

Nutrient Cycling by the Subterranean Termite *Gnathamitermes tubiformans* in a Chihuahuan Desert Ecosystem

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Summary. We estimated the density of subterranean termites *Gnathamitermes tubiformans* at $800,000 \cdot \text{ha}^{-1}$ for a standing crop biomass of $2 \text{ kg} \cdot \text{ha}^{-1}$. Predation losses were estimated to be $5.73 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ representing the major release of nutrients from termites to surficial soil layers. Nutrient fluxes from termites to predators amounted to $410 \text{ g N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, $33 \text{ g S} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and $19 \text{ g P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. These fluxes account for 8% of the litter N, 1.5% of the litter P and 2.9% of the litter S. The termites fixed an estimated $66 \text{ g} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ atmospheric N and returned an estimated $100 \text{ g} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in the surface gallery carton. Since losses of elements from subterranean termites were greater than standing crops, we estimated an annual turnover of N at 3.5 times per year, P of 2.5 times per year, and S of 2.5 times per year.

Since surface foraging, predation and alate flights are pulse regulated by rainfall, nutrient flows through subterranean termites are episodic and releases of nutrients accumulated in termite biomass precedes or is coincident with productivity "pulses" of some shallow rooted plants. We propose that subterranean termites are important as regulators in desert nutrient cycles.

Introduction

Chew (1974) suggested that although consumers process only a small fraction of the energy fixed in ecosystems, hence appear to be relatively unimportant in energy flow, they may serve to regulate the rates of ecosystem processes like nutrient cycling. Similar suggestions have been made by Mattson and Addy (1975).

Termites are prominent, if not visible, consumers in most deserts (Ghilarov 1962; Boullon 1970; Lee and Wood 1971; Bodine and Ueckert 1975; Haverty et al. 1975) and have been estimated to consume as much as 50% of the net primary production in Chihuahuan desert ecosystems (Johnson and Whitford 1975). Termites are excellent organisms for a test of Chew's hypothesis because organisms estimated to process such a large fraction of the net primary production should also have large and measurable effects on nutrient cycles.

Consumption and food preference of desert termites have been examined (Haverty and Nutting 1975; LaFage et al. 1976; Spears et al. 1976; Johnson and Whitford 1975) but there are no measurements of rates of consumption of non-woody desert plants or litter by subterranean termites. Estimation of the contribution of termites to nutrient cycles requires estimates of that

portion of the potentially available nutrients (in dead plants and litter) consumed by termites and released to the rhizosphere and higher trophic levels. Novel physiological adaptations such as nitrogen fixation (Beneman 1973; Breznak et al. 1973; French et al. 1976; Schaefer and Whitford 1976) need to be assessed in the perspective of nitrogen inputs and outputs of termites. Since desert subterranean termites were estimated to consume a large fraction of the standing crop of dead plant material each year (Johnson and Whitford 1975) and because of their unique nitrogen metabolism (French et al. 1976), we hypothesized that termites would play a major role in nutrient cycling in a desert ecosystem. We further hypothesized that termites would be more important in nitrogen cycling than in phosphorus or sulfur cycles. This study was designed to examine role of the subterranean termite *Gnathamitermes tubiformans* (Buckley) (Isoptera: Termitidae) in nitrogen, phosphorus, and sulfur nutrient cycles in a Chihuahuan desert ecosystem.

Methods

Our studies were conducted on the New Mexico State University Experimental Ranch 40 km NNE of Las Cruces, Dona Ana County, New Mexico, on an alluvial piedmont. The desert shrub vegetation is predominantly soaptree yucca, *Yucca elata*, creosote bush, *Larrea tridentata*, and mormon tea, *Ephedra trifurca*, with perennial clump grasses and ephemeral forbs accounting for most of the ground cover. The 100-year annual rainfall average \pm one standard deviation is 211 ± 77 mm with more than half occurring between 1 July and 30 September from convective storms (Houghton 1972). June is the hottest month with mean temperature maxima of 36°C , and January is the coldest with mean maxima of 13°C .

All termites collected were *Gnathamitermes tubiformans* (Buckley). Termite colony density was estimated by the bait technique using two large grids of toilet tissue rolls (Haverty et al. 1975; Johnson and Whitford 1975; Haverty et al. 1976; LaFage et al. 1976). Numbers of active foragers collected on the rolls were converted to numbers per hectare. Colony foraging areas were delimited spatially by determining whether or not termites collected from adjacent rolls reacted aggressively to each other. Aggressive behavior was a vigorous attack involving rapid motion and shearing of joints or body sections with the mandibles. The termites exhibiting such behavior were scored as foragers from different colonies.

The total number of termites per ha. was derived with Nutting's estimate (in Johnson and Whitford 1975) of 10,000 termites per colony for *G. perplexus*, a closely related species, multiplied by the estimated colony density. Area estimates of numbers of actively foraging termites were made at the same time although these numbers are known to seriously underestimate the total numbers of termites in a colony (Haverty 1974; Johnson and Whitford 1975). Samples were collected alive from the bait rolls and held at 0°C for later drying and analyses.

