

The order Isoptera and the importance of cellulose

The Isoptera, or termites, is an order of relatively primitive insects and is often lumped into a greater taxonomic group, the Dictyoptera, that includes the cockroaches (Blattodea) and the Mantises (Mantodea). The Dictyoptera itself is part of the greater collection of orthopteroid insects, such as grasshoppers, crickets and katydids, all of which have biting and chewing mouthparts (among other shared characteristics). The relationships between and among the various groups within the Dictyoptera and its place among the other orthopteroid taxa are handled well by Boudreaux (1). The phylogeny of the order Isoptera is presented in the works of Krishna (2) and Thorne and Carpenter (3). These works are recommended to readers interested in the relationships between these taxa.

The entire order Isoptera is eusocial (4). Thus, termites are not independent or solitary insects, as are other wood destroying organisms such as buprestid beetles, bark beetles, or siricid wasps. Due to their social structure, different termites are assigned different tasks within their colonies (division of labor). These divisions of labor divide termites into physically modified specialists, or castes. Labor is divided in a number of ways; for example, reproduction (queens, kings, supplementary reproductives, and winged alates), defense (soldiers in most species), and other activities such as tunnel construction, egg/brood care, limited defense, and (most important to humans) feeding. This final group of responsibilities belongs to the most versatile of the termite castes, the workers. They also represent the largest group of termites within a colony, as most individuals are workers, with much fewer soldiers, and even fewer still reproductive caste members (5). In the lower termites, such as the subterranean termites that are responsible for much damage to buildings, the workers are sometimes referred to as "pseudergates", or false workers, to indicate their prolonged ability to molt into other caste forms if required by the colony. It is generally thought that colonies are founded by a single pair of reproductives, but more recent genetic evidence suggests that this is not necessarily the case in some species (6). Kofoid (7) provides a still-relevant overview of basic termite biology, colony initiation and structure.

Most termite species are xylophagous, feeding on the lignocellulosic xylem of woody plants. For many years, termites were thought to be unable to produce any of their own cellulases for feeding. For this reason, it was argued that termites would always require the symbiotic association of microorganisms (protozoa, bacteria, or fungi) to produce these enzymes. Otherwise they could not obtain any nutrients from their food. Although this has now been demonstrated to be not entirely the case, it is still clear that a strong symbiotic relationship exists between termites and specific microorganisms. A requirement

Chapter 13

Termite Physiology in Relation to Wood Degradation and Termite Control

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The importance of termites (order Isoptera) in the degradation of wood (cellulose, hemicellulose, and lignin collectively) is discussed, and the relative contributions of termite enzymes and intestinal microfauna (protozoa and bacteria) are presented. We also provide an overview of the areas of cellulose degradation, and physiological (enzymatic and pheromonal) means of termite control. Discussion includes the currently known hormones and pheromones with application in control measures, and some reasons for their current use (or lack of use) in termite control. Termites are social insects, and hormonal/pheromonal control measures often do not have the same results as are expected with solitary pest species. Finally, a short discussion of the current trends in research on feeding and foraging behavior of subterranean termites is presented.

of symbionts for feeding is thought to have laid the groundwork for the eventual development of eusociality in the termites. More primitive ancestors of the termites, cockroaches of the family Cryptocercidae, share some of the same species of microfauna with the remaining member of the most primitive extant termite family Mastotermitidae (8). This information, along with comparative data from mitochondrial cytochrome oxidase subunit II, endo- β -1,4-glucanase, and ribosomal RNA, has led Lo *et al.* (9) to connect these two groups phylogenetically, a relationship also supported by Thorne and Carpenter (3), and McKittrick (8). Since microfauna are present in the hindguts of termites, they must be replenished at each molt (hindgut and foregut integuments are shed with the exuviae). This can be done by proctodeal feeding (direct anal feeding from one individual to the next) or through trophallaxis (regurgitated food passage between individuals). It is expected that proctodeal feeding is more important for transfer of microfauna, since the feces will have already passed through the donor's hindgut when they are expelled for the recipient. Note that although the hindgut is ectodermal in origin, absorption of nutrients does occur across the hindgut integument in termites (10).

