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The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem

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Summary. Rainfall simulation at an average intensity of 124 $mm \cdot h^{-1}$ was used to compare infiltration and run off on arid areas where subterranean termites had been eliminated four years prior to the initiation of the study (termite free) with adjacent areas populated by subterranean termites (termites present). Infiltration rates on termite free plots with less than 5% perennial plant cover were significantly lower 51.3 ± 6.8 $mm \cdot h^{-1}$ than rates on comparable termites present plots 88.4 ± 5.6 $mm \cdot h^{-1}$. On plots centered on *Larrea tridentata* shrubs, there were no differences in infiltration rates with or without termites. Plots with shrub cover had the highest infiltration rates 101 ± 6 $mm \cdot h^{-1}$. Highest run-off volumes were recorded from termite free <5% grass cover plots and the lowest from plots with shrubs. There were no differences in suspended sediment concentrations from termites present and termite free plots. Average bed load concentration was more than three times greater from termite free, <5% cover plots than from termites present, <5% cover plots.

The reduction in infiltration, high run-off volumes and high bedloads from termite free areas without shrub cover is related to increased soil bulk density resulting from the collapse of subterranean galleries of the termites that provide avenues of bulk flow into the soil. Subterranean termites affect the hydrology of Chihuahuan desert systems by enhancing water infiltration and retention of top soil. The presence of a shrub canopy and litter layer cancels any effect of subterranean termites on hydrological parameters. Since approximately 2/3 of the area is not under shrub canopies, subterranean termites are considered to be essential for the maintenance of the soil water characteristics that support the present vegetation.

Wood and Sands (1978) in a review of the role of termites in ecosystems summarized the data on soil transport, nest construction, extent of foraging galleries and chemical and physical properties of termite mounds. They state that, in tropical areas, sub-surface termite galleries are commonly so numerous as to collapse under-foot. They cite several workers who have commented that this dense network of galleries must affect porosity and aeration, infiltration, storage and drainage of water, and growth of plant roots. Wood and Sands (1978) indicate that measurements of the effect of termites on these soil parameters have yet to be made and that such measurements are crucial to a proper understanding of the total influence of termites on soils.

On arid watersheds in the Southwest, subterranean termites are important detritivores, processing a large fraction of plant litter and organic debris in these systems (Haverty and Nutting 1975, Johnson and Whitford 1975, Whitford et al. 1982). Activities of subterranean termites could be important in the maintenance of hydrologic stability through subsurface tunneling and soil profile disturbance. Subsurface tunneling is extensive as evidenced by the high density of foraging groups recorded on a desert watershed by Johnson and Whitford (1975). The extensive subsurface tunnels and galleries may provide improved water infiltration capacity, soil-water storage capacity and subsequent increased primary productivity.

However, surface depositions by termites of translocated, subsurface soils as gallery carton is generally of finer texture than surrounding surface soil (Whitford et al. 1982). This deposited material may serve as a source of readily detachable sediments that can be transported over the surface with overland flow following rain events. This would lead to an appreciably higher loss of surface soils from termite inhabited areas.

Our rainfall simulation studies were designed to examine the effects of subterranean termites on infiltration and runoff on a desert watershed. We utilized plots on areas from which termites had been eliminated and plots with active termite colonies to examine hydrologic parameters.

Methods and materials

The studies were conducted on the Long Term Ecological Research (LTER) watershed on the New Mexico State University Ranch 40 km NNE of Las Cruces, N.M. The dominant vegetation is creosotebush, *Larrea tridentata*. The long term average precipitation is 225 $mm \cdot yr^{-1}$ with more than 70% of the yearly average from summer conventional storms, July–October. Measurements were made on large research plots (1200 m^2 each) which had been treated with chlordane (TM) at 10.3 $kg \cdot ha^{-1}$ in 1977. By spring 1979, all common taxa of arthropods had recolonized the treated plots except for the subterranean termites. Untreated plots were compared to plots from which termites had been eliminated.

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During late September and early October 1981, we estimated gallery carton production on the site in randomly selected 1-m^2 plots along 100-m transects traversing the selected study site. No carton material was found within the chlordane plot boundaries.

On a separate transect, gallery carton was collected at random together with a sample of bare soil immediately adjacent to the gathered material. These paired samples were analyzed for nitrogen content by a microkjeldahl digestion technique (Thomas et al. 1967). Two 500-g samples of carton were analyzed for particle-size distributions using a sieve-hydrometer combination procedure modified from Bowles (1978).

Before initiating rainfall simulations, we randomly selected 5 open soil surfaces and 5 areas at 0.5 canopy radius under creosotebush canopies on both the treated and untreated study areas. Soil samples, each approximately 12 cm diameter × 10 cm deep, were excavated and excavation volumes determined using a sand-funnel apparatus. These samples were used to estimate treated and untreated soil bulk densities (Blake 1965) and total porosities (Vomocil 1965). Lastly, the characteristic particle-size distributions of treated and untreated soils were obtained from these samples using a combination wet sieve-hydrometer analysis (Bowles 1978).

