4. Discussion

4.1 Chemical control of termites

The consciousness of adverse impacts of chemicals for pest control necessitates the application of different control methods. These methods range from the adoption of an integrated pest management approach to the development of new, more selective, and environmentally acceptable generations of chemicals. One group of these chemicals are insect growth regulators (IGRs) such as juvenile hormones (JHs), their synthetic juvenile hormone analogues (JHAs) and chitin synthesis inhibitors (CSIs). Grenier and Grenier (1993) reported that the IGRs physiologically interfere with normal insect development and the formation of the developmental stages. This occurs either by metabolic interference during the moulting process of the larvae (moult-inhibitors) or by superimposition of the normal endocrine control of development (hormone analogues and hormone mimetics).

4.1.1 Juvenile hormones in insects in general

The JHs are secreted by the corpora allata and released into the hemolymph. Their mode of action is not well understood so far. The current knowledge was summarised by Pallaske (1997). During the normal development of insect larvae the level of JH is generally high but is slowly decreasing to a low level towards the end of the last larval instar. Each time larval growth exceeds the capacity of its cuticle; a short lasting peak of ecdyson induces moulting of the larva to the next stage. In the presence of JHs moulting results in another larval stage, whereas in the absence of the JHs moulting leads to pupa or adult. Wigglesworth (1970) pointed out that injection of JH induces cecropia pupae to moult into second pupae instead of adults.

JHAs act the same way as JHs and their mode of action was summarised by many investigators. Following the findings that a wide variety of chemicals can mimic the action of naturally occurring JHs (Slama *et al.*, 1974, Staal1975), the effects of a number of JHAs as control agents against insects were intensively investigated (Howard and Haverty, 1979). Chemicals as isoprenoid

juvenoids, like hydroprene, methoprene, and epofenonane were first tested for their efficiency against insects. Later, the 4-phenoxyphenyl juvenoids such as fenoxycarb had been tested and proved to be highly efficient and effective as JHAs against many insects (Dorn *et al.*, 1981; Masner *et al.*, 1981, 1987, Oberlander *et al*,1997). Like most other JHAs, the effects of fenoxycarb are mainly morphogenetic. Metamorphosis as summarised by Grenier and Grenier (1993), is disturbed or blocked at the end of the last larval instar, leading to:

- Permanent larvae with the possibility of development into normal adults on untreated food in the cockroach *Blattella germanica or* unable to produce normal adults on untreated food in *Spodoptera littoralis* (Lepidoptera).
- Supernumerary larval instars, with the possibility to get normal adults on untreated food in *Galleria mellonella* (Lepidoptera).
- Larva/nymph intermediates in *Adoxophyes reticulana* (Lepidoptera) and larva/adult intermediates in the bug *Oncopeltus fasciatus.*
- Inhibition of the second part of the metamorphosis only in the pupa and the final adult ecdysis in the mosquito *Culex pipiens*.

Other influences not linked to methamorphosis are:

- The caste differentiation as in ants and termites.
- Yolk synthesis perturbed in fire ants.

4.1.2 Juvenile hormones in termites

So far, the application of JHAs on termite species was found to produce a diversity of effects. These effects are:

- Differentiation of workers into presoldiers (French, 1974; Haverty and Howard, 1979; Springhetti, 1974 and Wanyony, 1974).
- Feeding deterrence (Su *et al.,* 1971; French *et al.,* 1979 and Doki *et al.,* 1984).
- Eradication of hindgut microbial fauna (French *et al.*, 1979 and Howard, 1984).

The JHA fenoxycarb has been investigated so far in lower termites. It was concluded that fenoxycarb could influence termite physiology, specifically in

the view of morphogenetic and oogenic effects. Morphogenetic effects of fenoxycarb are induction of caste differentiation and stimulation of moulting (Jones, 1989).

4.1.3 Chitin synthesis inhibitors (CSI) in insects in general

The chitin synthesis is generally taking place in the membrane coupled multienzyme complex as described by Verloop and Ferrell (1977). Chitin biosynthesis consists of a series of steps involving the enzymes acetyl-CoA-synthetase, glutamine-transaminase, phospho-glucosamine-trans-acetylase phosphoacetylglucosmine-mutase, chitin-UDP-AG-pyrophosphorylase and UDP-N-AG-polymerase (Pallaske *et al.*, 1993).