Much of the interest in the Isoptera in the United States has been based on their economic importance. However, globally, termites are known for ecological contributions in breaking down cellulosic litter, and improvement of soils through aeration and nutrient cycling (11-13). While there are species in North America representing four of the five to seven termite families, only two families are considered economically important in terms of wood destruction. These are the drywood termites (family Kalotermitidae) and the subterranean termites (family Rhinotermitidae). The activities of termites are estimated to cost homeowners in the USA over \$1 billion annually (14). These costs are due mainly to the activities of subterranean termites, especially those belonging to the native North American genus *Reticulitermes* Holmgren, and the introduced species *Coptotermes formosanus* Shiraki. Due to their destructive potential, these species have been the subjects of much research on termite control technology (15-18). The following sections provide an overview of the current state of knowledge in using pheromones, physiological modifications, foraging behavior and nutritional ecology in the prevention of termite-based cellulose degradation. In discussing various species, it will soon become evident that the major effort rests on the Rhinotermitidae, due to its economic importance and subsequent representation in the literature.

The overall biology of the Isoptera is well beyond the scope of this article, but the reader is referred to a second chapter in this book (19), as well as to Kofoid (7), Krishna and Weesner (20), and Grassé (21) for further information. For information on the evolution of eusociality in the Isoptera, the reader should consult Bartz (22), and Myles and Nutting (23), contrasting their work with Hamilton (24, 25).

Pheromones

While hormones and pheromones are both chemical messengers in biological systems, designed to produce specific cell responses, they differ mainly in their target organisms. Chemicals that cause altered cell chemistry in the same individual that produced the chemicals are called hormones. Chemicals produced by an individual that alter the cell chemistry and behavior of another individual are pheromones. These definitions are nothing new, and certainly further subdivisions of each category exist. In our discussion, however, we will treat them separately, with hormones discussed in the Physiology section below.

Another reminder of the fact that termites differ from most other wood destroying insects in that they are eusocial is the type of pheromones that they produce. The following paragraphs illustrate the importance of trail-following pheromones in termites, due to their potential value in control efforts. For detailed descriptions of the glands involved in pheromone production by termites see Grassé (21).

Trail-following pheromones are perhaps the best studied pheromones aiding in the foraging and wood destroying behavior of termites. These pheromones are deposited from the sternal gland on the ventral abdomen (26). Many subterranean termites appear to use the same compound, cis-cis-trans-3,6,8-dodecatrien-1-ol, to mark trails to indicate food availability. Termites can be induced to follow artificial trails of this compound, either as extracts from the sternal gland (27), or extracts from decay fungi (28), and possible pheromone-based applications to termite control have been discussed since the 1960s. However, Grace (29) found that this compound may present a problem for long-term use in misguiding termites, since they acclimate to its presence over time. Other researchers (26, 30, 31) have presented evidence for multiple components in the trail-following pheromone blend, but no minor components have as yet been isolated or chemically identified. If identified, such minor components could encourage further development of control methods employing synthetic trails or of baits with more attractive matrices.

In addition to trail-following pheromones, other pheromones have promise for manipulation in termite control. As discussed below, soldier and nymph inhibition pheromones produced and distributed through the colony to maintain caste proportions (32-34) may have potential uses in combination with juvenile hormone applications to termite colonies. Inhibition of these pheromones, thought to be produced by termites, could derail the caste proportion systems of termite colonies. However, such pheromones must first be isolated and identified.

Physiology

Certain agricultural insect pests can be controlled using mimics of a certain insect hormone called juvenile hormone. Juvenile hormone is essentially an anti-adult hormone (35). By using analogues (such as methoprene and hydroprene) of this compound, advancement to the adult stage can be suppressed and the juveniles induced to form supernumerary larval forms. While this may not directly kill the larvae, it affects the population as a whole by preventing reproduction (only adult insects have functional reproductive organs).

As social insects, termites use a slightly modified hormone chemistry. The majority of termites in a colony are immature forms rather than true adults, and juvenile hormone is used in a different manner from solitary species. With termites, caste may depend on the juvenile hormone concentration in the termite's environment. Lenz (32) presents evidence that suggests the role of nutrition in the development of different castes among termites. His studies used the juvenile hormone analogues (JHAs) altozar (ethyl-3,7,11-trimethyldodeca-2,4-dienoate) and altsid (isopropyl-11-methoxy-3,7,11-trimethyldodeca-2,4-dienoate), and various levels of nutrients from plain filter paper to wood decayed by brown rot fungi. Essentially, his work showed a positive influence of nutrition on subsequent molting of lower termite workers that had been exposed to JHA compounds into nymphs and reproductives. In contrast, those workers on relatively low nutritional diets tended to molt into soldiers when exposed to JHA compounds. Different termite species were able to control extraneous soldier development to different degrees; those with higher natural soldier proportions were better able to deter the formation of new soldiers, while those with naturally low soldier proportions became inundated with soldiers. Evidence from *Nasutitermes nigriceps* (Haldeman) suggested that higher termites may also be affected by JHAs in this manner (32). Lenz (32) suggests that the soldiers are essentially juvenile hormone sinks, perhaps by producing a compound that inhibits its production from the corpora allata of the workers. Henderson (36) further expanded upon the concept of termite soldiers as juvenile hormone sponges. Work by Lüscher (33) has indicated that higher termites have less plasticity in their developmental 'programming' than lower termites, such that adjustments to caste can only be made at relatively few points along their developmental pathways. There are five known juvenile hormones (0-III, plus 4-methyl juvenile hormone I; 35), and *R. flavipes* has been shown to use the juvenile hormone III in induction of soldier development (34). Prestwich (34) was also able to identify the juvenile hormone binding proteins within *R. flavipes*, and suggested that the mechanism for inhibiting soldier development by lower termite soldiers is the release of a pheromone that inhibits these proteins.

