

Potential of Insect Growth Regulators as Termiticides: A Review

by

Nan-Yao Su¹ and Rudolf H. Scheffrahn¹

ABSTRACT

Effects of insect growth regulators (IGR's) against termites and factors affecting test results are reviewed. It is a generally accepted hypothesis that IGR-induced production of excessive presoldiers and soldiers would overburden the tasks of the remaining worker nestmates. However, doubt exists that IGR's alone can disrupt the social homeostasis that is maintained by many other inter-linked factors. Results from previous studies indicates that IGR's may be more effective as control agents against species with lower natural soldier proportions.

INTRODUCTION

Determination of caste formation in termites is strongly influenced by the endocrine system (Lüscher 1976, Yin and Gillott 1975). Lüscher (1958) first suggested that juvenile hormone (JH) regulated soldier formation in the drywood termite, *Kalotermes flavicollis* (Fabr.). This hypothesis was confirmed in experiments whereby presoldier and soldier formation was induced by implanting *corpora allata* (Lüscher and Springhetti 1960, Lebrun 1967), and further elucidated when presoldiers were produced after injection of a synthetic JH (Lüscher 1969).

Termite colonies contain optimal proportions of the soldier caste which have apparently evolved to most efficiently provide for the defense of the colony (Wilson 1971, Haverty 1977). A hypothesis has been forwarded that juvenile hormone analogs (JHA's), which induce excessive soldier formation, may be used to disrupt the

¹Ft. Lauderdale Research and Education Center, University of Florida, IFAS, 3205 College Ave., Ft. Lauderdale, FL 33314

integrity of a termite society, leading to the destruction of the entire colony (Haverty 1977, Hrdý and Křeček 1972, Hrdý 1973). Howard and Haverty (1979a), who previously reviewed literature on this subject, raised questions that need to be considered before insect growth regulators (IGR's) can effectively be used in termite control. Their questions include effects of group size, population heterogeneity of test insects, colony origin and habitat, season, temperature, roles of endosymbionts, synergistic effects when used with other termiticides, etc. Although a considerable amount of work had, at that time, been conducted on the caste-inducing effects of many synthetic compounds that mimic JH activity (Howard and Haverty 1979a), their practicality for termite control had not yet been demonstrated. This article updates the information which has been published in the last decade and discusses the termiticidal potential of IGR's.

Insect Growth Regulators and Target Species

IGR's and termite species to which they were exposed are summarized in Table 1. Studies involving juvenile hormones or juvenoids showing negative results were excluded. Of the 20 species tested, the following ten subterranean species are considered of economic importance (Edwards and Mill 1986): *Reticulitermes lucifugus* (Rossi) and *Reticulitermes santonensis* Feytaud in Europe, *Mastotermes darwiniensis* Froggatt and *Nasutitermes exitiosus* (Hill) in Australia, *Coptotermes amanii* (Sjöstedt) in Africa, *Coptotermes niger* Snyder in central America, *Heterotermes indicola* (Wasmann) in India, *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks) in the United States, *Reticulitermes speratus* (Kolbe) in Japan, *Reticulitermes flaviceps* Oshima in China, and *Coptotermes formosanus* Shiraki found world-wide. Only two drywood species of economic importance, *K. flavicollis* and *Cryptotermes brevis* (Walker), have been tested for their susceptibilities to IGR's.

Methoprene and hydroprene were most frequently tested, mirroring their wide market appeal for control of other economically important insects. Of the four new IGR's that became commercially available during the 1980's (Table 1), fenoxycarb has the greatest potential for termite control due to its availability and effectiveness against other insect pests.

Table 1. List of insect growth regulators (IGR's) and termite species which responded to their exposure

