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Review Article

Exploitation of semiochemicals for the management of pest and beneficial insects with special emphasis on cotton cropping systems in Australia: A Review

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ABSTRACT: This paper examines semiochemicals, substances or mixtures of substances produced by one species that influence the behaviour of receptor organisms, from the perspective of their potential in a sustainable pest management context. Particular reference is made to *Helicoverpa* spp. and their natural enemies on cotton and to those chemical components derived from the inner tissues and organ surfaces of plants The post-alightment behavioural sequence of insect pests such as *Helicoverpa* spp. which lay eggs on plants which are not a food source, includes the sensing of small quantities of many types of chemical substances that may include free amino acids, organic acids, sugars, secondary metabolites, vitamins, minerals, growth regulators, etc. Detection of these substances on the leaf or organ surfaces of the plant provides specific information to the female insect on plant health, physiology and nutrition that guides the insect to either accept or reject the plant for oviposition. Three behaviour manipulation methods for pest management have been identified as (1) a behaviour of the pest, (2) a means by which the behaviour is manipulated appropriately, and (3) a method that utilizes the behavioural manipulation method for the protection of the resource from the pest. Stimuli that act over long distance such as chemical stimuli (e.g. attractants and repellents) and visual stimuli influence the insect's encounter with the plant. After the insect has landed, short range stimuli such as stimulants and deterrents, which occur on the organ or leaf surfaces of the plant, guide the insect to either accept or reject the plant for oviposition or feeding. In terms of beneficial insects, stimuli that act over long distances (eg. Food spray products) can be used to attract and conserve natural enemies of pests, enhancing their effectiveness as pest control agents. Food spray products attract natural enemies to an area through volatile compounds emitted by the products to increase the predator to prey ratio, predator searching activity and predation of pests in the cropping system. There is potential for plants which are not normally encountered by pest or beneficial insect species to function as a source of behaviour-modifying chemical signals, perhaps having different effects on different pests and beneficial insects. In general, semiochemicals are inherently different from synthetic insecticides in terms of their efficacy and impact on the environment and human health.

KEY WORDS: *Helicoverpa armigera, Helicoverpa punctigera,* semiochemical, integrated pest management, secondary plant compounds, attractants, repellents, deterrents.

INTRODUCTION

Cotton crops in Australia, as in the rest of the world, are attacked by a wide range of pests. Many insect species have been recorded in Australian cotton, but, only 6 are regarded as major pests, with another 17 considered minor pests (Hearn and Fitt, 1992; Fitt, 1994). The key pests in decreasing order of importance are *Helicoverpa* spp. (*Helicoverpa armigera* Hubner and *H. punctigera* (Wallengren)); two spotted mites (*Tetranychus urticae* Koch); green mirid (*Creontiades dilutus* (Stål)); thrips (*Thrips tabaci* Lind.) and aphids (*Aphis gossypii* Glover). *Helicoverpa* spp. occur in all regions and are considered the most important economic insect pests of cotton and other field crops (Fitt, 1989, 1994). The two local species are polyphagous, highly mobile and feed preferentially on young growing tips or reproductive structures of cotton plants. The estimated cotton crop losses due to *Helicoverpa* spp. in Australia in the 1996/97 season were valued at A$161.7 million despite the expenditure of A$87.2 million on control (Adamson *et al.,* 1997). During the 1998-99 season, it has been estimated that A$200 million was spent on pest control (Dallas Gibb, pers comm.). The control of these pests relies exclusively on the use of synthetic insecticides. Over-reliance on synthetic insecticides, together with the associated problems of insecticide resistance, disruption of beneficial insects and environmental pollution has cast doubt on the long-term classical synthetic insecticide approach. The focus of the Australian cotton industry, therefore, is to reduce its dependence on synthetic insecticides.

As a result, introduction and adoption of transgenic cotton crops by the industry has reduced their importance (Wilson *et al.,* 2005). The transgenic cotton crops contain a *Baccillus thuringiensis* (Bt) gene which expresses Cry 1AC and 2AB toxins that are toxic to *Helicoverpa* spp. and other lepidopteran pests when ingested (Wilson *et al*., 2005). Thus, the introduction of the transgenic cotton crops and the transition from conventional to transgenic cotton has given growers the platform to undertake a true integrated pest management (IPM) program to minimize synthetic insecticide use. Consequently, synthetic insecticide use against *Helicoverpa* spp. has reduced by 75-80% (Wilson *et al*., 2005). However, growers still face the problems of *Helicoverpa* spp. resistance, as well as the emergence of silverleaf whiteflies, green mirids, green vegetable bugs, aphids, two-spotted mites, mealybugs, pupae busting and soil pests such as wire worms as significant pests. Besides, use of cheaper broadspectrum insecticides such as pyrethroids, endosulfan, fipronil, disruption of beneficial insect activities, yield loss and high cost of cotton production are considered other constraints. This has led to a strong push by the industry towards an integrated pest management (IPM) system and research into alternative methods of pest control that can be used to integrate or supplement transgenic cotton crops.

The use of behaviour-modifying compounds such as feeding deterrents or antifeedants, oviposition deterrents, attractants, repellents, mating disruptants etc., that reduce insect feeding or egg laying without killing pests has intuitive appeal, because, such compounds are safer to non-target organisms such as beneficial insects and can reduce the use of synthetic insecticides.

