—— REVIEW ARTICLE ——

USE OF INFOCHEMICALS IN PEST MANAGEMENT WITH SPECIAL REFERENCE TO THE BANANA WEEVIL, *COSMOPOLITES SORDIDUS* (GERMAR) (COLEOPTERA: CURCULIONIDAE)

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Abstract—Infochemicals play an important role in the biology of many insect species. An understanding of their role in plant-herbivore-carnivore interactions can be used in the development of tools for the enhancement of environmentally benign alternatives to synthetic pesticides. This review discusses how chemical information mediates ecological interactions between organisms and the role of infochemicals in integrated pest management. Infochemicals can be used in pest monitoring and in pest control, through mating disruption, mass trapping and to aggregate herbivores at delivery sites for biological control agents. Particular emphasis is placed on the potential of using pheromones and kairomones in the management of the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), a pest in plantations of East African highland banana and plantain in most banana-growing regions of the world. *Cosmopolites sordidus* produces an aggregation pheromone that attracts both males and females. This pheromone has been identified and synthesised and is being recommended as an effective agent in the trapping and control of the weevil. The synergism between banana plant extracts (kairomones) and the synthetic pheromone in attracting *C. sordidus* should be better exploited. Future research areas that can provide information for the development of an infochemical-based trapping system for the management of *C. sordidus* are discussed.

Key Words: infochemicals, kairomones, aggregation pheromone, Coleoptera, banana weevil, *Cosmopolites sordidus*, biological control, pathogenic fungi, predators, synergism

Résumé—Les sémiochimiques jouent un rôle important dans la biologie de beaucoup d'espèces d'insectes. La compréhension de leurs rôles dans les interactions plante-herbivore-carnivore peut-être utilisée pour le développement d'outils destinés à améliorer les techniques de luttes alternatives aux pesticides de synthèse. Cet article montre comment l'information chimique agit sur les interactions écologiques entre organismes et, discute du rôle des infochimiques dans la gestion intégrée des ravageurs. Les sémiochimiques peuvent être utilisés pour surveiller et contrôler les ravageurs, à l'aide de la technique de la confusion sexuelle et du piégeage de masse et pour rassembler les ravageurs en un lieu donné pour les agents de lutte biologique. Une attention particulière a été portée au rôle potentiel de l'utilisation des phéromones et des kairomones dans la gestion du charançon du bananier *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), un ravageur

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des plantations de bananiers des hautes terres d'Afrique de l'Est et de la plupart des zones productrices de bananes dans le monde. *Cosmopolites sordidus* émet une phéromone d'agrégation qui attire aussi bien les mâles que les femelles. Cette phéromone a été identifiée et synthétisée et son utilisation recommandée pour piéger et contrôler efficacement le charançon. Le synergisme entre les extraits de bananier (kairomone) et la phéromone de synthèse dans l'attraction de *C. sordidus* devrait être mieux exploité. Les futurs domaines de recherches pouvant fournir des informations pour le développement d'un système de piégeage à base d'infochimiques pour la gestion de *C. sordidus* sont discutés.

Mots Clés: sémiochimiques, kairomones, phéromone d'agrégation, Coleoptera, charançon du bananier, *Cosmopolites sordidus*, lutte biologique, champignon pathogène, prédateurs, synergisme

INTRODUCTION

All organisms utilise information they perceive from their environment to maximise fitness, e.g. by improving food location, reproduction and predator avoidance. Information on environmental conditions is often available through chemical cues (Bell and Carde, 1984; Carde and Bell, 1995; Dicke, 1999a). Chemicals involved in conveying information in intra- and inter-specific interactions between organisms are termed 'infochemicals' (Table 1) and constitute a subcategory of semiochemicals (Dicke and Sabelis, 1988).

Chemical information is regarded as a key factor mediating behavioural and ecological interactions between insects and plants. The study of chemicals mediating interactions between organisms, either within the same species (pheromones) or from different species (allelochemicals), forms the research field of chemical ecology (Metcalf and Metcalf, 1992; Roitberg and Isman, 1992). In recent years, increased research attention has been directed towards the role of chemical information in arthropod biology (Whittaker and Feeny, 1971; Bell and Carde, 1984; Metcalf and Metcalf, 1992; Roitberg and Isman, 1992; Carde and Bell, 1995; Dicke, 1999a; Dicke and Vet, 1999).

In this review, chemically mediated interactions between organisms and the role of infochemicals in pest management are discussed. Our objectives are to summarise how infochemicals have been used in pest control, indirectly through monitoring and directly through mating disruption, mass trapping and by integration with biological control methods. Limited information is available on infochemicals and the banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). We therefore review the existing literature on coleopterans so as to gain an insight into the possible role of infochemicals in the development of an integrated pest management programme for *C. sordidus* and in particular the development of an infochemical-based trapping system for the control of this weevil.

CHEMICAL INFORMATION IN ECOLOGICAL INTERACTIONS

Chemicals produced by plants and insects play a major role in the behavioural responses that determine the performance, survival and development of the insects (Vet and Dicke, 1992). The chemicals involved in transmission of information between individuals of the same species are termed pheromones (Table 1). These include sex pheromones, aggregation pheromones and trail pheromones (David and Birch, 1986; Ridgway et al., 1990; Agelopoulos et al., 1999; Bartelt, 1999). Sex pheromones are produced by one sex (usually the female) and attract members of the opposite sex for mating. By comparison, aggregation pheromones lead to aggregation of members of both sexes resulting in mating and aggregation at a food source (Foster and Harris, 1997). These are often produced by males. Male-produced aggregation pheromones have been demonstrated for a number of weevil species such as *Rhynchophorus palmarum* (L) (Rochat et al., 1991), *R. cruentatus* (Weissling et al., 1993), *R. phoenicis* (Fabricus) (Gries et al., 1993), *Metamasius hemipterus* (L) (Giblin-Davis et al., 1994a), *C. sordidus* (Budenberg et al., 1993a), and *Sitophilus* spp. (Walgenbach et al., 1983). Social insects, such as ants and termites, often produce trail pheromones by which individuals may guide other members of the colony to food sources

Table 1. Infochemical terminology according to Dicke and Sabelis, 1988

Infochemical:	A chemical that, in the natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioural or physiological response
Pheromone:	An infochemical that mediates an interaction between organisms of the same species whereby the benefit is to the origin-related organism [(+, -) pheromone], to the receiver [(-, +) pheromone], or to both [(+, +) pheromone]
Allelochemical:	An infochemical that mediates an interaction between two individuals that belong to different species.
Allomone:	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response that is adaptively favourable to organism 1 but not to organism 2.
Kairomone:	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when contacts an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response that is adaptively favourable to organism 2, but not to organism 1.
Synomone:	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when contacts an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response that is adaptively favourable to both organism 1 and 2.