IGR	Termite	References
JHA-II(1)	Rhinotermitidae <i>Reticulitermes santonensis</i>	Hrdy & Krecek 1972
JHA-III(2)	Rhinotermitidae <i>R. santonensis</i>	Hrdy & Krecek 1972
Farnesenic acid ethyl & alkoxy deriv.	Kalotermitidae <i>Kaloterms flavicollis</i> <i>Postelectrotermes nayari</i>	Springhetti 1974, 1976 Varma 1977
	Hodotermitidae <i>Zootermopsis angusticollis</i>	Wanyonyi & Luscher 1973 Luscher 1974a Yin & Gillott 1975
	Rhinotermitidae <i>R. santonensis</i> <i>Prohinoterms simplex</i>	Hrdy et al. 1979 Hrdy et al. 1979
Triprene	Mastotermitidae <i>Mastotermes darwiniensis</i>	French & Robinson 1978
	Rhinotermitidae <i>Reticulitermes flaviceps</i>	Chu et al. 1974
Methoprene	Kalotermitidae <i>K. flavicollis</i> <i>Cryptotermes brevis</i> <i>Bifiditermes beesoni</i>	Lenz 1976 Hrdy et al. 1979 Afzal & Ahmad 1982a
	Rhinotermitidae <i>Heterotermes indicola</i> <i>Reticulitermes flavipes</i>	Lenz 1976 Lenz 1976 Howard & Haverty 1978, 1979b Haverty & Howard 1979 Howard 1980, 1983
	<i>R. flaviceps</i> <i>Reticulitermes lucifugus</i> <i>R. santonensis</i> <i>Reticulitermes virginicus</i>	Chu et al. 1974, Dai 1980 Lenz 1976 Hrdy et al. 1979(3) Howard & Haverty 1979b Haverty & Howard 1979
	<i>Coptotermes amanii</i> <i>Coptotermes niger</i> <i>Coptotermes formosanus</i>	Lenz 1976 Lenz 1976 Su et al. 1985 Jones 1987a Haverty et al. 1989
	<i>P. simplex</i>	Krecek et al. 1981
	Termitidae <i>Nasutitermes nigriceps</i>	Lenz 1976 Hrdy et al. 1979(3)
	<i>Macrotermes michaelseni</i>	Okot-Kotber 1980a,b
Hydroprene	Mastotermitidae <i>M. darwiniensis</i>	French & Robinson 1978 French et al. 1979

Table 1. List of insect growth regulators (IGR's) and termite species which responded to their exposure (cont.).

IGR	Termite	References
	Kalotermitidae	
	<i>K. flavicollis</i>	Lenz 1976
	<i>B. beesoni</i>	Afzal & Ahmad 1982a,b
	<i>Neotermes castaneus</i>	Hrdy et al. 1979
	<i>N. jouteli</i>	Hrdy et al. 1979
	<i>Incisitermes schwarzi</i>	Hrdy et al. 1979
	<i>Cryptotermes brevis</i>	Hrdy et al. 1979
	Hodotermitidae	
	<i>Z. angusticollis</i>	Wanyonyi & Luscher 1973 Luscher & van Doorn 1976
	<i>Z. nevadensis</i>	Wanyonyi & Luscher 1973 Wanyonyi 1974 Luscher & van Doorn 1976
	<i>Hodotermes mossambicus</i>	Luamba 1980
	Rhinotermitidae	
	<i>Heterotermes convexinotatus</i>	Hrdy et al. 1979
	<i>H. indicola</i>	Lenz 1976.
	<i>R. flaviceps</i>	Chu et al. 1974
	<i>R. flavipes</i>	Lenz 1976
	<i>R. santonensis</i>	Haverty & Howard 1979
	<i>R. lucifugus</i>	Hrdy et al. 1979
	<i>R. virginicus</i>	Lenz 1976
	<i>C. amanii</i>	Haverty & Howard 1979
	<i>C. niger</i>	Lenz 1976
	<i>C. formosanus</i>	Hrdy et al. 1979
	<i>P. simplex</i>	Hrdy et al. 1979
	Termitidae	
	<i>Nasutitermes exitiosus</i>	French 1974
	<i>N. nigriceps</i>	Lenz 1976 Lenz & Westcott 1985
	<i>Macrotermes subhyalinus</i>	Meyer & Luscher 1973
	<i>Microcerotermes</i> sp.	Faragalla et al. 1985
Difflubenzuron (Dimilin)	Rhinotermitidae	
	<i>H. indicola</i>	Doppelreiter & Koriath 1981
	<i>R. flavipes</i>	Doppelreiter & Koriath 1981
	Termitidae	
	<i>Microcerotermes</i> sp.	Faragalla et al. 1985
Fenoxycarb	Rhinotermitidae	
	<i>R. virginicus</i>	Jones 1984
	<i>C. formosanus</i>	Jones 1984, 1987b, Su et al. 1985
Ro 16-1295(4)	Rhinotermitidae	
	<i>R. virginicus</i>	Jones 1984
	<i>C. formosanus</i>	Jones 1984, 1987b, Su et al. 1985
AY22,243(5)	Kalotermitidae	
	<i>B. beesoni</i>	Afzal & Ahmad 1982a

Table 1. List of insect growth regulators (IGR's) and termite species which responded to their exposure (cont.).

