropod-present treatment (T− M+). In the plot with termites, 56.5% of the original litter biomass remained in cylinders after 6 months, with 48.5% remaining at the end of the 12-month experiment. In plots without termites, an average of 77.9% of the litter remained after 6 months, with no significant further loss at the end of one year (Fig. 1).

Microarthropod densities in the litter showed that in the (T− M+) treatment, microarthropod density was significantly higher than in the (T+ M+) treatment during all months of the experiment with the exception of September (Fig. 2). Densities of microarthropods in both plots showed significant increases during the first 3 months, then slowly decreased throughout the experimental period. Highest densities occurred in September in both plots (Fig. 2).

Discussion

In this study, we found that the consumer rate regulation hypothesis of Chew (1974) could not be applied without reservation to decomposition processes in the Chihuahuan Desert. In the Chihuahuan Desert, unlike other ecosystems, only termites played an important role in the breakdown of surface fluff grass litter; microarthropods had no measurable effect. If sufficient dead fluff grass and other preferred foods are available, subterranean termites will preferentially utilize fluff grass litter, hence the apparent discrepancy in the use of creosotebush leaf litter by termites reported by Fowler and Whitford (1980) and Whitford et al. (1982b). Our data show the important role of termites in the disappearance of surface fluff grass litter, where termites accounted for more than 51.5% of the organic mass loss after one year. The greatest percentage of organic mass loss was from July to December in plots where termites were present. That time period coincides with the termite surface activity (Johnson and Whitford 1975; Whitford et al. 1982b).

Several studies have shown (Santos et al. 1981; Whitford et al. 1981a; Santos and Whitford 1981b; Whitford et al. 1982a; Parker et al. 1984; Santos et al. 1984) that microarthropods play an important role in the decomposition of buried litter and roots in the Chihuahuan Desert. Although there were large numbers of microarthropods present in the litter, there were no differences in mass loss of fluff grass when microarthropods were excluded.

Seastedt (1984) reported a range of faunal impacts on decomposition rates. The effects of soil/litter fauna on decomposition ranged from values not significantly different from zero in mixed pasture grasses to almost 70% in blue grama grass (*Bouteloua gracilis*). When Madge (1969) used insecticide to exclude microarthropods from *Eucaluptus paucifolia* foliage, he found that microarthropods were contributing 38% to the rate of decomposition. In our study, the decay rates in plots with microarthropods and also without microarthropods and termites were the same (K= 0.050). The differences appeared in plots where termites were present. The decay constant (K) equaled 0.723 in plots with termites, suggesting that termites may account for more than 90% of the disappearance of litter.

The rate of decomposition can be affected by many factors. In this study, microarthropods were found to have no effect on the rate of decomposition, which is contrary to the findings of other investigators in other ecosystems (Seastedt 1984). We calculated the amount of food consumption by microarthropods using the biomass data and consumption equations in Reichle (1968), Franco et al. (1979) and Luxton (1982). Using the equation:

$$Y = 0.063X^{0.68 \pm 0.129}$$

where Y = dry weight of food consumed; X = dry body weight

from Reichle (1968), microarthropods were estimated to consume just 0.0013 g of fluff grass litter per cylinder in a year. If we assume that all of the microarthropods ate a mass of litter equal to their body weight and used the average density multiplied by 365 days, we calculate that the amount of litter consumed by microarthropods per year is 0.044 g per cylinder. This is only 0.4% of the original fluff grass mass per cylinder. Such a low percentage is not detectable from the background variation in mass loss from the cylinders due to spatial heterogeneity. The contribution of microarthropods to decomposition is much higher in forest and grassland (Luxton 1982) than in deserts. Whitford et al. (1981a) found that microarthropods exhibit diurnal migration from the litter to the soil to avoid dryness and high temperatures. However, Whitford et al. (1981a) found that many taxa of soil microarthropods, including the cryptostigmatid mites (oribatids) that feed on fungi and litter (Krantz 1975), are active in the litter layer for several hours each day, even when soils are dry. The major reason why microarthropods appear not to have affected the fluff grass litter disappearance is because of their low densities. Densities of microarthropods in this study were much lower than those found by Parker et al. (1984). Even though microarthropods come to feed on the surface during certain times of the day, the densities are so low that they do not have measurable effects on decomposition rates.

Parker et al. (1984) provided evidence that in the absence of microarthropods, nematodes regulated the rate of mass loss and mineralization in buried litter and roots. This does not occur in fluff grass litter on the soil surface because on plots with only microflora, protozoans and nematodes, mass loss did not differ from plots with microarthropods present. This also could have resulted from low populations of microarthropods and inactive (anhydrobiotic) nematodes in the dry litter (Whitford et al. 1981a).

In conclusion, termites were the only arthropods that contributed to the disappearance of fluff grass litter. Microarthropod densities were so low that if they contributed to a fluff grass disappearance, the percentage was too low to measure.