The objective of this review is to provide background information on the current and potential use of semiochemicals or behaviour modifying compounds for insect pests and beneficial insect management particularly of *Helicoverpa* spp. and other sucking pests on cotton and other field crops. The roles of semiochemicals in host selection and in influencing the behavioural sequence leading to feeding and/or oviposition are discussed. The review also discusses chemicals on the leaf surfaces of host plants, what is known about these leaf surface chemicals and other relevant leaf chemical constituents and how these can affect the oviposition behaviour of adult insects particularly *Helicoverpa* spp. which do not feed on the host plant, but nevertheless can determine its quality before depositing their eggs. The role of these semiochemicals in enhancing the efficicacy of natural enemies of *Helicoverpa* and other important pests are also enumerated. In addition, this article also reviews the feeding behaviour of *Helicoverpa* larvae in relation to the leaf surface chemistry of the host plants, particularly cotton and the implication of this feeding behaviour for the survival of *Helicoverpa* larvae. Future research directions and the most promising areas for further study in relation to exploiting behaviour modifying compounds to manage key pests on cotton have been suggested in this review.

1. What are semiochemicals?

Semiochemicals (literally, “signaling chemicals”) are chemical compounds emitted by one organism that modify the behaviour of an organism receiving the signal (Tinsworth, 1990). Rodriguez and Niemeyer (2005) defined semiochemicals as molecules involved in chemical communication within and between insect species and employed for pest control.

The natural plant chemical compounds which influence the behaviour of insects can be described as secondary plant compounds (SPCs). As well as functioning as cues stimulating an insect’s “interest”, many SPCs have evolved in plants to actually protect against pest infestation (Tingle and Mitchell, 1984). This has led to several examples of SPCs being used as botanical insecticides to reduce pest damage when applied to crop plants. Some SPCs extracted from non-host plants and then sprayed on host plants can change the behaviour of a pest, particularly moths, which then avoid the host plant (Tingle and Mitchell, 1984). Unfortunately, numerous studies into the effects of SPCs on pests have used the paradigm for insecticide screening: focusing on compounds that kill pests – not compounds with potential to modify and/or ameliorate damaging pest behaviours. Consequently, potentially useful compounds with more subtle modes of action that could lead to novel products have been overlooked. Such compounds attract or repel pests over considerable distances; or stimulate or deter both feeding and egg-laying following contact.

In Australia, semiochemicals are being classified as synthetic insecticides, but, semiochemicals are not biocides by themselves, but their ability to control pests may rely on their capacity to cause changes in the behaviour of insects such as pest attraction (Del Socorro *et al*., 2003, Del Socorro and Gregg, 2004; Grundy *et al*., 2006), attraction of beneficial insects (Mensah, 2002a), aggregation or mating disruption (Walker and Welter, 2001), oviposition deterrence of adult insects such as *Helicoverpa* spp. (Mensah, 1996; Mensah, 2000), feeding deterrence of larvae and nymphs of pests (Mensah, 2000) and lure and kill by association of attractive semiochemicals with chemical pesticides (Pyke *et al*., 1987; El-Sayed *et al*., 2009; Mensah and Macpherson, 2010). The feeding deterrent effect of most semiochemicals could cause larvae or nymphs of pests to stop feeding and die of starvation and may be construed as direct kill (Mensah, unpublished). The environmental benefits associated with the use of semiochemicals are (1) safety for humans and other non target organisms, (2) reduction of pesticide residues in food and the environment, (3) increased activity of natural enemies of pests and (4) increased biodiversity in managed agro-ecosystems (Kelly *et al.,* 2003; Rodriguez and Niemeyer, 2005). Therefore, semiochemicals are inherently different from synthetic insecticides in terms of their mode of action and subsequent impact on the environment and human health.

In 1979, the United States Environmental Protection Agency (EPA), Office of Pesticide Program (OPP), recognized that semiochemicals were inherently different from synthetic insecticides and so made a policy statement encouraging the development and registration of semiochemicals as safer alternatives to conventional pesticide products (Tinsworth, 1990).

2 Role of Semiochemicals in the behavioural sequence leading to pests and beneficial insect oviposition

Oviposition is an important step in an insect's reproductive process. This step ensures the continuity of the species generation and any mistakes committed by the adult female in selecting an oviposition site will affect the offspring dearly. For lepidopteran insects such as *Helicoverpa* spp. that do not feed on the host plant, the oviposition step is particularly crucial because the hatching larvae are often not very mobile (neonate stage) and thus depend on the judicious choice of food plant by the adult female (Chew and Robbins, 1984; Feeny *et al*., 1983; Renwick, 1989). Adult females exhibit a wide variety of behavioural characteristics whilst determining the quality or health of the host plant before ovipositing large proportion of their eggs on the plant.

Searching, orientation, encounter, landing, surface evaluation and acceptance or rejection is the sequence of behavioural events leading to oviposition by lepidopteran insects (Kogan, 1977; Renwick and Chew, 1994). Searching, orientation and encounter events are very difficult to differentiate (Jones, 1992) and therefore will be considered in this review as the first stage of the behavioural sequence.

