

Analysis of Above-ground Gallery Construction by the Subterranean Termite *Gnathamitermes tubiformans* (Isoptera: Termitidae)

WILLIAM P. MACKAY, JAMES H. BLIZZARD,
JACQUELINE J. MILLER, AND W. G. WHITFORD

Department of Biology, Box 3AF, New Mexico State University,
Las Cruces, New Mexico 88003

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ABSTRACT *Gnathamitermes tubiformans* (Buckley), a common termite species in the northern Chihuahuan Desert of North America, builds mud galleries around standing dead vegetation and other food materials after periods of rain. The termites graze only the surface of standing dead branches, tissues highest in nitrogen content. We hypothesized that termites invest more energy in gallery construction than they obtain from the wood they consume. We estimated energy costs of gallery construction from analysis of gallery material and construction behavior of the termites. In addition to obtaining a food source relatively high in nitrogen, the estimated energy that termites obtain from the wood is six orders of magnitude greater than the energy invested in gallery construction. Therefore, the termites obtain much more energy from wood than they invest in gallery construction.

Gnathamitermes tubiformans (Buckley) is an important decomposer of organic matter in the Chihuahuan Desert (Parker et al. 1982, Whitford et al. 1982a). It also plays an important role in nitrogen cycling (Schaefer and Whitford 1981). Subterranean termites, such as *G. tubiformans*, also affect the vegetative composition of the ephemeral flora (Parker et al. 1982).

Above-ground activity of *G. tubiformans* occurs when soils are wet, following rains between April and November. At such times termites construct mud galleries around dead (and occasionally living) branches of several species of desert shrubs, forbs, and grasses. The galleries may protect termites from desiccation, but as they are very porous, their primary importance may be as protection from predators. We observed that although termites construct galleries up to a height of a meter above ground level (Fig. 1), they consume only surface material on the dead stems to a depth of ca. 0.5 mm. We formulated two hypotheses: First, branch surfaces are higher in nitrogen than are subsurface tissues and this explains why the termites do not consume more of the branches. Second, cost (in terms of energy) of gallery construction is greater than the energy termites obtain from eating the wood. Therefore, termites invest energy in construction to obtain the high-nitrogen food source.

Materials and Methods

Study Site. The study was conducted on the LTER (Long Term Ecological Research) Jornada Site located 40 km NNE of Las Cruces, Dona Ana County, N. Mex. The long-term average annual

precipitation is 210 mm, 55% of which occurs between July and September as convectional storms. Summer maximum air temperatures average 40°C and winter air temperatures regularly fall below 0°C. The site is dominated by creosote bush (Whitford et al. 1982b).

Wood Nitrogen. Wood samples were collected in the field and analyzed for total nitrogen content in mid-January and mid-December 1983. The bark was removed from the living branches (bark was not present on the dead branches). The surface material was scraped off to a depth of ca. 0.5 mm; the second layer consisted of the next 1 mm of material. The heartwood was removed by splitting the branches. The resulting material was ground and passed through a #40 mesh sieve. Nitrogen analysis was done with a micro Kjeldahl technique (Tecator manual, Digestion System 40). Hydrogen peroxide was not used in the analysis and the samples (0.1 g) were placed in the Tecator Digestion System for ca. 1 h until the system reached 370°C and left for an additional 1 h at 370°C.

Gallery Material. Gallery material was collected in October 1983, when the termites were active above ground. The length and diameter of sections of gallery were recorded and the gallery was taken to the laboratory for drying, weighing, and particle size analysis.

Results

Higher levels of total nitrogen were found on the outer surfaces of dead branches of four desert perennial plants in January and December of 1983 (Fig. 2-4). There was no consistent pattern to distinguish between the nitrogen levels of standing

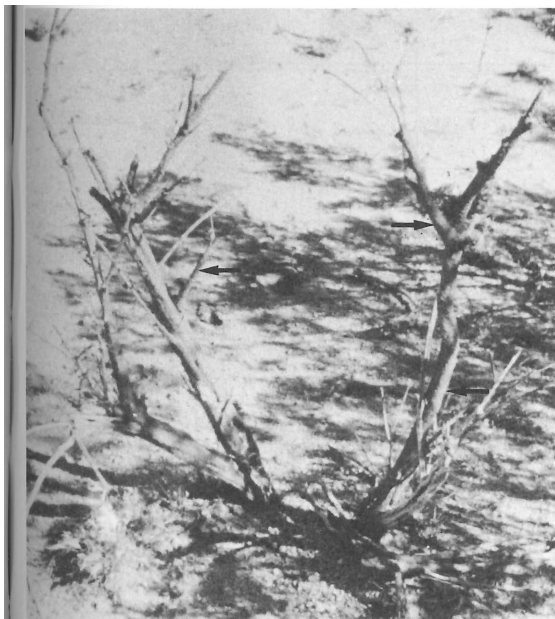


Fig. 1. Gallery system of *G. tubiformans* around branches of a standing dead creosote bush.