Chitin synthesis inhibitors such as diflubenzuron, hexaflumuron, triflumuron, and flufenoxuron are benzoyl urea compounds. They act on insects by disturbing the deposition of chitin of the insect cuticle so that the moulting process is inhibited and the postembryonic development will be stopped. Pallaske (1997) stated that the target enzyme for the benzoyl urea compounds is the UDP-N-AG-polymerase (chitinpolymerase). He stated that some benzoyl urea compounds such as dichloro benzoyl urea allow the attachment of the UDP-NAG to the chitinpolymerase and liberate the UDP, thereby suppressing the polymerisation.

Other studies conducted by Post *et al.* (1974) on the CSI diflubenzuron showed that this compound is a competitive inhibitor of chitinpolymerase. Moreover the histological investigation of Marks and Sowa (1974), and Ker (1977demonstrated that the region of increased DOPA deposition between exo - and endocuticula is missing in animals treated with CSIs. This absence of DOPA indicates that there is a lack of chitin matrix for deposition.

The CSI flufenoxuron was tested by Pallaske *et al.* (1993) and Valcke and Pallaske (1995) and was found to be the most appropriate moult inhibitor for insect control examined so far due to its efficacy against insects, its non-solubility in water, and the absence of repellence towards insects. So far flufenoxuron has been tested on various insects but there are no studies regarding its effect on termites.

4.1.4 Chitin synthesis inhibitors in termites

In lower termites, the CSIs do not only act on the larvae but also on the workers, which may undergo many moults after their differentiation (Peppuy *et al.*, 1998). In higher termites, CSIs can only act on the larval stages, since the workers do not moult after their differentiation.

4.1.5 Outline of present work

In the present study the efficacy of the juvenile hormone analogue fenoxycarb (phenoxy-ethyl-carbamate) and the chitin synthesis inhibitor flufenoxuron (acylurea) and their combinations were tested against workers of the subterranean termite *R. santonensis*. Workers were exposed to three kinds of treatments: oral, contact, and topical application of the IGR. Studies included repellence, mortality, and the induction of caste differentiation. In addition, the transferability between termites by feeding, and the inhibition of moulting were investigated. Furthermore, these laboratory experiments have been extended to the field, testing the acceptance of these chemicals by *Microtermes* species (Macrotermitinae, higher termites).

4.2 Effect of fenoxycarb on *R. santonensis* workers:

4.2.1 Mortality

When filter papers impregnated with the JHA fenoxycarb were offered as source of food, concentrations of up to 32 ppm did not produce any significant mortality in R. santonensis workers. This agrees with other studies that demonstrated no toxicity for JHAs. However, mortality of treated termites was caused in this and other studies by the fact that JHA induces the moulting of workers into presoldiers, which afterwards become soldiers. Presoldiers and soldiers belong to dependent castes, which are not able to feed by themselves but have to be fed by workers. The induction of soldier production out of workers results in low numbers of workers, which are not able to feed the increasing number of soldiers and this ultimately leads to increased mortality. Therefore, some investigators have reported that a variety of JHAs indirectly lead to the death of termites by the induction of soldier production. The findings of Hrdy (1972) and Hrdy and Kreicek (1972) on R. lucifugus santonensis, Chu et al., (1974) on R. flaviceps, Varma (1977) on Postelectrotemes nayari; Lenz (1976) on Kalotermes flavicollis, Coptotermes amani, Heterotermes indicola, Nasutitermes nigriceps and Howard and Haverty (1979) can be cited as examples.

This indirect mortality caused by JHAs is dose dependent. Lelis and Everaerts (1993) studied the effect of methoprene (JHA), orally applied on *R. santonensis*. They found that concentrations of 24, 120 and 240 μ g/mg or less resulted in <10% mortality. Concentrations of 480 μ g/mg and 960 μ g/mg led to 80% and 100% mortality, respectively (Lelis and Everaerts, 1993).