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References

Anderson JM, MacFayden A (1976) The role of terrestrial and aquatic organisms in decomposition processes. British Ecological Society Symposium, Vol 17. Halsted Press, Wiley Publishing Company, New York, pp 375–396

Chew RM (1974) Consumers as regulators of ecosystem: An alternative to energetics. Ohio J Sci 72:359–370

Crossley DA Jr (1970) Role of microflora and fauna in soil systems. In: Pesticides in the soil: ecology, degradation and movement, International Symposium – Pesticides in the Soil. Lansing, Michigan, pp 30–35

Douce GK, Webb DP (1978) Indirect effects of soil invertebrates on litter decomposition: elaboration via analysis of a tundra model. Ecological Modelling 4, 339–359

Edwards CA, Heath GW (1963) The role of soil organisms in the breakdown of leaf material. In: Doeksen T, Drift J van der (eds) Soil organisms. Amsterdam, North Holland Publishing Company

Edwards CA, Reichle DE, Crossley DA Jr (1970) The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle DE (ed) Analysis of temperate forests ecosystems. Springer, New York, pp 147–172

Elkins NZ (1983) Potential mediation by desert subterranean termites in infiltration, run off, and erosional soil loss on a desert watershed. Ph D, New Mexico State University, p 137

Elkins NZ, Whitford WG (1982) The role of microarthropods and nematodes in decomposition in a semi-arid ecosystem. Oecologia (Berlin) 55:303–310

Fowler HG, Whitford WG (1980) Termites, microarthropods and the decomposition of senescent and fresh creosotebush (*Larrea tridentata*) leaf litter. J Arid Environ 3:1–6

Franco PJ, Edney EB, McBrayer JF (1979) The distribution and abundance of soil arthropods in the northern Mojave Desert. Journal of Arid Environments 2:137–149

Houghton FE (1972) Climatic guide, New Mexico State University, Las Cruces, NM 1851–1971. New Mexico State University Agricultural Research Report 230:1–20

Johnson KA, Whitford WG (1975) Foraging ecology and relative importance of subterranean termites in Chihuahuan Desert ecosystems. Environ Entomol 4:66–70

Krantz GW (1975) A manual of acarology. First edition. Oregon State University Press, Corvallis

Lee JJ, Inman DL (1975) The ecological role of consumers – An aggregated systems view. Ecology 56:1455–1458

Ludwig JA, Whitford WG (1981) Short-term water and energy flow in arid ecosystems. In: Goodall S Perry (ed) Arid land ecosystems – structure, functioning and management, IBP. Great Britain, Cambridge University Press, pp 271–299

Luxton M (1982) Quantitative utilization of energy by the soil fauna. Oikos 39:342–354

MacFayden A (1963) The contribution of the microflora to total soil metabolism. In: Doeksen J, Drift van der J (eds) Soil organisms. Amsterdam, North Holland Publishing Company

Madge DS (1969) Litter disappearance in forest and savanna. Pedobiologia 9:288–299

Mattson WJ, Addy ND (1975) Phytophagous insects as regulators of forest primary production. Science 190:515–522

Noy-Meir J (1974) Desert ecosystem: Higher trophic levels. Annual Review of Ecology and Systematics 4:195–214

Parker LW, Fowler HG, Ettershank E, Whitford WG (1982) The effects of subterranean termite removal on desert soil nitrogen and ephemeral flora. J Arid Environ 5:53–59

Parker LW, Santos PF, Phillips J, Whitford WG (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual. Ecological Monographs 54:339–360

Reichle DE (1968) Relation of body size to food intake, oxygen consumption and trace element metabolism in forest floor arthropods. Ecology 49:538–542

Santos PF, DePree E, Whitford WG (1978) Spatial distribution of litter and microarthropods in a Chihuahuan desert ecosystem. J Arid Environ 1:41–48

Santos PF, Elkins NZ, Steinberger Y, Whitford WG (1984) A comparison of surface and buried *Larrea tridentata* leaf litter decomposition in North American hot deserts. Ecology 65:278–284

Santos PF, Whitford WG (1981) The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. Ecology 62:654–663

Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Ann Rev Entomol 29:25–46

Simons WR (1973) Nematode survival in relation to soil moisture. Mededelingen van de Landbouwhogeschool te Wageningen 73:1–85

Wallwork JA (1970) Ecology of soil animals. McGraw Hill, Inc, London

Whitford WG, Bryant M (1979) Behavior of a predator and its prey: the horned lizard (*Phrynosoma cornutum*) and harvester ants (*Pogonomyrmex* spp.). Ecology 60:686–694

Whitford WG, Freckman DW, Elkins NZ, Parker LW, Parmalee R, Phillips J, Tucker S (1981a) Diurnal migration and responses to simulated rainfall in desert soil microarthropods and nematodes. Soil Biol Biochem 13:417–425

Whitford WG, Meentemeyer V, Seastedt TR, Cromack K Jr, Crossley DA Jr, Santos PF, Todd RL, Waide JB (1981b) Exceptions to the AET model: Deserts and clear-cut forests. Ecology 62:275–277

Whitford WG, Repass R, Parker LW, Elkins NZ (1982a) Effects of initial litter concentration and climate on litter disappearance in a desert ecosystem. Am Midl Nat 108:105–110

Whitford WG, Steinberger Y, Ettershank G (1982b) Contributions of subterranean termites to the "economy" of Chihuahuan Desert ecosystems. Oecologia 55:298–302

Witkamp M, Crossley DA Jr (1966) The role of arthropods and microflora in breakdown of white oak litter. Pedobiologia 6:293–303

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