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Physical and chemical alteration of soil by two subterranean termite species in Sonoran Desert grassland

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Heterotermes aureus and *Gnathamitermes perplexus* are dominant factors in soil turnover, litter decomposition and nutrient cycling in the Sonoran Desert below 1200 m. Together they move *c.* 744 kg/ha of soil to the surface each year. They increase the clay content of surface soils by 21 kg/ha/year by selectively bringing up soil richer in clay. They alter the pH from slightly acidic to basic, mainly by bringing lime to the surface. They enrich the soil with organic C, total N, Ca, Mg, K and Na as a result of digesting plant material and depositing feces and/or saliva in their workings at the surface. Both are general feeders, but their characteristic attacks on different sets of preferred litter components tend to be complementary. Nutrients released by *Heterotermes* may remain in its workings for months or years, while those of *Gnathamitermes* are released within weeks or months by the first heavy rains.

Introduction

From 1971 to 1976, we investigated the role of subterranean termites in the detritus cycle of the Sonoran Desert near Tucson, Arizona. A major portion of this research concerned the foraging behavior of two dominant species of subterranean termites (Nutting, Haverty *et al.*, 1973; LaFage, Nutting *et al.*, 1973). We identified and quantified the environmental factors correlated with foraging activity of *Heterotermes aureus* (Synder) (Haverty, LaFage *et al.*, 1974) and *Gnathamitermes perplexus* (Banks) (LaFage, Haverty *et al.*, 1976) and described the foraging territories of *H. aureus* (Haverty, Nutting *et al.*, 1975).

While studying the foraging activity of termites at baits on the soil surface, we noticed that foragers of both species pack their workings with soil, as do many other termites (Lee & Wood, 1971*a*). Although we had not designed our program to consider their effects on soil, we were able to recover samples sufficient to present the following information on the amount and characteristics of the soil which these termites bring to the surface.

Methods

Our study site was at the upper limit of the Sonoran Desert, 40 km south of Tucson, Arizona, U.S.A, at an elevation of 940 m on the Santa Rita Experimental Range. It is a shrub-invaded, desert grassland, characterized by scattered small trees, shrubs and cacti. The soil is formed from outwash alluvium, characteristic of much of the Sonoran Desert.

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Annual rainfall averages 30 cm and is divided equally between summer and winter rainy seasons. Air temperatures typically range from near 40°C in mid-summer to a few degrees below 0°C during the winter months. Soil surface temperatures are very high (*c.* 60°C) during midday in summer, and frost may form on the surface for a few hours in winter.

Eighteen months prior to establishment of our study site, most of the large standing vegetation had been knocked down by chaining. All superficial and partly buried wood was removed from a 40 × 40-m area to eliminate most of the natural food for termites. The wood was immediately replaced with toilet paper rolls which served as bait, set out in a grid at 1-m intervals over the entire area (LaFage, Nutting *et al.*, 1973). Foraging behavior was monitored intensively on a 30 × 40-m block of these baits for 53 weeks (Haverty, LaFage *et al.*, 1974; LaFage, Haverty *et al.*, 1976). The remaining 10 × 40-m strip was left undisturbed for other purposes and provided the data for our soil analyses. While there were no controls *per se* for these studies, foraging populations were studied in a series of 50-m^2 plots in a nearby natural area (Haverty & Nutting, 1975*a*, *b*). However, it seemed impractical to try collecting the soil packed into the irregular workings in the many types of plant material encountered there.

The bait proved to be very attractive to *H. aureus* and *G. perplexus* and, furthermore, had the advantage of not attracting any of the other four subterranean species in the area