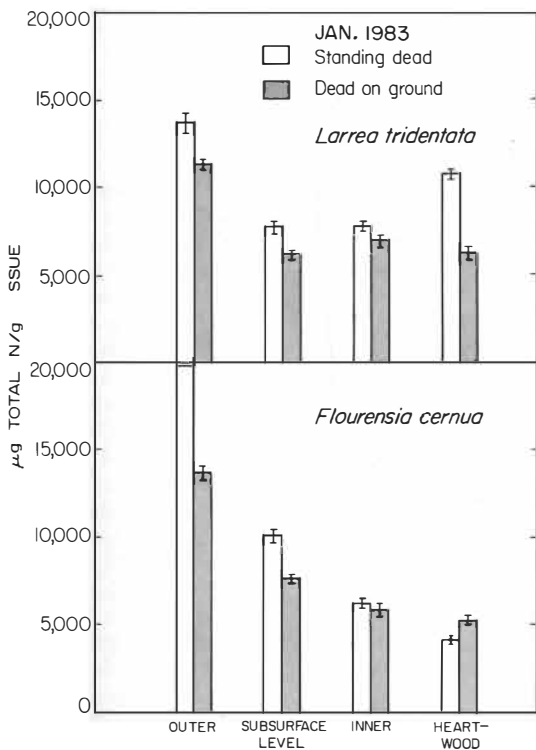


Fig. 2. Total nitrogen levels of wood of creosote bush (*Larrea tridentata*) and tarbush (*Flourensia cernua*) in January 1983. Both standing dead and dead on ground are indicated. In all cases $n = 2$. The outer level

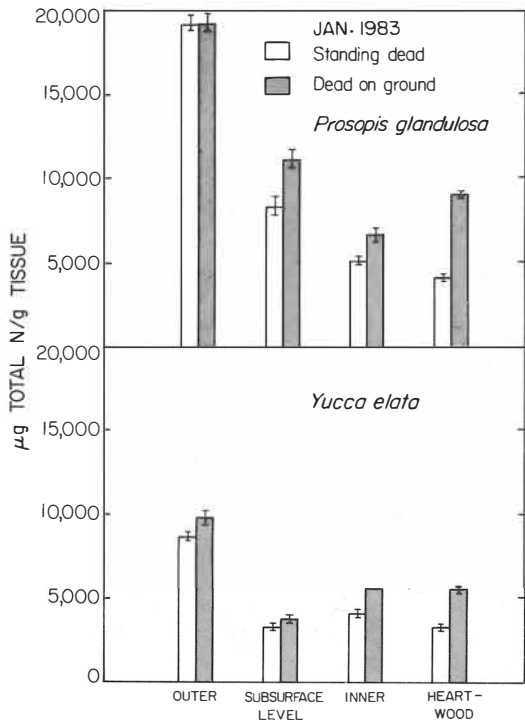


Fig. 3. Total nitrogen levels of wood of mesquite (*Prosopis glandulosa*) and soap-tree yucca (*Yucca elata*) in January 1983.

dead branches and those dead on the ground. In January, standing dead creosote and tar bush branches tended to have higher levels of nitrogen than those on the ground (Fig. 2). Dead branches on the ground tended to have higher nitrogen levels than those standing in mesquite and soap-tree yucca (Fig. 3). For creosote bush, the nitrogen content of dead branches on the ground was not significantly higher than the standing dead branches in December 1983 (Fig. 4). Termites grazed ca. 0.5 mm of surface material from the branches, the layer with the highest nitrogen level. Comparisons of grazed and ungrazed branches from the same plants demonstrate that the termites removed the surface material with the higher nitrogen levels (Fig. 5).

Observations of gallery construction suggested that termites expended a large amount of energy to obtain a small return. Therefore, we estimated the energy cost of gallery construction and the energy the termites obtained from the wood ingested.

A mixture of several sections of gallery material

← corresponds to the outer 0.5 mm of the branch. The subsurface is a 1-mm layer immediately below outer level. The inner level is the following 1 mm and the heartwood is the innermost part of the branch.