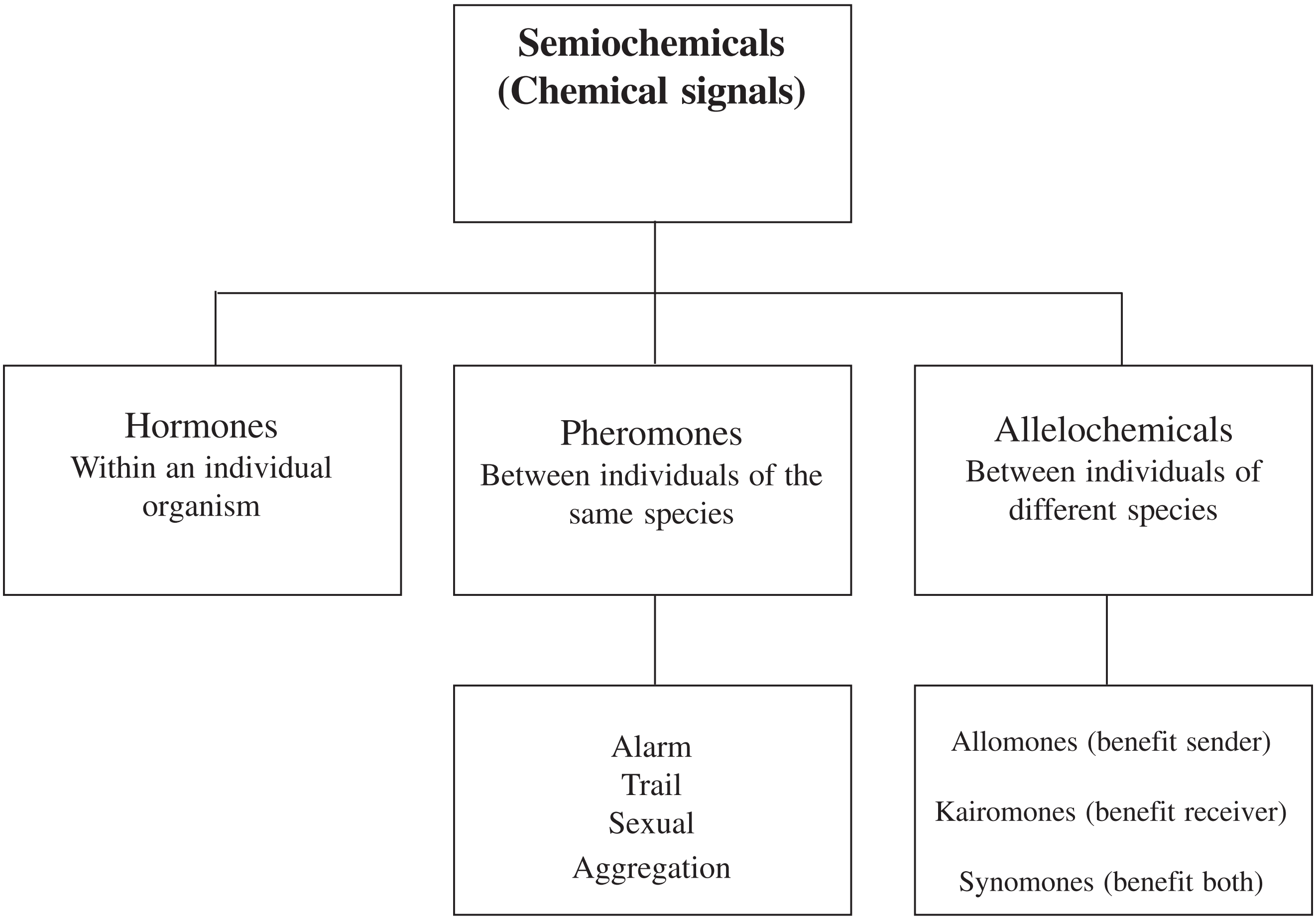

Fig. 1. Terms of chemical signals commonly used for various semiochemicals

This is followed by landing, contact evaluation and acceptance or rejection. All stages of the host find and acceptance sequence depends on a wide variety of cues both sensory (Renwick and Chew, 1994) and chemical cues (Renwick, 1989). However, experiments to differentiate between the mechanisms involved in searching, orientation and encounter are difficult to perform (Morris and Kareiva, 1991). Most studies in this area have focused on visual factors such as colour, shape and size of the host plants (Prokopy and Owens, 1983; Stanton, 1983). However, Mitchell *et al*. (1991) reported that many lepidopteran insects use airborne volatiles emitted from plants to locate their host in contrast to visual cues such as colour, shape and size of the host plant. Since, adults of *Helicoverpa* spp. are known to migrate and also lay most of their eggs during night time (Fitt, 1989), it is possible that they may utilize airborne volatiles to locate their host plants rather than such visual cues, which are of potentially greater importance during daylight.