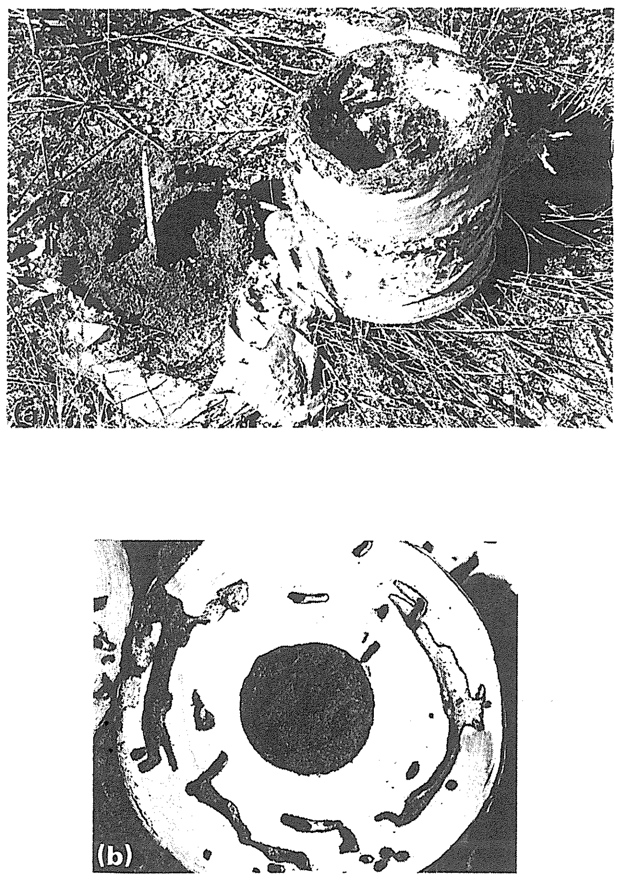

Figure 1. (*a*) Toilet paper roll with foraging cavity packed with soil by *Gnathamitermes perplexus*. (*b*) Toilet paper roll with deep, penetrating galleries and carton construction characteristic of foraging by *Heterotermes aureus*.

(Haverty & Nutting, 1975*b*). Each species attacked the rolls in a manner easily distinguishable from the other. *G. perplexus* foraged over the lower surface of the roll and packed its excavations with soil (Fig. 1*a*), whereas *H. aureus* drove narrow galleries farther into the roll causing the bottom surface to appear as if it had been drilled (Fig. 1*b*). The foraging territories of these two species overlapped and we often found both species foraging in contiguous, but separate galleries in the same roll.

At the end of one year, 211 rolls (a block of 110 plus 101 randomly chosen rolls) were harvested from the 420 rolls in the undisturbed strip, and all soil was carefully removed from the termite workings in them. Of these, 21 rolls had been attacked solely by *H. aureus*, 158 solely by *G. perplexus*, 26 by both species (an occasional roll contained no soil), and six remained untouched. For comparison with this termite-modified soil, samples (*c.* 350 g each) were trowelled up from the top 5 cm of undisturbed soil at four randomly chosen places, each equidistant between two adjacent rolls. All soil from each roll was weighed after drying at 24°C and 30% relative humidity, since the requirements of certain subsequent chemical analyses precluded further drying. Because the amount of soil in most of the rolls was insufficient for a complete series of analyses, the soil from all rolls harvested in each group or treatment (i.e. *H. aureus* only, *G. perplexus* only, both species together, and control) was pooled. Four subsamples for each group were analyzed for 20 separate chemical and physical characteristics by the Soil, Water and Plant Testing Laboratory, Department of Soils, Water and Engineering, University of Arizona. Pooling of the individual soil samples prevented our making statistical comparisons between soil groups. However, since the samples were pooled and thoroughly mixed, the estimates of the mean value for each chemical and physical parameter should be very precise.

Results

On the undisturbed, 420-m^2 study plot, *H. aureus* foraged over 22·3% of the area and *G. perplexus* over 87·2%, while their territories overlapped on 12·3% of the area. From the combined weights of soil in each group and assuming that a roll subtended 1 m^2, we estimate that, during the year of foraging (November 1971–November 1972), *H. aureus* moved soil to the surface at a rate of 70·3 kg/ha/year (mean 70·6, 95% confidence interval 22·4 g/roll for 21 rolls), *G. perplexus* at a rate of 574·9 kg/ha/year (mean 76·8, 95% confidence interval 7·9 g/roll for 146 rolls), and the two species together on overlapping territories, 99·0 kg/ha/year (mean 80·4, 95% confidence interval 18·2 g/roll for 24 rolls). In sum, they transported soil to the surface at a combined rate of *c.* 744·2 kg/ha/year. Both species brought up soil richer in clay than adjacent surface soil, and contributed to a small increase in soil pH (Table 1). These two termites, particularly *Heterotermes*, also added organic carbon to the surface soil. Only *Heterotermes* increased the quantity of nitrogen. *Heterotermes* increased NH_4 and *Gnathamitermes*, NO_3 in surface layers. Finally, both species contributed to a considerable increase in PO_4, Na, Mg and soluble salts, while *Heterotermes* alone increased K (Table 1).

