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LIGNOCELLULOSE DIGESTION IN TERMITES

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Abstract. Termites obtain energy from wood through a sequence of distinct processes. Chewing exposes the plant cell wall, enzymes from the host and its symbionts cleave polysaccharides, and microbial fermentation produces acetate. Direct evidence for host nutrition comes from Reticulitermes flavipes, where acetate occurs in the haemolymph and termite tissues oxidise it. Lignin can undergo structural change during gut passage, but its fate cannot be inferred from cellulose loss. Uzbek studies of Anacanthotermes link food preferences with regional evidence on gut bacteria. The fraction of ingested carbon reaching the host as acetate remains unmeasured.

Keywords: termite digestion · lignocellulose · host cellulase · hindgut fermentation · acetate · Anacanthotermes



Figure 1. Digestive tract of a *Reticulitermes flavipes* worker. Dashed line separates host-dominated tissues (left) from hindgut (right). Photo by J. A. Smith, from Scharf et al. [3], figure 1A. Original figure and CC BY credit.

Scope and approach

This narrative review follows plant carbon from ingested fibre to host tissues. It compares regional and international studies by species, gut compartment and type of measurement (table 1) [1–3, 18–23].

Table 1. Measurements that distinguish physical processing from chemical breakdown.

Component or step	Informative observation	What the observation establishes
Fragmentation	Reduced particle size or altered exposed surface.	Physical access has changed. A polymer chain may still be intact.
Cellulose	Shorter glucan chains or sugars released from a defined cellulose substrate.	Glycosidic bonds have been cleaved under the conditions examined.
Hemicellulose	Changes in xylan or other named polysaccharides and their products.	A specified part of the cell-wall matrix has been transformed.
Lignin	Changes in aromatic units or interunit linkages in matched feed and residues.	The aromatic polymer has been modified. Its carbon fate needs separate evidence.

Plant fibre and its digestive partners

The mandibles reduce wood to particles, exposing cellulose microfibrils embedded in a matrix of hemicelluloses and lignin. Enzymes cleave the carbohydrate chains. Lignin undergoes a different set of reactions (figure 2) [1, 4–6].

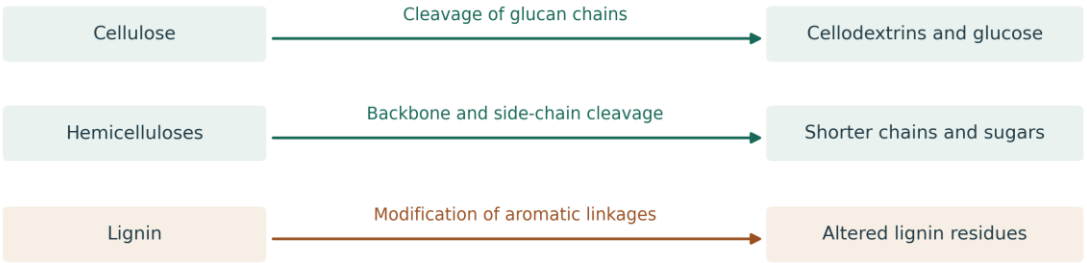


Figure 2. Chemical outcomes for three plant-wall constituents. Sugar release identifies carbohydrate hydrolysis. Changes in aromatic linkages require separate measurements. Conceptual synthesis of [1, 4–6].

In isotope-labelled wood fed to *Nasutitermes*, lignin lost major interunit linkages and methoxyl groups during gut passage [5]. Xue et al. also found differences in residual polysaccharides between poplar fed to *Nasutitermes* and pine fed to *Cryptotermes* [6].

Both the wood and the host varied in that comparison.

Host enzymes and microbial partners

The termite *Reticulitermes speratus* encodes its own endoglucanase, which cleaves bonds within cellulose chains [4]. In *R. flavipes*, combining the host and hindgut fractions increased glucose release [3]. The hindgut contains several protist genera (figure 3), so the activity of the combined fractions cannot be assigned to one organism.