We selected 3 vegetational cover regimes common to both areas – 1) low cover (less than 5% cover of fluff-grass, *Erioneuron pulchellum,* clumps), 2) medium cover (more than 10% but less than 15% grass cover), and 3) creosote cover (directly under the center of a creosotebush having a mean canopy diameter of greater than 1-m).

Five plots in each of the 3 cover regimes were selected and staked, with the exception of the medium cover, chlordane-treated plots, which we were forced to omit because of the lack of accessible grass densities sufficient to meet the minimum cover requirement (Whitford et al. 1982). Two soil samples were taken from immediately outside the plot frame with 7 cm × 5 cm deep sample tins at 0–5 cm and 5–10 cm soil depths and were used to determine the gravimetric moisture and organic matter content of the soils associated with each plot.

Simulation rainfall was produced using a calibrated nozzle and constant pressure pump system adjusted to produce equal rainfall, drop size, and velocity to the plots. The nozzle was mounted on a boom that was swung over and centered on the plot. A near constant-intensity, simulated rainfall averaging 124 $mm \cdot h^{-1}$ across a plot was used.

The standard plot was a 1-m^2 steel frame fabricated from 12.7 cm wide strips of 0.31 cm steel plate. This frame was driven into the ground to isolate the plot from the effects of run-on and interflow. The downslope side of the frame consisted of a lipped galvanized flashing tray which, when installed, was flush with the soil surface across the width of the plot normal to the direction of maximum slope. Runoff from the plot emptied into a 8.2 cm I.D. PVC pipe and was pumped into a collecting tank fitted with a Stephens depth recorder. Each plot received two simulated rains of 45 min duration. The period of time between simulated rain events was at least 24 h and never more than 48 h.

During simulated rainfalls, we recorded times of initial water ponding on the surface and runoff (drip initiation off the tray). After runoff had begun, a secondary pump was engaged for 15 to 45 sec at 5 min intervals in order to transfer the accumulated water and sediment from the PVC channel to the collection tank. After each simulation the hydrograph recorder was stopped and final rainfall depths were recorded.

After the final depth of runoff in the collection tank was recorded, the total volume was vigorously agitated and 5 water samples, each approximately 130–150 ml, were immediately taken. Three of these, used to estimate suspended sediment concentration, were sealed and stored. Approximately 2-ml of chlorine were added to the two remaining samples as a biostatic agent and these samples were put on ice. In the lab these samples were frozen until nitrogen and phosphorus assays could be made. The remaining runoff volume in the tank was removed except for the bottom 7–10 cm (approximately 10 ± 1). This water and the large particulate sediment it contained were saved in order to estimate bedload sediment.

Immediately following the end of each dry (first) simulation, a large sheet of plastic was laid over the plot frame to eliminate interim evaporative losses.

Three water samples from each run were taken for measurement of suspended (fine) sediment loads. Sediment loads were analyzed using a filtering process. Each sample was run through a vacuum Buchner filter. This filter trapped all material larger than very fine silts. If the filtrate remained cloudy, a second filtration was performed using a standard millipore vacuum procedure employing a Gelman stainless steel apparatus with 0.2 micron Metricel membranes (47 mm diameter). Oven-dry weights (60° C for 48 h) of these filters gave total suspended sediment weights per sample.

Each bedload sample was measured for total volume and allowed to air dry, transferred to aluminum plates and oven-dried at 60° C for 72 h to obtain final dry weights of each sample.

Two water samples from each simulator run were analyzed for nitrogen and phosphorus content. Immediately upon thawing, each sample was processed by a modified microkjeldahl digestion (Thomas et al. 1967) and aliquots were subsequently independently analyzed for nitrogen and phosphorus content using colorimetric procedures (Thomas et al. 1967, Watanabe and Olsen 1965).

The difference between rainfall intensity and runoff rate provided an infiltration rate estimate for each time period. These infiltration rate estimates were fitted using an inverse exponential model (Horton 1939) to obtain a best-fit decay plot for each run. The selected model was of the form

$$\ln \text{infiltration rate} = mt + b, \text{ or infiltration rate} = e^b e^{mt},$$

where m = slope of the decay, b = infiltration-rate intercept (i.e., calculated initial infiltration rate extrapolated from rate decay), and t = an incremental time variable. This manipulation supplied intercept and slope values for each simulation along with infiltration rate estimates at each minute. An estimate of the final measured infiltration rate was obtained by averaging the final two 5-min values from the hydrograph.

The bulk density data of chlordane-treated and untreated, open (low cover) and creosotebush-covered soils were analyzed using a single classification one-way analysis of variance (Sokal and Rohlf 1969). Particle-size distributions for these soils were compared by taking geometric means of percent finer material at selected points and apply-

Table 1. Comparison of soil bulk density and total porosity between chemical treatments and cover regimes. Sample number for all treatment groups is 5. Tukey's Q values are provided for significance testing between 2 or 4 means at $P<0.05$. Values are means ± 1 s.d.