(Blum, 1974; Bell and Carde, 1984). Other pheromones produced by phytophagous insects include anti-aggregation pheromones that ensure adequate spacing when resources are limited (Prokopy, 1981), oviposition-deterring pheromones that females use to mark the hosts on which they have laid eggs (Heard, 1995), and alarm pheromones that serve to warn conspecific insects of impending danger (Bowers et al., 1972). Knowledge of pheromones for carnivorous insects is still rudimentary, with a few pheromones indicated for parasitoids (e.g. egg marking pheromones) and predators (Aldrich, 1999).

Herbivores are known to use plant volatiles (kairomones) to locate a food plant (Visser, 1986). When herbivores feed on a plant, cell damage results and there is release of volatiles from the wound site (Dicke et al., 1990). The amount of volatiles released by herbivores or by herbivore-infested plants may affect herbivore response to the plant. The response to an information source by the herbivore may depend on physiological state, previous experiences and abiotic conditions (Dicke et al., 1998). Host plant selection by herbivores may be affected by infochemicals from competitors (Schoonhoven, 1990) and natural enemies (Grostal and Dicke, 1999).

Chemical information on herbivore presence and identity may be essential for successful location of herbivores by carnivores. Plants may respond to herbivore attack by producing chemical cues that attract carnivorous predators to themselves (Dicke, 1999 a,b). The herbivore-damaged plant may emit relatively large amounts of plant volatiles that are not emitted or only emitted in trace amounts by mechanically damaged plants (Dicke et al., 1990). The amount of plant volatiles released after herbivore attack may be different among species, plant genotypes, and plant parts and can be affected by abiotic and biotic factors such as species, instars and densities of the herbivores (Vet and Dicke, 1992). Corn seedlings release large amounts of volatile terpenoids after damage inflicted by *Spodoptera* caterpillars, which attract the larval parasitoid *Cotesia marginiventris* (Turlings et al., 1990). Similarly, the predatory mite *Phytoseiulus persimilis* is attracted by spider mite-induced volatiles produced by bean or cucumber plants (Dicke et al., 1990). The anthocorid predators (*Anthocoris nemorum* and *Orius* spp.) (Heteroptera: Anthocoridae) were attracted to pear trees infested by pear psylla under field conditions (Drukker et al., 1995). Prey searching and location is not the only

process triggered by herbivore-induced plant volatiles. Some predators such as *Metasyrphus corollae* (Syrphidae), *Chrysopa carnea* (Chrysopidae) and *Coccinella septempunctata* (Coccinellidae) use these chemical cues to select oviposition sites (Lewis, 1977; Shonouda et al., 1998; Steidle and van Loon, 2002).

INFOCHEMICALS AND INSECT PEST CONTROL

Infochemicals, and pheromones in particular, have been used widely in pest management and have been reported to have the advantage of being non-toxic to humans and arthoropods (David and Birch, 1986; Ridgway et al., 1990; Agelopoulos et al., 1999). Pheromones perform most effectively when employed as part of an integrated control programme, where they can be used either indirectly for monitoring (Wall, 1989), or directly to manipulate pest populations (Griffiths et al., 1991). They offer the prospect of establishing contact with microbial control agents by attracting pests into an environment where these agents might be best preserved. This can apply to fungal pathogens, mobile insect predators and parasitoids (Pickett, 1988). The knowledge on infochemical use by plants, herbivores and carnivores can be utilised in the development of new integrated pest control strategies.

Pheromones

Successful chemical identification of insect pheromones (Butenandt et al., 1959) led to an interest in pheromone research. Pheromones were considered a new generation of pest control agents and rapid progress was made in the identification and isolation of pheromones from a wide range of insects (Table 2). Sex and aggregation pheromones are common among weevils. However, the state of knowledge of weevil pheromones varies broadly among species. For some, there is only an indication that a pheromone exists but for others, there have been detailed behavioural and physiological studies, chemical isolation, identification, pheromone synthesis, and commercial development (Table 2).

Pheromones and other behaviour modifying chemicals hold a great potential as tools for pest management (Silverstein, 1981; Phillips, 1997; Agelopoulos et al., 1999; Suckling, 2000).

Pheromones have been used in both monitoring insect populations and in direct control (Phillips, 1997; Agelopoulos et al., 1999). Pheromone traps provide an easy and efficient way of detecting insect populations in the field and in storage facilities (Phillips, 1997). Control of insect pests can be achieved either by mating disruption (Burkholder and Ma, 1985) or by mass trapping using pheromone baited traps that lure insects to their death (Giblin-Davis et al., 1994a) (Table 2). Pheromones also have the potential to lure pests into traps containing entomopathogens that the visiting pests would then spread throughout their population (Vega et al., 1995; Klein and Lacey, 1999).

Although there have been limited successes, the potential exists for using pheromones to control coleopteran populations by mass trapping. The advantage is that, with few exceptions, coleopterans use aggregation pheromones, attracting both sexes which negatively affect the reproductive capacity of the population (Trematerra, 1997; Bartelt, 1999). This makes mass trapping using aggregation pheromones theoretically possible, in contrast to the systems with female-produced sex pheromones where more than 90% of males must be captured to effect any depletion of the following generation (Bartelt, 1999). Mass trapping is most promising for insect pests with low fecundity, slow population buildup, limited dispersal and long life span (Giblin-Davis et al., 1996a). Pheromone traps are species-specific and the negative impact on non-targets is limited. Other benefits of using pheromones in pest management include their low costs and low potential for development of pest resistance.

