

Semiochemical Mediation and Manipulation of *Reticulitermes* Behavior (Isoptera: Rhinotermitidae)

by

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ABSTRACT

Chemical mediation plays a critical role in termite social communication, orientation, foraging, and defense. Current knowledge of *Reticulitermes* spp. behaviors in response to chemical stimuli is reviewed, with an emphasis on studies with *R. hesperus* and *R. flavipes*. *Reticulitermes* spp. are the most serious subterranean termite pests of structures in North America, Europe, and parts of Asia, and new control methods are needed to replace persistent and non-selective pesticide applications. Behavioral chemicals, particularly those involved in food location and acceptance and trail-following, offer promise in the development of baiting systems, repellent wood preservatives, and other novel approaches to subterranean termite control.

INTRODUCTION

Naturally produced chemicals that influence insect behavior (semiochemicals) are accepted tools, or potential tools, in integrated pest management programs (Nordlund *et al.* 1981). Such chemicals are also extremely important in termite (Isoptera) communication, orientation, food location, defense, and maintenance of social homeostasis. The variety of known termite semiochemicals and their roles in mediating termite behavior have been reviewed generally by Stuart (1969), Moore (1974), Howse (1984), and Prestwich (1983, 1988). Species in the Holarctic subterranean termite genus *Reticulitermes* Holmgren (Rhinotermitidae) are the predominant termite pests of urban structures in North America, Europe, and parts of Asia (Harris 1970; Weesner

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1970; Edwards & Mill 1986). Both preventative and remedial control of this genus has long depended upon the application of persistent soil insecticides. Even with this non-selective control method, termite behavior is of interest, as evidenced by the continuing concern over the relative importance of repellency versus toxicity in defining soil pesticide efficacy (Su *et al.* 1982; Jones 1989; Grace 1990b). Moreover, mark-release-recapture studies of *Reticulitermes flavipes* (Kollar) foraging populations (Grace *et al.* 1989a; Grace 1990d) have demonstrated that placing a "chemical barrier" in the soil around threatened structures has little to no effect on termite populations outside of that narrow band of treated soil. Since a *Reticulitermes* colony foraging population can consist of several million workers (Grace *et al.* 1989a), alternative termite control techniques, such as baiting systems, are needed to reduce the threat represented by these constantly foraging termites. Behavioral chemicals may be useful components of such techniques (Rust *et al.* 1988). The present paper reviews recent studies of *Reticulitermes* chemically-mediated behavior, with an emphasis on the possible practical applications suggested by these studies.

POSITIVE BEHAVIORAL RESPONSES

Trail-following. *Reticulitermes* species lay chemical trails with secretions from the sternal gland, an epidermal gland located in the anterior portion of the fifth abdominal sternite beneath the fourth abdominal sternite (Smythe & Coppel 1966; Quennedey 1971). Matsumura *et al.* (1968, 1969) and Tai *et al.* (1969) identified the straight chain alcohol cis-3,cis-6,trans-8-dodecatrien-1-ol as the trail pheromone of *Reticulitermes virginicus* Banks. This alcohol also elicits trail-following in other *Reticulitermes* and *Coptotermes* species (Matsumura *et al.* 1972), and was considered by Ritter & Coenen-Saraber (1969) to be the pheromone of *Reticulitermes santonensis* (Feytaud). Honda *et al.* (1975) proposed it as the pheromone of *Reticulitermes speratus* (Kolbe), and this was recently confirmed by Yamaoka *et al.* (1987) and Tokoro *et al.* (1990a, 1990b). Tokoro *et al.* (1989) also identified this dodecatrienol as the trail pheromone of *Coptotermes formosanus* Shiraki. The principal active component of extracts of the sternal gland of *Reticulitermes hesperus*

Banks is a triple-unsaturated C₁₂ primary alcohol (Grace 1986), and Kaib *et al.* (1982) demonstrated that cis-3-dodecen-1-ol elicited trail-following in *Reticulitermes lucifugus* (Rossi) and 11 termite species in other genera. Because cis-3,cis-6,-trans-8-dodecatrien-1-ol (Matsumura *et al.* 1969; Ritter & Coenen-Saraber 1969) and possibly other compounds inducing trail-following (Watanabe & Casida 1963; Grace & Wilcox 1988) are found in fungus-decayed wood, a likely termite food source, identification of this alcohol as a pheromone from extracts of homogenated termites has been justly criticized (Stuart 1969). However, the chemical evidence from studies with solvent soaks of whole termite bodies (Tokoro *et al.* 1989, 1990a) or excised sternites (Grace 1986) combined with that of comparative bioassays with extracts of different portions of the termite body (Howard *et al.* 1976; Runcie 1983; Grace 1986) point to a dodecatrienol as the major component of the trail pheromone of *Reticulitermes* and *Coptotermes* species. The different responses of different species to analogues suggests that the shape of the receptors, however, is species specific (Prestwich *et al.* 1984). With *R. hesperus*, the same sternal gland fraction elicited initiation of trail-following and orientation (fidelity) to the trail (Grace 1986; Grace *et al.* 1988b), but the naturally-laid trail may contain other components (Runcie 1987), and minor components may impart species specificity (Moore 1974; Howard *et al.* 1976; Kaib *et al.* 1982; Tokoro *et al.* 1989).