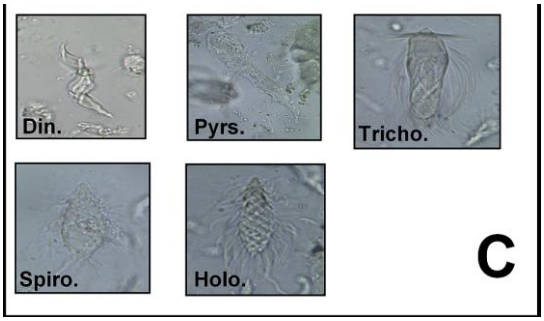


Figure 3. Hindgut protists in *R. flavipes*. From the upper left: *Dinenympha*, *Pyrsonympha*, *Trichonympha*, *Spirotrichonympha* and *Holomastigotes*. Cropped from Scharf et al. [3], figure 1C. Panel sizes do not provide a common scale. Original CC BY figure.

Table 2. Three digestive arrangements documented in termites [1–3, 7, 8, 17].

Example	Who processes the fibre?	Feature that changes the interpretation
Reticulitermes spp.	Host tissues, hindgut flagellates and associated prokaryotes.	A whole-hindgut preparation includes several interacting partners.
Wood-feeding Nasutitermes spp.	Host enzymes and a prokaryotic gut community without cellulolytic flagellates.	Bacteria attached to wood fibres can contribute strongly to xylan breakdown.
Fungus-growing Macrotermes natalensis	The Termitomyces fungus on the comb, together with the termite and its gut community.	An important phase of plant decomposition takes place outside the gut.

Hindgut fermentation and acetate uptake

Oxygen penetrated 150–200 µm into the peripheral hindgut contents of *R. flavipes* and *Nasutitermes lujae* [9]. In *R. flavipes*, hydrogen also varied with distance from the gut wall [11].

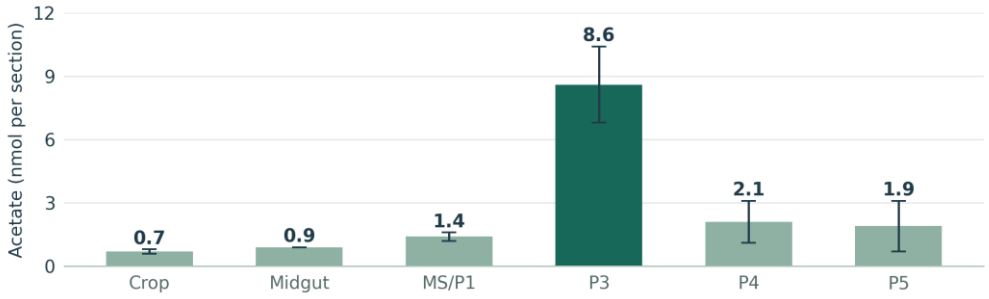


Figure 4. Acetate pool per gut section in *Nasutitermes corniger*. Means and mean deviations are from two pooled measurements of 40 sections each. MS/P1 combines the mixed segment and first hindgut segment. P3 is the enlarged hindgut paunch. Redrawn from table 1 of Köhler et al. [10].

In *N. corniger*, the enlarged P3 compartment held a mean of 8.6 nmol of acetate, compared with 0.9 nmol in the midgut (figure 4) [10]. The pool size records how much was present when sampled. A production rate also requires a time interval.

Microbes generate acetate directly from sugars or by reducing carbon dioxide with hydrogen. The latter pathway has been demonstrated both in a termite-gut community and in termite-derived spirochetes [13, 14]. Methanogens can also consume hydrogen (figure 5) [1, 2].

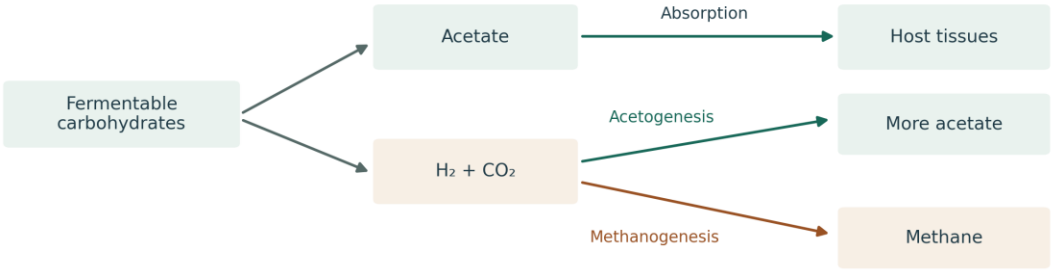


Figure 5. Selected fates of fermentation products. Both routes to acetate can contribute to the host-accessible pool. Arrows indicate the direction of reactions or transport. Based on [1, 12–14].