Discussion

Many termites transport soil to the surface in the course of building covered runways, shelters and mounds, or in packing their workings with soil (Lee & Wood, 1971*a*). We have suggested (Collins, Haverty *et al.*, 1973) that this habit may reduce or stabilize temperature within their above-ground cavities. We are aware that there may not be a one-to-one correspondence between rate of soil movement into the toilet rolls and that into the original complement of dead wood. If the termites preferred the paper or found it easier to work, our estimate might be high but if they switched partly to underground wood and other detritus (which we feel was negligible), then our estimate might be low. Nevertheless,

Table 1. *Physical and chemical characteristics of soil brought to the surface by* Heterotermes aureus *(Snyder) and* Gnathamitermes perplexus *(Banks) compared to adjacent, undisturbed surface soil in an Arizona desert grassland. Means are based on four subsamples from pooled collections*

Characteristic	Soil: Adjacent	*Heterotermes*	*Gnathamitermes*
Sand (% by wt.)	74·8	75·6	76·8
Silt (% by wt.)	23·7	20·8	19·6
Clay (% by wt.)	1·5	3·6	3·6
pH	6·8	7·9	7·6
Carbon, organic (% by wt.)	0·7	1·7	1·0
Nitrogen (Kjeldahl) (% by wt.)	0·3	0·43	0·03
NH_4 (% by wt.)	0·001	0·011	0·001
NO_3 (p.p.m.)	13·8	9·4	18·1
PO_4 (p.p.m.)	9·5	18·5	12·4
Exch. K (meq./100 g)	0·39	0·68	0·42
C̈ (p.p.m.)	9·0	11·5	7·5
Na (p.p.m.)	1·7	10·1	7·0
CO_3 (p.p.m.)	0·0	0·0	0·0
HCO_3 (p.p.m.)	14.6	81·8	56·2
Soluble K (p.p.m.)	6·4	17·7	8·0
Ca (p.p.m.)	4·3	18·0	10·1
Mg (p.p.m.)	0·9	3·4	1·7
SO_4 (p.p.m.)	16·3	14·5	14·0
Soluble salts (meq./100 g)	0·7	0·17	0·11
Soluble salts (p.p.m.)	50·0	120·0	78·0

our point is that *Heterotermes aureus* and *Gnathamitermes perplexus* are capable of moving soil at a combined annual rate of nearly 3/4 metric tonnes/ha, and must be among the principal movers of soil in this part of the Sonoran Desert. Whitford (1980) reported that *Gnathamitermes tubiformans* (Buckley) in the neighboring Chihuahuan Desert moved 243 and 178 kg/ha/year during 1978 and 1979. This is considerably less than our rate of 575 kg/ha/year for *G. perplexus* alone. These rates are probably not strictly comparable, however, because Whitford measured the 'galleries around dead plant parts' while we weighed soil packed into eaten-out parts of toilet rolls and whatever shelters remained on their outer surfaces at the end of the study. *G. perplexus* did very little shelter building over the sparse vegetation between rolls. We did not include shelters, so our estimate of its soil transport rate could be low for this reason as well.

These rates of soil movement are impressive for a desert ecosystem, but appear trivial when compared with those of mound-building termites in the savannas of Australia and Africa, where mounds may occupy up to 30% of the soil surface and contain up to $2{\cdot}4 \times 10^6$ kg of soil/ha (Lee & Wood, 1971*a*; Watson, 1977). The main difference between the mound-builders and these desert subterranean termites is that mounds withhold soil (both in the mound and, sometimes, on its barren surface area) from productivity for decades or even centuries (Lee & Wood, 1971*b*), whereas we suspect that most of the soil brought to the surface by *Gnathamitermes* is usually eroded and returned to the A horizon within a year or two, and that by *H. aureus* certainly within 10 years.

Since there are no earthworms in this site, most of the re-sorting of the soil horizons is done by the arthropod fauna, principally ants and termites, and assorted burrowing mammals. Ants excavate subterranean nests and noticeably accelerate this activity during the summer rainy season. For example, multiple nest entrances of the leaf-cutter *Acromyrmex versicolor* (Pergande) are ringed with large, fresh soil craters during this season. Although we have not quantified soil movement by ants or burrowing mammals, we suspect that termites move as much soil to the surface as both of these groups combined. It is important to note that ants and mammals rarely build with the soil they move; they simply remove it from their subterranean cavities to the surface around the entrance. Termites, however, construct runways, shelters and sheeting by cementing together soil particles with saliva, fecal material and, occasionally, undigested particles of wood (Lee & Wood, 1971*a*). This results in significant physical and chemical changes in the soil which they bring to the surface.