Monitoring

Pheromones have been used for monitoring pest populations of crop pests and orchard pests (Wall, 1989), stored products pests (Burkholder, 1990) and forestry pests (Borden, 1993). Monitoring can assist in detecting the arrival of dispersing and migrating insect pests, timing of control measures, risk assessment and population density estimates (McVeigh et al., 1990; Howse et al., 1998). Monitoring involves establishing a quantitative relationship between pheromone trap catches of a particular pest and the plant damage caused by it. The relationship is then used to define trap catch values that could be used to identify the economic

Table 2. Examples of weevils and beetle species of which pheromones have been reported and chemically identified

Species	Subfamily	Principal damage	Source	Identified?	Chemical / commercial name	Type of use	Reference
Anthonomus grandis Boheman (boll weevil)	Curculioninae	Cotton buds, bolls	Male	Yes	Granlure, grandisol	Monitoring	Tumlinson et al., 1969; Hardee et al., 1972
Conotrachelus nenuphar (Herbist) (plum curculio)	Cryptorhynchinae	Unripe fruit of apple, plum	Male	Yes	Grandisoic acid (8)	–	Eller and Bartelt, 1996
Cosmopolites sordidus (German) (banana weevil)	Rhynchophorinae	Banana plant corms	Male	Yes	Cosmolure+	Mass trapping	Budenberg et al., 1993a Beauhaire et al.,1995 Jayaraman et al.,1997
Cylas formicarius (Fabricius) (sweet potato weevil)	Apioninae	Sweet potato vines, roots, tubers	Female	Yes	(Z)-3-dodecen-1-ol (E)-butenoaete	Monitoring, mass trapping	Jansson et al., 1989 and 1993
Dynamis borassi (Fabricius) (palm weevil)	Rhynchophorinae	Inflorescence and crown of palms	Male kairomone	Yes	Ferrugineol	–	Giblin Davis et al., 1997
Diaprepes abbreviatus (L) (West Indian sugarcane root stalk borer)	Otiorrhynchinae	Citrus foliage	Male and female	No	–	–	Harari and Landolt, 1997
Popillia japonica (Newman) (Japanese beetle)	Rutelinae	Plant flowers, fresh leaves, grasses	Female	Yes	Japonilure	Monitoring	Tumlinson et al., 1977
Prostephanus truncatus (Horn) (larger grain borer)	Bostrichidae (family)	Storage grains	Male	Yes	Trun-call	Monitoring	Cork et al., 1991
Metamasius hemipterus (L.) (West Indian sugarcane borer)	Rhynchophorinae	Sugarcane, banana, palm stems	Male	Yes	Ferrugineol	Mass trapping	Giblin-Davis et al., 1994a
Rhynchophorus cruentatus (Fabricius) (palmetto weevil)	Rhynchophorinae	Palm stems	Male	Yes	Rhynchophorol	Mass trapping	Weissling et al., 1993
Rhynchophorus ferrugineus (Asian palm weevil)	Rhynchophorinae	Palm stems	Male	Yes	Ferrrugeneol	Mass trapping	Hallett et al., 1993
Rhynchophorus palmarum (L.) (American palm weevil)	Rhynchophorinae	Palm stems	Male	Yes	Rhynchophorol	Mass trapping	Rochat et al., 1991
Rhynchophorus pheonicis (F.) (African palm weevil)	Rhynchophorinae	Palm stems	Male	Yes	Phoenicol	Mass trapping	Gries et al., 1993
Sitophilus granarius (L.) (granary weevil)	Rhynchophorinae	Stored grains	Male	Yes	Sitophilate	Mass trapping, monitoring	Walgenbach et al., 1983
Prostephanus trunctus (Horn) (larger grain borer)	Bostrichidae (family)	Storage grains	Male	Yes	Trun-call	Monitoring	Cork et al., 1991

threshold level of a pest for which control measures are necessary (Suckling, 2000). The monitoring systems have enabled more effective targeting of all major pest control tactics including pesticides and biopesticides (Suckling, 2000).

Although commercial advances in pheromone-related pest monitoring and control technology have tremendous potential (Howse et al., 1998; Smit et al., 1997), there remain challenging technological issues in the development and use of monitoring and control systems (Suckling, 2000). These include the design of attractant release systems, trap design and deployment systems, data analysis and interpretation and the development of expert decision systems. Obtaining quantitative information about pest populations from trap catch data has proved difficult in many cases, especially for strongly flying, highly mobile species which may be able to escape from sticky substances commonly used in insect traps (Srivastava et al., 1992). In some cases pest species have been trapped successfully in the field but their presence did not correlate well with pest density and damage levels (David and Birch, 1986). There have also been examples of insect species not being caught by ineffective traps and causing crop damage (Tadas et al., 1994).

Mating disruption

Mating disruption involves permeating the pest environment with sex pheromones so that the probability of a female being found by a male, mating and laying viable eggs is reduced below a point where economically significant damage occurs (Carde and Minks, 1995; Evenden et al., 2000). Pest control by use of synthetic pheromones to disrupt normal mating behaviour is now operational for a number of lepidopteran species such as the pink boll worm, *Pectinophora gossypiella*, the cotton boll worm, *Helicoverpa armigera* and the rice stem borer, *Chilo suppressalis* (Campion et al., 1989; Hall et al., 1994; Carde and Minks, 1995; Cork et al., 1996; Tamhankar et al., 2000). Use of pheromones in mating disruption of coleopteran pests has been reported for *Cylas formicarius* (F) (Mason and Jansson, 1991) and for the African sweet potato weevils, *C. brunneus* and *C. puncticollis* (Downham et al., 2001).

One potential weakness of mating disruption is that this technique provides no safeguards against migration of mated females from outside the area treated with a disruptant (Carde and Minks, 1995). Thus, mating disruption can work best as an area-wide management tool (Staten et al., 1997) rather than being used by an individual farmer. A high population density of the target insect can also limit the control efforts especially if there is competition between synthetic and female-produced plumes (Carde and Minks, 1995). Lures involved in mating disruption should be formulated to release at sufficiently high rates to prevent mating (Suckling, 2000). Effective mating disruption requires a high proportion of males failing to mate females and therefore, long-lived species that can mate on multiple occasions are more difficult to control (Suckling, 2000).

