Effect of Increased Soil Moisture and Reduced Soil Temperature on a Desert Soil Arthropod Community

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Abstract: The effects of soil moisture and temperature on arthropod communities were experimentally examined in the northern Chihuahuan Desert of New Mexico. Shaded plots were established which lowered the soil temperature several degrees; some plots received artificial rainfall to increase soil moisture. Shading reduced soil temperature at 5-cm depth 7-10 C.

Soil moisture at 5 cm accounted for most of the variation in surface activity of subterranean termites (r values between 0.3 and 0.7). Termites did not respond to temperature differences. When all soils were at field capacity, there was no difference in termite activity in shaded and unshaded plots. There were higher densities of microarthropods in litter bags on the shaded plots than on the unshaded plots. Numbers of microarthropods were an order of magnitude larger in litter bags on watered and shaded plots than on other plots. Lower litter temperatures apparently affect litter arthropods more than increased soil moisture. Shade had no effect on ant colonies but there were fewer colonies on the watered plots.

There was between 40 to 50% mass loss from creosotebush leaf litter after 7 months on all plots. Water and soil temperature had no effect on decomposition rates.

Introduction

Temperature extremes and water availability are considered to be the most important factors limiting production, activity of desert organisms and ecosystem processes in deserts (Noy-Meir, 1973, 1974; Whitford *et al.*, 1981, Whitford *et al.*, 1983). The frequency, amount and seasonal occurrence of precipitation are thought to affect productivity, litter decomposition and behavior of soil biota (Whitford *et al.*, 1981). Noy-Meir (1973) proposed a "pulse-reserve" hypothesis for desert organisms in which rainfall sets off a pulse of activity that is rapidly reduced, but some energy is stored "reserved" to await the next pulse. If desert organisms behave as predicted by the "pulse reserve" hypothesis, simulated rainfall events should trigger intense activity of various groups of soil organisms.

Recent work indicates that moisture may not be as important as once thought as a regulator of the activity of soil biota. Whitford *et al.* (1982a) found no effect of rainfall on disappearance of leaf litter. They suggested that the desert soil decomposer community has evolved adaptations that allow those organisms to process surface litter independently of rainfall, and that soil temperature could be the most important parameter affecting the rate of litter removal. Hence, rates of decomposition in North American deserts are considerably greater than predicted based on the actual evapotranspiration and lignin content, which are good predictors of decomposition in more mesic environments (Whitford *et al.*, 1983).

Subterranean termites *Gnathamitermes tubiformans* are the most important processors of dead plant material and dung in the northern Chihuahuan desert (Johnson and Whitford, 1975; Whitford *et al.*, 1982b). Termites are active aboveground during the rainy seasons, especially in the autumn, when they can be found in accumulations of litter or producing mud galleries on dead plant material (MacKay *et al.*, 1985). Ettershank *et al.* (1980) reported that termites locate large food objects such as cow dung

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pats and *Yucca* spp. logs by sensing the thermal shadows in the soil that are produced by such objects on the soil surface. Whitford *et al.* (1982b) found that termites build galleries on scattered food items at the end of the summer rainy season. Ants capture termite workers on the soil surface in midsummer (Whitford, 1978; Whitford *et al.,* 1980), and one of us (WGW) has found termite workers in surface litter accumulations on a number of occasions. However, available data were insufficient to predict surface activity of subterranean termites on the basis of soil moisture and soil temperature. We, therefore, designed a study in which we manipulated both soil temperature and moisture to provide the data for predicting surface activity of termites and to examine the effects of these factors on the activity of other groups of Chihuahuan desert soil arthropods.

STUDY AREA

The study was conducted on the LTER (Long Term Ecological Research) Jornada site located 40 km NNE of Las Cruces, Dona Ana Co., New Mexico. The vegetation is sparse, consisting of annual plants (*Erigonium trichopes* Torr., *E. abertianum* Torr. etc.), perennials (*Baileya multiradiata* Harv. and Gray), sub-shrubs (*Zinnia grandiflora* Nutt., *Xanthocephalum sarothrae* (Pursh) Shinners) and a few shrubs (*Larrea tridentata* (DC) Cov.). The long-term average annual precipitation is 210 mm, 55% of which occurs during July-September as convectional storms (Whitford *et al.*, 1982a). Summer maximum air temperatures average 40 C and winter air temperatures regularly fall below 0 C (Whitford *et al.*, 1982a).