Trail-following consists of recruitment to the trail (Traniello 1982), initiation of trail-following, fidelity or orientation to the lateral boundaries of the trail space (Bossert & Wilson 1963), and orientation along the longitudinal axis of the trail (Grace *et al.* 1988a). Recruitment implies a social context that is rarely considered in laboratory assays with displaced termite workers (Hall & Traniello 1985). Assays by Runcie (1987) with variously aged *R. flavipes* trails laid under different circumstances indicated that a second volatile component may serve to distinguish active trails from abandoned trails, although the presence of food was not prerequisite to its deposition. Termite preference for trails laid to food sources and the greater longevity of such trails, in contrast to those laid by exploring or displaced workers (Runcie 1987), indicates a concentration-dependent initiation response, and suggests that quantity rather than quality of trail pheromone may

be involved in recruitment in *Reticulitermes*.

Grace *et al.* (1988a) demonstrated with dichloromethane extracts of the sternal gland of *R. hesperus* that initiation of trail-following, trail fidelity, and rate of locomotion along the trail were concentration dependent. Moreover, *R. hesperus* workers were able to detect pheromone concentration gradients on artificial trails, and selectively followed such trails to the high-concentration termini, even if this required reversing their direction of travel midpoint on the trail and retracing their path (Grace *et al.* 1988a). Similarly, Clément *et al.* (1988) reported that European *Reticulitermes* could follow gradients of terpenes from pine wood through the soil to locate food sources. These findings are significant from an applied standpoint, since they suggest that foraging subterranean termites could actually be directed towards a toxic bait or an area of pesticide treated soil by presenting them with a concentration gradient of a compound inducing trail-following. In lieu of the actual pheromone, either fungal extracts (Amburgey & Smythe 1977), readily synthesized analogues (Kajiwara *et al.* 1978), or commercially available chemicals such as several ink solvents (Becker 1966; Beard 1974) could be applied. Although decayed wood baits (Esenther *et al.* 1961) placed in the soil may create short-range chemical gradients in the surrounding soil, development of a practical "pied piper" method to influence long-range termite foraging behavior is challenging.

Attraction, arrestment, feeding stimulation, and preference. In most laboratory assays with termites held in small containers, attraction (orientation) to or arrestment (cessation of locomotion after contact) by chemical stimuli cannot be readily separated and are perhaps better grouped under the term "preference" (Grace *et al.* 1989b). Similarly, in two-choice or multiple-choice assays measuring food consumption, increased feeding on a particular substrate may result from either preferential orientation to this substrate (attraction), arrestment on the substrate after contact, or response to feeding stimulants in the substrate. Again, use of the general term "preference" (e.g., Delaplane & LaFage 1989) indicates that one or a combination of these factors is operative. Use of more specific terminology would imply a degree of discrimination not found in most termite bioassays. Although the development of more discriminating assays is certainly desirable, the reductionist approach is mitigated by the need to provide

the appropriate physical and behavioral context for these soil-dwelling social insects.

Becker (1948, 1965) reported a preference of *R. lucifugus* for pine wood decayed by several fungi, including *Gloeophyllum trabeum* (Pers. ex Fr.) Murr. (Basidiomycetes: Polyporaceae). Extraction of chemical fractions inducing this preference from *G. trabeum* (Esenther *et al.* 1961; Allen *et al.* 1964) and subsequent identification (Matsumura *et al.* 1969) of a principal active component as cis-3,cis-6,trans-8-dodecatrien-1-ol stimulated interest in combining termite "attractants" with insecticides or pathogens (Lund 1969). Other wood and fungal extracts also elicit positive behavioral responses in *Reticulitermes* (Smythe *et al.* 1967; Becker *et al.* 1972; Becker 1976; Carter & Mauldin 1981; Jones *et al.* 1983; Grace & Wilcox 1988; Grace *et al.* 1989b; Grace 1990a). However, interest in termite baits focused on use of the decayed wood itself (Esenther & Coppel 1964) rather than extracted or synthesized chemicals, with Esenther & Gray (1968) first demonstrating suppression of *R. flavipes* activity in the field with dechlorane (mirex) coated blocks. The long search for alternative nonrepellent and slow-acting bait toxicants continues to date (e.g., Prestwich *et al.* 1983; Jones 1984; La Fage 1984; Su & Scheffrahn 1988; Grace 1990e; and other papers in this symposium). Carvalho & Prestwich (1984) prepared toxic analogues of dodecatrienol, and the use of pathogens such as *Metarhizium anisopliae* and *Beauveria bassiana* (Zoberi & Grace 1990; Tamashiro, Grace, & Jones, in preparation) or insecticidal dusts (Grace & Abdallay 1990; Grace 1990f) in baiting systems is also under investigation. Applications of dusts or formulated pathogens to termite foragers would take advantage of mutual grooming behavior, trophallaxis, and cannibalism to transmit the toxicant through the colony.