	Chlordane-treated		Untreated	
	Open	Under canopy	Open	Under canopy
Soil bulk density (g/cm^3)	1.99 ±0.18	1.77 ±0.14	1.70 ±0.10	1.66 ±0.13
Total porosity (%)	24.9	35.5	35.8	37.4

F = 9.83* (Single-classification anova)
$Q_2 = 0.093$
$Q_1 = 0.137$

* Significant at 0.05 level

ing independent two-way analyses of variance (model I) (Brownlee 1965).

Infiltration rate decays were determined by linear regression and *t*-tests to indicate significance among mean treatment differences (Goodnight 1979). All other data were analyzed using the appropriate analysis of variance and Tukey's multiple range test (Sokal and Rohlf 1969).

Results

Less than 5.0 mm natural precipitation occurred during the period of simulations with the maximum 1-day event equalling 1.25 mm (on January 13). No precipitation was recorded on the site during the six-week period immediately prior to study initiation (August to October).

The gallery carton harvested from transects totalled $30.4 \pm 16.2\ g \cdot m^{-2}$. No gallery carton was observed on chlordane-treated plots during the study. Particle-size analysis of carton material produced a fractional composition of 23.8% coarse sand (0.5–1.0 mm), 32.1% medium to very fine sand (0.062–0.50 mm), 26.1% silt (0.004–0.062 mm) and 18.0% clay (0.004).

Although the average nitrogen content was higher in carton, $681.2 \pm 80.4\ mg \cdot g^{-1}$, the variation was great and not significantly different from the soil, $x = 663.7 \pm 82.8\ mg \cdot g^{-1}$ ($P<0.15$).

The soils of the site were similar in terms of bulk density with the exception of chlordane-treated, open soils which had significantly higher bulk density (and therefore lower total porosity) (Table 1).

Table 2 presents critical points of the particle-size distribution analyses for the four soil types. These data indicate that vegetative cover significantly affected the sand-silt break and the characteristic D_{50} and D_{86} points, probably resulting from energy dissipation and soil deposition through aeolean processes, while chlordane treatment had no discernible significant effect on any of the tested soil particle-size parameters.

Plot characteristics and soil parameters

Organic matter content in soils at 0–5 and 5–10 cm depth was essentially the same for the treatment combinations

Table 2. Soil particle size parameter comparisons among chemical treatments and cover regimes for soil samples from the study site. Numbers represent parameter means ($n=5$) in percent finer ±1 s.d. Values in parentheses are arcsine transformations. Letter superscripts indicate levels of significance from Tukey's Q range tests for comparison of 4 means at the 0.05 level. F values are from analyses of variance for each tested parameter

Tested soil parameter:
Percent finer than 0.062 mm (sand-silt break)

Chlordane-treated		Untreated	
Open	Under canopy	Open	Under canopy
24.08 ±4.13	38.32 ±2.41	21.46 ±3.46	41.04 ±4.18
(0.2434 ±0.0428)^a	(0.3926 ±0.02060)^b	(0.2164 ±0.0355)^a	(0.4144 ±0.0455)^b

F = 17.34***
Q_4 (significance levels indicated) = 0.037
$Q_2 = 0.029$

Tested soil parameter:
Percent finer than 0.004 mm (silt-clay break)

Chlordane-treated		Untreated	
Open	Under canopy	Open	Under canopy
8.44 ±1.04	9.80 ±1.11	8.90 ±1.33	9.24 ±2.85
(0.0845 ±0.0105)	(0.0982 ±0.0112)	(0.891 ±0.0134)	(0.0926 ±0.0287)

F = 1.34 (No significant difference at 0.05 level)
*** ($P<0.0001$)

Tested soil parameter: D_{50}

Chlordane-treated		Untreated	
Open	Under Canopy	Open	Under canopy
8.44 ±1.04	9.80 ±1.11	8.90 ±1.33	9.24 ±2.85
0.276 ±0.027^b	0.153 ±0.057^a	0.299 ±0.029^b	0.138 ±0.025^a

F = 9.31***
Q_4 (significance levels indicated) = 0.031
$Q_2 = 0.025$

Tested soil parameter: D_{86}

Chlordane-treated		Untreated	
Open	Under canopy	Open	Under canopy
1.55 ±0.34^a	2.35 ±0.41^b	1.78 ±0.46^a	2.58 ±0.62^b

F = 2.94*
Q_4 (significance levels indicated) = 0.38
$Q_2 = 0.26$

** ($P<0.0005$)
* ($P<0.05$)

Table 3. Comparison of regression slopes for infiltration on plots with termites present and termites absent and different vegetative cover. Slope values represent pooled estimates of the decay slopes using all treatment replicates simultaneously. F-statistics and r^2 values deal with fit between observed rates and the regression model, t = statistics for t-test using slope estimate and H_0: slope = 0. Replicate average r-square is the mean ($n = 5.4$ for creosote cover, dry runs) ± 1 s.d. of the treatment replicates' values. Superscripted letters indicate significant treatment differences (= 0.05) based on t-test comparisons of dry and wet run means, compared separately. Asterisks associated with dry run means indicate significant difference between dry and wet run means for that treatment

