CHEMICAL DEFENCE IN TERMITES – ECOLOGICAL ASPECTS

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SUMMARY

In a study carried out in the Federal District of Brazil, it was found that the defensive secretions produced by the nasute soldiers contain a variety of components, including monoterpenes. The monoterpenes were toxic on topical application to certain species of ant. Synthetic samples of these monoterpenes also acted as feeding repellents for the giant anteater. Soldiers with mechanical defence mechanisms rarely produce secretions which include the toxic secretions mentioned above. They appear to depend entirely on their powerful mandibles for colony defence. Species with defensive strategies based on chemical components produce large numbers of workers to feed them. This high investment in soldier production has resulted in a low investment in building activities and at the same a reduction in nest fortifications. The lack of a fortified nest is, however, compensated for by the toxic soldier secretions. The high soldier/worker ratio and the multidirectional action of the chemical secretions resulting from their volatility, allow the nasute species to forage on leaves and grasses on the soil surface. These food resources are rarely used in nest construction.

The corollary of this defensive strategy is found in species in which the soldiers have specialised in mechanical defence. These produce few soldiers and invest more energy

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in constructing nests more resistant to the attack of vertebrate predators. Such termites generally forage in galleries and feed on humus, depositing large quantities of soil which is used in constructing very resistant mound nests.

RESUMEN

Defensa quimica en los termites : aspectos ecologicos

En un estudio llevado a cabo en el Distrito Federal de Brasil, se encontró que las secreciones defensivas producidas por soldados nasutes contienen una amplia variedad de componentes, los cuales incluyen varios monoterpenos. Estos monoterpenos fueron tóxicos en aplicationes tópicas en ciertas especies de hormigas. Muestras producidas sintéticamente de éstos monoterpenos también actuaron como repelentes alimenticios del oso hormiguero. Los soldados de especies cuyos mecanismos de defensa son mecánicos, raramente producen secreciones que incluyen los compuestos tóxicos indicados anteriormente. Ellos parecen depender completamente de sus fuertes mandibulas para defensa de la colonia. Especies con estrategias defensivas basadas en compuestos quimicos, producen soldados de pequeño tamaño y en gran número y requieren por ello de un gran número de obreros para su alimentación. Esta alta inversion en la producción de soldados ha resultado en una baja inversión en actividades de construcción y al mismo tiempo en una reducción en la fortificación de sus nidos. La falta de un montículo fortificado es sin embargo compensada por los compuestos tóxicos en las secreciones de los soldados. La amplia relación soldado - obrero y la acción multidireccional de las secreciones quimicas debido a su volatilidad, permite a las especies nasutes de abastecerse con hojas y gramineas sobre la superficie del suelo. Estos recursos alimenticios son raramente utilizados en la construcción del montículo.

Lo opuesto a esta estrategia defensiva es encontrado en especies cuyos soldados se han especializado en defensas de tipo mecánico. Estas producen pocos soldados e invierten más energia en las actividades de construcción de montículos más resistentes al ataque de vertebrados depredadores. Estos termites generalmente se abastecen bajo protección y a menudo se alimentan en humus depositando grandes cantidades de suelo, el cual es usado en la construcción de monticulos de gran resistencia.

INTRODUCTION

Division of labour among different morphological castes is a marked characteristic of termite colonies. The soldiers are largely responsible for defence and have morphological adaptations for this function. Some species have soldiers with strong, thick mandibles specialised for mechanical defence whilst others have vestigial mandibles but produce complex defensive secretions. Although extensive literature on the chemical compositions of these secretions has become available in recent years (Prestwich, 1979) little is known of their action against natural predators or of their influence on other aspects of termite ecology. During three years fieldwork in the cerrado vegetation of central Brazil, observations were made on a series of termite species, their defensive strategies and ecology (Coles, 1980). In parallel with this fieldwork, chemical studies on soldier secretions were undertaken at Southampton University (Walmsley, 1981).

METHODS AND RESULTS

Chemical composition of soldier defence secretions

Soldiers and workers from 45 termite species were collected from excavated mounds and foraging parties. These were placed separately in vials of pure dichloromethane (Koch Light) and sent by air to Southampton University. Soldier-specific compounds were determined by analysing the volatile fraction of secretions using a variety of techniques including mass spectroscopy, gas chromatography and nuclear magnetic resonance spectroscopy (Walmsley, 1981). Several monoterpenes e.g. Limonene, phellandrenes, pinenes, were commonly found with diterpenes in the secretions of nasute species. Soldiers from species of the primitive genus *Syntermes* contain the monoterpene cis-β-ocimene and various sesquiterpenes. *Armitermes euamignathus*, also in the Nasutitermitinae but with a well-developed nasus and mandibles, contained no terpenoid compounds but only the straight chain hydrocarbons tri-, tetra- and pentadecane. The majority of species with soldiers adapted for mechanical defence eg. *Orthognathotermes gibberorum, Termes bolivianus* and *Cavitermes parmae*, have no volatile soldier-specific compounds.