Okot-Kober *et al.* (37) examined the effects of *n*-sulfenylcarbamate pro-insecticides (precursors of fenoxycarb analogues) as JHAs in several lower termite species. While the compounds did induce increased soldier proportions, this increase could be inhibited by the presence of natural soldiers in the laboratory arenas. Such natural adjustment of soldier proportions argues against the successful use of JHAs for purposes of termite control.

Of the control methods currently available for subterranean termites, the most recent has been the development of various baits (16-18, 38). Bait development was plagued for quite a few years by the need for a nonrepellent and slow-acting toxicant that would induce delayed mortality at a distance from the bait itself, thereby removing concerns about learned avoidance (38). The first commercially available bait for subterranean termite control was the Sentricon Colony Elimination System™ (Dow AgroSciences), which uses a unique physiological approach to address this issue. The active ingredient for this bait is hexaflumuron, a benzoylphenyl urea compound. Lenz *et al.* (39) showed that both hexaflumuron and triflumuron (another benzoylphenyl urea) affected subterranean termites (*C. acinaciformis* [Froggatt]) more quickly than higher termites (*Nasutitermes exitiosus* [Hill]). Their study also demonstrated concentration-dependent differences among species in susceptibility, with the rhinotermitids (subterranean termites) dying more rapidly and from lower concentrations of both materials.

Benzoylphenyl ureas, such as diflubenzuron and hexaflumuron, interrupt the formation of an intact integument during molting, leading to death of the insect during ecdysis. However, the exact mechanism of this inhibition is not yet understood. It is known that these compounds affect chitin synthesis such that chitin is not properly laid down in the new procuticle of the insect during apolysis. Many of the theoretical considerations of how these compounds function relates to chitin synthetase, the enzyme responsible for the conversion of UDP-*n*-acetylglucosamine residues into chains of *n*-acetylglucosamine residues or chitin. Theories for the actual mode of action vary from the potential for a metabolite of benzoylphenyl ureas inhibiting chitin synthetase to the inhibition of UDP-*n*-acetylglucosamine passage across cell membranes. While the exact nature of the mode of action for hexaflumuron may still be unknown, the inhibition of chitin synthetase is thought to be a very good candidate. A full discussion of the theories of benzoylphenyl urea mode of action is provided by Retnakaran (40).

While hexaflumuron has provided a very useful bait system (17, 18), there will always be room for improvement (39). In the next section, we discuss some new information on the feeding and foraging behaviors of termites, and how this may improve bait applications.

Feeding

Since we are ultimately concerned with the destruction of cellulose, we must consider all the active participants in its breakdown. In the Rhinotermitidae (subterranean termites), these participants are the termites, through chewing and mechanical (and some enzymatic) breakdown of wood (cellulose), and the symbiotic protozoa and bacteria found in the termite hindgut. The protozoa participate by the further enzymatic degradation of cellulose in the hindgut, producing acetate which is absorbed by the termite as a nutrient (41-43). Since wood contains a low proportion of nitrogen, the termites must also find a way of accumulating nitrogen (11). This is accomplished in part by symbiotic bacteria present in the termite alimentary canal (44-46). While the bacteria are considered accomplices in the destruction of cellulose, in the Rhinotermitidae they are secondary to the more important cellulase-producing protozoa of the hindgut.

Termite hindgut microfauna species and number vary with termite species. Perhaps the most recent and elaborate work on the various species of microfauna in a single species of termite has been performed with *C. formosanus*, the Formosan subterranean termite (47-52). This species is a member of the Rhinotermitidae, is very aggressive in its wood foraging (53), and even uses less energy than some other subterranean termites (*R. flavipes*, 54). Most importantly, as a model for protozoan cellulose degradation, it is quite simple, having only three species in its hindgut (55). These species, from largest to smallest, are *Pseudotriconympha grassii* Koidzumi, *Holomastigotoides hartmanni* Koidzumi, and *Spirotrichonympha leidy* Koidzumi. The largest protozoan, *P. grassii*, resides in the anterior end of the hindgut, while the smallest, *S. leidy*, resides mostly in the posterior of the hindgut, with *H. hartmanni* found throughout the hindgut (48). Each of the three protozoans is thought to metabolize only certain types of cellulose within the *C. formosanus* hindgut (50-52). Defaunation followed by an examination of termite survivorship on various types of cellulose indicated that *P. grassii* could utilize only cellulose with high degrees of polymerization, similar to natural wood (50).