One problem with the use of semiochemicals in termite control is volatility and rapid degradation of these compounds, which could be overcome by use of stable analogues or chemical protection (Grace 1990c). A second problem identified in laboratory assays with *G. trabeum* extracts is habituation, or a learned decrement in response after repeated exposure to a stimulus (Grace 1989). Habituation may be more of a problem in laboratory assays of potential bait toxicants than in the field, where conditions are less static and the baits would present a food reward along with the

"attractant" stimulus.

In the absence of a chemical gradient to lead foraging termites to toxic (or pathogenic) bait stations, we will have to rely upon careful bait placement (based upon prior inspection or pre-baiting) and random foraging for termites to locate the baits. In fact, the high level of foraging activity and large size of *R. flavipes* colonies (Grace *et al.* 1989a) strongly suggests that truly "attractive" baits, although desirable, will not be essential for efficacy of baiting techniques, so long as the baits are not actually repellent or deter feeding. On the other hand, semiochemicals would be extremely useful as masking agents for otherwise unpalatable toxicants. There is precedence for this in nature, in that some plant materials such as *Pinus ponderosa* Dougl. ex Laws. contain compounds eliciting positive orientation responses (Grace *et al.* 1989b) as well as containing compounds toxic to termites (Carter 1976; Grace *et al.* 1989b). Terpenes found in pine wood that are toxic to *Reticulitermes* (Clément *et al.* 1988; Lemaire *et al.* 1990) are repellent in high concentrations, but elicit positive orientation (along a gradient) at low concentrations (Clément *et al.* 1988).

A range of solvent extracts from the stem bark, sapwood, and heartwood were taken from both a tree species frequently infested in Toronto by *R. flavipes*, horsechestnut (*Aesculus hippocastanum* L.) (Hippocastanaceae), and one rarely infested, tree of heaven (*Ailanthus altissima* [Mill.] Swingle) (Simaroubaceae) (Cooper & Grace 1987). Bioassays revealed that extractives were present in both trees that elicited positive and negative orientation responses (Grace 1990a). However, the ratio of positive to negative components, and the relative amounts (yield) of each component, were strongly correlated with the observed pattern of termite infestation. Of 12 different solvent extracts from each tree species, 7 of the horsechestnut extracts elicited positive orientation responses and 3 elicited negative responses; versus only 2 positive responses to tree of heaven extracts and 7 negative responses (Grace 1990a).

Sex pheromones and other exocrine products. With the exception of defensive secretions, no extensive repertoire of pheromones comparable to that known from ants has yet been described for termites, although their social interactions are certainly as complex as those of social Hymenoptera. Clément *et al.*

(1988, 1989) identified *n*-tetradecyl propionate as a sex attractant pheromone from the sternal gland of *R. flavipes*. This suggests the possibility of monitoring or trapping out alate swarms, although efficacy of this as a control measure is questionable considering the importance of neotenic and colony budding in founding new *Reticulitermes* colonies. Pheromone traps might, however, be efficient monitoring tools.

Although its function is unknown, a complex exocrine gland was described on the legs of *R. lucifugus* by Bacchus (1979). Products of this gland could conceivably be involved in defense or trail-following.

NEGATIVE BEHAVIORAL RESPONSES

Repellency and feeding deterrence. These negative stimuli are somewhat easier to discriminate in bioassays than their positive counterparts by observing the insects' behavior, although "non-preference" is really all that is conveyed by a measurement of reduced feeding alone on a particular substrate. Floyd *et al.* (1976) conducted one of the few studies of contact repellency alone with *R. lucifugus*, correlating electroantennogram responses with qualitative observations of foragers avoiding paths containing various suspected repellent quinones and monoterpenes in a plastic "nest box." Additional studies of this type would help illuminate the molecular basis of negative behavioral responses.