Mass trapping

The aim of mass trapping is to control insect species by capturing a very large proportion of the pest population by deploying pheromone traps in sufficient numbers. Such an approach assumes that a reduction in the adult population will lead to a further population decrease in the next generation (Birch and Haynes, 1982). In mass trapping strategies it is important to know the proportion of the population that is captured and the relationship between this proportion and the reduction in the population of the next generation. In lepidopterans, mass trapping using sex pheromones has varying degrees of area-wide and prolonged success (Kehat et al., 1980; Mafra-Neto and Habib, 1996; Tamhankar et al., 2000). This may have two causes: (1) the sex pheromone (produced mostly by females) attracts only males (and then not all of them) and (2) the males are polygamous and a small proportion of untrapped males can continue to fertilise a substantial number of females with high egg laying potential (Tamhankar et al., 2000).

Several studies have tested the potential of the mass trapping strategy for the control of coleopteran insects. This strategy was tested against the spruce bark beetle, *Ips typographus* (L)(Bakke, 1981), the Japanese beetle, *Popillia japonica* Newman (Ladd and Klein, 1982), the boll weevil *Anthonomus grandis grandis* Boheman (Hardee, 1982), the European bark beetle, *Scolytus multistriatus* (Marsham) and the ambrosia beetle *Gnathotrichus sulcatus* (LeConte) (Birch and Haynes, 1982). Some authors (Oehlschlager et al., 1995; Alvarez, 1996) have reported successful

suppression of the pest populations by use of mass trapping. Use of pheromone traps significantly reduced the damage from *Cylas* infestation on potato plants in the Dominican Republic (Alvarez, 1996). Oehlschlager et al. (1995) described a 17-months mass trapping trial in Costa Rica during which the population density of the weevil *Rhynchophorus palmarum* in a 30 ha commercial palm plantation was substantially reduced using 6 traps/ha. Cost-benefit analyses of using pheromones in mass trapping for successful studies have, however, rarely been carried out.

Mass trapping using pheromones should be considered as one component of a set of pest management practices. Deployment of traps alone may not result in suppression of a pest population, especially when the target insect is abundant and has a high multiplication rate (Birch and Haynes, 1982; Weislein, 1992; James et al., 1996). Cuthbert et al. (1977) indicated that large numbers of naturally attractive sites (e.g. crop residues) competed with traps and hence reduced the trapping effect of scolytid beetles, *S. multistriatus*. Therefore, to suppress populations of the elm bark beetle, *S. multistriatus* (Birch and Haynes, 1982) and the spruce bark beetles, *Ips typographus* (Weislein, 1992), mass trapping should be conducted in conjunction with rigorous sanitation programmes. The same is true for the mass trapping of *Carpophilus* spp. in stone fruit orchards (James et al., 1996) and *R. palmarum* in plantations of African oil palm (Oehlschlager et al., 1995).

High trap densities and high trapping frequency are often needed to obtain satisfactory levels of population suppression (Lloyd et al., 1981). Continuous trapping of *A. grandis* at high population levels indicated that as many as 92 % of the males emerging from a population were captured with a trap density of 14 traps/ha (Lloyd et al., 1981). Such high trap densities are not practical as they render the technique too costly. In contrast, with low population levels, a density of 2.5 traps/ha resulted in a high rate of elimination of *A. grandis* (Legget et al., 1989). Mass trapping tends to be more effective at low population densities as was reported for *A. grandis* (Lloyd et al., 1981; Legget et al., 1989; Ridgway et al., 1990).

Two major questions have always been raised regarding trap density (David and Birch, 1986; Howse et al., 1998). First, what trap density is required to adequately sample the pest population? Second, at what density do traps interact thereby influencing the size of the catch in the individual traps? Answers to these questions will help in optimising trap placement that is critical to the success of mass trapping efforts.

Trap effectiveness

A number of factors influence the rate of captures of insects in pheromone traps. Pheromone dose and release rate influence how traps perform relative to natural pheromone sources and thus determine how well they attract insects (Muirhead-Thompson, 1991; De Groot and De Barr, 1998). Insects may respond to the colour of a trap and certain trap designs capture insects more efficiently (Giblin-Davis et al., 1996b; Smit et al., 1997; De Groot and De Barr, 1998). In field studies using aggregation pheromones as trap baits, all trap colours tested were equally efficient in attracting *M. hemipterus* to ground-mounted bucket traps (Giblin-Davis et al., 1996a) and *R. palmarum* to tree-mounted traps (Oehlschlager et al., 1993). *Anthonomus grandis* responded positively to yellow from a distance of approximately 7 m and at 2 m the majority of weevils orient to this colour rather than the pheromone (Legget and Cross, 1978). Placement of the traps near, within, or away from the host plants may affect the trap capture depending on the link between the host and mate finding (McNeil, 1991; Muirhead-Thompson, 1991). Catches may also correspond to the timing of placement of the traps in populations with distinct generations (Jansson et al., 1991).

Trap catches in most cases correlate to environmental factors such as wind direction and speed, rainfall and temperature (Jansson et al., 1989; Sappington and Spurgeon, 2000). Wind speed and direction may alter pheromone plume shape and size, and create pheromone concentration gradients within the plume. Upwind orientation by insects to pheromones is well known, but information on the influence of wind is not available for ground-dwelling insects where wind speed is negligible. Little research has been carried out to examine the influence of relative humidity on pheromone-mediated communication in Coleoptera. For Lepidoptera, Miller and McDougall (1973) found a negative relationship between trap catch and relative humidity in a 12-year trapping study on the

spruce budworm. Responsiveness of pests to pheromones has been demonstrated to increase with temperature (Burkholder and Bousch, 1974; Burkholder and Ma, 1985). Variation in pheromone trap catches with temperature may be attributed to increased response in the receiver and better distribution of the chemicals.

The trap efficiency is further affected by the pest biology. Mated females of *A. grandis* were less responsive to male-produced sex pheromone (grandlure) than virgin females, both in laboratory bioassays and in field tests (Hardee et al., 1969). In insect species in which virgin females are trapped, the reduction in the subsequent generation may be directly related to the proportion removed from the population. If females are trapped after mating and after having laid some eggs, the efficiency of the method decreases. If males were trapped, a very large proportion probably would have to be captured before there is a noticeable impact on the next generation. This is true for many insect species in which both males and females are capable of mating many times (Borden, 1977).

