

The effects of subterranean termite removal on desert soil nitrogen and ephemeral flora

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Total soil nitrogen and ephemeral plant density and biomass on plots treated with chlordane to eliminate termites were compared with untreated control plots at the Jornada validation site in the Chihuahuan desert. Total soil nitrogen in the 0-2.5 and 10-20 cm depths was significantly higher for treated compared to control plots. Other than increased soil N at the above two depths, the elimination of termites did not alter the spatial distribution of nitrogen around *Larrea tridentata*. Soil N in both treated and controlled plots was higher under the shrub canopy than in open areas, on the east side of shrubs than on the west, and in the surface soils than at lower depths.

There was no significant difference in total biomass between untreated and treated plots, although a trend existed for higher values on treated plots. There was significant reduction in biomass of *Descurianea pinnata* and *Eriastrum diffusum*, whereas biomass of *Lepidium lasiocarpum* increased on termite-free compared to the control plots. These differences in structure of the ephemeral plant community are attributed to an increase in soil nitrogen at the soil surface resulting from termite removal. There were no measurable differences in the late summer ephemeral plant community, which was a reduced subset of the annuals present during the late spring.

Introduction

Consumers can affect ecosystem structure and function indirectly by regulating decomposition rates, nutrient cycling and primary productivity (Chew, 1974; Lee & Iman, 1975; Mattson & Addy, 1975). In the Chihuahuan desert, Johnson & Whitford (1975) estimated that termites were the most important consumers, processing more than half of the estimated annual primary production. Termites were estimated to consume 7 per cent of the total annual woody production in the Sonoran desert (Gist & Sferra, 1978). Mound-building termites retard nutrient turnover by concentrating and retaining nutrients in the mound by using feces as a food source and as structural material and by cannibalism (Lee & Wood, 1971; Watson, 1977). Non-mound-building termites appear to enhance cycling of nutrients in the Sudan (Lee & Wood, 1971). Schaefer & Whitford (1981) concluded that termites played a key rôle in the nitrogen cycle in the Chihuahuan desert ecosystem providing rapid turnover and redistribution through termite predators. However, the non-mound-building termites in the Sonoran desert may move nutrients below the rooting zone of shrubs (Gist & Sferra, 1978).

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Termites also possess symbiotic nitrogen-fixing gut bacteria which may provide an important input of nitrogen into desert ecosystems (Benemann, 1973; Brynak, Brill *et al.*, 1973).

The termites (*Gnathamitermes tubiformans* and *Amitermes wheeleri*) in the Chihuahuan desert are non-mound-building subterranean termites and their rôle in nutrient cycling and soil fertility is not fully understood. Chihuahuan desert termites might be taking nutrients below the rooting depth making them unavailable to plant growth. Therefore, we hypothesized that the removal of termites would increase soil fertility and primary productivity.

Since productivity in the Chihuahuan desert is nitrogen-limited (Ettershank, Ettershank *et al.*, 1978), we chose soil N as our fertility index. We expected an increase in ephemeral plant biomass because they are shallow rooted and respond to a lower level of nitrogen fertilisation than *Larrea tridentata* (creosotebush), the dominate shrub (Ettershank, Ettershank *et al.*, 1978). To test these hypotheses we established a series of field plots in 1977 with and without termites. Above-normal rainfall from November 1978 to April 1979 provided the necessary abundant ephemeral flora.

Methods

These studies were conducted on the Jornada Validation Site at the New Mexico State University Experimental Ranch located in the center of the E $\frac{1}{2}$ of section 12, township 21S, Range 1E. Termites were eliminated on four, 30 × 40-m plots by spraying chlordane (octachloro-4,7-methanotetrahydroindane) at a rate of 10 kg/ha in November 1977. Four untreated plots were also established and used as controls. Chlordane initially reduced soil microarthropod numbers. However, by February 1979 microarthropod numbers on chlordane plots were not significantly different from control plots (Santos & Whitford, unpublished data). There was no evidence of termites on the treated plots throughout this study.