At one time, microfauna were thought to be responsible for all cellulase activity in termites, but this is not the case. Termites from both the Termitidae (*Trinervitermes trinervoides* [Sjöstedt], 56; *Macrotermes natalensis* [Haviland], 57; *Nasutitermes takasagoensis* [Shiraki], 58) and the Rhinotermitidae (*C. formosanus*, 49; *R. speratus* [Kolbe], 59) have been shown to produce cellulases of their own. In both families, these endogenous cellulases are endo- β -1,4-glucanases and β -D-glucanases (49, 58), and their activities extend to areas beyond the hindgut of the termite. It is thought that the termite-produced cellulases are regurgitated from the midgut and are active on wood (or cellulose) fragments throughout the alimentary canal (49, 51). It should be pointed out that

although they also produce cellulases from their midgut epithelial cells, termites of the subfamily Macrotermitinae do not rely upon protozoa for the remainder of their cellulases (57). Instead they cultivate a symbiotic fungus in their colonies, which contains cellulases that are transferred to the termite after feeding upon the fungus.

Yoshimura (48, 52) developed an overview of cellulose degradation in *C. formosanus*. Following mechanical degradation of the wood with the mouthparts into smaller pieces, the endo- β -1,4-glucanases and β -D-glucanases produced in the termite midgut break down the cellulose matrix into smaller, although still indigestible, sections. From there the fragments travel to the hindgut and are encountered first by *P. grassii*, which produces a cellulase that operates on highly polymerized cellulose. The less polymerized pieces will be encountered by *H. hartmanni* throughout the hindgut, and are broken down, thus completing the breakdown of cellulose itself into acetate. In the hindgut, *S. leidy* is thought not to degrade cellulose directly, but instead acts as a host for methanogenic and nitrogen fixing bacteria (48).

Current interest in termite breakdown of cellulose has also encouraged new research on the means by which termites locate their food in the first place. Subterranean termite foraging behavior and food-finding capabilities are currently being studied by a number of researchers (60-62), using two-dimensional foraging arenas (similar to ant farms) to observe tunneling. Both *R. flavipes* and *R. virginicus* (Banks) will use pre-existing tunnels in their movement through two-dimensional space; however, they show less preference for moving along guide wires placed in the sand (60). Re-use of existing foraging tunnels has also been observed by Grace and Su (18) in field studies of termite reinvasion of baited sites. *R. flavipes* and *C. formosanus* were found to show an increase in the number of tunnels produced prior to (compared with after) reaching a food source, suggesting a greater searching investment by the termites during the initial phases of food acquisition (61). Puche and Su (61) argue that the tunnel formation by these species can be adequately modeled using fractal analysis. Robson *et al.* (63) discovered that subterranean termites have patterns to their search behavior that, in the absence of other cues, evenly divide the foraging area so as to maximize the likelihood of food discovery. Campora and Grace (62) noted that a pattern of successive radial foraging tunnels (similar in appearance to spokes of a wheel) was created as termites encountered either wood in the soil or substrate anomalies such as a hollow space. Overall tunneling efforts shifted towards those parts of the arenas where food (or substrate anomalies) were first encountered. In nature, it may be rare for subterranean termites to be food-limited (11), since wood is a resource that few other organisms utilize. Thus, development of radial search patterns triggered by multiple anomalies in the soil rather than solely by discovery of wood (i.e., less selective patterns) would seem to make sense so long as such

anomalies are in fact associated with food a majority of the time. Such improved understandings of termite foraging strategies hold promise for improving termite control, particularly with respect to bait placement and monitoring efficiency.

Conclusions

Understanding the feeding behavior, protozoa, and hormone/pheromone physiology of economically important termites will expedite development and improvement of new technologies for controlling pest species. Behavioral examinations will lead to improved bait implementation, particularly better bait placement and improved monitoring methods. Knowledge of the relationships between symbiotic microfauna and their termite hosts could well lead to new control methods targeting metabolic pathways in the degradation of cellulose within the termite gut. The current successful use of chitin synthesis inhibitors in subterranean termite baits provides a good example of a physiologically-based control strategy. Certainly, additional strategies will be spawned by current research efforts.

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