METHODS

Experimental design. — We established four plots, each 3.5 m by 12.5 m, at the end of May 1983. Two of the plots were shaded by suspending three layers of dark green nylon netting approximately 0.2 m above the soil surface to reduce solar insolation. A sprinkler system was constructed to water one of these plots. A similar sprinkler system was used to water one of the unshaded plots. The second unshaded plot served as the control. This provided a complete factorial design of an unmodified control, a shaded plot, shade + water plot and a water only plot. No large shrubs were present in the plots which would provide shade.

The watered plots received approximately 12 mm of water per irrigation at irregular intervals throughout the summer. We buried two Westcor soil psychrometers in each plot at 5 cm and 15 cm depths. The psychrometers contain thermocouples for measuring soil temperature in addition to soil moisture tension. The dates and amounts of artificial and natural rainfall are presented in Table 1.

Termite activity. — A grid of 96 points (4 x 24 ca. 0.5 m apart) was laid out in each of the plots. A 12.5-cm-diam tin can was pressed to approximately 6-cm depth at each of the points and the soil inside the can removed. Approximately 50 g of mixed dead plant litter (senescent stems and leaves of *Baileya multiradiata, Erioneuron pulchellum* and *Larrea tridentata*) were placed in each of the resulting depressions (Whitford *et al.*, 1982b). Sufficient litter to provide a 3- to 4-cm layer was pressed into each depression to provide a compost layer of suitable food.

Eight depressions were checked at each sampling time in random order for termite activity, 2 or 3 days after watering. The litter was removed from each depression and the numbers of termites in and under the litter were recorded. The litter was replaced and the depressions marked to exclude them from further examination. At the same time, temperature and humidity readings were taken under the litter bags (in 1984) using a humidity probe, and at the 5-cm and 15-cm depths (both years) of all plots using a HR-33T dew point microvoltmeter (Westcor Inc.). Measurements were made at 2-hr intervals for 12 or 24 hr. The litter was removed and replaced with fresh litter at the end of each sampling period. We assume that surface activity reflects the relative density of termites in each of the plots.

Solar insolation was measured with a pyrohelimeter placed in the plots. The instruments took readings at ca. 20 cm above the soil surface.

Microarthropod densities and decomposition rates. —Thirty fiberglass-mesh litter bags (*see* Santos *et al.*, 1984, for details) containing 10 g of fresh air-dried creosotebush (*Larrea tridentata*) leaf litter were placed on the soil surface in each of the four plots on 30 June 1983. The bags were retrieved at 0800 MST 30, 90 and 180 days after placement in the field. Microarthropod populations in the litter bags were estimated by placing the litter into modified Tullgren funnels, followed by heat extraction into water for 72 hr (Santos *et al.*, 1978). The litter was then oven-dried (60 C for 72 hr) and burned in a muffle furnace at 600 C for 8 hr to determine organic matter content by mass loss. Since the bags were infiltrated with various quantities of mineral soil, it was necessary to correct the dry masses of litter. The following equation, modified from Santos and Whitford (1981), was used to calculate the percent mass remaining:

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

where %r = Percent of organic mass remaining
I = Dry weight (dried 72 hr at 60 C and corrected for handling error based on 10 samples)
C = Inorganic (ash) content of litter as a proportion of 1.
S = Inorganic (ash) content of soil under bags as a proportion of 1.
A = Ash weight after burning in the muffle furnace.
F = Final dry weight of each sample after collection
Si = Estimated inorganic content of the soil (mean of 10 muffled soil samples)

Effect on ant populations. —Nests of the five most common ant species, *Pheidole xerophila* Wheeler, *Ph. rugulosa* Gregg, *Ph. militicida* Wheeler, *Pogonomyrmex (Pogonomyrmex) desertorum* Wheeler and *P. (Ephebomyrmex) imberbiculus* Wheeler were tagged in each of the plots before the experiment was begun (14 June 1983). On 2 November 1983 the nests were recounted and retagged and the numbers of inactive nests and new nests were recorded.