	Estimated slope	$P > \|T\|$, H_0 : slope = 0	Estimated standard error	$P > F$ (regr'n)	r^2	Replicate average r^2
Dry runs						
Low cover						
Untreated	-0.00923^{a1}	0.0001	0.00071	0,0001	0.94	0.90 ± 0.07
Treated	-0.02680^{b1*}	0.0001	0.00160	0.0001	0.87	0.90 ± 0.03
Medium cover						
Untreated	-0.00912^{a1}	0.0001	0.00067	0.0001	0.83	0.91 ± 0.06
Treated	–	–	–	–	–	–
Creosote cover						
Untreated	-0.01016^{a1}	0.0001	0.00181	0.0001	–	0.98 ± 0.02
Treated	-0.00854^{a1}	0.0001	0.00148	0.0001	–	0.97 ± 0.03
Wet runs						
Low cover						
Untreated	-0.00830^{a2}	0.0001	0.00066	0.0001	0.77	0.81 ± 0.12
Treated	-0.01828^{b2}	0.0001	0.00181	0.0001	0.69	0.78 ± 0.13
Medium cover						
Untreated	-0.00759^{a2}	0.0001	0.00054	0.0001	0.81	0.83 ± 0.88
Treated	–	–	–	–	–	–
Creosote cover						
Untreated	-0.00870^{a2}	0.0001	0.00070	0.0001	0.84	0.92 ± 0.03
Treated	-0.00801^{a2}	0.0001	0.00041	0.0001	0.92	0.95 ± 0.02

(average $x = 0.8 \pm 0.3\%$). Soils under creosotebush canopies were appreciably richer in organic matter ($x = 2.1 \pm 0.8\%$). The chlordane-treated soils with creosotebush canopy also had a significantly higher organic content in the upper 5 cm ($4.5 \pm 0.6\%$). Soil moisture was relatively constant among treatments in the upper 5 cm $x = 1.9 \pm 0.3\%$), although chlordane-treated, low cover soils had a significantly lower moisture content ($1.3 \pm 0.4\%$) than similarly vegetated untreated soils ($2.0 \pm 0.2\%$). Since soils were similar, different antecedent moistures were probably the result of different porosities. At the 5–10 cm depth, soil moisture was also relatively constant, but significantly higher ($x = 4.3 \pm 0.5\%$). At both depths, soils under creosote canopies had slightly higher moisture.

Water quality

There were no significant differences in total nitrogen and phosphorus in the run-off water on termite free and control plots or with differences in vegetative cover ($P > 0.1$). Mean nitrogen concentration in the run-off was 0.055 ± 0.053 g $N \cdot ml^{-1}$ and mean phosphorus concentration was 0.032 ± 0.038 g $P \cdot ml^{-1}$.

Time to initial ponding and runoff

On untreated dry soil plots with varying degrees of cover, ponding was generally observed first on low cover plots, next on medium cover plots, and last on plots under creosotebush canopies. Ponding occurred on low cover plots in less than one-half the average time required for creosotebush cover plots (2 min 5 s $\pm$ 15 s and 5 min 33 s $\pm$ 9 s, respectively). A similar response sequence was observed during the wet runs, though less extreme, and less time was required to achieve ponding on all cover regimes. This same response pattern was noted on chlordane-treated plots for both dry and wet simulations. At the low cover, treated plots exhibited ponding in somewhat less average time than untreated plots (1 min 32 s $\pm$ 34 s vs. 2 min 5 s $\pm$ 15 s), but no real difference was observed between creosotebush cover plots.

The patterns observed associated with ponding carried over onto the time required for runoff initiation. Time to runoff was much greater on plots associated with creosote cover on both chlordane- and untreated soils than on any other treatment-cover combination. Chlordane treated low cover, dry plots had average time to runoff reduced by almost 50% compared to low cover, untreated plots (4 min 34 s $\pm$ 33 s vs 8 min 1 s $\pm$ 26 s). Increased grass cover tended to significantly lengthen the time required for runoff initiation, but to a much lesser degree than creosotebush canopy association.

Infiltration

Comparison of calculated decay function slopes from all treatments produced no significant differences between decay slopes of all dry run treatments and wet run treatments, contrasted separately, or between dry and wet runs of any given treatment, with one very notable exception. The pooled slope estimate for chlordane-treated, low cover plots was more than twice as large as that for any other treatment, for both dry and wet runs (Table 3). A slope reduction was observed for wet runs from all treatments, but

Table 4. Mean final measured infiltration rates ±1 s.d. estimated for each treatment. F value is for a single classification ANOVA. Superscripted letters indicate results of Tukey's multiple range comparisons for dry run means and wet run means, performed separately

	Dry runs		Wet runs	
	Chlordane treated	Untreated	Chlordane treated	Untreated
Low cover ($mm \cdot h^{-1}$)	51.3±6.8	88.4±5.6	55.4±4.8	84.8±3.0
Medium cover ($mm \cdot h^{-1}$)		92.7±3.8		90.7±3.0
Creosotebush cover ($mm \cdot h^{-1}$)	106.4±9.7	100.6±6.1	99.6±2.0	97.5±2.3