The pheromone trap efficacy is also influenced by interaction of the cropping system and the biology of an insect pest (Hebblethwaite, 1989). For polyphagous pests that have non-crops as host plants, uncultivated areas and weed populations are important elements of the farming system relevant to pest incidence. For pests having only one crop as host, the pattern of cultivation and proportion of land cultivated are some of the factors that determine their importance. The pheromone trapping efficiency is influenced by the cropping patterns (monocropping or mixed cropping), but it is also possible that within a cropping pattern there are still zones where the pest may be more important than elsewhere which may affect the trap catches. To develop an effective pheromone trapping system, biological information, such as the number of generations per year, range of host plants, dispersal rate, distribution pattern and migratory potential of the pest is generally needed (Borden, 1977).

Kairomones

Many insects use kairomones to find their host plants (Visser, 1986). Among the coleopterans, the boll weevil, *A. grandis*, orients to volatile chemicals emanating from its host plant cotton (Hardee et al., 1966) and also responds to crushed cotton squares (Dickens, 1989). Colorado potato beetles are attracted to volatiles from undamaged potato plants (Visser, 1986) but volatiles from mechanically damaged or herbivore-damaged potato plants elicit a stronger attraction in the beetles (Bolter et al., 1997). Female and male sugarcane stalk borer weevil, *Diaprepes abbreviatus* (L) were reported to be attracted to volatiles from damaged food (Harari and Landolt, 1997). Male and females of the plum curculio, *Conotrachelus nenuphar* (Herbst) are similarly attracted to host odour (Prokopy et al., 1995). Several studies have demonstrated the attractiveness of pseudostem and sugarcane stalk odours to palm weevils in the field (Giblin-Davis et al., 1994b). Mixtures of odorants synergistically attracted the Japanese beetle, *Popillia japonica* (Tumlinson et al., 1977) and bark beetles (Byers, 1992). There are hardly any data about the maximum distance from which kairomones can attract insects.

The efficiency of the kairomones in attracting insects depends on the odour quality and/or the amount released. Bark beetles prefer to attack and colonise dying trees that have odours that are distinctively different from those of healthy trees (Metcalf and Metcalf, 1992). Fermented plant tissues produce a spectrum of odorants that are significantly different from those released by healthy plants (Metcalf and Metcalf, 1992; Giblin-Davis et al., 1994b; Braimah and van Emden, 1999; Rochat et al., 2000). Fermented sap exuding from dead or wounded palms was highly attractive to *R. cruentatus* (Giblin-Davis et al., 1996a). Moist fermenting tissue from various palm species, fruits, sugarcane, pineapple and molasses are similarly attractive to palm weevils (Giblin-Davis et al., 1994b). In olfactometer bioassays, kairomones triggered the primary attraction of African palm weevils, *R. palmarum*, to oil palm. Fermentation processes were important to elicit this behaviour (Rochat et al., 2000).

In addition to being used as attractants of insects to traps, kairomones can be used to enhance attractiveness of insects to pheromone-baited traps (Phillips et al., 1984; Giblin-Davis et al., 1994b; Cerda et al., 1999). They may also be used in the dissemination of entomopathogens to target insects (Vega et al., 2000). Plant-produced kairomones that mediate host selection by phytophagous insects could also be exploited to enhance breeding for host plant resistance.

Synergism between pheromones and kairomones

Host plant volatiles (kairomones) are known to enhance the effectiveness of pheromone traps in attracting weevils (Dickens, 1984; Phillips et al., 1984; Giblin-Davis et al., 1994b; Cerda et al., 1999). In the pine weevil *Pissodes nemorensis*, the male-produced aggregation pheromones grandisol and grandisal were attractive in the field only when deployed with odours from the host plant (Phillips et al., 1984). The maize weevil, *Sitophilus zeamais*, responded significantly more to male-produced pheromones deployed with grain than to either pheromone or grain separately (Walgenbach et al., 1987). Ambrosia beetles in the genus *Gnathotrichus* utilise male produced pheromones that act synergistically with the host-derived compounds α-pinene and ethanol (Borden et al., 1980). Green leaf volatiles have a synergistic effect on the attraction of the boll weevil to its pheromone (Dickens, 1984). The combination of *R. palmarum* weevils and palm stem was attractive to both sexes of this species, and males without host material were not attractive to either sex in field trials (Rochat et al., 1991). Attraction of palm weevils by the synthetic pheromone rhynchophorol is synergised by the addition of host material, such as palm stem or sugarcane (Oehlschlager et al., 1993), or by host odour compounds, such as ethyl acetate (Jaffe et al., 1993). Attraction of male and female *R. cruentatus* to male pheromone 5-methyl-4-octanol (cruentol) is synergised by volatiles from host plant material, such as Sabal palm stem tissue (Giblin-Davis et al., 1994b). The response in the field of the West Indian sugarcane borer, *M. hemipterus*, to the aggregation pheromone was enhanced by fermented and fresh plant volatiles (Giblin-Davis et al., 1994a). Increasing quantities of sugarcane or host tissue generally increase attractiveness of pheromone-baited traps to *M. hemipterus* (Oehlschlager et al., 1993; Giblin-Davis et al., 1994b).

INFOCHEMICALS AND BIOLOGICAL CONTROL

Predators and parasitoids

There has been increasing interest in the implementation of biological control programmes using parasitoids and predators and the efficacy of these natural enemies may be enhanced by infochemicals (Vet and Dicke, 1992; Dicke, 1999a). Application of infochemicals in pest control is, however, impossible without knowledge of the behaviour induced by these chemicals (Gross, 1981). Infochemical use, both within and between species can be utilised in pest management by either exploiting the way the natural enemy responds or by manipulating the source of the infochemical (Dicke et al., 1990; Bottrell et al., 1998). For example, infochemicals can be used to enhance the searching efficiency, host utilisation and reproductive capacity of natural enemies (Lewis and Nordlund, 1985; Noldus, 1989; Renwick, 1992; Bottrell et al., 1998).