TABLE 1.—The application of water and the natural rainfall occurring in 1983 on the experimental plots in cm of precipitation

Date	Water application	Natural rain
7 June	2.4	
8 June	1.2	
14 June	1.2	
4 July	1.2	
18 July	1.2	
7 August		0.2
10 August		0.1
22 August	1.2	
25 August		2.2
26 August		0.3
9 September		1.7
Mid-September	1.2	
30 September		0.8
3 October		1.6
6 October		0.4
10 October	1.2	

RESULTS

Soil temperature and moisture. — Shading by nylon netting reduced the solar insolation by ca. 42% (Fig. 1). During the day this resulted in a 7-10 C reduction in soil temperature at the 5-cm depth in the watered plots and a 4-12 C reduction at the 5-cm depth in the unwatered plots (Fig. 2). The watered plots were usually a few degrees cooler than the unwatered plots (Fig. 2). Soil moisture at the 5-cm level was increased to field capacity on the watered plots; unwatered plots remained dry. The shaded unwatered plot was slightly dryer than the control plot in the morning (Fig. 2), suggesting that the nylon netting reduced the amount of condensation or dew deposition.

Termite activity. — The effects of shading and water addition on termite activity were tested on 3 days at 2-hr intervals during all hours of the day in 1983 and 2 days at 0800-0900 MST in 1984. In June 1983, the unwatered soils were at −45 to −60 bars (−4 to −6 MPa); the water-treated soils were at field capacity (Fig. 2). At midday the temperatures were reduced ca. 6-10 C at the 5-cm depth and 2-5 C at the 15-cm level in the shaded plots. Multiple linear regression analysis demonstrated that soil moisture at the 5-cm depth was the only parameter affecting termite activity and accounted for a large portion of the variation ($r = 0.68$, $p < 0.01$ in June 1983, $r = 0.56$, $p < 0.01$ in July 1983, $r = 0.32$, $p < .05$ in May 1984). The experiment was repeated on 12 October when all four plots were at field capacity (Fig. 2). At midday the control plot was 4.5 C above the shade plots at the 5-cm level. The watered plot was 6.5 C above the water plus shade plot. None of the treatments had a significant effect on termite activity.

The equations developed from the multiple regression analysis were used to predict the point at which the soils were too dry for aboveground activity of the termites. The

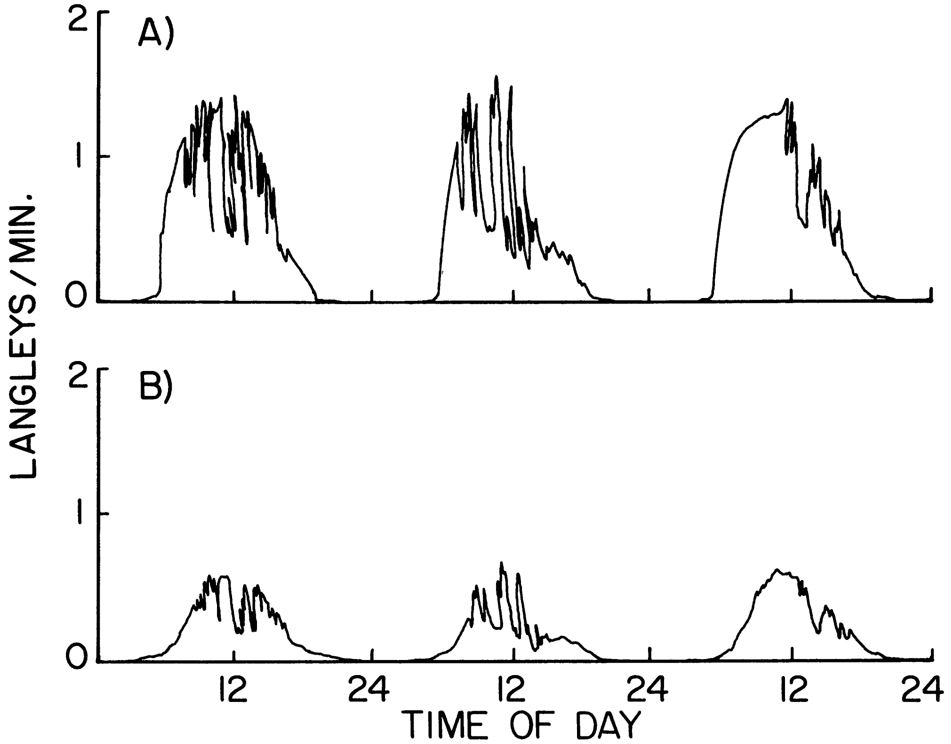

Fig. 1. — A comparison of the solar insolation in the control (A) and shaded plots (B), based on tracing of a pyrohelimeter in June 1983