Recent studies have reported that insects have odorant-binding proteins (OBPs) that provide the initial molecular interactions for chemical signals (semiochemicals) such as pheromones and host odours and are thought to transport the semiochemical molecules across the antennal sensillum lymph to the olfactory receptors (ORs) (Zhou *et al.,* 2009). All insect OBPs have six highly conserved cysteine residues, (Krieger *et al.,* 1993) which form disulphide bridges that stabilise the 3D structure (Stadler *et al.,* 2000). This sequence motif has been used for genome-wide identification and annotation of OBP genes in a range of insect species (Zhou *et al.,* 2004). OBPs in lepidopteran species are usually divided into different subfamilies; the PBP, the GOBP (Zhou *et al*., 2009) and the antennal-binding protein X homologues (ABPx) (Zhou *et al.,* 2009). PBPs of Lepidoptera are either specific to, or highly enriched in, the antennae of male moths and have been shown to bind the sex pheromones produced by females (Maida *et al.,* 2005). However, PBPs have been found in the antennae of females and in male sensilla, which are not pheromone-sensitive (Maida *et al.,* 2005). GOBPs are usually expressed equally in the antennae of both sexes, consistent with a proposed role in the detection of host volatiles (Zhou, *et al.,* 2009). ABPxs display limited sequence homology to PBPs and GOBPs but, have the same sequence motif of the conserved cysteine residues as PBPs and GOBPs (Zhou *et al*., 2009). No specific role has yet been proposed for them (Zhou *et al.,* 2009).

After the insect alights on a plant, contact perception of both physical and chemical characteristics of the leaf or other organ surface becomes the most important factor in determining the suitability of the host for oviposition. The behaviour of many herbivorous insects immediately after arriving on the plant indicates that are evaluating the plant as a potential food source or oviposition site (Blaney, 1970).

2.1 Searching, orientation and encounter of the host plant by the insect

The searching behaviour of moths and butterflies has been extensively reviewed (Morris and Kareiva, 1991; Jallow, 1998). Their conclusions suggest that the predominant sensory cue for host location is visual, with shape and colour playing a major role (Prokopy and Owens, 1983). However, Ramaswamy *et al*. (1987) reported that *H. virescens* females can choose between cotton and groundcherry even when olfaction and vision are prevented, indicating the importance of plant volatiles in host location. The important role of plant volatiles in the orientation of various moths to their host plants has also been reported (Renwick and Chew, 1994; Hartlieb and Rembold, 1996). Volatiles emanating from flowering cotton and maize may act as long range attractant for *H. armigera* females allowing the moths to concentrate within areas of flowering hosts (Hedin, 1976; Hopper, 1981). A similar suggestion has been made for *H. punctigera* on lucerne and peas (Cullen, 1969). Substantial research has been done on the effect of plant volatiles acting as oviposition stimulants or deterrents for moths (Renwick, 1990; Renwick and Chew, 1994), but little is known about long range perceptible host plant signals.

Hartlieb and Rembold (1996) suggested that ovipositing *H. armigera* females are strongly attracted by volatiles from pigeon pea stream distillate which stimulates two behavioural reactions important for host finding: orientation to the odour source from a distance and landing. They identified several sesquiterpenes in the distillate. Knowledge of long range perceptible plant signals will benefit the management of these moths because of the potential to attract these insects to non-hosts, or to assist in the breeding of crop varieties that may prevent moths locating them as host plants. The contact between a moth's orientation toward preferred and non preferred plants has been used to identify attractants involved in pre-oviposition behaviour. For example, the cabbage looper oriented towards volatiles from a susceptible variety of soybean, but was repelled by volatiles from a resistant soybean line (Khan *et al.,* 1987). The attraction of moths to plant volatiles is not always related to the finding of a suitable host for oviposition because, the insects have to undertake contact evaluation of the plant before deciding to accept or reject it. In pigeon pea/cotton interplants more *Helicoverpa* spp. moths were found on the pigeon pea when it was in flower compared to cotton, however, more eggs were laid on the cotton crop than on the pigeon pea (Mensah and Singleton, unpublished data). The responses of moths to floral volatiles do not necessarily indicate orientation to an oviposition site, because, many insects alternate bouts of nectaring with bouts of oviposition (Hartlieb and Rembold, 1996).

2.2 Landing of the insect on the host plant

The final step in the orientation process is the landing of the moth on the plant. According to Renwick and Chew (1994), landing may be triggered by either physical or chemical cues or a combination of both. The role of vision is well documented (Prokopy and Owens, 1983; Mensah and Madden, 1992; Mensah, 1996), and colour and shape of the leaves are particularly important (Singer, 1993; Stanton, 1984). The host abundance or quality during a particular season may change the landing frequencies of the orientating moths (Jackson *et al.,* 1984). However, in night-flying *Helicoverpa* spp., volatile chemicals may play a more important role than colour in promoting landing on a host plant such as cotton. The role of plant volatiles in eliciting landing has been suggested in several reviews (Jackson *et al.,* 1984), although the observed effects may often be attributed to attraction (Saxena and Goyal, 1978). According to Saxena and Goyal (1978), citrus volatiles cause a higher frequency of visits by *Papilio demoleus*. Stimuli that prevent or discourage landing on non-hosts or unsuitable hosts play an important role in the selection of oviposition sites. Such stimuli can also be utilised as repellents to manage these pests. Several attractants, arrestants and repellents that may be involved in handling or avoidance behaviour have been identified (Norris, 1990; Waage and Hedin, 1990).

2.3 Leaf surface evaluation of the host plant by the insect

This step in the oviposition process is very crucial in the life cycle of the insect, because, it is the final decision process for the female to accept or reject the plant for oviposition. Therefore, a mistake at this stage in gathering leaf surface information by the female, may lead to oviposition on an unsuitable plant which may affect the survival of the offspring and the continuity of the generation.