IGR	Termite	References
JHA-A(6)	Rhinotermitidae <i>Reticulitermes speratus</i>	Doki <i>et al.</i> 1984 Tsunoda <i>et al.</i> 1986
S-31183(7)	Rhinotermitidae <i>R. flavipes</i> <i>C. formosanus</i>	Su & Scheffrahn 1989 Haverty <i>et al.</i> 1989 Su & Scheffrahn 1989

- (1) methyl 10-chloro-3,7,11-trimethyl-2 dodecenoate
- (2) ethyl 10-epoxy-3,7,11-trimethyl-2,6-dodecadienoate
- (3) tetrahydrofuryl analog of methoprene
- (4) 2-[p-(m-Fluorophenoxy)phenoxy] ethyl ethylcarbamate
- (5) methyl Z-10, 11-epoxy-7-ethyl-3, 11-dimethyl-E, E2, 6-tridecadienoate
- (6) ethyl [2-(p-phenoxy phenoxy)ethyl] carbamate
- (7) 2-[1-methyl-2(4-phenoxyphenoxy) ethoxy] pyridine

Doppelreiter and Koriath (1981) provided the only positive data on the effect of a non-JHA IGR. Although their laboratory study demonstrated the ecdysis inhibitory effect of a chitin synthesis inhibitor, diflubenzuron (Dimilin), against *H. indicola* and *R. flavipes*, results from subsequent testing with Dimilin on field colonies of *Microcerotermes* species were mixed (Faragalla *et al.* 1985). A preliminary study with cyromazine also showed no effects against *C. formosanus* (Su and Scheffrahn, unpublished data).

EFFECTS OF IGR'S ON TERMITES

Most researchers reported production of presoldiers or other intercastes following IGR exposure (Table 2). Overt toxicity is the second most frequently reported result. Howard and Haverty (1978) indicated that hind-gut protozoans found in *R. flavipes* were killed by IGR's and suggested starvation-induced mortality. Their observation was confirmed by French *et al.* (1979) on *M. darwiniensis*.

Table 2. Reported effects of IGR's on termites.

Effect	Reference
Presoldier production:	Afzal & Ahmad 1982a,b, Chu <i>et al.</i> 1974, Dai 1980, Doki <i>et al.</i> 1984, Faragalla <i>et al.</i> 1985, French 1974, French & Robinson 1978, Haverty & Howard 1979, Haverty <i>et al.</i> 1989, Howard 1983, Howard & Haverty 1978, 1979b, Hrdý 1972, 1976, 1985, Hrdý & Křeček 1972, Hrdý <i>et al.</i> 1979, Jones 1984, 1987a,b, Křeček <i>et al.</i> 1981, Lenz 1976, Lenz & Westcott 1985, Lüscher 1960, Lüscher & van Doorn 1976, Okot-Kotber 1980a, b, Springhetti 1974, 1976, Su & Schefrahn 1989, Su <i>et al.</i> 1985, Tsunoda <i>et al.</i> 1986, Varma 1977, Wanyonyi 1974, Wanyonyi & Lüscher 1973, Yin & Gillott 1975
Intercaste production:	Afzal & Ahmad 1982a,b, Chu <i>et al.</i> 1974, Doki <i>et al.</i> 1984, Haverty & Howard 1979, Howard 1983, Howard & Haverty 1978, Hrdý 1972, 1976, 1985, Hrdý & Křeček 1972, Hrdý <i>et al.</i> 1979, Jones 1984, 1987a,b, Lenz 1976, Lenz & Westcott 1985, Luamba 1980, Meyer & Lüscher 1973, Springhetti 1974, 1976, Tsunoda <i>et al.</i> 1986, Varma 1977, Wanyonyi 1974
Toxicity:	Afzal & Ahmad 1982a, Chu <i>et al.</i> 1974, Dai 1980; Doki <i>et al.</i> 1984, Haverty & Howard 1979, Howard 1983, Howard & Haverty 1978, 1979b, Hrdý 1972, 1985, Hrdý & Křeček 1972, Lenz 1976, Lenz & Westcott 1985, Okot-Kotber 1980a, b, Springhetti 1974, Varma 1977
Neotenic production:	Afzal & Ahmad 1982a,b, Dai 1980, Springhetti 1974, 1976, Wanyonyi 1974, Wanyonyi & Lüscher 1973, Yin & Gillott 1975
Ecdysis inhibition:	Doppelreiter & Koriath 1981, Haverty & Howard 1979, Howard & Haverty 1978, Hrdý & Křeček 1972, Lenz 1976, Wanyonyi 1974, Varma 1977

Table 2. Reported effects of IGR's on termites (cont.)