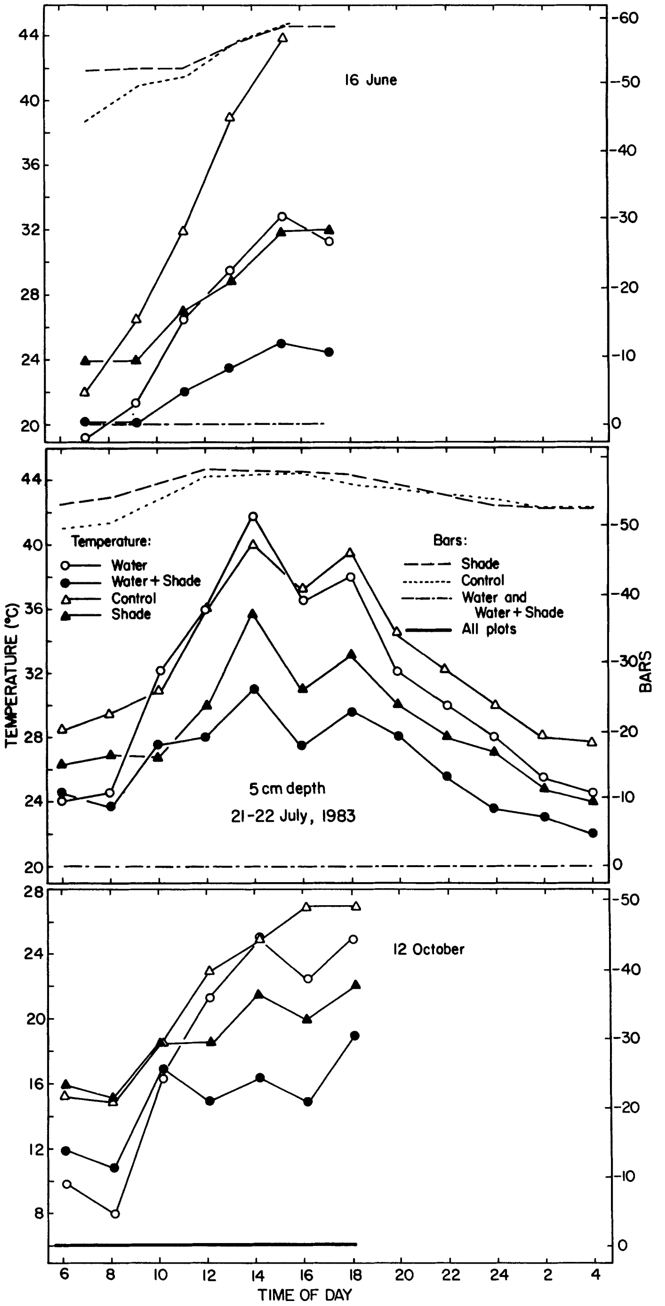

Fig. 2.—Modification of soil temperature and soil moisture at the 5-cm level in the experimental plots on three separate dates during 1983

equation for June 1983 was: $Y = -0.06X + 3.35$; for July 1983: $Y = -0.05X + 3.05$; and for May 1984: $Y = -0.04X + 1.81$. We let $Y = 0$ to solve for X. We predicted that termites should stop aboveground foraging when the soil moisture ($X \pm$ SD) is less than -5.4 ± 0.2 MPa.

Termites were more active at night and early morning than at midday (Fig. 3). This was true in the watered plots during the summer months of June and July (Fig. 3). In