Most phytophagous insects, immediately after landing on a plant, commence the evaluation of array of sensory or chemical information on the plant surface (Renwick and Chew, 1994; Eigenbrode and Espelie, 1995). The chemical subset of these stimuli or "chemical search image" plays an important role in host plant recognition (Stadler, 1986). For ovipositing insects such as *Helicoverpa* spp. that do not contact the inner tissues of the plant, but test only the leaf surface, recognition and selection of the host plant after landing could be determined by small quantities of many types of chemical substances that come from the inner tissues of the plant and that are present on the plant surface; for example, free amino acids, organic acids, sugars, secondary metabolites, vitamins, minerals and growth regulators (Tukey, 1971; Derridj *et al*., 1992). These substances, especially secondary metabolites, could give species-specific information to a phytophagous insect (Soldaat *et al*., 1996). Many secondary metabolites, however, are large molecules that do not diffuse through the membranes and cell walls easily and thus are unlikely to be present on the leaf surfaces of all plants. In contrast, primary metabolites are present on the leaf surface of all plants (Tukey, 1971).

Recent developments in chemotaxonomy have shown that plants can be discriminated against on the basis of their internal proportion of primary metabolites (Soldaat *et al*., 1996). Yeoh *et al.* (1984) described species-specific amino acid proportions in leguminous plants. It has also been shown that proportions of free amino acids in the leaf surfaces of maize and sunflower are very stable and affect host selection of these plants by the moth *Ostrinia nubialis* (Derridj *et al*., 1989). Plant surface chemicals that stimulate oviposition have been isolated for *H. zea* on corn (Wiseman *et al*., 1988), *Heliothis subflexa* on groundcherry (Mitchell and Heath, 1987) and *H. virescens* on tobacco (Jackson *et al*., 1984). Mitchell *et al*., (1990) also isolated oviposition stimulant compounds for *H. virescens* from leaves and squares of cotton plants. Rembold and Tober (1985) showed that *H. armigera* females responded differently in oviposition trials to odours obtained by pulling air over the leaf surfaces of seedlings of two cultivars of pigeon pea. Tingle *et al*. (1989) also found that *H. subflexa* females displayed positive flight responses to odours emanating from washings from leave surfaces of its host, groundcherry. It is also known that *H. virescens* can choose between cotton and groundcherry even when olfaction and vision are prevented indicating that chemoreception alone allow discrimination of host plants in this species (Ramaswamy *et al*., 1987).

These findings clearly support the suggestion that leaf or organ surfaces of plants contain chemicals which provide information to the insect by contact regarding the suitability of the host plant for oviposition. The female moths obtain this information from the leaf surface by fluttering, wing fanning, walking and ovipositor dragging after the initial contact with the leaf surface before oviposition. Surface cues on the leaf that discourage biting or oviposition before any damage occurs should benefit the plant (Chapman, 1977). Similarly, female moths should benefit from rapid assessment of host quality on the basis of host surfaces cues (Chapman, 1977).

2.4 Acceptance or rejection of plants by the insect

For ovipositing moths that do not feed on the plant, surface cues of the plant play a major role in the final decision to oviposit or not (Schultz, 1988). Rothschild and Schoonhoven (1977) demonstrated that *Pieris brassicae* assesses egg load of plants by means of surface leaf cues. Since this study, chemical cues mediating egg laying and distribution or avoidance of occupied foliage has been reported for moths (Poirer and Borden, 1991). Hartlieb and Rembold (1996) demonstrated that a sesquiterpene mixture from a pigeon pea distillate in a 1:50 dilution, stimulated egg laying on the pigeon pea. However, increasing concentration of the sesquiterpenes resulted in the rejection of the plant for oviposition. This means that the orientation and oviposition on pigeon pea are elicited by different optimum stimulus concentrations. The kairomone concentration that attracts *H. armigera* females to pigeon pea is, at a higher concentration, active as an oviposition deterrent, whereas a lower concentration of the same kairomone can stimulate egg laying. At what growth stage of the pigeon pea does it produce oviposition deterrent or stimulant kairomones? What other factors affect the production of the oviposition deterrent and stimulant kairomones? An understanding of these issues will enhance effective utilization of pigeon pea as trap or refuge crops in cotton. Sesquiterpenes have rarely been found as insect attractants or ovipositional stimulants, whereas aliphatic short chain alcohols and monoterpenes are more common semiochemicals (Metcalf, 1988). Some sesquiterpenes (I-humulene, I-bulnesene and J-caryophyllene have been identified in cotton plants (Elzen *et al*., 1985). Methyl esters of fatty acids have been reported as oviposition deterrent compounds for *O. nubiialis* (Thiery and Quere, 1991).

Mitchell *et al*. (1990) washed the leaf surfaces of susceptible tobacco (NC2326) and resistant tobacco (TI 1112) and 1 ml of each extract was pipetted onto the centre of a piece of white broadcloth, as an oviposition substrate. They reported that *H. virescens* laid more eggs on cloths treated with susceptible extract and very few eggs on cloths treated with resistant tobacco extract indicating that the moth can differentiate between the susceptible and resistant plants by leaf surface contact. The result was consistent with those of Jackson *et al*. (1984), who conducted similar competitive tests outdoors in small field cages. The positive ovipositional response recorded from *H. virescens* from the leaf wash of susceptible tobacco was due to the presence of duvane diterpenes and conversely, the ovipositional nonpreference displayed by the moth towards the resistant tobacco was due to the lack of or reduced level of duvane diterpenes (Jackson *et al*., 1991).