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Densities of the shrub species *Larrea tridentata*, *Yucca elata*, *Ephedra trifurca* and *Xanthocephalum sarothrae* were estimated by the wandering quarter method (Cantana 1963). Stems and leaves were sampled and dried for elemental analyses. Canopy height and width were measured for each shrub to determine volumes. Canopy biomass (partitioned into leaf and stem material) was estimated from canopy volume by the regression equations of Ludwig et al. (1975). The pools of nutrient elements N, P, and S for the leaf and stem material of each species were estimated by multiplying elemental concentrations by the dry weight per hectare, and summing for each element. Densities of the annual forbs and grasses were estimated by the point-center-quarter method (Cottam and Curtis 1956). All aboveground material was harvested, dried, weighed, and elemental pools estimated.

Surface litter was swept from 20 randomly placed 1 m² quadrats. The litter was separated from fine soil particles on a 24-mesh sieve, and from large particles and gravel by water flotation. The litter was skimmed and dried, hand sorted into categories (rabbit fecal pellets, wood, fallen yucca, *Astragalus spp.* stems, *Cryptantha spp.* and other) and weighed. Sub-samples were ground to 40 mesh for elemental analyses.

The harvesting of plant parts by termites was estimated by a modified litter bag technique. Seven dominant forb and grass species were harvested at the end of July and dried. Approximately 10 g of each species were weighed and placed in each of 10-coarse (1.3 mm holes) and 10-fine (0.6 mm holes) mesh bags. The coarse mesh admitted termites; the fine mesh did not. These were set in the field on 8 August 1979 in 4 × 5 grids of 5-m spacing in an alternating (checkerboard) fashion, and left undisturbed until 16 January 1980 when they were collected, sealed in plastic bags and scored for evidence of termite attack. Scoring was based on the presence of termite gallery carton on the bag surface in contact with the soil.

Plant material in each bag was separated from the carton and soil over a 24-mesh sieve. Each plant species was sorted into four groups: course mesh attacked by termites (CA), coarse mesh not attacked (CN), fine mesh attacked (FA), and not (FN). The plant material by species in each group was combined, dried, weighed, and ground to 40 mesh. Differences in weight loss between CA and CN were taken as termite consumption of each plant type. Differences between FA and FN provided estimates of decomposition enhancement by gallery carton. Carton from CA bags and soil from CN bags were analyzed for nitrogen and compared to estimate the flow of nitrogen gallery carton to the rhizosphere. Elemental concentrations and weight before and after the experiment were determined to estimate flux of N, P, and S in the different treatments. Weight loss percentages were arcsine transformed and compared with one-way ANOVA (Sokal and Rohlf 1969). Elemental concentrations were compared for difference with factorial ANOVA and t-tests, and the relationship between weight loss and carton construction was fit by linear regression. Soil and carton nitrogen samples were analyzed using the modification of Stewart et al. (1964). Samples for P and S analysis were digested in a two-stage process adapted from Black (1965) and Nes (1979). Aliquots of the diluted digest were analyzed for phosphorus as phosphate in the Molybdivanadophosphoric acid absorbance method (Kitson and Mellon 1944). Sulfur was determined as sulfate by turbidity of the barium precipitate (Black 1965; Nes 1979).

Laboratory measurements of acetylene reduction were used to estimate nitrogen fixation rates (Hardy et al. 1973). Live termites were field-collected and divided into groups of 30–50 in 20 × 200 mm glass tubes sealed with rubber septa. The atmosphere in the tubes was replaced with a gas mixture of 79% argon, 20.9% oxygen and 0.032% carbon dioxide to avoid competition between nitrogen and acetylene for the nitrogenase enzyme active sites. Acetylene and ethylene produced were measured by a Varian 600 gas chromatograph. Ethylene production was measured at 45 and 160 min after injection of acetylene. The relative amounts of each gas were converted to micromoles of ethylene produced by using the equations of McNabb and Geist (1979). Ethylene produced in the first hour was taken as the activity of the nitrogenase enzyme. Based on electron transport, the theoretical relative ratio of ethylene produced: nitrogen fixed is 3:1 (Kleiner 1975), but a value of 4.1:1 was used, based on comparative assays with isotopically labeled N₂ (Potts et al. 1978).

Table 1. Termite populations, alate production and forager predation; as biomass and nutrient inventories

Category	g ha ⁻¹	g N ha ⁻¹	g P ha ⁻¹	g S ha ⁻¹
Population ^a	2,000	140	6.5	12.5
Alate ^b Production	727	63	3.0	2.0
Forager ^c Predation	5,000	349	16.3	31.3
Total losses	5,727	412	19.3	33.3

^a (80 colonies ha⁻¹) × (10,000 termites colony⁻¹) × (0.0025 g termite⁻¹)

^b (800,000 termites ha⁻¹) × (0.10 alates termite⁻¹) × (0.0091 g alate⁻¹)

^c (2,000,000 termites ha⁻¹) × (0.0025 g termite⁻¹)

Results

Based on the numbers of colonies from the bait grids, 11 in 1,600 m² and 9 in 1,152 m², we estimated an average of 80 colonies · ha⁻¹. The study area thus had an estimated 800,000 termites · ha⁻¹ which at 400 termites per gram dry weight yields 2,000 g · ha⁻¹ (Table 1). Based on the number of termites found when the rolls were examined, the active forager estimate was 48,000 · ha⁻¹, or 6% of the colony total. Alates were estimated at 0.13% of the population for *G. perplexus* in southern Arizona in a dry year (Nutting and Haverty 1976) and at 10% of colony population for the Amitermitinae in general (Lee and Wood 1971). We used 10% of 800,000, or 727 g · ha⁻¹ for the alate production since rainfall was near normal during the study period (Table 1).

