Effects of Insect Growth Regulators on Subterranean Termites: Induction of Differentiation, Defaunation, and Starvation[1]

MICHAEL I. HAVERTY[2] AND RALPH W. HOWARD[3]

ABSTRACT

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Exposing groups of *Reticulitermes flavipes, R. virginicus,* and *Coptotermes formosanus* to methoprene and hydroprene had concentration-dependent morphogenetic and lethal effects on the *Reticulitermes* species but no effect on *Coptotermes*. Methoprene was not directly toxic to *R. flavipes*. Instead, most lethal effects probably result from starvation induced by elimination of termites' symbiotic protozoa and from trophic demands placed on them by the many presoldiers present. A small proportion of the mortality resulted from ecdysis failures.

Soldier differentiation in termites depends on the juvenile hormone (JH) titer at specific intervals of the molting cycle of nymphs and larvae (Lüscher 1976, Yin and Gillott 1975a, b). The titer of JH and the resulting proportion of soldiers is presumed to be controlled by pheromones produced by either the reproductives (stimulates) or soldiers (inhibits) (Lüscher 1972). Exposing larval or nymphal termites to exogenous JH or insect growth regulators (IGRs) with juvenile hormone activity produces superfluous presoldiers (Chu et al. 1974, French 1974, Hrdý 1972, 1976, Hrdý and Krěček 1972, Lenz 1976a, b, Lüscher and van Doorn 1976, Springhetti 1974, Varma 1977, Wanyonyi 1974, Wanyonyi and Lüscher 1973). Some of these authors also report that occasionally associated with these "soldier flares" was substantial mortality to both the undifferentiated termites and the newly molted individuals. Such mortality was ascribed either to incomplete ecdysis or to overt toxicity of the IGR to the termite. We (Howard and Haverty 1978) have indicated that the effects of IGRs on subterranean termites are more complex than previously realized. Here we report our findings on how 2 IGRs (methoprene and hydroprene) affect 3 termite species economically important in the United States: *Reticulitermes flavipes* (Kollar), *R. virginicus* (Banks), and *Coptotermes formosanus* Shiraki (Rhinotermitidae).

Materials and Methods

Termites

Reticulitermes spp. used in this study were freshly collected from infested pine logs in the DeSoto National Forest, ca. 32 km N of Gulfport, Miss. *C. formosanus* were obtained from infested cypress snags at Lake Charles, La., and were maintained in culture for at least 2 yr. All experiments utilized "workers." Obtaining individuals of equivalent age and instar is nearly impossible because of asynchronous molting and our inability to identify individuals within a given instar quickly and effectively. As a result we used any larva that had reached the third instar, a threshold size we could easily identify. Each of the experiments described used different source colonies.

Experimental Units

These were plastic cylinders 5.0 cm in diam by 3.5 cm high containing a single 47 mm diam cellulose filter pad disk (ca. 0.5 g – Gelman Instrument Co.[4]). The filter pads were treated at levels ranging from 0.0 to 2.5 mg active ingredient (AI)/pad with 1 ml of either hydroprene (ethyl-3,7,11-trimethyl-2,4-dodecadienoate) or methoprene (isopropyl [2E,4E]-11-methoxy-3,7,11-trimethyl-2,4-dodecadienoate) solution and then air-dried in a fume hood. We prepared treatment solutions from dilutions of the emulsifiable concentrate (EC) of hydroprene (0.72 kg AI/liter) or methoprene (0.48 kg AI/liter) (screening experiments), or from technical grade methoprene (95% AI) diluted in acetone (protozoa and toxicity effects experiments). Before adding the termites, the treated pads were moistened in their containers with 1 ml deionized water. Then, 30 workers were placed in each experimental unit and all units were held in an incubator for up to 4 wk. *Reticulitermes* sp. were held at 25° ± 1°C; *C. formosanus* at 28° ± 1°C.