It is also known among moths that chemicals extracted from non-host plants and sprayed onto known acceptable host plants can exhibit varying levels of deterrence by ovipositing females (Tingle and Mitchell, 1984). This could mean that identification of the chemicals stimulating oviposition or feeding presents opportunities for characterization of the behavioural and physiological factors regulating this essential process in the life cycle of the pest. Further, it may prove possible to mask such chemicals, thereby deterring oviposition, using other products, or greatly reduce or eliminate them from otherwise desirable cultivars through genetic manipulations, so imparting a degree of resistance to pest attack.

Epicuticular waxes and leaf surface lipids have also been suggested as potential cues used by ovipositing females to reject or accept a plant for oviposition (Eigenbrode and Espelie, 1995). Major classes of these plant epicuticular lipids have been reported (see review by Eigenbrode and Espelie, 1995). The epicuticular lipids of a plant can vary with plant part, age and environmental conditions (Baker, 1982). The epicuticular lipid composition of the abaxial leaf surface may differ dramatically from that of the adaxial surface (Bocovac *et al*., 1979) and this may affect egg distribution on the host plant.

Fiala *et al.* (1990) studied the relationships between the plant oviposition preference of *O. nubilalis* and the biochemical composition of the host plant, particularly maize. The *O. nubilalis* is a night flying insect similar to *Helicoverpa* spp. in Australia. The insect prefers plants, especially at twilight, which are richest in soluble carbohydrate contents and further selects those having the richest leaves, without any feeding (Fiala *et al*.,1985; Derridj *et al.,* 1986). To accept or reject a plant for oviposition without feeding, the insect needs to detect the quality of the plant on the leaf surface. Plants have pores or micropores in the cuticle and in the cell wall of epidermal cells which could promote the leaching of water soluble compounds from the inside of the leaf surface (Charmel, 1986; Miller, 1986). These may allow the moths or insects, which do not feed on the plant before making an oviposition decision, to determine the quality of the plant from the surface. The molecules leaching onto the plant surface are diverse and include soluble carbohydrates, free amino acids, organic and phenolic acids, terpenes and alkaloids (Merall, 1981). Derridj and Fiala (1983) observed a positive correlation between oviposition preference of European corn borer female moths and low molecular weight carbohydrates on the leaf surfaces of two corn hybrids. The method for collecting soluble substances on the leaf surface has been described in detail (Fiala *et al*., 1990).

In addition to the plant compounds involved in species recognition, other chemicals, particularly those containing nitrogen, can provide information to ovipositing females on the relative quality of a particular species or individual (Thompson and Pellmar, 1991). Changes in nitrogen levels are often accompanied by changes in other chemical constituents on the leaf surface of plants particular sugars, secondary carbohydrates (Thompson and Pellmyr, 1991). Thompson and Pellmyr (1991) sampled neighbouring pairs of ragwort plants; one of which had and egg mass, the other did not and found that cinnabar moths selected plants with high concentration of both nitrogen and sugars on the leaf surface. Plants poor in nitrogen and sugars on the leaf surfaces were less likely to receive eggs (Thompson and Pellmyr, 1991). The effects of nitrogen-containing alkaloids which are positively correlated with total-nitrogen and negatively correlated with soluble carbohydrate levels, have been shown to have no effect on oviposition (Thompson and Pellmyr, 1991).

Though ovipositing female moths are capable of detecting suitable host plants just through contact with the leaf surface, ovipositional “mistakes” ie ovipositions onto plant species outside the normal range of acceptable hosts, are common (Singer, 1984). Such mistakes may be the raw material for host shifts. They may mark the broadening of the number of plant species used by an insect population, favouring females that save time in searching for hosts by adding this species to those they use. Alternatively, these mistakes may mark the beginnings of a complete shift onto a new plant species. On the other hand, they may simply serve to select against females that are less specific than others in their choice of host plants (Futuyama, 1983). *Helicoverpa* spp. particularly *H. armigera*, undertake “distress” laying similar to ovipositional mistakes when given oviposition substrates or plants they do not prefer. Such a behaviour usually complicates host preference trials in the laboratory and makes it impossible to translate these results to the field.

2.5 Oviposition preference and larval performance

A major working hypothesis on the evolution of oviposition behaviour is that females will select plant species that will maximize the survival of the larvae (Rausher, 1982; Thompson and Pellmyr, 1991). Studies so far reviewed suggest that ovipositing female moths, after landing on a plant, can detect the quality and therefore suitability of the plant for oviposition on the leaf surface. An important question is whether the biochemical composition of the leaf is detectable by the larvae by contact. Hedin *et al*. (1988), reported that the first stage larvae of *H. virescens* can detect and avoid feeding on glands that contain gossypol when they hatch from the eggs. When the larvae leave the cotton terminal where the eggs hatched, they move onto small squares and then prefer to feed along the calyx crown until they moult into the second stage when they are unaffected by gossypol and then consume the glands (Parrott *et al.,* 1983). Further studies have shown that the young *H. virescens* larvae feed less on squares of high gossypol plants than those with low densities of gossypol (Parrott *et al*., 1989). It has been suggested that anthocyanin-containing cells surrounding the gossypol glands deter the neonate larvae from feeding and thus tissues containing toxins are avoided (Bernays and Chapman, 1994).