In April 1979 treated and control soils were analysed for total soil nitrogen. Since the nitrogen in desert soils is distributed spatially around shrubs (Barth & Klemmedson, 1978), we sampled soils at four depths (0–2.5, 2.5–5, 5–10 and 10–20 cm), three distances from the canopy center ($\frac{1}{2}$, 1 and 2 canopy radii) and on both the east and west sides of each shrub. Five randomly selected creosotebushes were sampled per plot and these samples were pooled, mixed and sub-sampled for the nitrogen analysis. Total nitrogen was analyzed by microkjeldahl digestion (Bremner, 1965) and Conway microdiffusion determination of ammonium in the digest (Stanford, Carter *et al.*, 1973). The Conway microdiffusion method was modified by substituting 10 N NaOH for potassium carbonate. Soil nitrogen data were subjected to a randomized block analysis of variance and, when significance was observed at the $P = 0.05$ level, Tukey's Q values were calculated.

Due to the shrub induced spatial distribution of ephemerals (Muller, 1953; Patten, 1978; Sanchini & Jolls, 1982) we sampled ephemeral plants oth under *Larrea tridentata* canopies and in open areas between shrubs. Between-shrub or open areas were sampled by harvesting all ephemeral plants within 12, random, 1-m² quadrats per plot. Under-canopy vegetation was sampled by randomly selecting 10 creosotebushes per plot and removing all ephemeral plants. Canopy area was estimated from canopy diameter to allow for the conversion of ephemeral plant biomass to an area basis. All ephemeral plant samples were transported to the laboratory where they were sorted by species, counted, oven-dried at 60 °C for 72 h and weighed. Species were ranked according to their numbers. Plant nomenclature follows that of Correll & Johnston (1970). Both ephemeral numbers and biomass were examined by analysis of variance. Means were separated by the Duncans multiple range test ($P = 0.05$).

In October 1979 all live ephemeral plants within 12 random, 1-m² quadrats of each of the chlordane and untreated plots were harvested, dried and weighed.

Table 1. The effect of subterranean termite removal on the spatial distribution of mean total soil N ($\mu\text{g/g}$). With termites (+), without termites (-). Treatments which are underlined are not significantly different at the $P = 0.05$ level

Depth (cm)	Location											
	West						East					
	2		1		$\frac{1}{2}$		$\frac{1}{2}$		1		2	
	-	+	-	+	-	+	-	+	-	+	-	+
0-0.25	297	256*	277	251*	307	261	595	522	447	374	292	340
2.5-5	290	279	326	310	328	274	392	440	358	360	314	317
5-10	337	330	305	341	412	338	427	407	358	377	447	388*
10-20	408	330	349	369	478	356	452	307	370	288	348	396

* Denotes significance at the $P = 0.1$ level.

Results

Total soil N varied with both termite removal and relationship to shrub canopy. Soil N at the 0-2.5 and 10-20 cm depths was significantly higher ($P = 0.0455$) in the treated plots than in the control plots (Table 1). The difference between control and treated plots represents an estimate of the amount of nitrogen that may be removed by termites or $0.76 \text{ g N/m}^2/\text{year}$ under the shrub canopy. Soil N was higher on the east than the west side of creosotebushes (388 and $332 \mu\text{g N/g}$ soil respectively). Soil N also decreased with depth and distance from canopy center (Table 2).

The effect of termites on spring ephemeral density and biomass was species specific (Tables 3 and 4). Increased densities of four species (*Baileya multiradiata*, *Descurainia pinnata*, *Eriastrum diffusum* and *Lepidium lasiocarpum*) were observed in the shrub interspaces of termite free plots. *B. multiradiata* was more abundant on treated than on control plots but there was no significant difference in biomass, indicating a larger number of small *B. multiradiata* plants on the termite-free plots. The exclusion of termites resulted in a decrease in *E. diffusum* biomass and an increase in *L. lasiocarpum* biomass under the shrub canopy. There was no significant effect on total ephemeral density and biomass, although a trend existed for higher values on chlordane treated plots (Table 5). There were significantly higher densities and biomass ($P = 0.0001$) of total spring ephemerals under shrubs than in the open (Table 3).

The fall ephemerals on the plots represented a subset of those forbs that made up the spring flora (Table 6) and undoubtedly represented those species which survived and grew through the summer. There were no significant differences in biomass of all annuals or of the four dominants between the plots (Table 6).