4.2.2 Production of presoldiers

As described above, fenoxycarb tested against *R. santonensis* workers showed no toxic effect at all the concentrations used but rather induces the differentiation of workers to dependent presoldiers 9 days after the first treatment. Additionally to presoldiers, fenoxycarb also induces the moulting of workers into intercastes. These intercastes are intermediate forms between

workers and soldiers that never occur naturally, but only under the influence of JHAs. Whereas presoldiers subsequently moulted into full soldiers, the intercastes were cannibalised by the workers.

As soldier production by fenoxycarb was also found by French (1974) on *Nasutitermes exitiosus*, by Haverty and Howard (1979) on *Coptotermes formosanus*, *R. flaviceps* and Springhetti (1974) on *Kalotermes flavicollis*, and by Wanyony (1974) on *Zootermopsis nevadensis*, this substance seems to be generally effective on lower termites. The effect on higher termites is not known so far.

Other substances found to induce soldier production is the JHA Methoprene when applied topically on *R. santonensis* workers at 1, 2, 4, 6 and 8 μ g / mg (Lelis and Everaerts 1993), and S-31183 which induced 90% presoldiers in the Japanese damp wood termite *Hodotermopsis japonica* when applied at 10 and 30 μ g (Ogino *et al.*, 1993).

4.2.3 Factors influencing the efficiency of JHAs

Studies conducted so far indicated that the rate of differentiation of worker to presoldiers by JHAs could be attributed to a number of factors. These include the type as well as the concentration of the JHA used, the termite species tested, the method of application, the dosage used, the origin of the tested colony, the competence period, the caste composition, and the age of the individual castes as well as the feeding substrate used.

Treatments methods

Different application methods (oral, contact, topical as well as vapour administration) were used for different chemicals on different species at variable concentrations. This fact made the comparison of the obtained results difficult. In the present study, three methods were used to apply JHA to *R. santonensis*. These were oral and contact application to a group of workers and topical application to individual workers. GC-analyses indicated no difference in JHA-concentration in *R. santonensis* workers after oral and contact treatments. Also the comparison between the number of *R. santonensis* presoldiers produced following oral application and topical application showed no statistical differences (p > 0.05, calculated $\chi^2 = 1.579$,

tabulated $\chi^2 = 2.370$). However, workers exposed to treated surfaces (contact application) resulted in a lower production of presoldiers than after topical or oral treatments. This is probably due to the fact that higher amounts of fenoxycarb are brought into the termites by oral and topical treatments. Oral application works via feeding and contact and in topical application the amount applied is controlled by the investigator. In contact treatment, however, the termites take up only small amounts by random contact with the chemicals. Thus, for the control of termites oral application is preferable over the other methods.

A third method of JHA application, which was not used in this work but is worth being mentioned, is vapour application. The works of Hrdy (1976) on *Neotermes castaneus*, Meyer and Lüscher (1973) on *Macrotermes subhyalinus*, Wanyoni and Lüscher (1973) on *Zootermopsis angusticollis* and *Z. nevadensis*, (Hrdy 1976) and Wanyoni (1974) on *Z. nevadensis* are examples of applications of this method. However, Howard and Haverty (1979) considered vapour application as an insensitive method as large quantities of the JHAs are required to perform the test as compared with the other two methods.

Dose dependency

With respect to *dosage dependency*, my study 19 % soldiers were produced at 16 ppm and 39 % at 32 ppm fenoxycarb. Doki *et al.* (1984) reported that fenoxycarb applied to *R. speratus* on filter paper or topically induced at a lower dosis differentiation of workers to presoldiers, while at a higher rate it caused 100% indirect mortality (see above) of workers and presoldiers. This indicated that the survival rate might be proportional to the topically applied JHA dose. Likewise, Lelis and Everaerts (1993) examined dose dependency of the JHA methoprene on *R. santonensis*. Results demonstrated that when methoprene was topically applied to *R. santonensis* workers, at 1000, 2000, 4000, 6000 and 8000 ppm, the mortality rate was below 25% for all doses and there was no significant difference (p > 0.05) between doses. The highest transformation rate (70%) was achieved using 240 000 ppm of methoprene. Su *et al.* (1989) used 30 ppm S-31183 against *R. flaviceps* and reported a maximum presoldiers production of 84%, while at 750 ppm the maximum produced was 61.2 %. In *C. formosanus* they found 37% presoldiers were produced at 1500 ppm. On the other hand, Su *et al.* (1985, 1989) and Jones (1987) who worked on *C. formosanus* found insignificant statistical differences (p > 0.05) in presoldiers production in response to different concentrations of methoprene.