Determination of Effect of IGR Concentration on Soldier Differentiation and Mortality

Screening.—To establish the range of effective concentrations and to observe the effects at different concentrations, groups of 30 workers from one *R. flavipes* colony were placed on pads treated as above and observed for 4 wk at 2- to 3-day intervals. Each treatment concentration (0.078–2.5 mg AI/pad, Table 1) was replicated 5 times. We counted the number of live and dead termites, determined proportions of the various forms in each category, and assessed both behavior of the survivors and condition of the filter pad. At each inspection dead termites were removed to prevent microbial infection of survivors.

Expanded screening included *R. virginicus* and *C. formosanus* as well as *R. flavipes*. The procedures of the initial screening were followed with the exception that treatment levels ranged only from 0.0 to 0.5 mg AI/pad (Tables 2 and 3).

Determination of Protozoan Numbers

Unlike the other experiments in which the same insects were observed for the entire observation period, this experiment made it necessary to destroy some of the insects in each experimental unit to count their protozoans. Accordingly, different experimental units were examined at each observation date and not observed again. Observations were made on days 7, 10, 13, 17,

[1] Received for publication Dec. 11, 1978.

[2] Insecticide Evaluation Project, Pacific Southwest Forest and Range Experiment Station, P. O. Box 245, Berkeley, CA 94701.

[3] Forestry Sciences Lab., Southern For. Exp. Sta., Forest Service, USDA, P. O. Box 2008 GMF, Gulfport, MS 39503.

[4] Mention of a company or trade name is simply to identify a material and does not imply endorsement by the USDA.

Table 1.—Differentiation and mortality of *R. flavipes* exposed to various concentrations of methoprene and hydroprene for up to 29 days.

Concn mg AI/pad	Max percentage of presoldiers[a]		Percentage of mortality[a,b]					
	Presoldier		Worker		Presoldier		Incomplete molt	
	M[c]	H	M	H	M	H	M	H
0.000	0	0.2	8.0	17.3	0	0	0	0
0.078	56.0	58.7	25.4	26.0	65.4	61.3	9.3	8.0
0.156	16.7	52.7	46.0	30.0	21.4	60.7	32.6	9.3
0.313	0	29.3	96.6	54.0	1.3	36.7	2.1	9.3
0.625	0	25.3	100.0	44.0	0	32.6	0	23.3
1.250	0	4.7	100.0	94.0	0	5.3	0	0.7
2.500	0	0	100.0	100.0	0	0	0	0

[a] Mean of 5 replications.
[b] All treatments > 0.078 mg IGR/pad had 100% mortality by 29 days. The 0.078 mg methoprene/pad treatment had 58% total mortality and the 0.078 mg hydroprene/pad treatment had 72% total mortality.
[c] M = methoprene, H = hydroprene.

Table 2.—Differentiation and mortality of *R. flavipes* exposed to various concentrations of methoprene and hydroprene for 33 days.

Concn mg AI/pad	Max percentage of live termites[a]						Percentage of mortality[a]					
	Presoldier		Soldier		Intercaste		Worker		Presoldier		Incomplete molt	
	M[b,c]	H	M	H	M	H	M	H	M	H	M	H
0.000	0	0	0	0	0	0	12.0	12.0	0	0	0	0
0.016	57.3	0	4.0	0	3.3	0.7	13.3	6.0	12.0	0	0.7	0
0.032	56.0	6.7	2.7	0	0.7	0	28.7	4.7	43.3	0.7	0	0
0.063	54.7	33.3	0.7	5.3	0.7	0.7	34.0	12.0	56.0	4.7	0	0
0.125	5.3	57.3	0	0	0	0	81.3	41.3	11.4	57.3	7.3	1.3
0.250	1.3	62.0	0	0	0	0	84.7	32.0	3.3	65.3	12.0	2.0
0.500	0	38.7	0	0	0	0	95.3	56.0	0	22.7	4.7	5.3

[a] Mean of 5 replications.
[b] M = methoprene, H = hydroprene.
[c] Previously reported (Howard and Haverty 1978).

Table 3.—Differentiation and mortality of *R. virginicus* exposed to various concentrations of methoprene and hydroprene for 33 days.