Table 2. The effect on soil depth and distance from canopy on mean total soil N ($\mu\text{g/g}$). Values which are underlined are not significantly different at the $P = 0.05$ level

	Distance			Depth (cm)			
	$\frac{1}{2}$	1	2	0-2.5	2.5-5	5-10	10-20
East	443	363	355	428	401	363	360
West	364	316	316	382	344	301	301

Table 3. Comparisons of mean densities (no./m²) and mean biomass (g/m²) of all ephemerals on desert rangeland with termites eliminated (–) and plots with termites present (+). No significant difference in density or biomass at $P = 0.05$

	Canopies		Inter-shrub areas	
	+	–	+	–
Density	80 ± 23	107 ± 20	16 ± 11	20 ± 9
Biomass	24 ± 10	32 ± 19	4 ± 1	4 ± 1

Table 4. Comparisons of average biomass (g/m²) of dominant spring ephemeral plants in between and under shrubs on desert rangeland with termites present (+) and absent (–)

Plant species	Under shrub		Inter-shrub area	
	+	–	+	–
<i>Astragalus nuttallianus</i>	0.57	0.04	0.39*	0.04*
<i>Baileya multiradiata</i>	1.35	1.97	0.22	0.51
<i>Cryptantha crassisejala</i>	4.20	6.06	1.23	1.55
<i>Cryptantha micrantha</i>	1.09	0.50	0.19*	0.09*
<i>Descurainea pinnata</i>	5.56*	1.37*	0.44	0.30
<i>Dithyrea wislizenii</i>	0.15	0.95	0.02	0.01
<i>Eriastrum diffusum</i>	2.50*	0.87*	0.29	0.20
<i>Eriogonum abertianum</i>	0.07	0.12	0.49	0.06
<i>Eriogonum rotundifolium</i>	0.07	0.16	0.04	0.08
<i>Eriogonum trichopes</i>	0.63	0.04	0.03	0.02
<i>Lepidium lasiocarpum</i>	4.83*	13.04*	0.03*	0.08*

* Significantly different at $P = 0.05$ level.

Table 5. Comparisons of densities (no./m²) of dominant spring ephemeral plants in between and under shrubs on plots with termites present (+) and plots with termites absent (–)

Plant species	Under shrub		Inter-shrub area	
	+	–	+	–
<i>Astragalus nuttallianus</i>	0.10	0.91	0.58	0.24
<i>Baileya multiradiata</i>	1.93	3.35	0.38*	1.32*
<i>Cryptantha crassisejala</i>	8.96	16.27	2.79	4.14
<i>Cryptantha micrantha</i>	6.20	4.13	1.88	1.50
<i>Descurainea pinnata</i>	12.42	7.32	0.97*	3.16*
<i>Dithyrea wislizenii</i>	0.26	0.76	0.42	0.34
<i>Eriastrum diffusum</i>	20.07	14.21	2.38	2.34
<i>Eriogonum abertianum</i>	0.85	1.76	4.83	0.2
<i>Eriogonum rotundifolium</i>	1.11	1.42	0.46*	1.80*
<i>Eriogonum trichopes</i>	6.39*	0.49*	0.14	0.16
<i>Lepidium lasiocarpum</i>	15.28*	32.51*	0.14	2.80

* Significantly different at $P = 0.05$ as determined by Duncan's multiple range test.

Table 6. Comparisons of biomass (g/m^2) of the dominant fall ephemerals on plots with termites present (+) and termites absent (—)

Plant species	+	—
<i>Baileya multiradiata</i>	1.62	0.96
<i>Eriogonum abertianum</i>	0.15	0.46
<i>Eriogonum rotundifolium</i>	0.75	1.08
<i>Eriogonum trichopes</i>	0.39	0.39

The production-species rank curves for open and under-canopy ephemeral plant communities differed in that 10 and 6 species, respectively, accounted for 90 per cent of production (Fig. 1). Open-ground communities had a steep initial slope followed by a middle plateau indicating that dominance was concentrated in several species with moderate production. Under creosotebush canopies, however, dominance was concentrated in a few species. There was no difference ($P = 0.05$) in production-species rank between treated and control plots.