Ants are generally regarded as the most significant predators of termite workers (Wood and Sands 1978; Steppe, 1970) although Pianka (1973) found that termites made up 15.9%, 16.5% and 41.3% of the volume of stomach contents of lizards in the Kalahari, North American and Australian deserts, respectively. Several Chihuahuan desert bird species rely heavily on termites in their diets in breeding season (T. Marr, pers. comm.). Termites are reported to make up between 16% and 25.2% of the forage items of *Novomessor cockerelli* (Whitford 1978b; Whitford et al. 1981) which occur at densities of 2 colonies · ha⁻¹ on the study site. Although termites account for only 2% of the forage of *Pogonomyrmex spp.*, these ants are abundant and based on the data in Whitford (1978a) we estimated they take 1.4 × 10⁶ termites · ha⁻¹ · yr⁻¹. Since quantitative estimates were not available for losses to lizards and birds, we assumed that these predators take fewer termites than harvester ants and used 2 × 10⁶ termites · ha⁻¹ · yr⁻¹ or 5,000 g dry weight · ha⁻¹ · yr⁻¹ as a conservative estimate of predation losses (Table 1).

Because our attempts to quantitatively sample alate production failed, we were forced to use literature values. Alate predation has been reviewed by Nutting (1969) and has been characterized as resulting in mortality of virtually all alates produced. Basalingappa (1970) found in *Odonotermes assmuthi* that 99.5% of the alates did not survive to excavate the initial nest chamber, and that 88% of those that did were killed or died subsequently, yielding 99.94% mortality. Therefore, we assumed that the entire alate production was input to higher trophic levels (Table 1).

Perennial shrub nutrient inventories were dominated by *Y. elata* (Table 2), which provided 43% of the N, 56% of the P and 66% of the S; *L. tridentata* which contributed 45% of the N, 36% of the P and 22% of the S and *E. trifurca* which contained most of the remainder; 11.3%, 7.2% and 11.2% of the

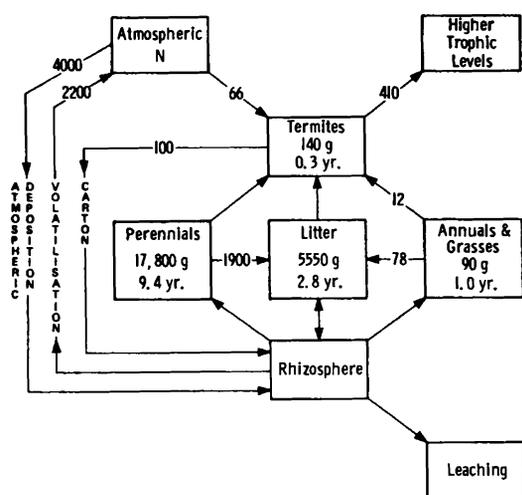


Fig. 1. Estimated nitrogen fluxes through subterranean termites in a Chihuahuan desert ecosystem. Quantities in the boxes are standing crops, the yr numbers in boxes represent turnover times for nitrogen in that compartment and numbers with arrows are the grams of nitrogen transferred in the direction of the arrow annually

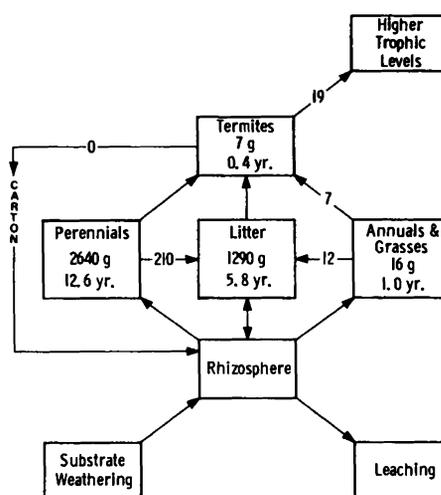


Fig. 3. Estimated phosphorus fluxes through subterranean termites in a Chihuahuan desert ecosystem. Method of presentation the same as Fig. 1

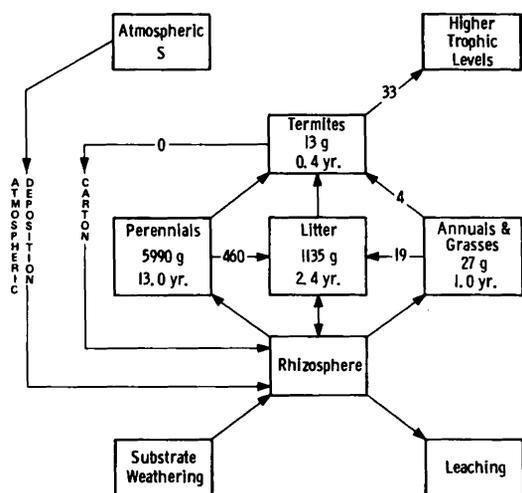


Fig. 2. Estimated sulfur fluxes through subterranean termites in a Chihuahuan desert ecosystem. Method of presentation is the same as Fig. 1

N, P, and S, respectively. The perennials accounted for most of the biotic N and S and more than half of the biotic P (Figs. 1, 2, and 3).

Perennial litter fall on the Jornada bajada was estimated at $200 \text{ kg} \cdot \text{ha}^{-1}$ (O'Brien, 1978). To estimate nutrient flux, the average percent composition of N, P, and S in the perennials was multiplied by that $200 \text{ kg} \cdot \text{ha}^{-1}$. With the exception of phosphorus, these percentages were consistent with values for woody and soft litter that was sampled (Table 3).