Biological action of defence secretions

Ant predators. A range of compounds was tested againts several species of ant common in the Distrito Federal. Small amounts of the synthetic compound being tested (0.15 μl/ant) were applied topically to the anterior dorsal thorax of each ant. Tests were carried out with 20 ants treated and 20

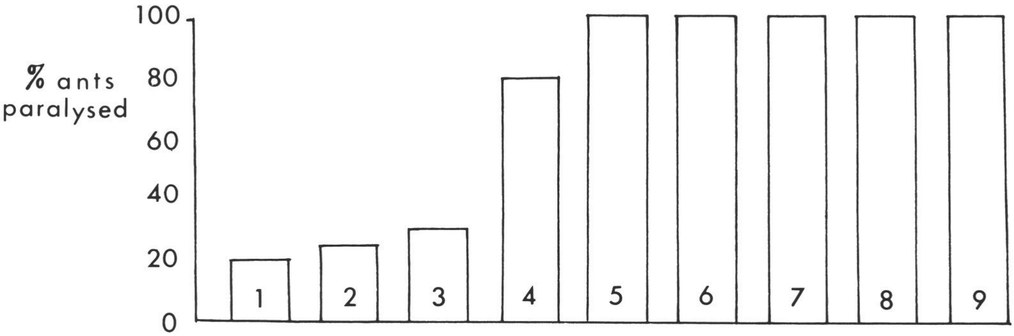

Fig. 1 – Maximum percentage of ants (*Camponotus* sp. A) paralysed by topical applications of test compounds (100 % conc., 0.15 μℓ/ant). Identification of the compounds tested is given below : 1 – n-pentadecane ; 2 – n-undecane ; 3 – myrcene ; 4 – β-pinene ; 5 – cis-β-ocimene ; 6 – α-thujene ; 7 – α-phellandrene ; 8 – α-pinene ; 9 – limonene.

Fig 1 – Porcentaje máximo de hormigas (*Camponotus* sp. A) paralizadas por aplicación tópica de compuestos probados (100 %) conc., 0.15 μℓ/hormiga). La identificación del compuesto probado esta marcada abajo.

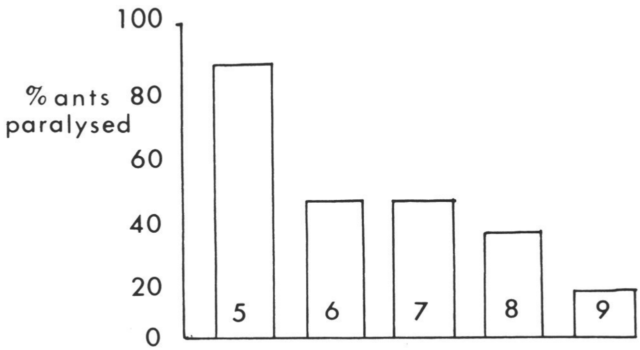

Fig. 2 – Time taken for five of the tested compounds to paralyse 100 % of the ants – *Camponotus* sp. A. (Topical application of 0.15 μℓ/ant to the dorsal, anterior thorax). Identification of the compounds is given below.

Fig. 2 – Tiempo necesario para que cinco de los compuestos probados paralizen 100 % de hormigas *Camponotus* sp. A. (aplicaciones tópicas de 0.15 μℓ/hormiga en el torax antero-dorsal). La identificación de los compuestos está marcada abajo.

as controls, in both open and closed petri dishes. The effects of the compounds tested varied both in severity and rapidity but in general produced paralysis and in some cases death. When death did not occur, paralysis lasted for several hours which would almost certainly lead to death under natural conditions due to predation and desiccation.

The varied effects of the compounds tested are shown in Fig. 1. The time taken to paralyse all the ants also varied and ranged from 16 minutes with 100 % concentrations of limonene and 92 minutes with cis-β-ocimene (Fig. 2). Dilutions of the most toxic monoterpenes were also tested. Ethanol, used as a solvent, was tested and shown to have no detectable toxic effect. Solutions of 80 % concentration had a more rapid toxic action than those of 100 % (Table 1). These differences are probably due to the solvent spreading the terpenes over the cuticle more effectively.