There are few cases of the application of infochemicals to manipulate the behaviour of predators in the field. However, data on the role of infochemicals in predator foraging have become available for some groups such as predatory mites (Sabelis and Dicke, 1985; Dicke and Sabelis, 1988), bark beetle predators (Aukema et al., 2000), heteropteran predators (Van Loon et al., 2000) and coccinellids (Liu and Sengonca, 1994; Steidle and van Loon, 2002). The predator *Rhizophagus grandis* (Gyll.) (Coleoptera: Rhizophagidae) is attracted to traps baited with a kairomone produced by the bark beetle *Dendroctonus micans* Kug (Coleoptera: Scotylidae) (Aukema et al., 2000) and in this way the predator distribution in the field can be monitored. The search time of predators may be reduced through increased aggregation at infested sites or kairomone sources (Vet and Dicke, 1992).

The performance of natural enemies can be enhanced by changing their environment by using infochemicals. Predators and parasitoids may be retained in the target area or their search and attack behaviour may be improved (Noldus, 1989; Lewis and Martin, 1990). Hagen et al. (1971) used artificial honeydew as stimulus to increase predation of *Heliothis zea* by *Chrysoperla carnea* (Stephens). The chemical provided both a kairomone and food supplement that increased predator density around cotton plants. Detailed behavioural studies in patches of cotton plants containing host larvae revealed that when nectar was present in the patch, the wasp *Microplitis croceipes* (Cresson), a parasitoid of *H. zea* larvae stayed longer and parasitised more hosts than when nectar was absent (Stapel et al., 1997). Similarly the release of a synthetic blend of the sex pheromone of *H. zea* in cotton increased parasitism of eggs from 21 % in control to 36 % in treated plots (Lewis et al., 1982).

A thorough behavioural analysis is needed for drawing conclusions on the role of infochemicals in predator and parasitoid foraging strategies and thus to employ such chemicals in pest control (Noldus, 1989; Dicke et al., 1990; Renwick, 1992; Dicke, 1999a). We need to: (i) know desirable traits of natural enemies and the mechanism(s) by which infochemicals influence these traits, (ii) have the technological ability to manipulate these traits prior to and/or after release, and (iii) know the potential negative effects such as the attraction of pest insects (Bolter et al., 1997).

Fungal pathogen dissemination

Although certain fungal pathogens have been recognised as potential biological control agents of insect pests (Kaya et al., 1993; Nankinga, 1994), their commercial use has been limited by technical problems to do with their delivery to the target pests (Kaya et al., 1993; Lacey et al., 1994; Nankinga et al., 1996; Nankinga and Ogenga-Latigo, 1996). Practical delivery of biocontrol agents to the damaged area of the plant remains a challenge because conventional application techniques are typically not cost effective and the target organisms are often difficult to reach. One possible mechanism of targeted delivery is by contaminating insects with pathogens and letting them spread the infective material (McLaughlin et al., 1969; Shapas et al., 1977; Pell et al., 1993; Lacey et al., 1994). Pheromone traps have been identified as possible lures for inoculation devices and subsequent pathogen dissemination (Vega et al., 1995; Klein and Lacey, 1999; Vega et al., 2000). The movement of infested hosts is considered to be one of most important ways in which a pathogen can be transmitted and dispersed to new habitats (Shapas et al., 1977; Vega et al., 2000). With an effective pheromone and luring device, it may be relatively easy to expose the attracted insects to a pathogen. These insects would then leave the trap on habituation to the pheromone and return to the crop disseminating the entomopathogen among their own population (auto-dissemination). The hoped for advantage of such inoculation rather than immediate killing with the insecticide would be the potential for the transmission of the pathogen to other insects in the immediate area, magnifying the effect of the treatment. It would be relatively easy in this inoculation technique to contaminate insect stages hidden inside the plant tissues with pathogens especially when the egg laying female is infested (Zimmermann et al., 1992). This technique allows for specific and targeted delivery of the bioactive agent that would not be possible using conventional methods (Vega et al., 2000). The effectiveness of the auto-dissemination delivery system of fungal pathogens may however be influenced by the biology (the population dynamics and rate of dispersal) of the target insects.

Various reports are available where pheromones have been used effectively in the dissemination of fungal pathogens (McLaughlin, 1969; Schwalbe et al., 1974; Shapas et al., 1977; Vega et al., 1995; Klein and Lacey, 1999). A bait containing a feeding stimulant and the protozoan, *Mattesia grandis* was effectively used in spreading the pathogen throughout cotton fields for the control of *A. grandis* (McLaughlin, 1969). In laboratory tests, 96% of the test insects placed in the inoculation devices treated with pheromone and pathogen got contaminated compared to 56% that picked pathogens from inoculation devices containing only *Mattesia* pathogens (Schwalbe et al., 1974). In the field, over 95% of the Japanese beetle (*Popillia japonica*) that passed through the auto-dissemination traps during a one-week period died within the 10-day observation period while the control mortality during the same period was 8% (Klein and Lacey, 1999). The inoculative device becomes practical especially when the trap is baited with a pheromone lure that aggregates insects of both sexes (Vega et al., 1995).

## INFOCHEMICALS AND BANANA WEEVIL CONTROL

Cosmopolites sordidus is considered to be one of the most serious pests of bananas (Stover and Simmonds, 1987). The insect can cause yield loss of up to 100 % (Sengooba, 1986; Koppenhoeffer et al., 1994) through sucker death, toppling and snapping (Sikora et al., 1989; Rukazambuga et al., 1998; McIntyre et al., 2002), and shortens plantation life spans if not controlled (Rukazambuga et al., 1998; Gold et al., unpubl. data). For information on biology and population dynamics of the banana weevil, see extensive reviews by Gold (1998) and Gold et al. (1999b).

Control of this pest has depended on the use of synthetic insecticides, which, though feasible

for larger commercial growers, is beyond the economic capacity of most banana producers in developing countries such as Uganda. Furthermore, *C. sordidus* is resistant to a wide range of chemicals (Collins et al., 1991; Gold et al., 1999a). There are hardly any bananas and plantain varieties identified with useful tolerance or resistance to *C. sordidus* (Ortiz et al., 1995). The control of the weevil by cultural methods such as mulching or the use of split pseudostem traps to catch and kill resident and invading weevil populations has been only partially successful (Okech et al., 1999; Gold et al., 2001). Trapping as a control method is influenced by environmental factors, weevil biology, trapping intensity and frequency (Bakyalire, 1992; Gold, 1998). Efficacy of trapping is also related to trap density, trap placement, quality of traps, size of traps and frequency of collection (Bakyalire, 1992; Ogenga-Latigo and Bakyalire, 1993; Koppenhoeffer et al., 1994). Re-invasion from neighbours' fields may be another problem (Okech et al., 1999; Gold et al., 2001). Enhanced trapping using infochemicals, including pheromones and kairomones, has been identified as a means that can be used to develop an effective method of trapping and controlling the weevil. Below we discuss the role of pheromones and kairomones, and their integration with biological control methods for the management of *C. sordidus*.