Soft litter contained 828 of the 1288 g (68%) of phosphorus, and a much smaller proportion of the nitrogen and sulfur (39% each) (Table 3) *Astragalus spp.* litter contributed a similar portion of the biotic pools of nitrogen and sulfur (42% and 36%), but only 15% of the litter phosphorus. The other categories together comprised between 17% and 25% of the three nutrients in the litter component. The forbs and grasses represented about 0.4% of the total biotic pools of each of the three nutrients. As an

Table 2. Density, standing crops and nutrient inventories in perennial shrubs

Species and category	No. ha^{-1}	kg ha^{-1}	g N ha^{-1}	g P ha^{-1}	g S ha^{-1}
<i>Yucca elata</i>	44				
live leaves		8.2	113	7	18
dead leaves		410.8	3,286	489	137
caudices		1,073.2	4,293	987	3,338
<i>Larrea tridentata</i>	35				
leaves		48.4	576	36	366
stems		771.0	7,401	917	1,210
<i>Ephedra trifurca</i>	158				
"leaves" ^a		168.2	1,905	177	853
stems		16.5	112	13	27
<i>Xanthocephalum sarothrae</i>	53				
leaves		4.3	77	7	18
stems		5.6	39	5	13
<i>Zinnia grandiflora</i>	67				
leaves		4.5	60	5	11
Totals $\pm 1 \text{ SD}$		2,551,160 $\pm 426,730$	17,862 $\pm 3,800$	2,643 ± 610	5,991 $\pm 1,280$

^a Green photosynthetic stems

example, 90 g of the 23,580 g of biotic nitrogen was in annual forbs and grasses. Considered as an input to the litter component, this represents between 3.9% and 5.4% of the annual flux of these nutrients to the litter.

We used the estimates of atmospheric contributions of nitrogen to desert biogeochemical cycles in West and Skujins (1978).

The ratio of annual flux of material or energy through a component divided by the storage in that component is the "turnover time" (Reiners 1972), also called "transit time" (Eriksson 1971). Values for energy turnover range from 10^4 days in temperate forests to 10^{-2} days in oceanic plankton (Pomeroy 1970). The rates of nutrient fluxes through the components in this desert ecosystem were calculated either as flux in or out

Table 3. Standing crops and nutrient inventories in litter categories, sampled from 20 1 m² quadrats

Category	g ha ⁻¹	g N ha ⁻¹ ^a	g P ha ⁻¹ ^a	g S ha ⁻¹ ^a
<i>Astragalus sp.</i>	94.2	2,351	171	404
<i>Cryptantha sp.</i>	12.9	80	26	17
Woody	37.7	422	57	82
Soft	232.2	2,148	878	444
<i>Yucca elata</i>	35.4	141	33	110
Fecal pellets	26.6	407	123	79
Totals	438.5	5,550	1,288	1,135
± SD	± 48.2	± 740	± 210	± 200

^a Weights multiplied by elemental contents

divided by storage in that component (Figs. 1, 2, and 3). For example, the nitrogen flux out of the perennial shrub component is 1,900 g·ha⁻¹·yr⁻¹; the perennial shrub nitrogen pool is 17,800 g·ha⁻¹ and the ratio is the turnover time: 17,800:1,900=9.4 years. Flux out of perennials into termites is small and was not included in the calculation of turnover time (Figs. 1–3). Similar calculations for phosphorus and sulfur yielded perennial shrub turnover times of 12.6 and 13.0 years, respectively. The turnover time of nitrogen in termites is derived from the pool in termites (140 g·ha⁻¹) divided by the flow out of termites (510 g·ha⁻¹·yr⁻¹), equals 0.27 years. The litter turnover was considerably slower, e.g. 2.5 years for N and S and 5.6 years for P. Termites turn over their N, P, and S 3.5 to 4 times per year (Figs. 1, 2, and 3). The dynamics of termite nutrient loss is seasonal: by alate flights and foraging activity. The timing of these nutrient flux pulses corresponds with the rapid growth of fluff grass, *Erioneuron pulchellum* which also responds to soil N amendment (Ettershank et al. 1978).

To balance their other fluxes, the termites had to harvest from 0.3% to 1.8% of the elements from the perennial and litter components annually. Nitrogen fixation rates were estimated at 7,700 μ moles per g termite for the 8 month activity period or 1,800 mg per termite. The energy expensive nature of nitrogen fixation (Kleiner 1975) makes it doubtful that this process would continue during the winter. There were an estimated 2,000 g. of termites per hectare, which yielded 100 g of nitrogen fixed per hectare per year. A similar experiment performed in November 1978 yielded an average of 0.19 micromoles N per gram of termites per hour, or 32 g of N per hectare per year. Since we do not know what factors control the nitrogen fixation in the hindguts of termites, we used the average of these rates, or 66 grams nitrogen fixed per hectare per year.