Table 3. Acetate availability and use in wood-feeding termites [12].

Measurement	Published observation	Biological interpretation
Acetate in hindgut fluid	57.9–80.6 mM across three wood-feeding species.	A concentrated extracellular pool was present.
Acetate production in R. flavipes	Estimated 20.2–43.3 nmol per termite per hour.	Production can be compared with respiratory demand on a time basis.
Acetate in R. flavipes haemolymph	9.0–11.6 mM.	Acetate was present in the fluid circulating through the host.
Oxidation by host tissue	Termite tissues converted acetate to CO_2.	Host metabolism can use absorbed acetate as a fuel.

In *R. flavipes*, estimated acetate production could supply 77–100% of respiratory demand under the study conditions [12]. Wood assimilation requires a separate carbon balance.

What comparative genomics can establish

Arora and colleagues sequenced 145 gut samples and used a subset of 129 assemblies to compare prokaryotic carbohydrate-active enzyme and binding-module categories [15]. Across that subset, they reported 346 categories. Glycoside hydrolases accounted for 205 of them (figure 6). The unit is a distinct category detected somewhere in the survey, so the chart describes functional diversity across the dataset.

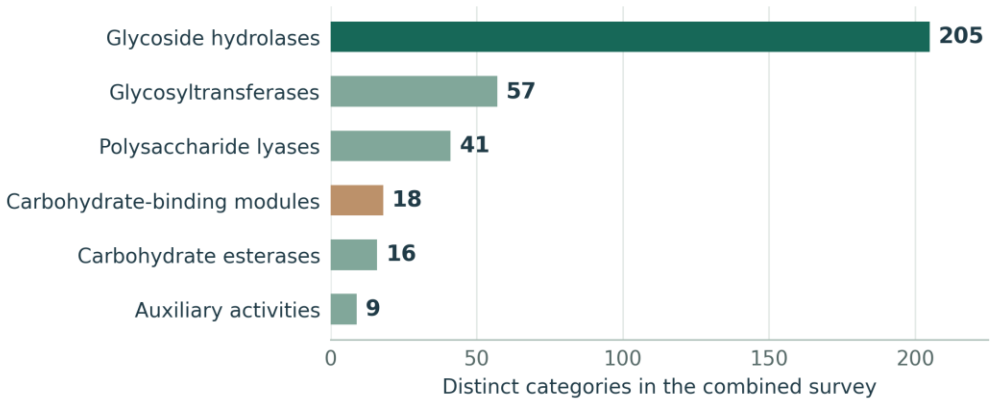


Figure 6. Number of distinct carbohydrate-active enzyme or binding-module categories in 129 gut metagenomes, from Arora et al. [15]. Carbohydrate-binding modules bind substrates and are distinguished from catalytic classes. The bars do not represent transcript levels or enzyme activities.

Linking gene sequences to activity

In wood-feeding higher termites, metagenomes and activity assays identified microbial contributions to cellulose and xylan hydrolysis [7]. Tokuda et al. traced much of the xylan degradation to spirochetes associated with ingested fibres [8].

A gene on a termite genome can be assigned to the host, while a microbial metagenome describes genes present in the associated community. Liu and colleagues compared genome assemblies for 45 termite species and two cockroaches [16]. That host-genome dataset complements the microbial survey. The counts from the two studies cannot be summed to obtain the enzyme complement of a typical termite because they sample different organisms and use different units.

Table 4. Evidence needed to move from genetic potential to carbon use [3, 7, 8, 12, 15].

Observation	Inference supported	Next question
A sequence matches a known enzyme family.	The sample contains a candidate function.	Is the gene expressed, and which substrate does its product act on?
A protein or transcript is associated with a fibre.	A candidate contributor is present at a plausible site.	Is cleavage of the proposed substrate measurable there?
Sugars appear in an activity assay.	Hydrolysis occurred under the assay conditions.	What happens to those products in the intact gut?
Diet-derived carbon reaches a host metabolite.	Carbon has crossed a defined physiological boundary.	How much crosses per individual and unit time?