Colony specificity

Colony specificity and origin was studied by Doki et al. (1984) in *R. speratus*. Whereas 0.08 mg/dish JHA gave 11.6 % presoldiers in one colony, the same amount produced 76.2 % in another colony. Laboratory experiments with *C. formosanus* (Haverty, 1979) and *R. flaviceps* (Haverty and Howard, 1981) revealed that under the influence of JHA, different colonies of the same species produced presoldiers and soldiers at different rates. Moreover, studies carried out by Su et al. (1985) and Jones (1987) both demonstrated a significant difference in response to IGRs among colonies of *C. formosanus*. Colonies differences might be related to genetical, nutritional variation or environmental factors which are unknown so far.

The age of the workers

The age of the worker is another component that influences the rate of presoldier production in addition to the concentration of JHAs. Okot-Kotber (1980 a and b) and Afzal and Ahmad (1982) related caste differentiating abilities to different worker instars. Okot-Kotber (1980 a) found that 0 to 6 days old larvae of *Macrotermes michaelseni* could differentiate into presoldiers when treated with a concentration of 12.5 µg JHA or less. Under the influence of JHAs presoldiers could be produced as early as the second larval instar in *Prorhinotermes simplex* (Hrdy *et al.*, 1979) and by the third larval instar in *M. michaelseni* (Okot-Kotber, 1980 b). Tsunoda *et al.* (1978) found that presoldiers were induced from every worker instar in *R. speratus*, obviously under the influence of JHAs, with a peak at the fifth instar.

Jones (1987) who studied the effects of methoprene on *C. formosanus* concluded that caste differentiation was somewhat affected by time. Su *et al.*, (1985) suggested that a *C. formosanus* colony maintained in culture for at

least two years may have become too mature to respond to the IGR. On the contrary, Jones (1987) reported that three–year-old workers of the same species, in another colony, differentiated into presoldiers.

As not all workers develop into presoldiers, at least in the termite species studied so far, it is concluded that caste differentiation depends on the age of the individuals (Doki *et al.*, 1984). Studies with individual termites with known age are necessary to solve this question.

Competence time

Lüscher (1960) first noted that larvae are capable of differentiation only at certain developmental stages. Okot-Kotber (1980a, 1985) indicated that *M. michaelseni* workers are most competent to differentiate into the presoldiers' stage from the 1st up to the 6th day of age. Dai (1980) also reported that the younger instars of *R. flaviceps* were more easily transformed into presoldiers than older larvae. On the contrary, in *R. speratus* the 5th instar pseudergates were found to be more responsive to IGRs than younger ones (Tsunoda *et al.*, 1986). The reason for differences in the response to JHA between termite individuals that is sometimes observed (e.g. absence, or delay of differentiation) might be that not all termite individuals that are exposed to JHAs are in the same developmental stages.