There was significantly greater weight loss from the termite attacked bags than those not attached (F 1,8 values range from 9.85 to 63, $p \leq 0.05$) except in *Astragalus spp.* (Fig. 4). The plants in unattached bags had elemental concentrations significantly different (t between 3.0 and 12.0, $n=3$, $p \leq 0.05$) from the initial values for that plant in the following species and elements: *Astragalus spp.*, N, P; *Aristida purpurea*, P; *Cryptantha spp.*, N, P; *Eriogonum rotundifolium*, N, S; *Erioneuron pulchellum*, P; *Lepidium lasiocarpum*, N, P, S; *Eriastrum diffusum*, N, P and S. The termite attacked bags had significantly different elemental concentrations (between 2.9 and 9.3, $n=3$, $p \leq 0.05$) from the initial values in: *A. purpurea*, S; *Cryptantha spp.*, N, S; *Eriogonum rotundifolium*, N, S; *Erioneuron pulchellum*, N, P; and all elements in *L. lasiocarpum* and *Eriastrum diffusum*. Those values

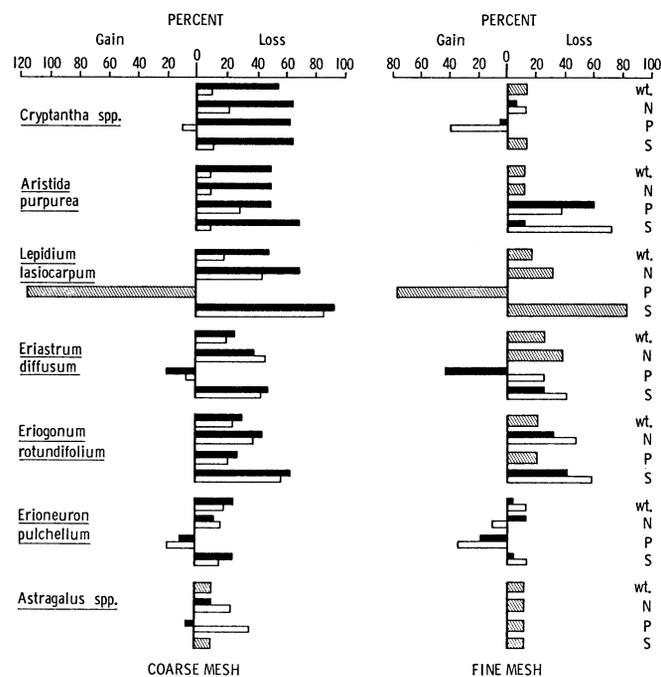


Fig. 4. Percent weight losses and gains of elements expressed as percent of original amount from coarse mesh bags (which allowed termite entry) and fine mesh bags (which excluded termites). The dark bars refer to bags attacked by termites, the light bars are for bags not attacked by termites and the cross-hatched bars indicate no significant difference between termite attacked bags and bags not attacked by termites. Although fine mesh bags excluded termites, the termites built gallery carton on bags scored as attacked

were multiplied by the plant weights before and after field exposure to yield a nutrient flux into or out of each plant type under each treatment (Fig. 4).

With a few exceptions, the nutrient losses paralleled weight losses (Fig. 4). In *L. lasiocarpum* in both treatments phosphorus increased by 116% while weight declined by 25.4% (unattached) and 48.2% (attached). This may be due to translocation of phosphorus into the litter by fungal mycelia, as has been noted in decomposing lodgepole pine needles by Fahey (1979). Phosphorus increased in all *E. diffusum* and *Erioneuron pulchellum* treatments (Fig. 4). Assuming that the differences in nutrient fluxes between the coarse mesh attacked and unattached was due to termites, we estimated that 13.9% of the nitrogen, 19.3% of the phosphorus, and 14.2% of the sulfur in the annual species are removed by termites or 12.2 g·ha⁻¹, 7.1 g·ha⁻¹, and 3.8 g·ha⁻¹ of N, P and S, respectively, are removed each year by termites. Losses from unattached bags yielded losses of 25.2 g·ha⁻¹, 1.5 g·ha⁻¹ and 10.0 g·ha⁻¹ of N, P and S per year by fungal and microbial action, and leaching.

The differences in weight loss between attacked and unattached fine mesh bags were not statistically significant, except for *Erioneuron pulchellum* (df 1,8 $t=7.14$, $p \leq 0.05$). Differences in mineral content between attacked and unattached bag treatments were statistically significant (t between 2.2 and 8.5, $n=3$, $p \leq 0.05$) for *Cryptantha spp.*, N, P; *Aristida purpurea*, P, S; *Eriastrum diffusum*, P; *Eriogonum rotundifolium*, N, S; and *Erioneuron pulchellum*, N, P. The only element measured which increased was phosphorus in *Cryptantha spp.*, *L. lasiocarpum*, *E. diffusum* and *E. pulchellum*. The unattached treatment of *E. pulchellum* had a nitrogen gain ($t=2.2$, $p \leq 0.05$). More sulfur was

Table 4. Standing crops and nutrient inventories in annual forbs and grasses

Species	g ha ⁻¹	g N ha ⁻¹	g P ha ⁻¹	g S ha ⁻¹
<i>Eriogonum</i> ^a <i>rotundifolium</i>	2,344	19.0	5.5	3.9
<i>Baileya</i> <i>multiradiata</i>	1,869	22.6	2.6	2.9
<i>Erioneuron</i> ^a <i>pulchellum</i>	1,226	9.9	2.9	2.0
<i>Cryptantha</i> ^a <i>spp.</i>	936	9.1	1.6	1.6
<i>Eriogonum</i> <i>albertianum</i>	720	11.6	0.5	2.0
<i>Dithyrea</i> <i>wislizenii</i>	543	7.3	0.5	4.3
<i>Aristida</i> ^a <i>purpurea</i>	307	1.6	1.8	0.4
<i>Astragalus</i> ^a <i>spp.</i>	205	5.4	0.3	0.8
<i>Eriastrum</i> ^a <i>diffusum</i>	134	0.8	0.3	1.8
<i>Lepidium</i> ^a <i>lasiocarpum</i>	29	0.2	0.1	0.1
<i>Solanum</i> ^b <i>eleagnafolium</i>	24	–	–	–
Unknown ^b	57	–	–	–
Totals ± 1 SD	8,394 ± 670	87.5 ± 8.7	16.1 ± 2.5	26.8 ± 3.2