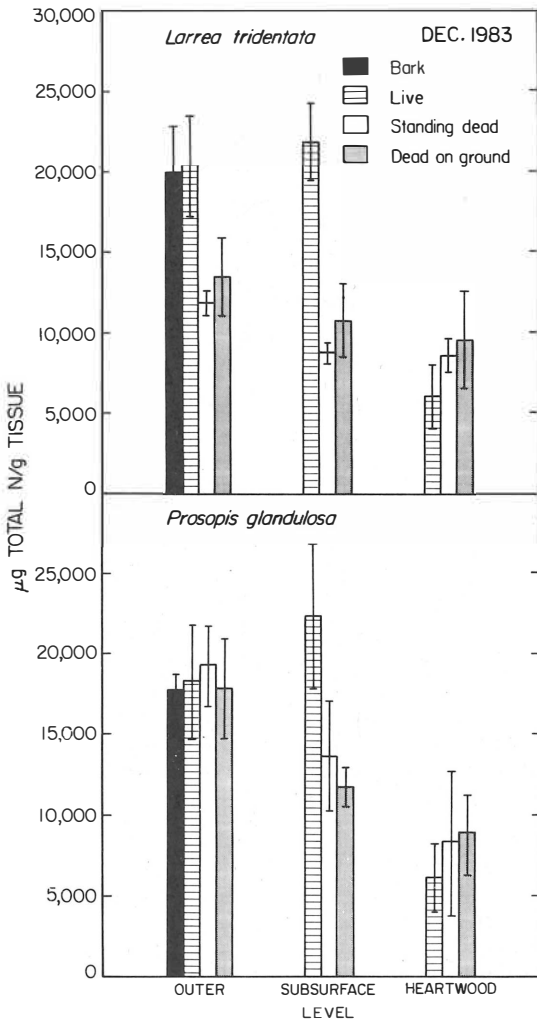


Fig. 4. Total nitrogen levels of creosote bush (*L. tridentata*) and mesquite (*P. glandulosa*) in December 1983. In the living material, the bark and the material immediately under the bark are both indicated in the outer layer. Levels are explained in legend of Fig. 2. In all cases $n = 4$.

was sieved to determine the size-class composition (Table 1). Most of the material was $<500 \mu\text{m}$ in diameter. This is the "mud" termites use to "cement" sand grains together to form the gallery. About 11% of the gallery material was composed of particles $\geq 500 \mu\text{m}$ in diameter. A total of 1,651 of these larger particles was present in a 6.47-g sample of gallery. Each termite carries a single particle in its mandibles, which it cements into place during gallery construction (W.G.W., personal observation). Therefore, the 6.47 g required 1,651 termite trips. Termites apply the material in the form of a mud that dries rapidly. Wetting experiments in the lab suggested that the mud is at least 15% water. Thus, the gallery in Table 1

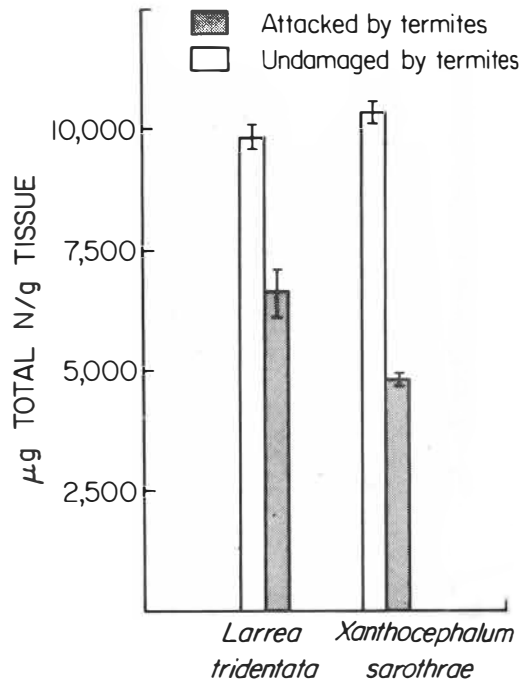


Fig. 5. Total nitrogen content of termite-stripped and undamaged standing dead wood of creosote bush (*L. tridentata*) and snakeweed (*Xanthocephalum sarothrae*). Samples for each species were collected from the same plant; $n = 4$ for creosote bush and $n = 2$ for snakeweed.