$F = 8.93$**; $Q_5 = 0.28$; $Q_2 = 0.19$

** ($P < 0.001$)

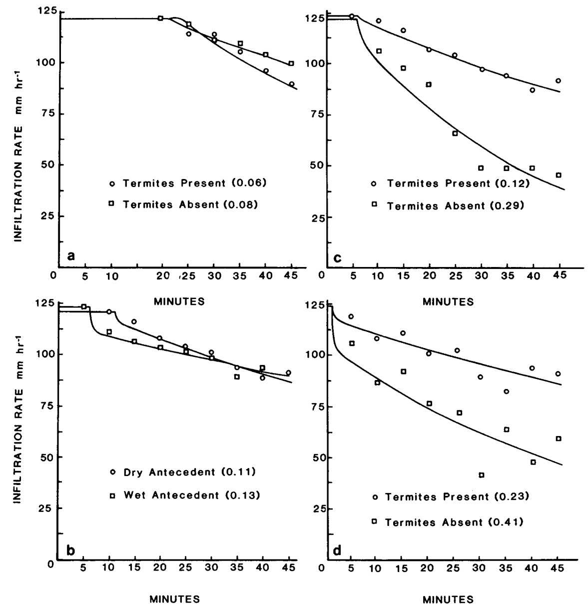

Fig. 1a–d. Representative plots of infiltration rate through time on field plots with varying plant cover. **a** is a plot centered on a *L. tridentata* shrub, **b** is a plot with medium grass cover of *E. pulchellum*, **c** is a low grass cover plot, dry antecedent conditions and **d** is a low grass cover plot with wet antecedent conditions

only for the chlordane-treated, low cover estimates was this reduction statistically significant. It is possible that the high simulated intensities effectively "swamped" antecedent moisture effects. The data summarized in Tables 4 and 5 indicate that creosote cover on treated and untreated plots retarded runoff initiation, but once runoff had started, the infiltration rates decayed on those plots generally faster than on either low or medium grass cover, untreated plots.

Chlordane-treated, low cover plots had a much lower average final measured infiltration rate than any other treatment for both dry and wet runs (Table 4).

Figure 1 provides graphic comparisons between treatment pairs of infiltration rate vs. time, using actual treatment replicates in which times to runoff and decay slopes closely approximated the respective treatment means for those parameters. These figures illustrate the highly significant hydrologic response differences found between some treatments, while indicating the absence of such parametric differences in other treatments.

Runoff volume

Termite free, low cover plots had the substantially greatest total water yields (dry: 38.1±3.30 mm, wet: 41.15±4.83 mm), followed by untreated, low cover (dry: 16.51±1.38 mm, wet: 21.84±1.27 mm), untreated, medium cover (dry: 12.95±1.01 mm, wet: 18.5±1.27 mm), and lastly treated and untreated creosote cover which exhibited very low and similar yields of approximately 5.33±3.05 mm (dry) and 7.37±1.78 mm (wet). Termite removal had little consistent or significant effect, for any measured hydrologic response parameter including water yield, on soils with creosotebush canopy, but treatment produced spectacularly different responses for these same parameters on bare or low vegetational cover areas.

Suspended sediment

The mean concentration of suspended sediment in runoff was not significantly higher from untreated, low cover, dry runs in comparison to treated dry runs (Fig. 2). The dry

Table 5. Treatment means and standard deviations ($n = 5$) of important rainfall and rainfall response parameters measured for each simulation run

	Chlordane-treated plots				Untreated plots					
	Low cover		Creosote cover		Low cover		Medium cover		Creosote cover	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Estimated average rainfall intensity (mm/h)	124.7 ±2.5	122.9 ±2.6	122.4 ±0.0	122.4 ±0.0	124.5 ±3.5	126.8 ±2.9	124.9 ±2.6	124.5 ±0.8	122.4 ±0.0	122.4 ±0.0
Average time to ponding (min:sec)	1:32 ±0:34	0:45 ±0:12	6:53 ±2:49	3:34 ±0:43	2:05 ±0:15	0:38 ±0:10	2:53 ±0:20	0:59 ±0:09	5:33 ±2:06	2:52 ±0:29
Average time to runoff (min:sec)	4:34 ±0:33	2:21 ±0:34	26:56 ±10:27	14:43 ±1:32	8:01 ±0:26	2:28 ±0:53	9:55 ±0:20	3:52 ±0:12	28:32 ±10:20	17:43 ±5:06
Average runoff volume (mm)	38.15 ±3.21	41.15 ±5.04	4.73 ±2.67	7.11 ±0.92	16.51 ±1.38	21.95 ±1.47	13.06 ±1.09	18.49 ±1.21	5.64 ±3.27	7.47 ±1.48