Effect	Reference
Feeding inhibition:	French & Robinson 1978, French <i>et al.</i> 1979, Jones 1987a,b, Lenz & Westcott 1985, Springhetti 1974
Gut symbiont defaunation:	French <i>et al.</i> 1979, Haverty & Howard 1979, Howard 1983, Howard & Haverty 1978
Pseudoimago production:	Varma 1977, Wanyonyi & Lüscher 1973, Wanyonyi 1974
Egg production inhibition:	Afzal & Ahmad 1982a, Howard 1980

FACTORS AFFECTING TEST RESULTS

1. Nutrition

Lenz (1976) demonstrated that laboratory groups of *K. flavicollis* fed on IGR-treated decayed wood produced more presoldiers than those fed on treated filter paper or sound wood. Although the higher protein content in decayed wood apparently enhanced presoldier formation at the individual level, he suggested that a well nourished colony may endure an alternation of caste composition whereas a poorly nourished colony would likely succumb. Studies with *C. formosanus* also agree with Lenz's (1976) finding as IGR-exposed groups fed on wood blocks produced more presoldiers (Su *et al.* 1985) and intercastes (Jones 1984) than those fed less nutritious materials. Contrary to these observations, a study by Howard and Haverty (1979b) indicated that absorbent paper pads, composed of refined cellulose, stimulated greater soldier differentiation in two *Reticulitermes* species than other diets including decayed sawdust. They noted, however, that the poor performance of the sawdust-fed termites may have been due to fungal contamination.

2. Caste Composition and Group Size

Lüscher (1961) hinted that chemical factor(s) released from existing soldiers inhibit formation of additional soldiers. Indeed,

the inhibitory effects of soldiers on presoldier production have been demonstrated in many termite species (Springhetti 1969, Haverty 1979, Haverty and Howard 1981, French 1974, Lenz 1976, Okot-Kotber 1983). Excess soldiers were usually starved or cannibalized by the workers (Morgan 1959, Lüscher 1961, McMahan 1966, Nagin 1972, Stuart 1972, Yin and Gillott 1975, Haverty 1979, Haverty and Howard 1981, Su and La Fage 1987). Under the influence of IGR's, some concluded that groups containing more soldiers generally produced fewer presoldiers (Hrdý 1976, Lenz 1976, Afzal and Ahmad 1982b), while others indicated that the presence of soldiers had negligible effects on presoldier production (Dai 1980, Howard 1983). Contradictory results seem to be species dependent. It may be more relevant for applied studies to use experimental groups containing soldier proportions approximate to those found in field colonies (Jones 1984, Su *et al.* 1985).

Shimizu (1963) first indicated there was a relationship between group size and soldier proportion. Smaller groups (orphan groups) of *C. formosanus* (Haverty 1979) and *Reticulitermes* species (Haverty and Howard 1981) generally contained lower soldier proportions than did larger groups. Increased group size, however, reduced presoldier formation of the termitid species, *Macrotermes michaelseni* (Sjöstedt) (Okot-Kotber 1983). Maki and Abe (1986), who examined 85 field colonies of a kalotermitid species, *Neotermes koshunensis* (Shiraki), also observed decreased soldier proportion in larger colonies.

Under the influence of IGR's, the presence of replacement reproductives reduced presoldier formation in small groups but did not affect larger groups of the kalotermitid, *B. beesoni* (Afzal and Ahmad 1982b). Groups size used in laboratory tests varied among studies mainly due to the availability of termites.

3. Competence Period and Colony Origin

Lüscher (1952) first noted that only at certain developmental stages (or "competence periods") could larvae and nymphs of *K. flavicollis* molt into the supplementary reproductive castes. Soldier formation by *K. flavicollis* (Springhetti 1972), and *Zootermopsis angusticollis* (Hagen) (Lüscher 1974a) was induced only when instars were of certain age. Yin and Gillott (1975) considered the early phase in the stadium as the competence period for

Z. angusticollis. Okot-Kotber (1980a) determined that the 0-6 day interval is a period when *M. michaelseni* workers are most competent to differentiate into the presoldier stage. Dai (1980) also showed that the younger instars of *R. flaviceps* were more easily transformed to presoldiers, while 5th instar pseudergates of *R. speratus* were found most responsive to IGR's (Tsunoda *et al.* 1986).

Other factors such as season and temperature (Lüscher 1974b, Haverty and Howard 1981, Afzal and Ahmad 1982b) have been suggested to affect presoldier formation of termites. Another factor to be considered is colony origin. Laboratory experiments with *C. formosanus* (Haverty 1979) and *R. flavipes* (Haverty and Howard 1981) demonstrated that different colonies of the same species produced presoldiers and soldiers at different rates. In separate studies, Su *et al.* (1985) and Jones (1987b) both showed significant differences in responses to IGR's among colonies of *C. formosanus*. Ages of field colonies of subterranean termites are difficult to determine but may be the primary cause of among colony variation with regard to IGR susceptibility. Competence period and nutritional factors may also be responsible for colony differences in IGR response. Whenever possible, these factors should be considered when testing IGR's against termites. Several different colonies should always be used.