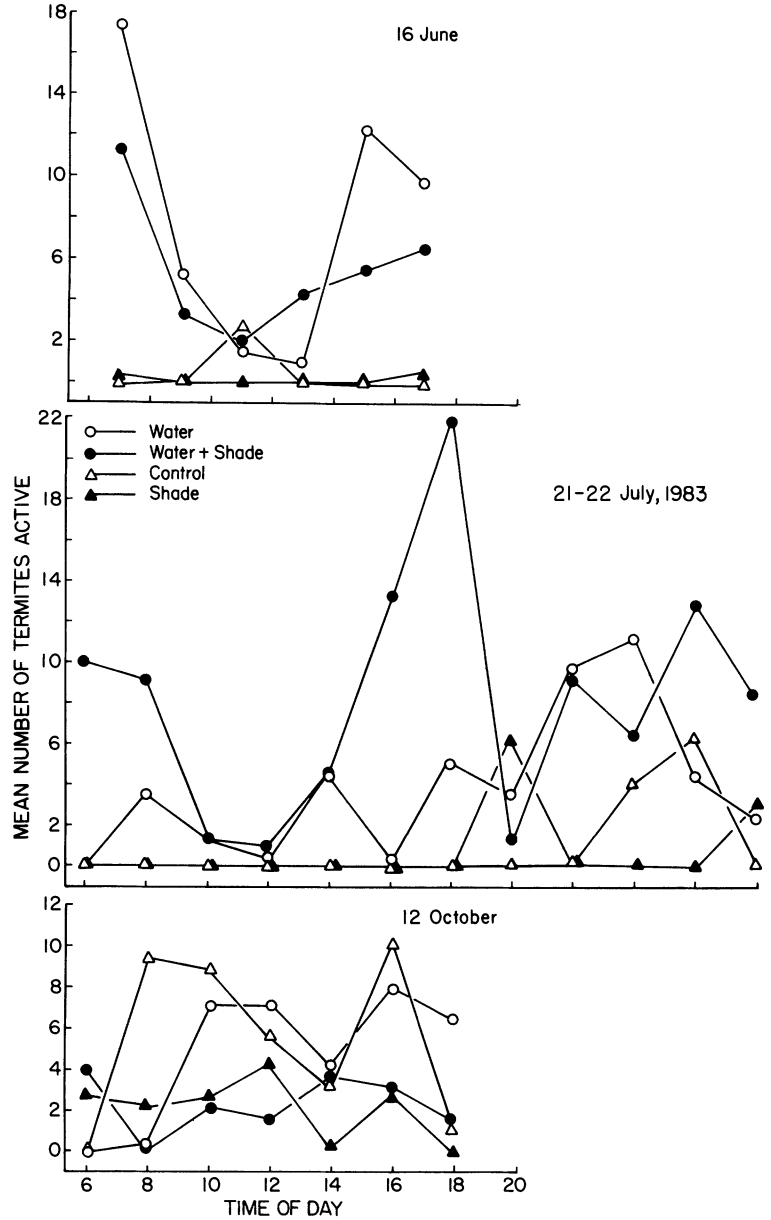

Fig. 3.—Diurnal surface termite activity in litter depressions in the experimental plots on 17 June, 21-22 July and 12 October 1983

October, the termites in the unshaded plots appeared to be more active, although temperatures at that time had no significant effect on their activity.

Microarthropod activity and decomposition rates. —Very few microarthropods were collected in August 1983 and January 1984, and it is thus impossible to discuss treatment effects on those days. In contrast, large numbers were collected on 3 October 1983 (Table 2). Two-way ANOVA comparisons of the numbers of individuals of each taxa found in the bags of the treatments indicated numerous significant treatment effects. Comparisons, made within each of the taxa using Duncan's multiple range test, indicate differences between the shade plus water and the other plots (Table 2). In most cases, there were no significant differences in the numbers of individuals or taxa in litter bags on the control and watered plots. Litter bags in the control plot had significantly more cunaxids and collembolans than did the watered plot. Litter bags in the shade plot had signifi-

TABLE 2.—Mean numbers of microarthropods collected from creosote litter bags in the experimental plots 96 days after the bags were placed in the field (3 October 1983). The data are based on 10 replicate bags from each of the four plots. Only those taxa with more than 50 individuals in total were compared. C = control, W = water, S = shade, W + S = Water and Shade. The data were analyzed using one-way ANOVAS and the means were compared using Duncan's Multiple Range Test. The treatments with different letters (a-d) are significantly different at the 5% level. p = predator, f = fungivore, d = detritivore