Concn mg AI/pad	Max percentage of live termites[a]						Percentage of mortality[a]					
	Presoldier		Soldier		Intercaste		Worker		Presoldier		Incomplete molt	
	M[b]	H	M	H	M	H	M	H	M	H	M	H
0.000	0	0	0	0	0	0	13.3	13.3	0	0	0	0
0.016	52.7	0	2.7	0	0	1.3	19.3	12.0	13.3	0	0.7	0
0.032	68.7	0	0	0	0	0.7	27.4	9.3	72.6	0	0	0
0.063	62.7	2.0	0	0	0	1.3	36.0	10.7	64.0	2.0	0	0
0.125	54.0	40.0	0	0	0	0	37.3	55.3	58.7	43.3	4.0	1.3
0.250	36.7	45.3	0	0	0	0	44.7	54.0	46.7	46.0	8.7	0
0.500	14.7	35.3	0	0	0	0	63.4	64.0	15.3	35.3	18.7	0.7

[a] Mean of 5 replications.
[b] M = methoprene, H = hydroprene.

20, and 23. One ml of IGR solution was applied to the filter pads so that each pad received 0, 0.016, 0.032, or 0.063 mg of methoprene. The treated pads were air-dried in a fume hood for one h and then placed in the plastic cylinders and moistened with one ml of deionized water. Thirty *R. flavipes* workers were then added to each unit. There were 3 replications for each concentration-day combination. One replication was set up on each of 3 consecutive days so that only 24 containers had to be checked on each observation day. We measured in each replication the number of live and dead workers, presoldiers, soldiers, and soldier-nymph intercastes, and the mean number of each of 4 species of protozoa in 5 live workers or presoldiers. Protozoan species observed were *Dinenympha* sp., *Pyrsonympha* sp., *Spirotrichonympha* sp., and *Trichonympha agilis* Leidy.

After counting termites in each container, we randomly selected 5 termites (both workers and presoldiers) by tumbling them in an empty container and using the 1st 5 to fall out. Samples of the populations of each protozoan species were measured by a modification of the method of Mannesman (1974). This modification involved mincing the termite hindgut on a shallow-well microscope slide rather than in the apparatus used by

Mannesman. For each replication of each concentration-day combination counts for each species of protozoa from the 5 termites were pooled. The resulting mean was used as the value for each replication. The 4 concentrations of methoprene were compared statistically by analysis of variance for each observation day and protozoa species. Data were transformed to the square root before analysis of variance. Significant differences were separated at the $\alpha = 0.05$ level by Tukey's procedure.

Determination of Overt Toxicity of Methoprene to R. flavipes

Twenty groups of 30 termites were totally defaunated (DF) by being held for one h at 15 psi O_2 + 30 psi CO_2 (Cleveland 1925), carefully returned to atmospheric pressure, allowed to revive for 2 h, transferred to moistened filter pads in cylindrical containers for 2 h, then covered and held overnight. Twenty groups of 30 normally faunated (NF) termites were also held overnight on moistened filter pads in covered containers.

Twenty filter pads were each treated with one ml acetone solution of methoprene (M) at a concentration of 5 mg AI/ml. A 2nd group of 20 filter pads was treated with one ml of acetone only (A). After the solvent had evaporated from the pads, they were placed in experimental units and each moistened with one ml of deionized water. Ten groups each of NF or DF termites were then transferred to containers with either A or M treated filter pads. Thus the 4 treatments, NFA, NFM, DFA, and DFM, were each replicated 10 times. Mortality was recorded for 27 days.

Results and Discussion

Effects of IGR Concentration on Differentiation and Mortality

Initial Screening.—Exposure of *R. flavipes* to concentrations of methoprene and hydroprene ranging from .078 to 2.500 mg AI/pad revealed a striking pattern of dosage dependent differentiation and mortality (Table 1). For both IGRs maximal differentiation to the presoldier form occurred at 0.078 mg/pad; likewise, overall survival was greatest at this dosage of both chemicals. As the concentration of each IGR increased, maximal proportions of live presoldiers steadily declined,with differentiation in methoprene units dropping off more quickly. No soldiers or intercastes were produced in either IGR group. Except for the 0.078 mg/pad dosage, all methoprene and hydroprene treatments resulted in total termite mortality before 29 days. For all concentrations of IGR, most mortality was not associated with ecdysis failures, but rather with the death of either workers or presoldiers. For both IGR treatments ecdysis failures were also concentration-dependent.