IGR'S AS TERMITICIDES

Hrdý and Křeček (1972) first suggested that excessive IGR-induced superfluous soldiers may disrupt the social balance of termite colonies. Because the worker caste is solely responsible for food intake in a colony, abnormally large proportions of dependent castes, such as soldiers, could lead to disruption of the homeostasis of the termite society. This optimistic view is held by some researchers (Haverty 1977, Howard and Haverty 1979a, Jones 1984, Su *et al.* 1985, Tsunoda *et al.* 1986). Workers of *C. formosanus* consume more wood in response to the presence of increased soldiers in experimental groups, but their wood-consumption rates decreased drastically when trophallactic demands from soldiers exceeded workers' food intake capacity (Su and La Fage 1987). Excess soldiers were starved or cannibalized until soldier proportions converged to a "stable" range

(Haverty 1979, Su and LaFage 1987). We suspect that artificially induced soldiers would meet the same fate in field situations should IGR's be introduced into the colony. Field trials with methoprene and hydroprene in Cuba, however, failed to yield an increase in soldiers or the decline of *Prorhinotermes simplex* (Hagen) colonies (Hrdý *et al.* 1979). They attributed this failure to the chemical instability of these compounds. This view is shared by Afzal and Ahmad (1982b) who stress that the effectiveness of an IGR had to persist long enough to encompass the competency period of the target insects.

Aside from the chemical instability, Hrdý *et al.* (1979) also raised a fundamental skepticism on the practical application of IGR's in termite control. Because the homeostatic regulatory mechanisms of a field colony are difficult to simulate in the laboratory, IGR's' effects observed from isolated foraging groups may be negated by some innate "homeostatic resistance" of a field colony. This is especially relevant when testing subterranean termites that naturally contain largely populated colonies. Noting that many environmental, physiological, and behavioral factors might affect the formation and maintenance of soldier proportions of termite colonies, Lenz and Westcott (1985) questioned if the introduction of IGR's alone could upset colony homeostasis which is balanced and maintained by an array of factors.

From his testing of IGR's against seven termite species, Lenz (1976) concluded that species with lower natural soldier proportions such as *K. flavicollis* respond better to IGR's than those with higher natural soldier proportions such as *C. amanii*. His conclusion is well supported by other studies which demonstrated that, when exposed to IGR's, *Reticulitermes* species (natural soldier proportions: 1-2%) generally produced more presoldiers and/or resulted in higher mortality than *C. formosanus* whose colonies generally contain 10-15% soldiers (Haverty 1977, Haverty and Howard 1979, Jones 1984, Su *et al.* 1985, Su and Scheffrahn 1989).

In a preliminary field trial with fenoxycarb baits, Jones (1988) observed an increase of presoldiers and soldiers in colonies of *Reticulitermes* species and a subsequent decline in their foraging activities. Her results are the first to demonstrate efficacy under field conditions and are encouraging for the potential of IGR's as termiticides. A comparison of her success with the previous failure

of field trials reported by Hrdý *et al.* (1979) with *P. simplex* (naturally high soldier proportion), further supports Lenz's (1976) conclusion and suggests that IGR's may be more effective against termites with lower natural soldier proportions such as *Reticulitermes* species.

ACKNOWLEDGMENTS

We thank M. I. Haverty and S. C. Jones for reviewing this manuscript. This article is Fla. Agric. Exp. Stn. Journal Series No. 8973.

REFERENCES

- Afzal, M., and M. Ahmad. 1982a. Effects of juvenile hormone analogues on colony foundation and caste differentiation in *Bifiditermes beesoni* (Gardner) (Isoptera: Kalotermitidae). *Mater. Org.* 17: 35-49.
- Afzal, M., and M. Ahmad. 1982b. Significance of existing castes on the future caste differentiation of *Bifiditermes beesoni* (Gardner) under the influence of a juvenile hormone analogue. *Mater. Org.* 17: 93-116.
- Chu, H.-H., J.-D. Dai, T.-F. Chen, M.-W. King. 1974. Induction of soldier differentiation in the termite, *Reticulitermes flaviceps* Oshima, with juvenile hormone analogues. *Acta Entomol. Sinica* 17: 161-165.
- Dai, J.-D. 1980. Induction and inhibition of caste-differentiating potentials in *Reticulitermes flaviceps* (Oshima). *Acta Entomol. Sinica* 23: 374-380.
- Doki, H., K. Tsunoda, and K. Nishimoto. 1984. Effect of juvenile hormone analogues on caste-differentiation of the termite, *Reticulitermes speratus* (Kolbe) (Isoptera: Rhinotermitidae). *Mater. Org.* 19: 175-187.
- Doppelreiter, V. H., and M. Koriöth. 1981. Entwicklungshemmung durch Diflubenzuron bei den Bodentermiten *Heterotermes indicola* und *Reticulitermes flavipes*. *Z. angew. Ent.* 91: 131-137.
- Edwards, R., and A. E. Mill. 1986. Termites in buildings. Their biology and control. Rentokill Limited. W. Sussex, U.K., 261 pp.
- Faragalla, A. A., A. I. Badawi, and A. I. Dabbour. 1985. Field evaluation of the effects of the juvenile hormone analogues (JHA's) and diflubenzuron (Dimilin) on termites of the genus *Microcerotermes* (Isoptera: Termitidae) in the central region of Saudi Arabia. *Sociobiology*, 11: 29-37.