Taxon	C	W	S	W + S
Class Arachnida				
Subclass Acari				
Suborder Mesostigmata				
Rhodacaridae (p) (unknown genus)	0	0.2	0	0
Suborder Prostigmata				
Anystidae (p) *Chaussieria* (?)	0	0.6	0	0.6
Bdellidae (p) *Spinibdella* sp.	0.1	0.2	1.4	0
Caligonellidae (p) *Calligonella* sp.	0.2	0.3	0.2	0
Cunaxidae (p) *Cunaxa* sp.	1.0^b	0.2^c	0.8^b	7.1^a
Eupodidae (f) *Eupodes* sp.	16.9^a	15.7^a	14.4^a	31.1^a
Nanorchestidae (f,d) *Speleorchestes* sp.	3.3^a	1.2^a	0 ^{a}	1.6^a
Pygmephoride (f,d) *Siteroptes* sp.	2.8^c	5.4^c	20.7b	212.0^a
Raphignathidae (p) (unknown genus)	0.3	0	0.2	0.3
Stigmaeidae (p) *Stigmaeus* sp.	0	0	0	1.5
Tarsonemidae (f,d) *Tarsonemus fusarii*	0 ^{b}	0 ^{b}	0 ^{b}	54.0^a
Trombidiidae (p) (unknown genus)	0	0.7	0.1	0.9
Tydeidae (f) *Tydeus* spp.*	6.6^b	3.9^b	12.7^b	85.4^a
Suborder Astigmata				
Acaridae (f,d) (unknown genus)	0.2	0	0	0
Subclass Pseudoscorpiones	0.1	0.8	0	0
Class Insecta				
Collembola (f,d) *(F. Isotomidae, F. Entomobryidae)*	1.7^c	0.7^d	5.6^b	17.2^a
Psocoptera (f,d) *(F. Liposcellidae)*	1.7^c	2.8^c	29.5^b	51.5^a
Totals of Means	34.9	32.7	85.6	463.2

*Possibly two species present

cantly more Pygmephoridae, Collembola and Psocoptera than the control and watered plots. Litter bags on the water plus shade plot had significantly more individuals of six taxa then litter bags on all of the other plots. The total number of microarthropods collected in the W + S plot was over an order of magnitude greater than the numbers collected in the control plot. Tarsonemid mites were found only in litter bags from the W + S plots.

We attempted to divide the microarthropods into two groups: predators and fungivores/detritivores. This was difficult as little is known about mite ecology (Krantz, 1975). For example, we placed the tydaeid mites in the fungivore detritivore group although they have also been reported to prey on bacteriophagous nematodes (Santos and Whitford, 1981). We also placed the Collembola in the same group, although they also feed on algae, microorganisms and living vegetation (Santos and Whitford, 1981). With that caveat in mind, we conclude that most of the microarthropods were fungivores/detritivores (Fig. 4). We collected a mean of over 450 such microarthropods per litter bag on the W + S plot compared to less than 100 per bag from the other three plots.

Microarthropods and termites are considered to be important in the decomposition of litter in deserts, although *Gnathamitermes tubiformans* prefers other types of litter over creosotebush litter (Fowler and Whitford, 1980; Santos and Whitford, 1981; Whitford *et al.*, 1983). Thus, one might expect that the litter in the W + S plot would have the highest rate of mass loss. This was not the case in our experiment. An analysis of covariance comparison (after an angular transformation of the data) of the slopes showed no significant difference between any of the treatments and the control. The percent organic material remaining in the litter bags dropped to between 50 and 60% after 7 months in the field (Fig. 5).

Effect on ant populations. —We expected that shade would reduce the soil temperature and induce the ants to move their nests. We compared the treatments to the control us-

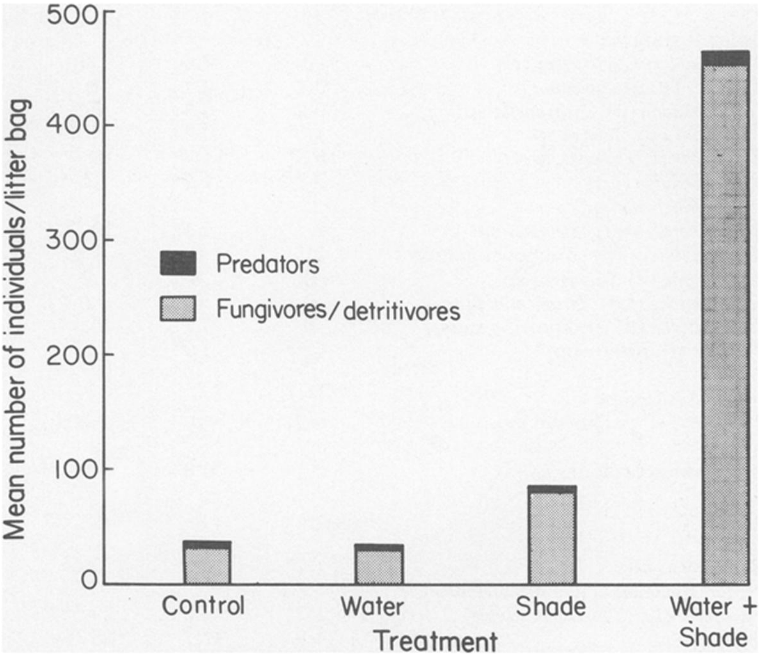

Fig. 4. —Comparison of the functional groups of mites in the experimental plots

ing chi square (Table 3). Shade had no effect on the five species. The watering treatments considerably reduced the numbers of nests in the plots.