Mammalian predators. Food preference experiments were carried out using captive giant ant-eaters (*Myrmecophaga tridactyla*) and eight termite species representing different types of soldier defensive adaptations (Nasutes – *Nasutitermes* sp. n. D, *Cortaritermes silvestrii* and *Velocitermes paucipilis*, Mechanical – *Cornitermes* sp. n. A, *Procornitermes araujoi* and *Syntermes dirus* ; Soldierless – *Grigiotermes metoecus* ; Intermediate – *Armitermes euamignathus*). Tests were repeated on 8 days with different sequences of presentation of the termites (Coles, 1980, Coles de Negret and Howse, 1983). The results indicate that species with nasute soldiers are eaten less than soldierless species and those with soldiers specialised in mechanical defence.

Three synthetic monoterpenes, known to be present in nasute soldier defence secretions were tested as feeding deterrents. All three compounds were effective but varied in their degree of feeding inhibition. Limonene was the strongest deterrent followed by β-pinene and cis-β-ocimene in the approximate ratios of 11 : 1, 5 : 1 and 2 : 1 respectively.

Foraging strategies

A detailed study of the foraging behaviour of three species from the genus *Syntermes* was carried out near Brasilia. The foraging of *Syntermes* species is crepuscular and nocturnal. They form above-ground foraging parties and the termites are unprotected by soil sheeting. Data on the length of foraging trails, soldier to worker ratios and morphological adaptations of the soldier caste were collected. General observations were made on the feeding behaviour of a further 50 termite species from 29 genera found near Brasilia. The type and location of foraging (i.e. above ground, under soil sheeting, in

Table I – Effects of various monoterpenes applied topically to selected and species, including paralytic effects (PT_{50}) and recovery times, RT_{50} (lethal effects).

Tabla I – Efectos de varios monoterpenes aplicados de manera tópica a varias especies de hormigas seleccionadas, incluyendo los efectos paralizantes (PT_{50}) y los efectos letales (RT_{50}).

Compound tested (0.15 $\mu\ell$/ant)	Conc. (%)	Ant species	Effect	PT_{50} (min.)	RT_{50} (min.)
(+)–limonene	100	A	+++	5.92	x
	80	A	+++	4.48	x
	60	A	++	11.95	1590
	40	A	+	–	
	20	A	0	–	
α-phellandrene	100	A	+++	13.65	>1000
	80	A	++	5.92	560
	60	A	+	8.23	12
	40	A	0	–	–
	20	A	0	–	–
	100	B	+++	9.57	–
	80	B	+++	10.16	–
	60	B	+++	12.64	–
	40	B	+	–	–
	20	B	0	–	–
(+)–α–pinene	100	A	+++	14.54	450
	80	A	+++	7.96	x
	80*	A	+	–	–
(–)–β–pinene	100	A	+++	11.85	220
	100	C	+	14.65	15–25
	100	D	++	38.25	90
α-thujene	100	A	+++	17.61	990
cis–β–ocimene	100	A	+++	–	–
n – undecane	100	A	+	–	–
n – pentadecane	100	A	+	–	–
	80	A	0	–	–
β–myrcene	100	A	+	–	–
Ethanol	100	A	0	–	–
	100	B	0	–	–

A : *Camponotus* sp. A
B : *Acromyrmex* sp. A
C : *Camponotus rufipes*
D : *Camponotus* sp. D

+++ : strong response
++ : medium response
+ : very weak response
0 : no difference from control response

x : no recovery apparent
– : not measureable
* : the lid of the petri dish was replaced with a gauze top in this experiment

the soil or in wood) was noted. Over 80 % of the above-ground foragers were found to have soldiers with monoterpenes in their defensive secretions. These same species have high soldier to worker ratios (Haverty, 1977, Redford & Coles de Negret, *in prep.*). Species with soldiers specialised in mechanical defence are generally restricted to foraging under the protection of soil sheeting or underground. These species have low soldier to worker ratios (Haverty, *op. cit.*, Redford and Coles de Negret, *op. cit.*).

The foraging strategies observed in the three *Syntermes* species reflect this general trend. *S. grandis* soldiers are adapted for mechanical defence and have a low frontal gland volume to head volume ratio. They produce no terpenoid compounds in their defence secretions (Baker et al., 1980), have a low soldier to worker ratio in foraging parties and form short above-ground foraging trails. *S. molestus* soldiers have a greater dependance on chemical defence with a relatively larger frontal gland volume to head volume ratio. They produce secretions rich in the monoterpene cis-β-ocimene (Baker et al., 1980), have high soldier to worker ratios in foraging parties and form long above-ground trails. *S. dirus* forms an intermediate between these two species.