Discussion

The increase in soil nitrogen at the 0–2.5 and the 10–20 cm depths in the absence of termites suggests that subterranean termites in the Chihuahuan desert are removing nitrogen that could otherwise be incorporated into the rooting zone of ephemeral plants. It also indicates they are removing more nitrogen than they are returning to the surface as gallery carton material. The subterranean termites in the Chihuahuan desert appear to be removing potentially available nitrogen from the system and thus tying it up in colony production where it is not available for plant production as has been suggested for the Sonoran desert (Gist & Sferra, 1978). These data suggest that,

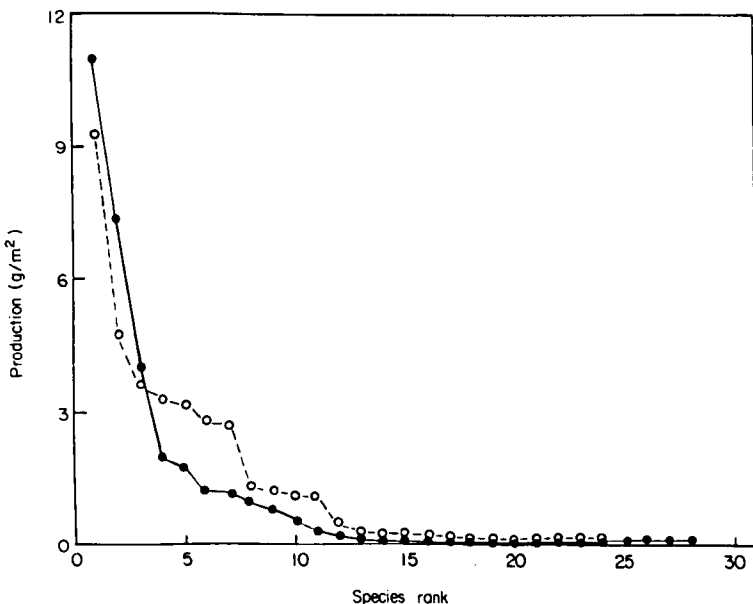


Figure 1. The relationship between species rank and production of spring ephemeral plants under creosotebush canopies (●—●) and in the open (○---○).

although termite biomass is rapidly turned over via predation (Schaefer & Whitford, 1981), they are still acting as a nitrogen sink in the Chihuahuan desert.

We had anticipated a marked difference in ephemeral biomass resulting from termite removal because Bodine & Ueckert (1975) reported that termite exclusion increased productivity in a west Texas grassland. However, we observed only a trend towards a higher ephemeral biomass with the removal of termites perhaps due to the slightly higher levels of nitrogen in the surface soil on the treated plots. This increase in nitrogen only represents 7 kg/ha/year, a rather low level of nitrogen input, of which the majority is probably tied up in the microfloral biomass involved in decomposition processes. In the west Texas grassland, Bodine & Ueckert (1975) attributed higher productivity to increased infiltration and enhanced water status of soils in general, resulting from a mulching effect of the slowly decomposing grass not consumed by termites.

We attribute the vegetative changes at the species level to low level changes in nitrogen and other soil nutrients at the soil surface where ephemeral seeds germinate. Such nutrient changes are likely to affect the growth, and hence the competitive ability, of ephemeral plant species. Individual species of the assemblage of spring annuals may be positively affected by low-level increases in soil nutrients.

These data document the importance of shrub canopies in the productivity of Chihuahuan desert ephemerals. As pointed out by both Muller (1953) and Patten (1978) shrub canopies modify the microclimate which enhances growth of ephemerals. Shrub canopies also modify soil fertility (as indicated by soil N) with soils under-shrub canopies having a higher fertility than inter-shrub areas. This shrub induced distribution of nitrogen has also been observed for other desert systems (Charley & West, 1977; West & Klemmedson, 1978). The lower numbers of ephemeral plant species contributing to the majority of the biomass under the shrub canopy when compared to inter-shrub areas may be a result of this higher soil fertility in the under-canopy area. However, it may also be a result of allelopathic chemicals (Rhoades, 1977). The higher soil fertility under the east side shrub canopies results from litter accumulation under that side due to the predominantly westerly winds (Santos, Depree *et al.*, 1978). This litter pattern probably contributes to the significant east-west distribution of soil nitrogen observed in this study which has also been observed by Barth & Klemmedson (1978). The growth of ephemerals under canopies of desert shrubs can thus be enhanced by edaphic as well as microclimatic factors.

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