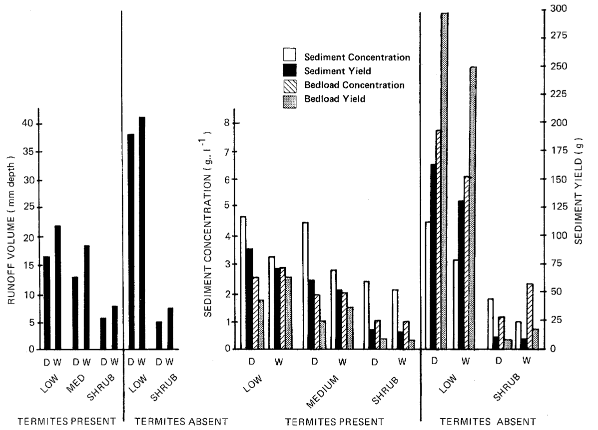

Fig. 2. Runoff and sediment characteristics from simulated rainfall on plots with termites present and termites absent. Values represent means for each treatment. For the sediment data, block bars are sediment yield values and the white bars are sediment concentration values. The first pair of bars (one white, one black) in each group of 4 are concentration and yield for suspended sediment, the last pair are concentration and yield for bedload sediment. *D* dry antecedent conditions and *W* wet antecedent conditions. □ Sediment Concentration; ■ Sediment Yield; ▨ Bedload Concentration; ▩ Bedload Yield

run concentration for both treatments was significantly greater than the subsequent wet run concentrations. The total suspended sediment yield was much greater from the treated plots, however, due to a significantly increased run-off volume. Suspended sediment concentration and yield were similar between the two untreated grass cover regimes.

Plots with creosotebush canopy had very low suspended sediment concentrations and yields compared to all other treatments. There was a significant difference between treated and untreated dry and wet runs with respect to concentration, but not in total yield for these shrub treatments with shrub canopy. Dry run means did not differ significantly from wet run means for either treatment.

Bedload

Average bedload concentration was over 3 times greater from treated, low cover, dry run plots than from untreated, low cover, dry runs (7.76 ± 0.97 g/l and 2.54 ± 0.46 g/l). Average total bedload yield showeed a 7-fold difference (296.8 ± 51.5 g vs. 42.3 ± 10.5 g) between these two treatments. Similar results were observed for wet run total yield and concentration means for these treatments. Increased grass cover significantly decreased mean bedload concentration and yield associated with untreated plots.

Wet runs of all treatments exhibited higher concentration and yield with the exceptions of untreated creosote cover and treated, low cover, both of which had lower wet run means. As with suspended sediment, creosote cover greatly depressed average concentration and yield irrespective of chemical treatment presence or absence (Fig. 2).

Discussion

The most important finding in this study is that in the absence of subterranean termites soil porosity is reduced thereby reducing water infiltration. The increased bulk density of the termite free soil probably resulted from back filling and collapse of termite gallaries during the four years following chemical exclusion. Soil infiltration capacity is predominately controlled by the presence and interconnection of these large soil pores (Edwards et al. 1979, Iverson et al. 1981). Differences in grass cover have also been shown to result in decreased run-off in semi-arid range lands (Smith and Leopold 1942, Lyford and Gashu 1969, Tromble et al. 1974, Tromble 1976). The elimination of termites has resulted in the virtual extinction of the only perennial grass, *Erioneuron pulchellum* (Whitford et al 1982). *E. pulchellum* responds to the water status of the upper 5–10 cm of soil (Brown 1983). Water content of the upper 5–10 cm would decrease because of the reduction in infiltration during the brief but intense convectional storms characteristic of this region. The reduction in porosity brought about by the absence of termites evidently initiated a spiral of degradation of the intershrub system: reduced soil moisture eliminating the fluff grass; less grass cover increasing erosion.

The changes in basic hydrological properties may have been responsible for shifts in species composition of the annual plants when termite free plots were compared with untreated plots (Parker et al. 1982). We have also recorded differences in litter fall patterns but not of litter quantities of creosotebushes on termite free plots that may be related to the hydrological changes or soil changes in intershrup spaces (unpublished data). Roots of the *L. tridentata* extend into soil of the intershrub spaces (Ludwig 1975) thus the water status of *L. tridentata* could be affected. This in turn could affect the timing of litter fall from this evergreen perennial.

The elimination of subterranean termites has resulted in gradual changes in the architecture (structural components) and processes in this ecosystem. The system is continuing to change at present and may continue to do so for years into the future. The elimination of termites has resulted in a net accumulation of nitrogen in the upper 5 cm of soil (Brown 1983). This is probably the result of reduced transport of organic matter from the soil surface deep into the soil by termite foragers. On this site, subterranean termites have been found to account for the removal of 40–60% of the standing crop of detritus during their period of peak activity in September through November (Whitford et al. 1982). Schaefer and Whitford (1981) documented the importance of these animals in nitrogen cycling processes in the Chihuahuan desert.