weighed at least 7.4 g at the time it was constructed. Each termite, therefore, carried 4.5 mg (7.4 g per 1,651 trips), more than twice its weight (wet weight of worker termites = $2.0 \text{ mg} \pm 0.3$, $n = 29$). A termite plus the particle and the mud it carries weighed ca. 6.5 mg. The amount of energy expended to raise this weight 1 cm is as follows: $(0.0065 \text{ g})(980 \text{ cm/s}^2)(1 \text{ cm}) = 6.37 \pm 0.3 \text{ g cm}^2 \cdot \text{s}^{-1} = 6.37 \text{ ergs}$, disregarding friction and assuming 100% efficiency. The net cost of moving an ant loaded with 1.4-fold its mean body weight approximately doubles over that of an unloaded ant (Nielsen et al. 1982). Assuming that energy costs of work for termites and ants are similar, we doubled the cost to $12.8 \text{ ergs} \cdot \text{cm}^{-1}$. A gram of gallery contained 255 particles, thus requiring 255 termite trips. A 1-cm length piece of gallery weighed ca. 0.15 g, requiring about 38 termite trips for construction. Therefore, the energy cost per centimeter is ca. 486 ergs. This is assuming that the height of the gallery system and mass per unit length are independent, which is not a valid assumption. Examination of the masses per unit lengths versus the total length of the gallery system showed that longer gallery systems in standing dead vegetation are more massive per unit length (Fig. 6). Apparently termites construct taller gallery systems of greater structural

Table 1. Size-class composition of material used by *G. tubiformans* in construction of gallery

Size class	Dry mass (g)	% Of total mass	Mean dry mass of particle ^a (mg) ±SD	No. of particles
X < 500 μm	5.77	89.1	—	—
500 μm < X < 710 μm	0.46	7.2	0.32 ± 0.03	1,347
710 μm < X	0.24	3.7	0.74 ± 0.06	304
Totals	6.47	100		1,651

^a Based on six subsamples of 10 to 100 individual particles each.

strength as taller gallery systems have a greater mass per cm than do shorter gallery systems.

We took into account the additive costs of termites raising their loads in the gallery system and the increase of mass per length of branch (Fig. 6) and calculated the costs of gallery construction (Fig. 7). The costs to construct heights up to 30 cm were relatively low. For heights from 40 to 50 cm, the costs rapidly increased.

The termites obtained more energy from the wood they removed than they invested in the production of the gallery system. For example, a 30-cm gallery system cost 0.042 J to construct. We scraped the surface of dead branches of snake-weed with a knife to approximate the amount of material grazed by the termites. A sample of 18 branches of various weights and diameters indicated that the termites removed 13 ± 0.6 SD mg·cm⁻¹. Using a value of 5,000 cal·g⁻¹ (MacKay 1981), this would be about 65 cal·cm⁻¹ or 270 J·cm⁻¹. From a 30-cm branch, the termites obtained 1,950 cal or about 8,100 J. Thus, they obtained

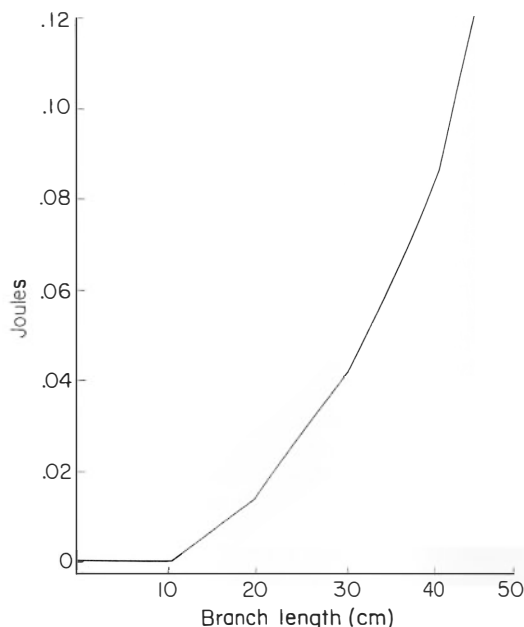


Fig. 7. Relationship between cost of construction of the gallery system of *G. tubiformans* and the height of the standing dead branches.

more than 193,000-fold as much energy as they invested in construction of the tunnel system. This is undoubtedly an underestimate of the actual costs, as we have disregarded the energy used to obtain the mud and sand particles, which may occur several centimeters below the soil surface. The construction of the gallery and grazing of the wood surface also require an energy investment. Our estimates are not accurate, but in any case the termites do receive much more energy than they invest, in addition to consuming tissues relatively high in nitrogen.

Discussion

We have found that *G. tubiformans* surrounds standing dead perennial branches with mud galleries, but consumes only surface tissues. We have shown that surface tissues of branches have higher levels of nitrogen than the subsurface, which may explain why termites consume only such tissues. Thus, the data support our first hypothesis. Our data clearly allow rejection of our second hypothesis, that the cost of construction of the gallery system would outweigh the energetic benefit that the termites would obtain from eating the wood, but they would construct galleries to obtain tissues higher in nitrogen. Actually, the termites obtain thousands-fold more energy than they invest.