Studies conducted in Australia have shown that *Helicoverpa* spp. females lay the same number of eggs on transgenic and non-transgenic crops (Wilson *et al.,* 2005; Del Socorro and Gregg, 2004; Del Socorro *et al*., 2003) suggesting that the adult moth cannot detect the Bt toxin by using surface chemical cues to discriminate against the transgenic plants as oviposition sites. The question is, can the larvae use surface chemicals as cues, even before their first bite, to discriminate against or change their feeding behaviour on a plant? If this is so, then such discrimination, particularly on transgenic cotton, may partially explain changes in larval movements and feeding behaviour which lead to higher than expected survival on transgenic plants. If the Bt toxin is not expressed uniformly in the plant tissues, then the larvae may avoid feeding on tissues high in Bt until they have grown to sufficient size that they are no longer strongly affected by the Bt protein. This will ensure the survival of the larvae because adult female moths are sometimes known to make “ovipositional mistakes” to expand their host range. In this situation, it is up to the larvae to test the host plant and correct the situation by changing their feeding behaviour to survive on the plant.

A plant commonly chosen for oviposition, but poor for larval survival or growth, may be a recent addition to a habitat and selection may not have had sufficient time to favour females that avoid that plant species (Thompson and Pellmyr, 1991). For example, transgenic cotton plants have been used in Australian cotton systems for about 10 years and selection may not have had sufficient time to favour females. It is possible that with time, females of *Helicoverpa* spp. females may discriminate against these plants as oviposition sites.

3.0 Behaviour manipulation methods for pest management

The manipulation of a pest's behaviour to protect a crop is a relatively new concept. According to Foster and Harris (1997), there are three principal elements of a behavioural manipulation method. They are (1) a behaviour of the pest (2) a means by which the behaviour is appropriately manipulated and (3) a method that utilizes the behaviour manipulation to protect the crop. The manipulation of the pest feeding on the crop or the finding of the crop or host plant is more likely to be useful for pest management than manipulation of insect or pest behaviours unrelated to the crop (for example, mating disruption) (Foster and Harris, 1997). If the feeding behaviour of the pest is manipulated successfully, it will ensure that the crop or resource is protected. However, successful manipulation of an unrelated behaviour may reduce the local population but, still not protect the resource because of immigration of outside populations which may be already mated into the protected area, as can occur in moths (Carde and Minks, 1995).

In an attempt to avoid the pitfalls of characterizing semiochemicals in terms of unanalyzed behavioural effects, Kennedy (1978) classified chemical stimuli that act over a long distance (finding-type behaviours) as attractants and repellents and those that act at a short distance (acceptance-type of behaviours) as stimulants and deterrents. Nevertheless, it appears that an earlier classification (Dethier *et al.,* 1960) has stood the test of time. This definition invokes oriented movements towards (attractant) or away (repellent) from the source of stimulus and the eliciting (stimulant) or inhibition (deterrent) of feeding or oviposition (Bernays and Chapman, 1994).

3.1 Utilization of semiochemicals in managing pests on cotton

In general, behavioural manipulation methods of both pest and beneficial insects involve some changes in pest behaviour and can be exploited in the use of semiochemicals to manage pests such as *Helicoverpa* spp. in agricultural crops such as cotton. Ultimately, the success of any particular strategy to manage *Helicoverpa* spp. in cotton will depend on the efficacy of the semiochemical product on the oviposition and feeding behaviour as well as toxicity to the pest on the host plant. There are several strategies for exploiting semiochemicals in managing pests especially *Helicoverpa* spp. on cotton crops in the field. These include use of semiochemicals to (1) attract and conserve beneficial insects to feed on pests on cotton crops, (2) use semiochemical lures with insecticides to attract-and-kill pests, (3) apply semiochemical onto cotton plants to deter pest oviposition and feeding, (4) apply semiochemical lures with insecticides to stimulate oviposition and feeding on another crop, (5) apply semiochemicals toxic to pests to cause direct mortality and (6) mix semiochemical with insecticides to enhance synergism.

3.1.1 Attracting and conserving beneficial insects

Cotton is grown in over 69 countries and across five continents (ICAC, 2006). Cotton is grown as short-lived annual monocultural or polycultural crops wherever it is grown. The major pests attacking cotton crops are mainly *Helicoverpa* spp. These pests are highly migratory and beneficial insects alone are unable to control the population successfully due to the rapid build up of the pest population. The insect attractants can be used to establish beneficial insects in cotton crops prior to *Helicoverpa* spp. arrival to give the beneficial insects enough time to establish and prey on these pests.