Both *G. perplexus* and *H. aureus* selectively bring up soil which is rich in clay and add an estimated 20·9 kg/ha/year to the soil surface (Table 1). This activity is a fairly common finding with many species around the world (Lee & Wood, 1971*a*; Pomeroy, 1976; Arshad, 1982). Thus, in addition to burying organic matter and turning or mixing the soil, they can also modify soil profiles.

Both species contribute to a small increase in soil pH by bringing soil from alkaline horizons below (G. R. Dutt, personal communication). These termites, particularly *Heterotermes*, also add a considerable amount of organic carbon (3·4 kg/ha/year) to the soil surface as a result of their feeding on plant material and habits of depositing saliva and fecal material along with the soil in their workings. This is also a fairly general occurrence (Lee & Wood, 1971*a*,*b*; Sarma, Tandon *et al.*, 1979), although there is usually little carbon in the outer parts of mounds (Malaka, 1977; Arshad, 1982).

Surprisingly enough, only *H. aureus* added significantly to the quantity of nitrogen in the soil (0·67 kg/ha/year). Of the available nitrogen, *Heterotermes* increased the NH_4 and *Gnathamitermes* the NO_3, although this may have resulted from attack by micro-organisms on organic debris left by the termites in their foraging areas. In the Chihuahuan Desert *G. tubiformans* added 95–272 kg/ha/year of gallery material, containing 14–40 g N/ha, to the soil surface over a 3-year period (Whitford, Freckman *et al.*, 1983). *H. aureus* leaves large amounts of organic carbon and nitrogen compared to *G. perplexus*; this may reflect differences in the way each manages its closed foraging environment.

Heterotermes is a general feeder, although it prefers certain species of fallen deadwood—stumps, trunks, branches and fragments of several species of trees, shrubs and woody cacti. It may remain in a piece of wood for a long time: weeks, months or longer, depending on size and suitability (Haverty & Nutting, 1975*a*). It uses relatively little soil, but plasters interior gallery surfaces with fecal material, builds tubes and fills some voids with true carbon (Lee & Wood, 1971*a*). While *Heterotermes* adds many important nutrients to the soil, most of them are within or under pieces of wood and remain unavailable until the wood has decayed, broken up and been leached of its 'packing'.

Gnathamitermes is also a general feeder with distinct preferences, generally different from those of *Heterotermes* (Haverty & Nutting, 1975*b*). It favors the weathered surfaces of wood and bark, dead stems and leaves of grasses and herbs, and dung of herbivores. To feed on exposed substrates, it builds foraging shelters over them made of soil particles cemented together with saliva rather than feces. These structures are made quickly as the foragers advance over plant materials and are soon abandoned, usually within a few days. *G. perplexus* may spend longer, perhaps weeks, beneath large pieces of wood and they often spot the surface of such feeding substrates with fecal material. Wind and rain break up their delicate constructions, and whatever nutrients they contain are washed out onto the soil surface with the first heavy rainfall (personal observations).

Parker, Fowler *et al.* (1982) measured significantly higher total nitrogen in Chihuahuan Desert soils after eliminating populations of *G. tubiformans* and *Amitermes wheeleri* with an insecticide. They attributed a trend toward higher total biomass of ephemeral plants in these areas, to the resulting increase of surface soil nitrogen. Bodine & Ueckert (1975) reported a considerable increase in the productivity of a west Texas grassland following similar treatment; however, they considered it a result of increased filtration and water retention resulting from the mulching effect of the accumulated litter not consumed by termites. Likewise, Arshad (1982) reported greater biomass and different species composition of grasses within the most active foraging radius of mounds of *Macrotermes michaelseni* in semi-arid Kenyan savanna. He attributed these differences not only to higher concentrations of nutrients, but to higher moisture levels and improved drainage as well.

Our findings emphasize how the foraging and building activities of two species of subterranean termites can affect the physical and chemical characteristics of native soils in one part of the Sonoran Desert. While these two dominant termites are general feeders, they tend to complement each other in their characteristic modes of attack on different sets of preferred litter components. *Heterotermes* returns considerably more nitrogen and organic carbon to surface soils than does *Gnathamitermes*, while both species increase many of the macronutrients in the soil they displace. The chemical additions made by *Heterotermes* probably remain in its workings for months or years, while those of *Gnathamitermes* are returned within weeks or months.

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