At the 3 highest IGR concentrations, termites became lethargic by day 11 and had chewed or eaten little of the filter pad. Termites in the other IGR treatment remained active and were observed consuming the filter pads.

Further Screening

Since initial screening clearly indicated that maximal differentiation with minimal mortality had been obtained with the lowest IGR concentration tested, we restricted further evaluations of the IGRs to concentrations < 0.5 mg AI/pad. Accordingly, methoprene and hydroprene at concentrations ranging from 0.016 to 0.5 mg/pad were tested against *R. flavipes, R. virginicus,* and *C. formosanus*.

There was no differentiation and little mortality in *C. formosanus* at any of the concentrations tested. The lack of response is especially puzzling since Hrdý (1976) observed presoldier development in this species after exposure to JHAs. Furthermore, Lenz (1976b) observed presoldier development in workers of *Coptotermes amanii* (Sjöstedt) and *C. niger* (Snyder) exposed to hydroprene and methoprene. We have no explanation for this phenomenon unless Lenz (1976b) is correct in his assertion that a termite species may react differently to the same chemical depending on the physiological condition of the insects in the colony at the time of exposure. Perhaps we simply did not expose *C. formosanus* to enough of either chemical. Our observations were made on only one colony, so no definitive conclusions can be drawn.

Tables 2 and 3 summarize the differentiation and mortality profiles for *R. flavipes* and *R. virginicus,* respectively. Unlike *C. formosanus,* both *R. flavipes* and *R. virginicus* were affected by the 2 IGRs with the differentiation effects commencing after 12–14 days. As indicated by Table 2, *R. flavipes* exposed to hydroprene produced a few presoldiers at 0.032 mg/pad and many presoldiers at greater concentrations. Presoldier induction by hydroprene in *R. virginicus* (Table 3) required concentrations of at least 0.063 mg/pad. For both species, concentrations of 0.125 mg hydroprene/pad or greater produced total mortality by day 28. Both species produced numerous presoldiers at 0.016 mg methoprene/pad, and both showed similar rates of mortality at the higher concentrations tested. Unlike in the initial experiment at high IGR dosage rates, some presoldiers in this experiment successfully molted to soldiers. Successful molting occurred more frequently for *R. flavipes* exposed to methoprene than for any other combination. Nymph-soldier intercastes were also produced in this experiment. These forms were induced by both IGRs in *R. flavipes* but only by hydroprene in *R. virginicus*.

The patterns of mortality in Tables 2 and 3 are similar to those in Table 1 for the initial screening experiment. Again, little mortality was caused by ecdysis failure. Most mortality resulted from deaths of workers and presoldiers. Termites were generally active and engaged in feeding on the filter pads.

Our experiments to this point had delineated the dosage-dependent morphogenetic and toxic properties of methoprene and hydroprene to *R. flavipes* and *R. virginicus*. Still to be answered, however, was why these IGRs were lethal to termites. At least 3 major hypotheses presented themselves: (1) mortality was a direct result of overt toxicity to the termites, (2) the termites were starving because the excess presoldiers placed a trophic burden on the remaining workers, or (3) the termites were defaunated by the IGRs and therefore starved to death. Some combination of these 3 was also possible.