Feeding substrate

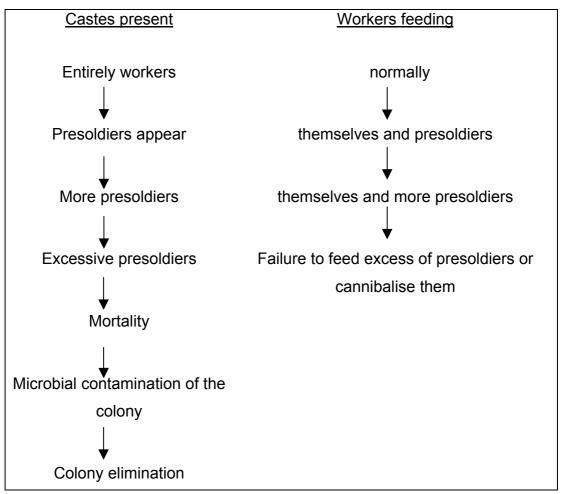
Studies conducted by Su *et al.* (1985) demonstrated that the feeding substrate influences the efficacy of JHAs. They stated that groups of *C. formosanus* termites fed on pine blocks treated with JHA survived better and produced more presoldiers than those fed on α -cellulose substrate. The results were not significantly different. However, Jones (1984) reported that *C. formosanus* fed on IGR impregnated α -cellulose produced no presoldiers at all. It is assumed that the low nutritional value of the cellulose prevents the differentiation.

4.2.4 Transferability of fenoxycarb among *R. santonensis*

In the present study, presoldier differentiation also occurred in untreated workers that were kept together with workers topically treated with 320 ppm fenoxycarb. Obviously fenoxycarb was transferred from treated workers (donors) to the untreated ones (recipients). In the case of oral application of 32 ppm, the amount of fenoxycarb transferred from treated to untreated termites via trophallaxis probably was inadequate to induce the differentiation.

Workers to presoldier differentiation were achieved at all ratios of treated to untreated workers tested. This indicates that the amount absorbed was always sufficient to induce the differentiation. However, the number of presoldiers produced increased with time, which could have been due to the accumulation of the substance with time. Moreover, a high ratio of donors to recipients resulted in a high induction of presoldiers that decreased as the ratio decreased. This could be explained by the accumulation of the JHA among nest mates. These results could be useful in field applications, as the foraging workers will always bring more substance incorporated with food that will be deposited and/or exchanged via trophallaxis.

The following suggests the proposed correlation between workers, feeding pattern, presoldiers production and colony fate in *R. santonensis.*



4.3 Effect of flufenoxuron on *R. santonensis* workers

4.3.1 Mortality

The mortality rate of *R. santonensis* exposed to flufenoxuron was found to be directly proportional to the concentration. Statistically highly significant differences (p < 0.01) in mortality were found between *R. santonensis* exposed to different flufenoxuron doses (1, 2, 10 and 20 ppm). The mortality increased with time due to the accumulative effect of the CSI. This demonstrates that flufenoxuron is suitable for termite control like other CSIs as for instance hexaflumuron and triflumuron.

However, because the mortality rate inflicted by different CSIs is species dependent, further studies with different species should be conducted before flufenoxuron is used against other termite species. Lenz *et al.* (1996) studied the impact of hexaflumuron and triflumuron on *Nasutitermes exitiosus* and *Coptotermes acinaciformis*. They reported no difference in mortality between the control and a range of 0 to 1000 ppm hexaflumuron and 0 to 5000 ppm triflumuron for *N. exitiosus* while exposure of *C. acinaciformis* workers to hexaflumuron at a concentration of 125 ppm or to triflumuron at a concentration of 126 ppm or to triflumuron) in *C. formosanus* and *R. flavipes*. They found that almost 100% mortality occurred after nine weeks of exposure even at the lowest hexaflumuron concentrations tested (125 ppm for *C. formosanus* and 31.3 ppm for *R. flavipes*).

Also the finding of this study that the mortality of CSIs is time dependent is in agreement with other studies. *C. formosanus* exposed to lufenuron for three weeks showed no significant differences in mortality to the controls at any of the concentration levels tested, but at six weeks it reached about 60 % (Su and Scheffrahn, 1996).

4.3. 2 Feeding deterrence

Flufenoxuron has no deterrent effect on the feeding of *R. santonensis* workers at the concentrations necessary to induce CSI. There were no significant

differences between the consumed weight of filter papers treated with different concentrations of flufenoxuron of 0.2 up to 20 ppm and untreated ones (control of 0.00 ppm). Field results with *Microtermes* also showed no deterrent effect for up to nine weeks. Thus, flufenoxuron seems to be more suitable for the control of termites than other CSIs, which have a dose dependent deterrent effect on termites.