Behavioral responses to wood extractives have generally been assessed in conjunction with feeding and mortality (Carter & Mauldin 1981; Carter *et al.* 1983; Grace *et al.* 1989b). Although current wood preservatives such as CCA (chromated copper arsenate) protect via high toxicity rather than repellency (Grace, unpublished data), contact repellency should provide equal or better protection. One microbicide, TCMTB (2-[thiocyan-omethylthio]benzothiazole), used in preservative formulations does act as a contact repellent to *R. flavipes* (Grace 1988). Toxic alkaloids from *Lycoris radiata* Herb. (Amaryllidaceae) act to deter termite feeding on Japanese rice paper manufactured in a traditional manner (Grace *et al.* 1986).

As mentioned earlier, the relative value of repellency and toxicity in preventing termite penetration of soil treated with termiticides

is a matter of debate. Very low concentrations of nontoxic repellents (Lewis *et al.* 1978) and repellent pesticides such as pyrethroids (Su *et al.* 1990) will prevent penetration, but may also degrade rapidly and do not reduce the exterior termite population threatening the structure. On the other hand, nonrepellent and slow-acting insecticides such as sodium borate (Grace 1990b, 1990f) slowly kill termites tunneling through the treated soil, but do not prevent penetration. One integrated approach might be to use both types of materials to treat different portions of termite-threatened properties.

Alarm, defense, and agonistic behaviors. Alarm in response to disturbance of a termite colony (by predatory ants, for example) appears to be transmitted by a combination of substrate vibration (head-banging), tactile cues, and pheromone release (Stuart 1963, 1988; Moore 1969). Both sternal gland (Stuart 1963) and frontal gland (Moore 1969) secretions have been suggested to play roles in alarm, as well as in trail orientation and defense. Zalkow *et al.* (1980, 1981) characterized cephalic secretions from *R. flavipes* and *R. virginicus*, but the significance of these compounds is not known as these authors were unable to demonstrate a role in alarm or defense. Terpenes secreted by European *Reticulitermes* have been characterized (Parton *et al.* 1981; Baker *et al.* 1982), with the diterpene geranyl-linalool representing the larger part of these secretions (Clément *et al.* 1988; Lemaire *et al.* 1990).

Observations by the author (unpublished) and other researchers (personal communications cited in Haverty & Thorne 1989) indicate that intraspecific aggression between *Reticulitermes* colonies is uncommon. Clément (1978, 1986) reported the absence of aggression between *R. santonensis* colonies, and a seasonal pattern to aggression between colonies of *R. lucifugus*. Interspecific aggression served to isolate *R. lucifugus banyulensis* from *R. lucifugus grassei* (Clément 1978). In addition to seasonal factors, cuticular hydrocarbon profiles may act as cues to stimulate or prevent agonistic behavior (Howard *et al.* 1982; Clément 1986, Bagnères *et al.* 1988), as in *Zootermopsis* species (Haverty & Thorne 1989). Theoretically, interference with perception of such cues could disrupt normal social interactions and result in destructive aggression within the colony.

Allomones. Chemicals used by predators of termites to attack

their prey may serve as the basis for development of more specific and environmentally acceptable insecticides. Clément *et al.* (1986, 1988) identified aggressive secretions from ants (*Monomorium* and *Crematogaster* spp.) as potent termiticides. Johnson & Hagen (1981) reported an apparent vapor-phase toxicant emitted by a Berothid (Neuroptera) larva, *Lomamyia latipennis* Carpenter, preying on *R. hesperus* that paralyzed termite workers before death but had no effect on several other insect species tested.

CONCLUSIONS

Currently, the use of semiochemicals in urban termite control is in somewhat the same stage that the application of behavioral chemicals to forest and agricultural pest management was 10–15 years ago. Our understanding of the role of chemical mediation in *Reticulitermes* ecology and behavior has advanced, a number of naturally-occurring compounds have been identified, and the potential value of these compounds and synthetic analogues in pest control is widely recognized. Interest in the development of new methods for controlling termites has been spurred in the past decade by the withdrawal of the persistent and non-selective organochlorine insecticides from the pest control arsenal in many parts of the world. Within the next few years, baiting systems for subterranean termite control should become a commercial reality, with semiochemicals incorporated to aggregate foragers or mask repellency. With growing interest in less toxic wood preservatives, termite repellents are logical candidates for use in wood protection. As these approaches are demonstrated to be efficacious and accepted as reliable, and our knowledge of termite behavior and semiochemicals increases, we can expect to see practical applications of increasingly creative techniques for manipulating termite behavior.

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