A test of these hypotheses was thus initiated. We decided to restrict the work to *R. flavipes* and methoprene for these experiments since there appeared to be little difference in responses between *R. flavipes* and *R. vir-*

Table 4.—Mean number of protozoans in a sample of the hindgut contents of *R. flavipes* after exposure to 4 concentrations of methoprene for up to 23 days. These values represent ca. 1/100 of total protozoan population in one termite.[a,b,c,d,e]

Concn mg AI/pad	Days after exposure					
	7	10	13	17	20	23
			Pyrsonympha sp.			
0.000	18.7a	31.7a	20.2a	31.3a	17.3a	29.9a
0.016	16.4a	21.2a	19.3a	14.3b	13.1ab	17.9a
0.032	14.0a	12.4a	2.1b	4.3b	5.5ab	0.6b
0.063	19.1a	11.0a	0.0b	0.4b	0.0b	0.0b
			Dinenympha sp.			
0.000	276.1a	309.1a	350.0a	297.5a	257.9a	340.7a
0.016	186.3ab	207.7ab	223.3b	181.5b	200.4ab	267.1a
0.032	159.6ab	126.1ab	52.9c	37.9c	40.9bc	42.0b
0.063	126.7b	86.6b	7.4c	1.6c	2.2c	0.0b
			T. agilis			
0.000	29.5a	29.4a	30.3a	23.9a	22.0a	31.4a
0.016	15.9ab	10.7b	12.7b	11.1b	15.7ab	12.7b
0.032	7.2b	4.6b	1.1c	0.7c	1.8b	0.6c
0.063	10.4b	1.8b	0.0c	0.1c	0.1b	0.0c
			Spirotrichonympha sp.			
0.000	7.6a	7.5a	9.4a	7.4a	5.2a	8.3a
0.016	6.6a	3.6b	8.2a	5.5ab	3.4ab	4.8ab
0.032	3.9a	3.1b	1.0b	1.5ab	0.6b	2.2ab
0.063	4.8a	2.4b	0.3b	0.3b	0.0b	0.0b

[a] Mean of 15 termites.
[b] After 13 days some workers had differentiated to the presoldier form; therefore, some means include values for the presoldiers also.
[c] Means in a column for each protozoan species followed by the same letter are not significantly different at the $\alpha = 0.05$ level by Tukey's procedure.
[d] The mean number of protozoa on day 0 in a 20-μl sample of hindgut contents of *R. flavipes* was 14.90 *Pyrsonympha*, 175.00 *Dinenympha*, 32.20 *T. agilis*, and 5.50 *Spirotrichonympha* (n = 10).
[e] A summation of these effects was reported earlier (Howard and Haverty 1978).

Table 5.—Mean number of *R. flavipes* presoldiers (PS) and % survival of the initial 30 termites after exposure to 4 concentrations of methoprene for up to 23 days. These termites were used in the evaluation of concentration effects of methoprene on symbiotic protozoans.

Concn mg AI/pad	Day[a]							
	13		17		20		23	
	PS	%	Ps	%	PS	%	PS	%
0.000	0.0	95.6	0.0	93.3	0.0	94.4	0.0	93.3
0.016	3.7	93.3	4.0	96.7	10.3	94.4	10.3	93.3
0.032	4.7	96.7	12.7	96.7	16.5[b]	96.7[b]	23.5[b]	93.3[b]
0.063	3.3	85.6	14.7	96.7	18.0	94.4	14.0[c]	90.0[c]

[a] Each pair of values (PS + %) represents the mean response from 3 separate groups of 30 termites.
[b] Mean response from 2 groups of 30 termites.
[c] Response from 1 group of 30 termites.

ginicus, and because methoprene induced differentiation at lower levels.

Effect of Methoprene on Symbiotic Protozoa

Table 4 indicates that methoprene in some manner kills the 4 major species of protozoans found in the hindgut of *R. flavipes*. Significant reduction in *Dinenympha* and *T. agilis* in termites was apparent after 7 days of exposure to 0.032 and 0.063 mg/pad. *Pyrsonympha* and *Spirotrichonympha* were significantly reduced by 0.032 and 0.063 mg/pad after 13 and 10 days, respectively. *T. agilis* appeared the most sensitive protozoa species since its numbers were significantly reduced by the 10th day at 0.016 mg/pad. Over the length of this test (23 days), termite mortality was not excessive (Table 5) even though protozoan populations dwindled to near zero by day 13 in termites exposed to 0.032 and 0.063 mg/pad of methoprene. Mortality similar to the earlier test (Table 2) was evident in the 0.032 mg/pad groups at days 20 and 23 and in the 0.063 mg/pad groups at day 23. Although the presoldier differentiation and survival in this test (Table 5) cannot be compared statistically with that of the previous test (Table 2), observations in this test are similar to those in the earlier test.