^a Plants selected for consumption experiment

^b Elemental analyses not performed

lost from the unattacked than the attacked bags containing *A. purpurea*, *E. diffusum* and *E. rotundifolium*, the last of which had a similar decrease in N. The phosphorus content of *A. purpurea* was reduced significantly ($t=3.9$, $p\leq 0.05$) in the unattacked bags. The same pattern of increases and decreases of nutrients in *L. lasiocarpum* was seen in both treatments of both experiments, suggesting nutrient flows in this species are little affected by termites. The weight loss was greater in the termite-attacked coarse bags, but there were no differences between treatments in the fine mesh bag experiment (Fig. 4).

Carton collected within CA bags was dried and weighed individually. These weights ($n=30$) were correlated positively with the weight of plant material removed. This correlation was best fit ($r=0.72$) by the line:

$$Y = 2.4X + 6.21$$

where X = g plant material removed and Y = g carton deposited. This correlation is not strong enough to predict soil movement from known consumption, or conversely to predict consumption from carton deposition measurements. However, it emphasizes the great amount of soil moved to the surface by termites.

Discussion

The nutrient budgets developed in this study provide one assessment of the importance of termites in this Chihuahuan desert ecosystem. Most of the estimates are conservative because we

were unable to measure all of the materials harvested by termites, have no measure of predation on termite workers by vertebrates, and were unable to obtain direct measurements of alate production. However, our estimates do provide some useful insight into the relative importance of subterranean termites in desert nutrient cycles and which fluxes are most important as potential rate regulators. Subterranean termites translocate large quantities of dead plant material into deep colony galleries. Nutrients in such material is thus not available to shallow rooted plants. Further, since termites use trophylactic feeding and dispose of old or damaged individuals by cannibalism (Wilson 1971) nutrients incorporated into termite tissue would tend to remain unavailable to plants. The nutrient budgets we developed demonstrates the importance of higher trophic levels in releasing nutrients from the subterranean termite nutrient sink. Nutrient flows by predation on workers and alates by ants, lizards and birds are the major returns to the surface soil and provide for rapid "turnover".

Subterranean termites, *Gnathamitermes tubiformans*, also construct gallery carton on plant material which is consumed and also on plant material not or incompletely consumed. Carton is a mixture of fine soil particles mixed with saliva and feces and is nitrogen enriched as we have shown in this study. This represents another significant pathway for nitrogen return to the soil. We have documented that *G. tubiformans* fixes atmospheric nitrogen and that a part of that nitrogen is probably made available to plants via the gallery carton. However, the data on N fixation raises a number of questions about the interpretation of the numbers obtained. Experiments by Breznak et al. (1973) with *Coptotermes formosanus* yielded 32 nanomoles ethylene per dry gram per hour. Beneman (1973) obtained 400 nanomoles ethylene per dry gram in 2.5 h with *Kaloterme minor*. Our estimate for *G. tubiformans*, while performed under similar experimental conditions, is substantially greater. Several factors may influence these results: (1) We use lower acetylene concentrations than either of the above-mentioned experiments. The effects of high acetylene concentrations on the termites and symbiotic bacteria are not known. (2) The other termite species examined were from mesic environments. Nitrogen content of their food is almost certainly higher, and Breznak (1973) showed reduction of nitrogenase activity in termites by supplementing the diet with ammonium salts. This would suggest less N fixation by termites on a higher N diet. (3) Environmental effects on termites themselves have not been examined. N-fixation experiments were done with a compressed gas mixture at 0% relative humidity. In one of our experiments where the same gas mixture was saturated (100% r.h.), acetylene reduction was not detectable. Experimental conditions reported by other workers did not include humidities.

"Turnover times" have been applied to ecosystem studies to assess the rate at which energy or material flows through ecosystem components (Reiners 1972). Although flux of nutrients through termites is relatively small, turnover times are extremely rapid. Since some of these nutrient releases are episodic, like that from alate flights, the maximum flux rate out of termite colonies are underestimated by mean annual values. Is there a regulatory value of relatively small flows of nutrients through ecosystems? Pomeroy (1970) pointed out that the important nutrients may not be present in a Liebig-limited sense, but only in the rate at which they are recycled. Stark (1972) recognized that although the input of pollen was quantitatively small ($1-3 \text{ kg/hg} \cdot \text{yr}^{-1}$), the timing of this input accelerated decomposition of fallen pine needles from which most of the mineral nutrients had already been leached. The small portion of the total phos-