Our analysis indicated that increased soil moisture had no significant effect on the microarthropod population (Table 2). This is contrary to other reports that microarthropod abundance in surface leaf litter is increased with increased moisture content (Whitford *et al.*, 1981). We were able to collect sufficient microarthropods only on 3 October 1983, a date which coincided with a natural rain event and which was also preceded by a period of rainfall leading up to the collection time (Table 1). Increased moisture may have led to an increase in microarthropods in the litter prior to the actual sampling date. Both temperature and moisture may interact to generate the observed results. A control plot that received no moisture (artificial or natural) would be needed to separate the effects of these two factors. Our data (Table 3) support the observation that temperature is the most important factor limiting the activity of microarthropods. We found more microarthropods in the S + W plot (Fig. 4) than we expected, but this may have been a result of a further reduction in temperature due to the evaporation of water (Fig. 2) and not directly an effect of moisture.

Discussion

The soil moisture at the 5-cm level was the only factor that significantly influenced aboveground foraging activity in the termite *Gnathamitermes tubiformans*. Other workers have suggested that aboveground foraging in subterranean termites is exogenously controlled by both soil temperature and moisture conditions (Badawi *et al.*, 1984; Haverty *et al.*, 1974; Haverty and Nutting, 1976; LaFage *et al.*, 1976; Ueckert *et al.*, 1976). We expected reduced soil temperature to increase aboveground activity because the decrease in soil temperatures in the autumn is accompanied by increased termite activity (Whitford *et al.*, 1983). However, *G. tubiformans* did not respond to the soil temperature difference observed in this study. We expected termites to respond to moisture, since the integument of subterranean termites is thin and delicate and may be susceptible to loss of body moisture through evaporation (Ueckert *et al.*, 1976). Soil temperature may act like an on-off switch in spring and autumn. From studies of termite activity at surface baits, we know that when temperatures of the upper 5 cm drop to near freezing, termite surface feeding ceases and does not resume until soil temperatures remain above freezing (Johnson and Whitford, 1975). However, when soil temperatures are favorable, soil moisture is the factor regulating activity in surface litter accumulations. Apparently, late summer precipitation is the factor which stimulates an increase in aboveground activity of termites.

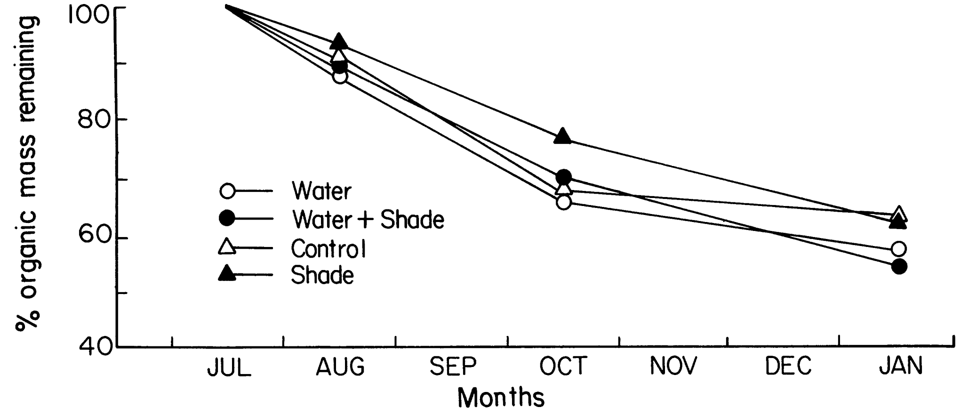

Fig. 5. — The results of the decomposition of creosotebush (*Larrea tridentata*) litter in fiberglass-mesh bags in the experimental plots

Our data suggest that reduced soil temperature or at least reduced insolation has a greater effect on litter microarthropod populations than does soil moisture. However, since we did not collect data on litter water content, we do not know if the shade-screening reduced wetting of litter bags by natural rainfall events. It is possible that the litter bags on the shade plots had higher water content than those on the other plots since the last sprinkler-delivered water was supplied in mid-September, 2 weeks before the retrieval of the litter bags.