Nest biology

Data on the mechanical resistance of termite mounds, the number of soldiers per unit time appearing at breaches, reconstruction activity by workers and numbers of inquiline termite species, were collected from a series of mounds (Coles, 1980). Termite species with nasute soldiers were found to build thin-walled fragile mounds which workers reconstruct slowly and with a high number of soldiers per unit time at breaches. Mounds of these species rarely have other inquiline termite species. Species with soldiers specialised in mechanical defence build thick-walled resistant mounds which workers reconstruct quickly but with a low number of soldiers per unit time at breaches. Multiple occupation of mounds of these species is very common and the inhabitants are protected then by both chemical and mechanical defence systems (Coles de Negret and Howse, 1983b, *in prep.*).

DISCUSSION

The defensive secretions produced by the nasute soldiers examined contain a variety of compounds including several monoterpenes which are toxic on topical application to certain ants. Synthetic samples of three of these monoterpenes were also shown to act as feeding deterrents to giant ant-eaters. Soldiers from species specialised in mechanical defence rarely produce secretions with these volatile toxic compounds. They appear to rely on large mandibles for defence.

The species *Armitermes euamignathus*, with soldiers specialised in both mechanical and chemical defence, presents an intermediate form of defence. Soldiers of this species produce no terpenoid compounds but straight-chain hydrocarbons which have little effect on topical application to ants. The mandibles alone are unlikely to provide an effective defence against potential predators. It is also doubtful that the slight toxic effects of the alkanes are enhanced by the cutting action of the mandibles because the hydrophobic nature of these compounds would allow them to penetrate the cuticular wax more quickly than body tissues. There remains the further possibility that the alkanes serve as «propaganda» pheromones against camponotine ants, common in the Distrito Federal, which produce similar compounds in their alarm pheromone. Ayre and Blum, 1971, and Blum, 1973, showed that camponotine ants produce un-, tri-, tetra- and pentadecane in alarm pheromones. Soldiers of *A. euamignathus* produce three of these alkanes in such large quantities (84 μg, 35 μg and 180 μg per soldier for tri-, tetra- and pentadecane respectively) that they may act as superpheromones disrupting the communication system of attacking ants thus reducing their potential as raiding predators.

The effects of different specialisations for defence in the soldier caste on the ecology of termite species is evident from the results presented above. Species with chemical defensive strategies produce many small soldiers and require a correspondingly high number of workers to feed them. This high investment in soldier production has resulted in a lower investment in building activities and reduced nest fortifications. The lack of a resistant mound is, however, compensated for by the toxic compounds in the soldier secretions. The high soldier to worker ratios and the multi-directional nature of the volatile secretions enables nasute species to forage above-ground for grass and leaves. This food source is rarely utilised in the construction of mounds. The corollary of this defence strategy is found in species with soldiers specialised in mechanical defence. These produce fewer soldiers and invest more heavily in building activities constructing mounds more resistant to attack by vertebrate predators. These termites generally forage under protection and often feed on humus, excreting large quantities of soil which is used to construct the hard mounds.

References

AYRE G.L., BLUM M.S., 1971. – Attraction and alarm of ants (*Camponotus* spp. – Hymenoptera : Formicidae) by pheromones. *Physiol Zool., 44*, 77-83.

BLUM M.S., 1973. – Comparative exocrinology of the Formicidae. *Proc. VII. Congr. IUSSI* (London), 23-24.

BAKER R., COLES H.R., EDWARDS M., EVANS D.A., HOWSE P.E., WALMESLEY S., 1980. – Chemical composition of the frontal gland secretion of *Syntermes* soldiers (Isoptera, Termitidae). *J. Chem. Ecol.*

COLES H.R., 1980. – Defensive strategies in the ecology of Neotropical termites. *Ph. D. thesis. University of Southampton.*

COLES de NEGRET H.R., HOWSE P.E., 1983a. – Preliminary observations on feeding preferences in the giant ant-eater, *Myrmecophaga tridactyla. In prep.*

COLES de NEGRET H.R., HOWSE P.E., 1983b. – Multioccupation of mounds in the defensive strategies of Neotropical termites. *In prep.*

HAVERTY M.I., 1977. – The proportion of soldiers in termite colonies ; a list and a bibliography. *Sociobiology, 2*, 199-216.

PRESTWICH G.D., 1979. – Chemical defence by termite soldiers. *J. Chem. Ecol., 5*, 459-480.

REDFORD K.H., COLES de NEGRET H.R., 1981. – Soldier to worker ratios and notes on the biology of central Brazilian termites. *In prep.*

WALMSLEY S., 1981. – The chemistry of the defensive secretions of South American termites. *Ph. D. thesis. University of Southampton.*