The concentration threshold of hexaflumuron for feeding deterrence was \geq 4000 ppm for *R. flavipes* and \geq 8000 for *C. formosanus* (Su and Scheffrahn, 1996). Feeding deterrence of lufenuron ranged between 50 and 100 ppm for *R. flavipes* and between 1000 and 2000 ppm for *C. formosanus* as reported by Su and Scheffrahn (1996). The differences between the concentrations that produced deterrence is probably related to the termite species examined and the type of baits offered. Impregnated filter papers were offered to *R. santonensis* (in the present study), sawdust to *R. flavipes* and *C. formosanus* (Su and Scheffrahn, 1996) and wooden blocks to *C. acinaciformis* (Lenz *et al.*, 1996).

Even at the same concentrations, the same compound (hexaflumuron) gave different mortality rates and feeding deterrence as reported by Lenz *et al.* (1996) and Su and Scheffrahn (1996). Laboratory experiments showed that neither hexaflumuron nor triflumuron (CSIs) were repellent to the mound building *C. acinaciformis* (Lenz *et al.* (1996).

4.4 The effect of combined fenoxycarb and flufenoxuron on *R. santonensis*

To verify the exact effect of flufenoxuron in combination with fenoxycarb on *R.* santonensis, a series of experiments was carried out using it alone or in combination with fenoxycarb at different concentrations. So far, apart from the present study, there are no studies available that examine the combined effect of JHA and CSI combinations on termites. The laboratory experiments on *R.* santonensis proved that fenoxycarb and flufenoxuron inflicted their expected effects (caste differentiation for the former compounds and chitin synthesis inhibition for the latter compounds) also when applied in combinations. When tested in combination at a very high concentration of 32

ppm fenoxycarb and 20 ppm flufenoxuron, 100% mortality was obtained after three weeks. A reduction of the used amount by 50% (16 ppm fenoxycarb and 10 ppm flufenoxuron), reduced mortality after three weeks by only 20%. No presoldiers were produced at these combinations and the high mortality (80-100 %) is likely to be due to the toxic effect of the flufenoxuron.

To make use of the presoldier-inducing effect of fenoxycarb, the amount of flufenoxuron was further reduced in additional experiments. Using fenoxycarb or low concentrations of flufenoxuron alone showed no toxic effect. However, when both compounds were applied in combination, 16 ppm fenoxycarb + 0.2 ppm flufenoxuron caused the same mortality as 2 ppm flufenoxuron alone. Thus, a synergism raised mortality up to a level, which was otherwise achieved only by a 10 fold higher concentration of flufenoxuron alone. This synergistic effect could be caused by the fact that flufenoxuron prevents the completion of the moulting process which is induced by fenoxycarb. This idea is supported by the fact that after combined treatment presoldier production and mortality are inversely correlated with the amount of flufenoxuron applied. At an application of 0.2 ppm flufenoxuron, presoldier production was high and mortality was low, whereas at an application of 2 ppm flufenoxuron presoldier production was low, but mortality was high. From the discussion above the following points can be made regarding the synergistic effect of fenoxycarb and flufenoxuron combinations on R. santonensis:

- Flufenoxuron is toxic to *R. santonensis* workers at high concentrations.
- The rate of this mortality is dose dependent.
- The mortality rate can be elevated if fenoxycarb is added to flufenoxuron.
- The LT₅₀ is inversely related to the concentration of the combined dose.

4.5 Acceptance of fenoxycarb and flufenoxuron on *Microtermes* species in the field

Duncan (1997) stated that for baits to be effective they must be edible to the foraging workers and made of a substance, which is attractive as food also when impregnated with chemicals. However, many chemicals tested so far for termite control did not meet these requirements but render attractive baits repellent to the termites. This was found when the results obtained from several laboratory experiments were extended to the field level by several investigators such as Haverty (1977), Haverty and Howard (1979), Jones (1984, 1989, 1990) and Su et al. (1991). In the present study, the acceptance of fenoxycarb and flufenoxuron for termites in the field was examined on the lawns of the University of Khartoum with colonies of *Microtermes*. The effect of 32 ppm and 320 ppm fenoxycarb and 20 ppm and 200 ppm flufenoxuron wooden baits driven into the soil were tested. Pine wood baits treated with either concentrations of fenoxycarb or flufenoxuron were accepted as food source by Microtermes for up to 6 weeks. After that, the consumption rate of treated baits became significantly smaller than control baits because of one or several of the following reasons:

- Continuous decline in the production of workers, as the majority of *M*. *lepidus* larvae differentiated into soldiers under the effect of the JHA carried into the nest. Jones (1989) stated that field colonies of *Reticulitermes* species exposed to fenoxycarb showed a subsequent decline in their foraging activity as a consequence of increased soldiers' production.
- Effect of flufenoxuron, which might have led to the death of *Microtermes* larvae by intervening with moulting. Lenz *et al.* (1996) suggested that if enough hexaflumuron enters the colony it can lead to the eradication of larvae and earlier stages of workers and nymphs of *C. acinaciformis* and *N. exitiosus* during moulting.
- It might be that *Microtermes* workers avoided the treated wooden baits or shifted their foraging activity to other food sources or performed a low foraging activity. This is in accordance with Su (1991,1994) and Forschler

and Ryder (1996) who evaluated the role of bait-toxicants in suppressing subterranean termite population and suggests possible shifting in foraging activity to avoid the IGR.

Whatever reason might have caused the decrease in consumption, it is important to note that termites had been feeding on the baits for up to 6 weeks. Based on the laboratory studies showing that the influence of fenoxycarb and flufenoxuron started already after 2 weeks, it can be assumed that this is enough time to cause effects (induction of presoldier differentiation, increased mortality) on the immature forms inside the colony.

4.6. Proposed control method for termites using fenoxycarb and flufenoxuron

The present study demonstrates that fenoxycarb and flufenoxuron affect termites by increasing mortality and inducing soldier production. In contrast to other chemicals they do not seem to exhibit significant deterrent effects. Furthermore, this is one of the first studies to demonstrate that fenoxycarb is actually transferred to the nest. Preliminary tests on a laboratory established colony of *Macrotermes* performed in the present study revealed that grass impregnated with fenoxycarb and dyed with 2% neutral red was accepted by foragers for feeding for up 6 months. When opening the nest after 6 months, no larvae but many presoldiers were observed inside indicating that many of the immature forms were influenced by fenoxycarb and moulted into soldiers. Furthermore, only few eggs were found that normally occur in the nest, indicating effects on oogenesis. Red coloration on the fungus garden clearly indicated that dye-treated food was accepted, collected and deposited into the fungus combs. Experiments with Microtermes colonies established in the laboratory showed a significant reduction of egg laying and a decrease in the number of larvae in colonies fed with fenoxycarb. These experiments clearly demonstrate that fenoxycarb is transferred inside the nest by foragers and fed to the reproductives. Thereby it also turns out that, apart from inducing soldier production, fenoxycarb probably affects fecundity of the reproductives. However, this has to be studied in further detail in the future.

Discussion

As most of the presented results have been obtained in the laboratory, it is still unclear whether the examined chemicals would also be effective in the field. Especially, it is unclear whether presoldiers induction by JHAs as demonstrated here in the laboratory also happens in field colonies. This lack of knowledge is because subterranean termites with no obvious boundaries of their nest render it difficult to trace the influence of the IGRs on the development inside the nest. Moreover, it is always difficult to know if a sufficient quantity of the treated bait was delivered inside the nest to affect the colony population or not. This question was raised for underground (Su, 1994; Su *et al.*, 1995 and Duncan, 1997) as well for above ground (Su *et al.*, 1997) baiting systems.

However, there are several field studies available indicating an increased production of soldiers due to JHAs or eradication and/or suppression of the colony due to CSIs (Jones, 1984, 1988, 1990; Lüscher, 1969; Lenz, 1976; Lenz *et al.*, 1996; Su, 1994; Su and Scheffrahn, 1989; Su *et al.*, 1997; Tsunoda *et al.*, 1997). Jones (1984, 1989, and 1991) reported that fenoxycarb led to increased production of presoldiers and soldiers in field colonies of *Reticulitermes* species.