We expected the decomposition rates of the watered shade plot to be much higher due to greater microarthropod and termite activity in that plot. The absence of such an effect is counter to conventional wisdom. Apparently the termites did not consume any of the creosotebush litter. We found no evidence of termite activity in the litterbags such as holes in the screen or gallery carton in the bags. The microarthropods were actually in the litter and should have had some effect on mass loss. Termites apparently do not consume creosotebush leaf litter if other more preferred materials are available (Fowler and Whitford, 1980; Whitford *et al.*, 1982b). Since we provided the preferred foods for our studies of termite activity, the termites had no need to use the *Larrea tridentata* leaves in the litter bags. Although there were large differences in microarthropod populations in the litter bags on the October sampling date, there were few microarthropods in the litter bags on the other sampling dates. It is, therefore, likely that the populations of microarthropods are not large enough for a sufficient period of time to make a detectable difference. This is similar to the conclusions of Silva *et al.* (1985), who used chemical exclusion and found that microarthropods had no measurable effect on fluff grass, *Erioneuron pulchellum*, decomposition in the northern Chihuahuan desert. Santos and Whitford (1981) experimentally demonstrated that microarthropods account for ca. 53% of the decomposition of buried mixed species litter. The data of Silva *et al.* (1985) and this study support the idea that decomposition processes in surface litter are very different from those in buried litter. Further, it appears that microarthropods must be present during the entire decomposition process, not just in pulses, to have any measurable effect on decomposition.

The temperature of an ant nest has been shown to have a direct effect on overall activity and determines the developmental rate of the immatures (MacKay, 1985). If nests of *Pogonomyrmex badius* are artificially shaded, soil temperature is reduced to a depth of 50 cm (Carlson and Gentry, 1973). The temperature reduction apparently interferes with the normal development of the brood and results in moving of the nest to a new site. In our study, we expected that the ants would move their nests from the shaded plots in response to temperature reduction, but this did not occur. However, the increased soil moisture on watered plots resulted in a reduction in the numbers of nests. We assumed the reduction in numbers of nests was due to migration and not to mortality of nests. Perhaps an increase in soil moisture caused an increase in brood pathogens, especially fungi.

Whitford *et al.* (1983) hypothesized that either temperature or moisture or a combi-

TABLE 3.—Net change in the numbers of nests from 14 June 1983 to 2 November 1983. (The numbers in parenthesis are the initial numbers of nests)

	Treatments			
Species	Water	Water + shade	Shade	Control
Ph. xerophila	−1 (6)	−2 (5)	+1 (4)	+2 (2)
Ph. rugulosa	−2 (6)	−1 (2)	+1 (5)	+1 (0)
Ph. militicida	−1 (2)	0 (2)	0 (3)	0 (1)
P. desertorum	−1 (3)	0 (1)	−1 (1)	0 (3)
P. imberbiculus	0 (2)	0 (1)	0 (2)	0 (0)
Chi-square	13.5***	12.0***	0.5ns	

*** indicates significance at $P < 0.001$

nation of the two limits activity of desert soil arthropods. Data from this study provide specific tests of that hypothesis. Aboveground activity of termites is limited by soil moisture, and soil temperature has relatively little effect, at least during the spring to autumn seasons. Increased soil moisture reduces ant populations and temperature has little effect. Reduced litter temperatures increases litter microarthropod populations; increased soil moisture has little effect. The effects of these factors on soil arthropods should be of great importance to the overall soil community as these groups of insects have been shown to be very abundant and extremely important in desert soils (MacKay, 1981; Santos and Whitford, 1981; Parker *et al.*, 1982; Whitford *et al.*, 1982b; Whitford *et al.*, 1983).

Acknowledgments.—We wish to thank Sonia Galindo and Amilton Ferreira for assistance in constructing the plots, Brenda Massad and Nora Silva for typing the manuscript. An anonymous reviewer provided many useful comments. The investigation was supported by grant BSR 821539 from the National Science Foundation to W. G. Whitford.

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SUBMITTED 4 MARCH 1985 ACCEPTED 6 MAY 1985