- French, J. R. J. 1974. A juvenile hormone analogue inducing caste differentiation in the Australian termite *Nasutitermes exitiosus* (Hill) (Isoptera: Termitidae). *J. Aust. Ent. Soc.* 13: 353-355.
- French, J. R. J., and P. J. Robinson. 1978. Feeding inhibition of *Mastotermes darwiniensis* Froggatt (Isoptera) on JHA surface treated plywood blocks. *Z. angew. Entomol.* 85: 360-364.
- French, J. R. J., P. J. Robinson, J. W. Creffield, and C. D. Howick. 1979. Effects of hydroprene on the feeding activity of *Mastotermes darwiniensis* Froggatt (Isoptera). *Z. angew. Entomol.* 87: 239-246.
- Haverty, M. I. 1977. The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). *Sociobiology* 2: 199-216
- Haverty, M. I. 1979. Soldier production and maintenance of soldier proportions in laboratory experimental groups of *Coptotermes formosanus* Shiraki. *Insectes Soc.* 26: 69-84.
- Haverty, M. I., and R. W. Howard. 1979. Effects of insect growth regulators on subterranean termites: induction of differentiation, defaunation, and starvation. *Ann. Entomol. Am.* 72: 503-508.
- Haverty, M. I., and R. W. Howard. 1981. Production of soldiers and maintenance of soldier proportions by laboratory experimental groups of *Reticulitermes flavipes* (Kollar) and *Reticulitermes virginicus* (Banks) (Isoptera: Rhinotermitidae). *Insectes Soc.* 28: 32-39.
- Haverty, M. I., N.-Y. Su, M. Tamashiro, and R. Yamamoto. 1989. Concentration-dependent presoldier induction and feeding deterrence: potential of two insect growth regulators for remedial control of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *J. Econ. Entomol.* 82: 1370-1374.
- Howard, R. W. 1980. Effects of methoprene on colony foundation by alates of *Reticulitermes flavipes* (Kollar). *J. Ga. Entomol. Soc.* 15: 281-285.
- Howard, R. W. 1983. Effects of methoprene on binary caste groups of *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). *Environ. Entomol.* 12: 1059-1063.
- Howard, R. W., and M. I. Haverty. 1978. Defaunation, mortality and soldier differentiation: concentration effects of methoprene in a termite. *Sociobiology* 3: 73-77.
- Howard, R. W., and M. I. Haverty. 1979a. Termites and juvenile hormone analogues: a review of methodology and observed effects. *Sociobiology* 4: 269-278.
- Howard, R. W., and M. I. Haverty. 1979b. Comparison of feeding substrates for evaluating effects of insect growth regulators on subterranean termites. *J. Ga. Entomol. Soc.* 14: 3-7.
- Hrdý, I. 1972. Der Einfluss von zwei Juvenilhormonanalogen auf die Differenzierung der Soldaten bei *Reticulitermes lucifugus santonensis* Feyt (Isoptera: Rhinotermitidae). *Z. angew. Entomol.* 72: 129-134.