Relative abundance also has a denominator. One family can gain a larger share because other families declined. Comparisons among related termites must additionally account for shared ancestry, especially when close relatives share a diet [15, 16].

Harvester termites in Uzbekistan

In laboratory and field trials, *Anacanthotermes turkestanicus* consumed sunflower and sweet sorghum stems [18]. Ganieva, Khashimova, Rustamov and Akhmedov also compared attraction to food baits [21]. These studies establish a food preference. Measuring acetate yield would require the amount ingested and the carbon recovered from it.

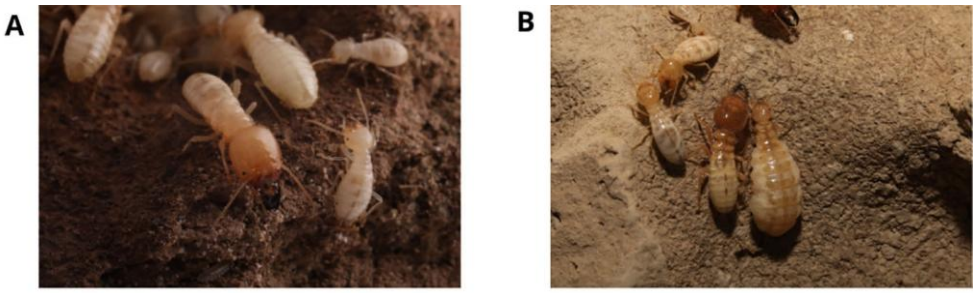


Figure 7. *Anacanthotermes ahngerianus* (A) and *A. turkestanicus* (B), the two species compared in the Uzbek gut survey. Photographs by Jan Šobotník, cropped from panels A and B of figure 1 in Togaev et al. [19]. CC BY 4.0.

Togaev et al. compared *A. ahngerianus* from Khiva District with *A. turkestanicus* from Khatirchi District (figure 7) [19]. Each species contributed one pool of 15 workers. Species, locality and habitat varied together, and variation among colonies could not be estimated.

Table 5. How local evidence can be carried into a study of digestion.

Local evidence	What is documented	What still requires measurement
Food trials and attractants [18, 21]	Use of selected substrates and responses to bait materials.	Ingested carbon, polymer-specific loss and metabolite yield.
Whole-gut DNA [19]	Taxonomic profiles and predicted functions in two pooled samples.	Enzyme activity and production rates in independent colonies.
Host identification [22]	Molecular confirmation of Amitermes rhizophagus in Uzbekistan.	The host identity of each new sample before comparing digestive traits.
Caste surveys [23]	The proportions of castes change across sampled nests and seasons.	Matched worker stages and collection dates for physiological comparisons.

Zakiryaeva, Utaganov, Ganieva and Rustamov compared gut regions of worker *A. ahngerianus* from Beruniy District, Karakalpakstan [20]. The hindgut had the largest cultivable bacterial count (figure 8). These counts measure growth in culture. They do not quantify cellulose breakdown or acetate absorption.

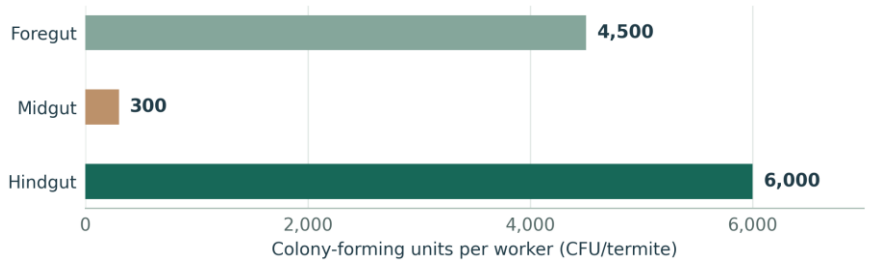


Figure 8. Cultivable bacteria reported for three gut regions of *A. ahngerianus* workers in Beruniy District [20]. Values are colony-forming units per termite for the indicated region. Values are the authors' general bacterial counts.

Conclusion

Evidence from wood-feeding termites links host and microbial enzymes to hydrolysis, fermentation to acetate, and acetate to host respiration [3, 4, 8, 12]. For Uzbek *Anacanthotermes*, the unresolved step is the transfer from a measured quantity of ingested plant carbon to acetate used by the worker [18–21].

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