Thus, this test provided strong evidence that methoprene at concentrations above 0.016 mg/pad caused either a reduction in the numbers or an elimination of symbiotic protozoa in *R. flavipes*. Such defaunation would, of course, result in the termite's being unable to utilize ingested cellulose and lead to its death by starvation. If many defaunated workers were superimposed on unusually large numbers of colony members like presoldiers and soldiers who are incapable of feeding themselves, the observed pattern of mortality in our experi-

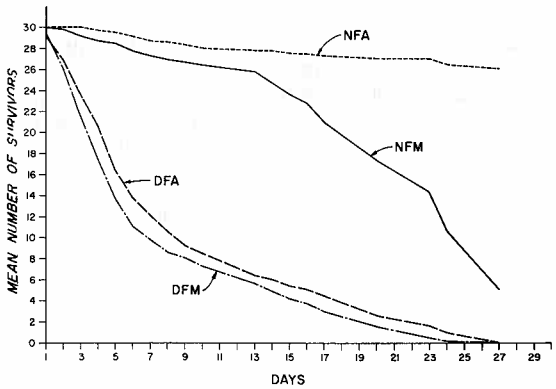

FIG. 1.—Number of live normally faunated (NF) or defaunated (DF) *R. flavipes* at various times after exposure to an acetone-treated paper pad (A) or a pad containing 0.5 mg of methoprene (M). Values are the mean of 10 groups of 30 workers for each of 4 treatments: NFA = normally-faunated on acetone-treated pad, NFM = normally-faunated on methoprene-treated pad, DFA = defaunated on acetone-treated pad, and DFM = defaunated on methoprene-treated pad.

ment would become explicable. The question remained, however, as to whether or not methoprene was overtly toxic to the termite itself.

Determination of Overt Toxicity of Methoprene to R. flavipes

Mortality in DFM groups was consistently more than but not much different from that of DFA groups (Fig. 1). Direct toxicity to the termites should have caused significantly greater mortality in the DFM group. Such was not the case. Mortality in the NFM groups was consistently greater than the NFA groups, the difference becoming pronounced on day 14. Survival in the NFM group was higher than in the groups exposed to 2.5 mg AI/pad in an earlier test (Table 1). This might be due to differences in the vigor of the 2 colonies used or to a difference in this species' reaction to methoprene in an EC rather than the technical grade material. Apparently, mortality in the DFA and DFM was caused mainly by starvation after defaunation. The severe conditions of the defaunation procedure undoubtedly also contributed to mortality. Likewise, mortality in NFM was apparently due to starvation as a result of methoprene-induced defaunation, which was probably complete by day 13 (Table 4).

Conclusions

The IGRs methorpene and hydroprene exhibit several concentration-dependent morphogenetic and lethal effects upon *R. flavipes* and *R. virginicus* workers. Such effects include induction of many presoldiers, soldiers, and nymph-soldier intercastes, and mortality from starvation and ecdysis failures. Experiments using *R. flavipes* and methoprene showed that the termites starved for 2 reasons: induced defaunation of their symbiotic protozoans; and excessive trophic demands caused by the disproportionate number of soldier forms present. While defaunation effects were not examined for *R. virginicus*, the essentially similar response of *R. virginicus* and *R. flavipes* to methoprene strongly suggests that the *R. virginicus* protozoa are also eliminated.

The effect of hydroprene on the symbiotic protozoa of *Reticulitermes* spp. has not been examined. The overall differences noted in morphogenetic and lethal effects between termites exposed to methoprene and hydroprene are great enough that analogous effects on the protozoan cannot be safely assumed. Finally, our results clearly show that methoprene is not overtly toxic to the termites themselves, but rather only eliminates, in some as yet unknown manner, their protozoan symbionts.

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