- Hrdý, I. 1973. Effect of juvenoids on termites and honeybees. Proc. 7th Int'l. Congr. IUSSI, London 1973, pp.158-161.
- Hrdý, I. 1976. The influence of juvenile hormone analogues on caste development in termites, p. 71. In M. Lüscher [ed.], Phase and caste determination in insects. Endocrine aspects. Pergamon Press, Oxford.
- Hrdý, I. 1985. The role of juvenile hormones and juvenoids in soldier formation in Rhinotermitidae, pp. 245-249. In J. A. L. Watson, B. M. Okot-Kotber, and CH. Noirot [eds.], Caste differentiation in social insects. Pergamon Press, Oxford.
- Hrdý, I., and J. Křeček. 1972. Development of superfluous soldiers induced by juvenile hormone analogues in the termite, *Reticulitermes lucifugus santonensis*. Insectes Soc. 19: 105-109.
- Hrdý, I., J. Křeček, and Z. Zusková. 1979. Juvenile hormone analogues: effects on the soldier caste differentiation in termites (Isoptera). Vestn. Cesk. Spol. Zool. 43: 260-269.
- Jones, S. C. 1984. Evaluation of two insect growth regulators for the bait-block method of subterranean termite (Isoptera: Rhinotermitidae) control. J. Econ. Entomol. 77: 1086-1091.
- Jones, S. C. 1987a. Effects of methoprene on *Coptotermes formosanus* (Isoptera: Rhinotermitidae). The Int'l. Res. Group on Wood Preserv. Doc. No. IRG/WP/1322. 8 pp.
- Jones, S. C. 1987b. Extended exposure of two insect growth regulators on *Coptotermes formosanus* Shiraki, pp. 58-61. In M. Tamashiro and N.-Y. Su [eds.], Biology and control of the Formosan subterranean termite. College of Trop. Agric. Human Resources, Univ. of Hawaii, Honolulu, HI.
- Jones, S. C. 1988. Field evaluation of several bait toxicants for subterranean termite control: a preliminary report. 19th Ann. Meeting of the Int'l. Res. Group on Wood Preservation Doc. No. IRG/WP/1376, 11 pp.
- Křeček, J., I. Hrdý, V. Jarolim, and Z. Wimmer. 1981. Antagonistic interaction between a juvenile hormone analogue and precocene I in *Prorethotermes simplex* (Isoptera). Acta Ent. Bohemoslov. 78: 266-269.
- Lebrun, D. 1967. La détermination des castes du termite à cou jaune (*Calotermes flavicollis* Fabr.). Bull. Biol. France et Belg. 101: 139-217.
- Lenz, M. 1976. The dependence of hormone effects in termite caste determination on external factors, pp. 73-89. In M. Lüscher [ed.], Phase and caste determination in insects. Endocrine aspects. Pergamon Press, Oxford.
- Lenz, M. and M. Westcott. 1985. Homeostatic mechanisms affecting caste composition in groups of *Nasutitermes nigriceps* (Isoptera: Termitidae) exposed to a juvenile hormone analogue, pp. 251-266. In J. A. L. Watson, B. M. Okot-Kotber, and C. Noirot [eds.], Caste differentiation in social insects. Pergamon Press, Oxford.

- Luamba, J. L. N. 1980. R ch rches sur le polymorphisme et aper u sur l'influence de l'analogue de l'hormone juv nile sur le d veloppement d'un termite, *Hodotermes mossambicus* (Isoptera: Hodotermitidae). *Bio. Ecol. Mediterraneenne*. 7: 169-171.
- L scher, M. 1952. Die Produktion und Elimination von Ersatzgeschlechtstieren bei der Termitenart *Kaloterme flavicollis* Fabr. *Z. vergleich. Physiol.* 34: 123-141.
- L scher, M. 1958. Ueber die Entstehung der Soldaten bei Termiten. *Rev. Suisse Zool.* 65: 372-376.
- L scher, M. 1960. Hormonal control of caste differentiation in termites. *Ann. N. Y. Acad. Sci.* 89: 549-563.
- L scher, M. 1961. Social control of polymorphism in termites, pp. 57-67, *In* Kennedy, J. S. [ed.], *Insect polymorphism*. Royal Entomol. Soc. London. Symposia No. 1., London.
- L scher, M. 1969. Die Bedeutung des Juvenilhormons f r die Differenzierung der Soldaten bei der Termitenart *Kaloterme flavicollis*. *Proc. VI. Congr. IUSSI, Bern*, pp. 165-170.
- L scher, M. 1974a. Die Kompetenz zur Soldatenbildung bei Larven (Pseuderg ten) der Termitenart *Zootermopsis angusticollis*. *Rev. Suisse Zool.* 81: 710-714.
- L scher, M. 1974b. Kasten und Kastendifferenzierung bei niederen Termiten, pp. 694-739. *In*: Schmidt, G. H. (Hersg.), *Sozialpolymorphismus bei Insekten. Probleme der Kastenbildung im Tierreich*. Stuttgart.
- L scher, M. 1976. Evidence for an endocrine control of caste determination in higher termites. pp. 91-103. *In* M. L scher [ed.], *Phase and caste determination in insects. Endocrine aspects*. Pergamon Press, Oxford.
- L scher, M., and A. Springhetti. 1960. Untersuchungen  ber die Bedeutung der Corpora Allata f r die Differenzierung der Kasten bei der Termitenart *Kaloterme flavicollis*. *J. Insect Physiol.* 5: 190-212.
- L scher, M., and J. van Doorn. 1976. Die Abh ngigkeit der Soldatenbildung bei der Termitenart *Zootermopsis* von der Dauer der Einwirkung des Juvenilhormon-analogons Altozar. *Rev. Suisse Zool.* 83: 939-942.
- Maki, K. and T. Abe. 1986. Proportion of soldiers in the colonies of a drywood termite, *Neotermes kosshunensis* (Kalotermitidae, Isoptera). *Physiol. Ecol. Japan.* 23: 109-117.
- McMahan, E. A. 1966. Food transmission within the *Cryptotermes brevis* colony (Isoptera: Kalotermitidae) *Ann. Entomol. Soc. Am.* 59: 1131-1137.
- Meyer, D. and M. L scher. 1973. Juvenile hormone activity in the haemolymph and the anal secretion of the queen of *Macrotermes subhyalinus* (Rambur) (Isoptera: Termitidae). *7th Int'l. Congr. IUSSI Proc.* 1973: 268-273.