Why don't the termites consume more of the branch? There are two possible hypotheses. First, the part of the branch below the outer surface is mostly carbon and not useful to the termites be-

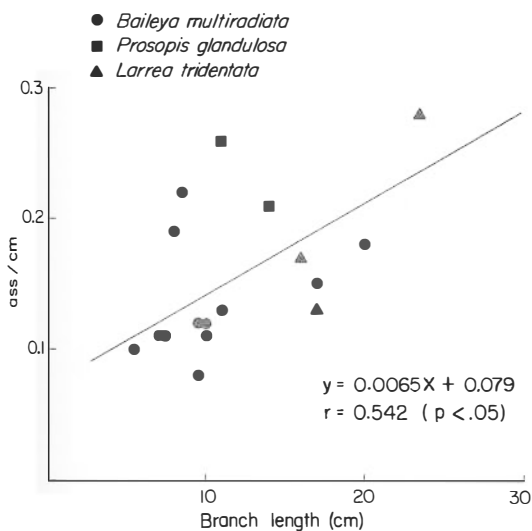


Fig. 6. Effect of mass/cm versus height of the gallery system of *G. tubiformans* on desert marigold (*Baileya multiradiata*), mesquite, and creosote bush.

cause they are not carbon-limited. We have evidence to support this hypothesis. The total masses of wood in the study area are quite high. Preliminary estimates range from 450 to over 7,000 kg·ha⁻¹ (unpublished data). Most wood present in the area is not attacked by termites during any one year. The termites also graze on leaf litter (Whitford et al. 1983), which is present in large quantities. It appears there is an overabundance of carbon available to the termites. Second, the branch is a structurally important component of the gallery system, when the gallery material is removed from the branch, the system is very fragile. We have two lines of evidence that tend to allow rejection of this hypothesis. First, termites graze only the surface, even when the branch has a diameter of up to 1.5 cm. Further grazing would not weaken the branch to the point where it would break. Second, termites occasionally eat all of the branches with diameters <3 mm. This may hasten the breakup of the gallery system, but by the time this happens, the termites have eaten most of the branch.

Ganhamitermes tubiformans is the most important organism involved in the mass loss of wood in the northern Chihuahuan Desert (unpublished data). Mass loss occurs from the outside in a process similar to what occurs in streams (Dudley and Andersen 1982) and much different from what occurs with wood in other terrestrial ecosystems (Abbott and Crossley 1982).

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References Cited

- Abbott, D. T., and D. A. Crossley, Jr. 1982. Wood litter decomposition following clearcutting. *Ecology* 63: 35-42.
- Dudley, T., and N. H. Andersen. 1982. A survey of invertebrates associated with wood debris in aquatic habitats. *Melandria* 39: 1-21.
- MacKay, W. P. 1981. A comparison of the ecological energetics of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Ph.D. dissertation, University of California, Riverside.
- Nielsen, M. G., T. F. Jensen, and I. Holm-Jensen. 1982. Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* (Formicidae). *Oikos* 39: 137-142.
- Parker, L. W., H. G. Fowler, G. Ettershank, and W. G. Whitford. 1982. The effects of subterranean termite removal on desert soil nitrogen and ephemeral flora. *J. Arid Environ.* 5: 53-59.
- Schaefer, D. A., and W. G. Whitford. 1981. Nutrient cycling by the subterranean termite *Gnathamiitermes tubiformans* in a Chihuahuan desert ecosystem. *Oecologia* (Berlin) 48: 277-283.
- Whitford, W. G., Y. Steinberger, and G. Ettershank. 1982a. Contributions of subterranean termites to the "economy" of Chihuahuan desert ecosystems. *Ibid.* 55: 298-302.
- Whitford, W. G., R. Repass, L. Parker, and N. Elkins. 1982b. Effects of initial litter accumulation and climate on litter disappearance in a desert ecosystem. *Am. Midl. Nat.* 108: 105-110.
- Whitford, W. G., D. W. Freckman, L. W. Parker, D. Schaefer, P. F. Santos, and Y. Steinberger. 1983. The contributions of soil fauna to nutrient cycles in desert systems, pp. 49-59. In P. Lebrun, H. M. Andre, A. deMedts, C. Gregoire-Wibo, and G. Wauthy [eds.], Proceedings, 8th International Colloquium of Soil Zoology, Belgium—New trends in soil biology. Dieu-Brichart, Louvain-La-Neuve, Belgium.

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