phorus pool released by microorganisms from decomposing litter in the tundra was suggested by Chapin et al. (1978, p. 109) to be the "bottleneck in the phosphorus cycle." Rehder and Schäfer (1978) suggested root exudates could stimulate nitrogen mineralization in alpine ecosystems, and thus potentially hasten nutrient fluxes through the rhizosphere. We view termites in the Chihuahuan desert in this context i.e. regulating the rates of recycling of nutrients, especially nitrogen and phosphorus. Our study suggests that the timing of the release of nutrients from termites may be as critical a feature as the forms in which the nutrients become available. Alate flights are initiated by the first summer convectional storms. These and later intense storms erode the nitrogen-enriched carton to the soil surface. Foraging by both termites and predators (Whitford and Ettershank 1975, Whitford 1978b, Johnson and Whitford 1975) tends to maximize predation at these times. If decomposition in deserts is "pulsed" by rainfall as Noy-Meir (1974) and others suggest, pulsed release of nutrients from termite colonies will influence these processes. If available nutrients in the surficial soil layers become limited during sporadic moist periods in the desert, then the coincident input of nutrients from termites would play an important role in desert nutrient dynamics.

Direct effects of termites on plant decomposition include a 14–20% removal of N, P, and S from annual forbs and grasses, and an inferred 1–6% removal of these nutrients from the perennials and litter. With the possible exception of seed consumers, we know of no desert consumer with such wide access to plant and litter nutrient pools. It appears that further utilization of these pools by termites is limited by their ability to establish colonies in the face of predation. The resultant patchy use of the environment, and the tendency for nutrients released from termites to be spatially concentrated by consumers, may have unrecognized effects on the structure of desert plant communities.

Indirect effects of termites on plant decomposition include one case of nutrient accumulation as a result of carton construction, and several of reduced losses of nutrients, perhaps by reducing leaching. Carton is washed from plant structures by rainfall during the summer convective storms or broken up by wind. If leaching losses are high at such times, then the carton may influence the transfer of nutrients to the rhizosphere beyond its own content.

Experiments involving termite removal with insecticides produced dramatic increases in forb and grass biomass and litter (Bodine and Ueckert 1975), and changes in diversity and dominance of annuals (Whitford et al. unpublished data). Insecticide effects of removing seed-harvesting ants and the rapid release of nutrients from dead insect biomass resulting from insecticides in these experiments need critical appraisal. Eventually, though, a steady state between plant uptake and microbial/fungal decomposition and leaching would obtain, and the distribution of nutrients in the soil column in the absence of termite nutrient dynamics could be examined. If annual plants depend partially on the episodic release of nutrients in termite carton and biomass, annual plant densities would be expected to decline after the initial increase, as nutrients released by decomposition are incorporated into perennial plant tissue, and become less available at the soil surface. An aspect of alate flights that has been noted (Ghilarov 1962) is the accumulation of alate wings on the soil surface. If alate wings are readily decomposable, they may act in a manner ecologically similar to Stark's (1972) pollen rain, and stimulate litter decomposition.

In spite of these termites' preference for dead plants and litter, they have been characterized as competing with rangeland

herbivores (Bodine and Ueckert 1975; Spears et al. 1975), and insecticide control measures suggested. We have shown that the role of termites in desert ecosystems is very different from cattle. It remains doubtful that the long-term effect of such insecticides will enhance either stability or productivity of desert ecosystems.

References

- Basalingappa S (1970) Environmental hazards to reproductives of *Odontotermes assmuthi* (Holmgren). Ind Sci Cong Assoc Proc 57(4): 409
- Beneman JR (1973) Nitrogen fixation in termites. Science 181:164–165
- Black CA (1965) Methods of soil analysis, Part 2: Chemical and microbiological properties. Amer Soc of Agron Inc Madison Wisc
- Bodine MC, Ueckert DN (1975) Effect of desert termites on herbage and litter in a shortgrass ecosystem in west Texas. J Range Mgt 28:353–358
- Bouillon A (1970) Termites of the Ethiopian region. In: K Krishna and FM Weesner, (eds), Biology of termites. Vol II Academic Press, NY p 154–280
- Breznak JA, Brill WJ, Mertins JW, Coppel HC (1973) Nitrogen fixation in termites. Nature 244:577–580
- Catana AJ, Jr (1963) The wandering quater method of estimating population density. Ecology 44:349–360
- Chapin FS III, Barsdale RJ, Barel D (1978) Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. Oikos 31:189–199
- Chew RM (1974) Consumers as regulators of ecosystems: an alternative to energetics. Ohio J Sci 74:359–370
- Cottam G, Curtis JT (1956) The use of distance measure in phytosociological sampling. Ecology 37:451–460
- Eriksson E (1971) Compartment models and reservoir theory. Ann Rev Ecol Syst 2:67–84
- Ettershank G, Ettershank J, Bryant M, Whitford WG (1978) Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. J Arid Environ 1:135–139
- Fahey TJ (1979) Decomposing lodgepole pine needles. Bull Ecol Soc Am 60:85
- French JRJ, Turner GL, Bradley JF (1976) Nitrogen fixation by bacteria from the hindgut of termites. J Gen Microbiol 95:202–206
- Ghilarov MS (1967) Termites of the USSR, their distribution and importance. In Termites in the Humid Tropics, UNESCO, Paris
- Hardy RFW, Burns RL, Holsten RD (1973) Applications of the acetylene-ethylene reduction assay for measurement of nitrogen fixation. Soil Biol Biochem 5:47–81
- Haverty MI (1974) The significance of the subterranean termite, *Heterotermes aureus*, as a detritivore in a desert grassland ecosystem. Ph D diss, University of Arizona Tucson Ariz
- Haverty MI, Nutting WL (1975) Natural wood preferences of desert termites. Ann Entomol Soc Amer 68:533–536
- Haverty MI, Nutting WL, LaFage JP (1975) Density of colonies and spatial distribution of foraging territories of the desert subterranean termite, *Heterotermes aureus* (Snyder). Environ Entomol 4:105–109
- Haverty MI, Nutting WL, LaFage JP (1976) A comparison of two techniques for determining abundance of subterranean termites in an Arizona desert grassland. Insectes Sociaux 23:175–178
- Houghton FE (1972) Climatic guide, New Mexico St. Univ., Las Cruces, New Mex, 1851–1971. New Mex Agr Res Rep 230:1–20
- Johnson KA, Whitford WG (1975) Foraging ecology and relative importance of subterranean termites in Chihuahuan desert ecosystems. Environ Entomol 4:66–70
- Kitson RE, Mellon MG (1944) Colorimetric determination of phosphorus as molybdivanadophosphoric acid. Anal Chem 16:379–383
- Kleiner D (1975) Fixation of atmospheric nitrogen by microorganisms. Angew Chem Int Ed 14:80–84
- LaFage JP, Haverty MI, Nutting WL (1976) Environmental factors correlated with the foraging behavior of a desert termite *Gnathamiotermes perplexus* (Banks) (Isoptera: Termitidae). Sociobiol 2:155–169