Since the removal of subterranean termites initiated a series of changes in soil properties and since there is no indication that any of the other soil organisms can compensate for that loss, we suggest that in the northern Chihuahuan desert, subterranean termites are "keystones" in the structure and function of that system. Paine (1969a, b) first used the term "keystone" in reference to predators that are responsible for the maintenance of structure in marine invertebrate communities. In an ecosystem context a "keystone" is a taxon that maintains both the structural and functional integrity of the system. At the time of this writing, the dominant perennial grass in the system, *E. pulchellum* has disappeared completely from the termite free plots; the dominat shrub, *L. tridentata* productivity has decreased, and the composition of the spring annual plant community has changed because of the direct and indirect effects of this consumer. Lee and Inman (1975) and Chew (1974) have suggested that consumers are important in ecosystems as rate regulators. Although *G. tubiformans* are consumers, they are consumers of dead plant material and probably affect rates indirectly by affecting nutrient cycling pathways. It is obvious that a detritus consumer such as *G. tubiformans*, is important in energy flow through the ecosystem based on the fraction of the annual net primary production it consumes (Johnson and Whitford, 1975; Whitford et al. 1982). This study documents another important function of some consumers in ecosystems, i.e. modification of the physical structure of the environment.

Soil translocation by *G. tubiformans* did not affect particle distribution densities within the upper 10-cm of soil. Some significant differences might have been found if this 10 cm soil profile had been divided into small depth increments and independently analyzed. Since soils under creosotebush canopies differ from intershrub soils by having higher percentages of both coarse sands and silts, creosotebushes apparently produce different erosional and aeolean depositional characteristics than open, intershrub regions.

Plots with shrubs had similar rate decays, response times, final measured infiltration rates and total runoff volumes, regardless of the presence or absence of termites. Soil structure was similar as was antecedent soil moisture and organic matter (soil and litter). The similarities were not therefore surprising. Plots with *L. tridentata* exhibited extremely different hydrological responses than did lower cover plots. This could result in part from the characteristic conical formation of the soils around the plant stem that allowed runoff to propagate away from the collection throughs on the back halves of the plots. This resulted in deep standing water within the plot frames. Also, plots with shrubs had litter cover of more than 40% of the total plot area. The litter tended to absorb and detain water, thereby significantly retarding runoff from these plots.

The increased concentration of suspended sediment on untreated plots may be related to lower litter cover interference or increased fine sediment supply due to termite carton production in litter and overstory canopies. The low concentrations and yields for both suspended and bedload sediment associated with runoff from under creosotebush canopies did not indicate a significant contribution by termites. Creosotebush microsystems appear to override termites in their vicinity. This probably resulted from the activity of other organisms that did not differ between the treated and untreated areas. In the shaded, organically rich subsystems represented by creosotebushes and their underlying soils, the multiple effects of biological activities not present in the surrounding intershrub areas might overshadow termite impacts with regard to soil structure modifications. This biological activity could account for the observed similarities in soil characteristics and hydrologic responses between treated and untreated creosote plots.

These studies were conducted during the season when termite effects on soil should be most pronounced (Whitford et al. 1982). A repeat of the study in late spring could yield different results. Schumm and Lusby (1963) noted significantly different seasonal runoff responses from watersheds resulting from rainfalls of similar total accumulation. The observed seasonal differences could not be explained on the basis of differences in precipitation intensities or antecedent moisture conditions. Since their study sites were lithosols with low vegetation coverage, the authors concluded that the seasonal changes were the result of seasonal variations in soil characteristics attributable to frost action. Data from the present study strongly suggest that although edaphic conditions certainly alter seasonal soil and vegetation characteristics, seasonal peaks of soil biological activity should also be considered as a possible component determining runoff on any watershed.

Chemical analyses of the runoff water demonstrated that great variation in nutrient yields exists over very short distances even for similar cover regimes. This variation most probably reflects spatially heterogeneous soils. Localized processes within the soil such as plant litter fall and animal excretion and death, nutrient mineralization and decomposition, uptake and exudation from plants and microbial transformation and immobilization of limiting nutrients, result in spatially variable nutrient yields. Nutrient movement with runoff, as a loss from the system, was essentially negligible. Based on observed concentrations, it would require over 15,000 l of runoff from a 1-m^2 area to remove 1 g of nitrogen and over 23,000 l to remove 1 g of phosphorus. The highest runoff volume recorded from any plot, with an average rainfall intensity of approximately 125 $mm \cdot hr^{-1}$ and duration of 45 min, was 40 l.

It is important to realize that although plots with shrubs yielded lower runoff and sediment, a strict quantitative comparison between these and low cover, intershrub plots is not warranted. Under natural rainfall conditions creosotebushes are not independent of intershrub areas but instead receive significant input of water and sediment from outside the perimeter of influence of any individual shrub. Also, much could be gained from rainfall simulation on creosotebush plots with the above-ground biomass removed. Under this denuded condition, hydrologic responses from the soil directly under a shrub crown could be analyzed without the complicating presence of the canopy.