Thus, it seems reasonable to assume that the IGRs are transferred into the nest and induce the production of presoldiers, intercastes, and soldiers (Fig. 37). This disrupts the caste ratio of the colony and interferes with the provision for enough food to colony mates, putting the existence of the whole group of workers at stake. These considerations are in accordance with the findings of many investigators like Su *et al.* (1971) and Doki *et al.* (1984). In *Microtermes* colonies the number of workers outnumbers that of soldiers throughout colony development (El Bakri, 1986, Mohamed, 1991). At a certain stage of the worker would continue to increase (El Bakri, 1986). This is geared to meet the colony demand for food. If excessive production of soldiers happened as a result of exposure to fenoxycarb, the workers will fail to perform their normal task. In natural colonies of *Reticulitermes* the proportion of soldiers is about 2%. A considerable increase above this level cannot be compensated by the feeding activity of the workers, thus leading to the extinction of the whole

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group (Lenz *et al.*, 1976). The importance of soldier to worker ratio was also demonstrated by Lenz *et al.* (1976) showing that *C. amanii* a species characterised by its higher soldier proportion showed decreased response to IGRs as compared with *Kalotermes flavicollis* that is characterised by its low soldier proportion.

Control of termites relies on the suitability of the substance to be accepted by the workers without any immediate effect, allowing transportation from the site of application inside the nest. Furthermore, these substances have to be distributed among nest mates by trophallaxis and grooming. Baits impregnated with biocides such IGRs will be the suitable way to achieve this goal thus providing the best and most appropriate control strategy. They have no impact on the environment, as they affect only termites that feed on baits but no non-target organisms. Thus, the use of IGRs and especially JHAs and CSIs seems to be a promising and environmentally safe alternative for the control of termites.

However, this has to be demonstrated in further studies, especially in the field because the control of subterranean termites is rather difficult due to the cryptic nature of their way of existing. There will always be unknown factors that influence the field findings. Future studies for termite control programmes especially of subterranean termites should focus on the following aspects:

- Acquiring knowledge on the biology and life history of the termite species.
- Determination of the initial size of the targeted termite population.
- Seasonal activity pattern.
- Factors affecting foraging and food finding behaviour.

A consistent and long term monitoring programme should follow for the assessment of the influence of these JHAs and CSIs on termites. Release-recapture method and morphometric markers used by Forschler and Jenkin (1999) and Evans et al (1998) can be adopted to provide an idea about the colony foraging area and the number of colonies available in the study area.

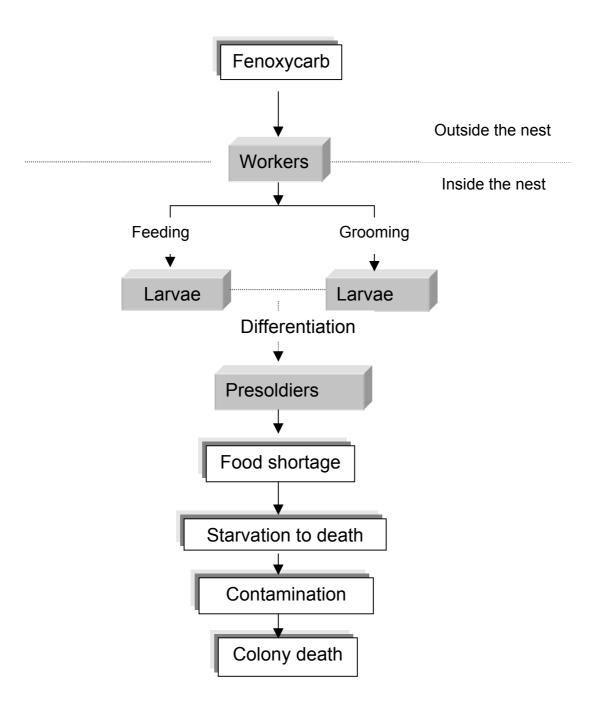


Fig. 37: Fate of the colony after exposure of workers to fenoxycarb