Pheromones

Evidence for a male-produced aggregation pheromone to which both females and males of *C. sordidus* respond was first provided by Budenberg et al. (1993a). Beauhaire et al. (1995) detected six male-specific compounds with electroantennogram (EAG) activity in volatile collections. They identified and synthesised sordidin (2,8-dioxa-1-ethyl-3,5,7-trimethy-lbicyclo[3.2.1]octane) (Fig. 1), which was the most abundant of the volatiles. The absolute stereochemistry of the natural sordidin was later determined (Mori et al., 1996; Fletcher et al., 1997). Ndiege et al. (1996) and Jayamaran et al. (1997) developed a large-scale synthesis of racemic sordidin that made field-testing possible. It was attractive to both males and females, confirming its function as an aggregation pheromone. This has been synthesised to provide cosmolure pheromones that together with traps are
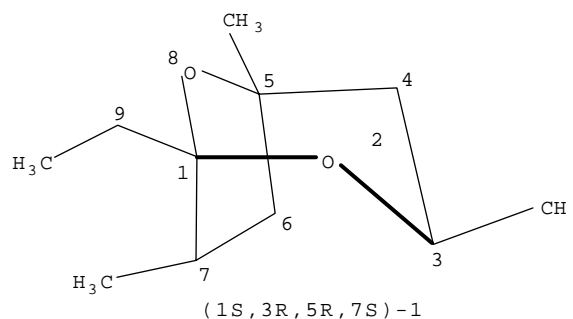
Fig. 1. Configuration of sordidin, a major component of the pheromone cosmolure+

commercially available from ChemTica International in Costa Rica.

The use of pheromone lures (cosmolure+) for trapping *C. sordidus* has been reported in Costa Rica as a promising option (Alpizar et al., 1999; Oehlschlager et al., 2000). Trials of mass trapping in plantations of banana and plantains with pheromone traps on plots of 1–250 ha in size, and traps at a density of four per ha were effective in reducing weevil damage to banana corms by over 60 % and bunch weight was increased by 20 % (Alpizar et al., 1999; Oehlschlager et al., 2000). Alpizar et al. (1999) proposed that trap density could be reduced once weevil populations and damage have been reduced to low levels. In Costa Rica, trap interference starts to decrease at a separation of 20 m (C. Oehlschlager, pers. commun.), and the effective radius was estimated to vary from 5 to 15 m. Consequently, a trap density of four traps/ha and moving them every month at regular space intervals was found effective to bring *C. sordidus* populations to low levels in the banana plantation in 4–5 months (Alpizar et al., 1999; Oehlschlager et al., 2000). Preliminary studies conducted in Uganda showed pheromones to be 18 times more attractive to *C. sordidus* than pseudostem traps (Tinzaara et al., 2000).

In laboratory and field studies, male-produced aggregation pheromones for some coleopteran insects are ineffective unless combined with host plant volatiles (Oehlschlager et al., 1992; Giblin-Davis et al., 1996a). The weevil appears to show a similar trend of synergistic combinations of species-specific pheromone and host plant volatiles (Ndiege et al., 1996; Jayaraman et al., 1997).

Mass trapping using infochemicals, especially pheromones, is particularly promising for the

control of *C. sordidus* since the weevils crawl and do not disperse, both sexes are attracted, and their reproductive capacity is low (Alpizar et al., 1999). Use of pheromones may provide a weevil control option that is less labour intensive compared to the use of pseudostem traps although costs are likely to increase as pheromones will require importation, distribution and storage. The development of the infochemical-based trapping system could also be used as a means of disseminating entomopathogens with baited traps which allow both entry and exit of weevils. Further research is necessary to develop these ideas.

Kairomones

Cuille (1950) first suggested that plant kairomones attract the banana weevil to the host plants. Volatiles from the susceptible AAA cooking banana attracted more weevils than the AB resistant dessert types (Budenberg et al., 1993b). Seshu Reddy et al. (1993) showed that baits of cooking bananas are more attractive to the weevil than those made of dessert bananas. Decaying banana material is more attractive than fresh material (Budenberg et al., 1993b) although it is reported that fresh pseudostems are more attractive than fermented material (Hord and Flippin, 1956; Delattre, 1980). *Cosmopolites sordidus* seems to prefer corm odours from plants with fruits to corm odours from young or adult plants, or from adult plants with flowers (Cerda et al., 1996). Preliminary studies conducted at ICIPE in Kenya indicate that use of kairomone-based trapping systems with processed and buried banana materials attract weevils (S. Lux, pers. commun.). This trapping system might be integrated with entomopathogens.

The potential of using banana kairomones, especially fermented tissues, as synergists to synthetic pheromones has not been well exploited, although there is information indicating that banana plant volatiles could be used to enhance the attractiveness of synthetic pheromones (Ndiege, 1996; Jayaraman et al., 1997). Further research is needed on host plant odours to optimise the use of kairomones in an infochemical-based trapping system for *C. sordidus* control.

Infochemicals and biological control of *C. sordidus*

Studies regarding the effect of infochemicals on the behaviour of predators of *C. sordidus* are currently not available. However, ant and non-ant predators for *C. sordidus* have been reported from Kenya (Koppenhoeffer et al., 1992), Uganda (Tinzaara et al., 1999, A. Abera, pers. commun.), and Cuba (Roche and Abreu, 1983; Bendicho, 1987). These predators were mostly found associated with weevil environments in rotten pseudostem tissues and in larval tunnels (Koppenhoeffer et al., 1992; Tinzaara et al., 1999). Attraction of predators by the volatiles from the plant-weevil complex has not been investigated yet. It is possibe that these predators are attracted to the weevil environments by volatiles produced by the host plant, the weevil or the weevil-plant complex. Although synthetic pheromones (cosmolure+) are known to be specific to *C. sordidus*, their effect on the behaviour of predators has not been investigated. Information on how infochemicals influence the behaviour of the predators may increase their chance of being used in the field as biological control agents.