- Lee KE, Wood TG (1971) *Termites and Soils*. Academic Press, London, Great Britain
- Ludwig JA, Reynolds JF, Whitson PD (1975) Size-biomass relationships of several Chihuahuan desert shrubs. *Amer Midl Natur* 94:451-461
- Mattson WJ, Addy ND (1975) Phytophagous insects as regulators of forest primary production. *Science* 190:515-522
- McNabb DH, Geist JM (1979) Acetylene reduction assay of symbiotic nitrogen fixation under field conditions. *Ecology* 60(5):1070-1073
- Nes P (1979) Routine measurement of total sulfur in biological material. *N Zeal J Sci* 22:269-272
- Noy-Meir I (1979) Desert ecosystems: Higher trophic levels. *Ann Rev Ecol Syst* 5:195-214
- Nutting WL (1969) Flight and colony foundation. In: Krishna and FM Weesner, eds. *Biology of Termites*, Vol I. Academic Press New York p 233-283
- Nutting WL, Haverty MI (1976) Seasonal production of alates by five species of termites in an Arizona desert grassland. *Sociobiology* 2:145-153
- O'Brien RT (1978) Proteolysis and ammonification in desert soils. In: NE West and J Skujins (eds), *Nitrogen in Desert Ecosystems*. Dowden, Hutchinson and Ross, Inc Strousburg, Penn p 50-59
- Pianka ER (1973) The structure of lizard communities. *Ann Rev Ecol Syst* 4:53-74
- Pomeroy LR (1970) The strategy of mineral cycling. *Ann Rev Ecol Syst* 1:171-190
- Potts M, Krumbein WE, Metzger J (1978) Nitrogen fixation in anaerobic sediments determined by acetylene reduction, a new ^{15}N field assay, and simultaneous total N - ^{15}N determination. In: WE Krumbein (ed), *Environmental Biogeochemistry and Geomicrobiology*. Vol 3: Methods, metals and assessment. Ann Arbor Science Publishers Inc Ann Arbor Mich
- Rehder H, Schäfer A (1978) Nutrient turnover studies in alpine ecosystems: IV. Communities of the central Alps and comparative survey. *Oecologia (Berl)* 34:309-327
- Reiners WA (1972) Structure and energetics of three Minnesota forests. *Ecol Monogr* 42:71-94
- Schaefer DA, Whitford WG (1979) Nitrogen fixation in desert termites. *Bull Ecol Soc Am* 60:128
- Sokal RR, Rohlf FJ (1969) *Biometry* WH Freeman and Co San Francisco
- Spears BM, Ueckert DN, Whigham TL (1975) Desert termite control in short-grass prairie: Effect on soil physical properties. *Environ Entomol* 4:899-904
- Stark N (1972) Nutrient cycling pathways and litter fungi. *Bio-science* 22:355-360
- Steppe W (1976) Invertebrate predation on termites of the African savannah. *Insectes Sociaux* 17:205-218
- Stewart BA, Porter LK, Beard WE (1969) Determination of total nitrogen and carbon in soils by a commercial Dumas apparatus. *Proc Soil Sci Soc Amer* 28:269-272
- Whitford WG, Ettershank G (1975) Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environ Entomol* 4:689-696
- Whitford WG (1978) Foraging in seed-harvester ants *Pogonomyrmex spp.* *Ecology* 59:185-189
- Whitford WG (1978b) Structure and seasonal activity of Chihuahuan desert ant communities. *Insectes Sociaux* 25:79-86
- Whitford WG, Depree E, Johnson P (1981) Foraging ecology of two Chihuahuan desert ant species: *Novomessor cockerelli* and *Novomessor albisetosis*. *Insectes Sociaux* 27:148-156
- Wilson EO (1971) *The insect societies*. Harvard Univ Press Cambridge Mass
- Wood TG, Sands WA (1978) The role of termites in ecosystems. In: MV Brian, (ed), *Production Ecology of Ants and Termites*. Cambridge Univ. Press, Cambridge, Great Britain p 245-292

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