- Morgan, F. D. 1959. The ecology and external morphology of *Stolotermes ruficeps* Brauer (Isoptera: Hodotermitidae) Trans. Royal Soc. New Zealand 86: 155-195.
- Nagin, R. 1972. Caste determination in *Neotermes jouteli* (Banks). Insectes Soc. 19: 39-61.
- Okot-Kotber, B. M. 1980a. Competence of *Macrotermes michaelseni* (Isoptera: Macrotermitinae) larvae to differentiate into soldiers under the influence of juvenile hormone analogue (ZR-515, methoprene). J. Insect Physiol. 26: 655-659.
- Okot-Kotber, B. M. 1980b. The influence of juvenile hormone analogue on soldier differentiation in the higher termite, *Macrotermes michaelseni*. Physiol. Entomol. 5: 407-416.
- Okot-Kotber, B. M. 1983. Influence of group size and composition on soldier differentiation in female final larval instars of a higher termite, *Macrotermes michaelseni*. Physiol. Entomol. 8: 41-47.
- Shimizu, K. 1963. Studies on caste differentiation in termites. III. Emergence of soldiers and supplementary reproductives of the Japanese termites *Leucotermes* (*Reticulitermes*) *speratus* (Kolbe). Japan. J. Appl. Entomol. Zool. 7: 207-212.
- Springhetti, A. 1969. Influenza dei reali di sostituzione di *Kalotermes flavicollis* Fabr. Annali dell' Università di Ferrera, Biologia 3: 49-64.
- Springhetti, A. 1972. The competence of *Kalotermes flavicollis* pseudergates to differentiate into soldiers. Monitore Zool. Ital. (N.S.) 6: 97-111.
- Springhetti, A. 1974. The influence of farnesenic acid ethyl ester on the differentiation of *Kalotermes flavicollis* Fabr. (Isoptera) soldier. Experientia 30: 1197-1198.
- Springhetti, A. 1976. The influence of soldiers on the action of farnesenic acid ethyl ester in *Kalotermes flavicollis* Fabr. (Isoptera). Monitore Zool. Ital. (N.S.) 10: 413-420.
- Stuart, A. M. 1972. Behavioral regulatory mechanisms in the social homeostasis of termites (Isoptera). Am. Zool. 12: 589-594.
- Su, N.-Y., and J. P. La Fage. 1987. Effects of soldier proportion on the wood-consumption rate of the Formosan subterranean termite (Isoptera: Rhinotermitidae). Sociobiology 13: 145-151.
- Su, N.-Y., and R. H. Scheffrahn. 1989. Comparative effects of an insect growth regulator, S-31183, against the Formosan subterranean termite and eastern subterranean termite (Isoptera: Rhinotermitidae). J. Econ. Entomol. 82: 1125-1129.
- Su, N.-Y., M. Tamashiro, and M. I. Haverty. 1985. Effects of three insect growth regulators, feeding substrates, and colony origin on survival and presoldier production of the Formosan subterranean termite (Isoptera: Rhinotermitidae). J. Econ. Entomol. 78: 1259-1263.

- Tsunoda, K., H. Doki, and K. Nishimoto. 1986. Effect of developmental stages of workers and nymphs of *Reticulitermes speratus* (Kolbe) (Isoptera: Rhinotermitidae) on caste differentiation induced by JHA treatment. *Mater. Org.* 21: 47-61.
- Varma, R. V. 1977. Influence of juvenile hormone analogue, farnesyl methyl ether on caste differentiation in termite *Postelectrotermes nayari* Roonwal & Verma, 1971. *Indian J. Exp. Biol.* 15: 564-565.
- Wanyonyi, K. 1974. The influence of the juvenile hormone analogue ZR 512 (Zoecon) on caste development in *Zootermopsis nevadensis* (Hagen) (Isoptera). *Insectes Soc.* 21: 35-44.
- Wanyonyi, K., and M. Lüscher. 1973. The action of juvenile hormone analogues on caste development in *Zootermopsis* (Isoptera). 7th Int'l. Congr. IUSSI Proc. 1973: 392-395.
- Wilson, E. O. 1971. *The insect societies*. Belknap, Cambridge.
- Yin, C.-M., and C. Gillott. 1975. Endocrine control of caste differentiation in *Zootermopsis angusticollis* Hagen (Isoptera). *Can. J. Zool.* 53: 1701-1708.