Our studies permit a relatively strong conclusion on the relative importance of the two opposing termite-mediated processes – a potentially increased and beneficial infiltration capacity due to extensive subterranean excavation versus a potentially increased and detrimental erosional loss of topsoil due to significant surface deposition of gallery carton on the soil surface. Termite exclusion on sparsely vegetated, intershrub areas of the study site watershed, which comprises approximately 80% of the total surface area, produced both reduced infiltration capacity and increased erosional soil loss. Termite activity on this watershed, and almost certainly on similar watersheds in arid and semi-arid regions of the Southwestern United States, appears to be a very beneficial ecological process allowing greater short-term soil water storage within primary rooting zones while effectively checking erosional losses of soil and organic matter.

Our studies, coupled with independent observtions on treatment plots associated with other investigations, support the following generalizations: (1) On an arid to semi-arid watershed with low vegetational density, the activity of subterranean termites is very significant factor in the regulation and maintenance of hydrologic responses. (2) On a desert watershed, termite activity is obviously beneficial in terms of enhancing water economy and topsoil stability. (3) Termite activity appears to have little effect on primary nutrient economy through either retardance or acceleration of nutrient movement associated with runoff. (4)

The complete cessation of termite activity for almost one-half of each year suggests that the extent to which termites might be affecting hydrologic responses on the watershed is likely to be variable during the year. (5) Creosotebush microsystems do not reflect significant termite mediation. Other biological and physical processes operating in and under creosotebush canopies apparently override termite activity in these microsystems, but their cover is only 20%.

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References

Blake GR (1965) Bulk density. In: Methods of Soil Analysis. No. 9 Monograph Series Part II, Black (CA), American Society of Agronomy, 374–390

Bowles JE (1978) Grain size analyses – mechanical and hydrometer methods. In: Engineering properties of soils and their measurement, McGraw-Hill, New York, 35–59

Brown MF (1983) Relationship between termites, straw amendment and growth of *Erioneuron pulchellum* in a Chihuahuan desert ecosystem. M.S. Thesis, New Mexico State University, Las Cruces, NM, p 109

Brownlee KA (1965) Statistical Theory and Methodology in Science and Engineering, John Wiley & Sons, Inc, New York, pp 316–317, 467–481

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

Edwards WM, van der Ploeg RR, Ehlers W (1979) A numerical study of the effects of noncapillary-size pores upon infiltration. Soil Sci Soc Amer J 43:851–856

Goodnight JH (1979) SAS procedure GLM. In: SAS User's Guide, 1979 edition, Helwig JT, Council KA (eds) SAS Institute, Inc, Raleigh, North Carolina, 245–265

Haverty MI, Nutting WL (1975) Density, dispersion and composition of desert termite foraging populations and their relationship to superficial dead wood. Environ Entomol 4:480–486

Horton RE (1939) Analysis of runoff-plat experiments with varying infiltration capacity. Transactions of the American Geophysical Union 7:693–711

Iverson RM, Hinckley BS, Webb RH, Hallet B (1981) Physical effects of Vehicular disturbances on arid landscapes. Science 212:915–916

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

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

Ludwig JA (975) Distributional adaptations of root systems in desert environments. In The below ground ecosystem: A synthesis of plantassociated processes, Marshall JK, Proceedings of U.S./IBP Interbiome Symposium, Fort Collins, Colo. Dowden, Hutchinson & Ross, Stroudsburg, Pa.

Lyford FP, Gashu HK (1969) Infiltration rates as affected by desert vegetation. Water Resources Research 5:1373–1376

Paine RT (1969a) A note on trophic complexity and community stability. Amer Nat 103:92–93

Paine RT (1969b) The *Pisaster-Tegula* interaction: prey patches, predator food reference and intertidal community structure. Ecology 50:950–961

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

Schaefer DA, Whitford WG (1981) Nutrient cycling by the subterranean termites *Gnathamitermes tubiformans* in a Chihuahuan desert exosystem. Oecologia (Berlin) 48:277–283

Schumm SA, Lusby GC (1963) Seasonal variation of infiltration capacity and runoff on hillsides in Western Colorado. J Geophysical Res 63:3655–3666

Smith HL, Leopold LB (1942) Infiltration studies in the Pecos River Watershed, New Mexico and Texas. J Soil Sci 53:195–204

Sokal RR, Rohlf FJ (1969) Biometry. WH Freeman and Co, San Francisco

Thomas RL, Sheard RW, Moyer JR (1967) Comparison of conventional and automated procedures for nitrogen, phosphorus, and potassium analysis of plant material using a single digestion. Agron J 59:240–243

Tromble JM (1976) Semi-arid rangeland treatment and surface runoff. J Range Manage 29:251–255

Tromble JM, Renard KG, Thatcher AP (1974) Infiltration for three rangeland soil-vegetation complexes. J Range Manage 27:318–321

Vomocil JA (1965) Porosity. In Methods of Soil Analysis. No. 9 Monograph Series Part II, Black CA, American Society of Agronomists, 299–314

Watanabe FS, Olsen SR (1965) Phosphorus determination from soil. Soil Science Society of America Proceedings 29:677–678

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

Wood TG, Sands WA (1978) The role of termites in ecosystems. In: Production ecology of ants and termites, Brian MV (ed) Cambridge Univ Press, Cambridge, 245–292

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