The potential of biological control of *C. sordidus* using indigenous entomopathogenic fungi has been recently investigated (Pena et al., 1995; Nankinga and Ogenga-Latigo, 1996; Nankinga et al., 1996; Nankinga, 1999; Schoeman and Schoeman, 1999; Nankinga and Moore, 2000). *Beauveria bassiana* showed a great potential for effective control of *C. sordidus* (Pena et al., 1995; Nankinga et al., 1996). One of the limiting factors is the lack of an effective delivery technique to the target insects (Nankinga, 1999). The potential of infected weevils being used in transferring pathogens to their uninfected counterparts was demonstrated by Schoeman and Schoeman (1999). Dissemination of *B. bassiana* using pseudostem traps was tested but found ineffective (Nankinga, 1999). The development of a pheromone lure could be used as a means for aggregating weevils to disseminate the entomopathogens. The use of pheromone lures as successful devices for dissemination of *B. bassiana* has been reported for other beetle species (Vega et al., 1995; Klein and Lacey, 1999). An above-ground ramp trap that allows both entry and exit of weevils (Alpizar et al., 1999; Oehlschlager et al., 2000; Tinzaara et al., 2000) could be used in this regard.

FUTURE RESEARCH NEEDS

Studies available indicate that there is a potential for using infochemicals to control *C. sordidus* (Alpizar et al., 1999; Oehlschlager et al., 2000; Tinzaara et al., 2000). Further information is needed to develop a cost-effective infochemical-based trapping method to control *C. sordidus*. Information is lacking on how infochemicals relate to weevil behaviour and environmental conditions. Other questions to be addressed are: does adult removal using infochemicals have an impact on weevil population dynamics and damage; and can infochemicals be integrated with other methods such as biological control?

The efficiency of the pheromone traps may be influenced, among other factors, by the physiological status of the pest, such as its reproductive maturation and mating status (Borden 1977; Jansson et al., 1991). Although pheromone lures are known to attract female and male weevils equally (Alpizar et al., 1999; Tinzaara et al., 2000), there is lack of information on the effect of the pest mating status and the age of *C. sordidus* on catches in pheromone-baited traps. We hypothesise that if mature and mated individuals do not respond to the pheromone lures, then trapping will cause limited suppression of the weevil population in the field.

Catches per trap are reduced when baited traps with synthetic pheromones are placed close to each other (trap interference) compared to widely spaced single traps (Schlyter, 1992; Byers, 1999). The effective trap radius has direct implications on the trap density used and the costs involved and therefore there is a need to get a more accurate value of the radius before pheromone traps can be used in mass trapping. Trap placement influences the capture rates for many insect pests (McNeil, 1991; Muirhead-Thompson, 1991). It is not clear whether the banana host plant has any influence on pheromone trap catches although we hypothesise that traps placed close to mats capture more weevils than traps placed between mats. Information is therefore required on the attraction range of the pheromone trap, its effective radius and on trap location relative to the host plant.

High trap densities may be needed to obtain high levels of pest population suppression (Howse et al., 1998), but they may not be practical especially to resource-poor farmers, as they render the method too costly. The trap density of four traps per hectare and moving the traps to new locations once a month was reported effective in reducing weevil populations to low levels within 4–5 months in Costa Rica (Alpizar et al., 1999). The assumptions here are: (1) the weevil movements are limited and there is no reinvasion of areas that have already been cleared; and (2) the traps remove a high proportion of weevils within the trap area in a month. The percentage population reduction using pheromone traps was however estimated using trap catch numbers and not overall population densities in the banana plantations. The effectiveness of a trap density of four traps per hectare needs to be evaluated under different agroecological conditions. Placing traps in the whole plantation without changing trap location monthly could be cost effective if the time taken to reduce weevil populations is low. Information is needed on the proportion of weevils trapped per unit area so as to make decisions on when to change the location of the traps (in case of mobile traps) and when to stop trapping when the population has been reduced to low levels. The rate of reduction of weevil population and damage using different trap densities needs to be determined. The question that should be answered here is which trap density is most cost effective. The pheromone trap catches need to be correlated to environmental factors such as wind direction, rainfall and temperature. Such information would assist farmers in managing their traps.

Deployment of pheromone traps alone may not result in pest population suppression when host material is abundant, providing good conditions for pest multiplication (Birch and Haynes, 1982; Vite and Baader, 1990; James et al., 1996). Many crop residues compete with traps, thereby reducing the effect of the traps. The effect of banana residue management on pheromone trap catches is not known. Mulching influences weevil movements in banana plantations (C. Gold and G. Kagezi, unpubl. data), but how much this would affect pheromone trap catches is not known. Therefore, the influence of farm management practices such as mulching and sanitation on pheromone trap catches needs to be studied.

Herbivore-damaged plants are known to produce volatiles that attract carnivores (Dicke, 1999a). Such volatiles may lead to increased carnivore density around the plant that may lead

to reduced herbivore damage. Predators of *C. sordidus* are normally found in weevil-infested rotten pseudostems and galleries (Koppenhoeffer et al., 1992; Tinzaara et al., 1999; A. Abera, pers. commun.). Are these predators attracted to such environments by volatiles produced by the host plant, weevil or the weevil-plant complex? The role of pheromones in influencing such an interaction has not been investigated.

The potential of using *B. bassiana* in Uganda to control *C. sordidus* was promising (Nankinga, 1999; Nankinga and Moore, 2000). However, one of the limiting factors is the lack of an effective delivery technique (Nankinga, 1999; Roy and Pell, 2000). Use of pheromone lures to infest beetles with *B. bassiana* and to disseminate it to other beetles is possible (Klein and Lacey, 1999; Vega et al., 2000), but needs to be studied for *C. sordidus*.

In conclusion, there is limited information on the use of infochemicals for the control of *C. sordidus*. However, according to the available information on other coleopteran insects, there is a potential for development of an infochemical-based trapping system for the control of *C. sordidus*. There are however research areas that need to be investigated to generate information for use in developing an infochemical-based trapping system for the control of *C. sordidus*. Research aimed at investigating some of the aspects mentioned in this review has been initiated in Uganda.

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