Semiochemicals are potential agents for use as attractants for beneficial insects in many agricultural crops such as cotton (Mensah *et al*., 2003, 2011). Application of supplementary food sprays to cotton crops can attract and enhance the establishment of beneficial insects, mainly predators, before pests such as *Helicoverpa* spp. arrived in a cotton crop in Australia (Mensah *et al*., 2003) and Benin (Mensah *et al*., 2011). Food spray products work by managing pests indirectly by attracting and conserving their natural enemies, which in turn control the pests (Mensah *et al*., 2011; Mensah, 1997; Walker *et al.,* 1996; Neuenschwander and Hagen, 1980). They can also deter lepidopteran pests such as *Helicoverpa* spp. and *O. nubilalis* laying their eggs on cotton and maize (Mensah *et al*., 2000). Studies by Mensah (2002 a, b) have shown that a predator-to-pest (*Helicoverpa* spp.) ratio ≥ 0.5 is acceptable when managing lepidopteran pests on cotton. Any ratio less than 0.5 could mean that the number of predators is insufficient to control the pests, resulting in the greater survival of pests such as *Helicoverpa* spp. Thus, application of semiochemicals such as food sprays (Mensah, 2002a) can attract and conserve beneficial insects such as predatory beetles, bugs, lacewings, spiders etc which will prey on *Helicoverpa* spp. eggs and larvae to reduce pest population and damage. Key predatory insects that can be attracted by the use of food sprays are given in Table 1.

3.1.2 Attract-and-kill strategy

This strategy has been used for many years in pest management in agricultural crops (El-Sayed *et al*., 2009;

Welham and Liburd, 2006). The technique involves the use of a semiochemical lure containing a toxicant (usually insecticide) to attract or lure the pest to another crop where the insect is killed after ingesting the semio-chemical lure. Many studies have used "attract– and–kill" strategies successfully against pest insects such as cotton bollworm and native budworm (Pyke *et al.*,1987), tephritids, house flies, tsetse flies (Jones, 1998), fruit flies (Cunningham and Steiner, 1972), pink bollworm (Haynes and Baker, 1986), coddling moth (Charmilot *et al.*, 2000), and light brown apple moth (Suckling and Brockerhoff, 1999). The attractants can be pheromones or other semiochemicals (De Souza *et al.*, 1992) and are formulated with a mortality agent that can be a toxin, a sterilant (Langley *et al.*, 1990) or a pathogen (Pell *et al.*, 1993).

Previous attract and kill formulations used against lepidopteran pests were based on pyrethroid insecticides (Miller *et al.*, 1990; Downham *et al.*, 1995) because, they exhibit a rapid knockdown effect (Suckling and Brockerhoff, 1999). For example, the attract and kill formulation (Sirene® CM) included a liquid containing pheromone, pyrethroid and a UV-absorber that was used against codling moth to reduce fruit damage in orchards of Switzerland (Charmilot and Hofer, 1997; Hofer, 1997). The response of *H. armigera* males to Sirene® CM in commercial cotton crops in Australia was studied but, the contact rate of *H. armigera* males to the formulation was found low to be effective and the study concluded that Sirene® CM might be ineffective in suppressing *H. armigera* infestations on cotton farms (Britton *et al.*, 2002). However, recently a moth attractant marketed in Australia by AgBiotech Pty Ltd as Magnet® consisting of a volatile blend and feeding stimulants that mimic the type of signals that lepidopteran adults look for when seeking nectar has the potential to attract lepidopteran pests in a wide range of crops (Del Socorro *et al.*, 2003; Grundy *et al.*, 2006).

Mensah and Macpherson (2010) studied attract and kill strategy by applying Magnet® mixed with toxicant (Larvin® 375) insecticide) to transgenic cotton crops and demonstrated a reduction of *Helicoverpa* spp. adult population of 91.5 per cent. This resulted in a reduction in the number of eggs and larvae on the treated cotton crops (see Figure 1).

Table 1. Predators of cotton pests that were attracted by supplementary food spray on commercial cotton crops. (Mensah *et al.,* **2002, a, b)**

Order	Family	Species	Group
Coleoptera	Coccinellidae	*Coccinella transversalis* Fabricius *Diomus notescens* (Blackburn)	Predatory beetles
	Melyridae	*Dicranolauis bellulus* (Guerin-Meneville)	
Hemiptera	Nabidae	*Nabis capsiformis* (Germar)	Predatory bugs
	Lygaeidae	*Geocoris lubra* (Kirkaldy)	
	Pentatomidae	*Cermatulus nasalis* (Westwood) *Ochelia schellenbergii* (Guerin-Meneville)	
	Reduviidae	*Coranus triabeatus* (Horvath)	
Neuroptera	Chrysopidae	*Chrysopa* spp.	Predatory lacewings
	Hemerobiidae	*Micromus tasmaniae* (Walker)	
Araneida	Lycosidae	*Lycosa* spp.	Spiders
	Oxyopidae	*Oxyopes* spp.	
	Salticidae	*Salticius* spp.	
	Araneidae	*Araneus* spp.	

3.1.3 Oviposition and feeding deterrent strategy

A deterrent is a chemical that inhibits feeding or oviposition behaviour when applied to a site where the behaviour normally occurs (Bernays and Chapman, 1994). In pest management, a deterrent is applied directly to reduce a pest's feeding or oviposition behaviour. The presence of deterrents at the surface of leaves plays a major role in discriminatory behaviour of ovipositing moths. However, in the case of a ployphagous insect it is likely that tolerance to deterrents is comparatively high.

Many plant extracts have been tested for deterrent activity on a variety of insects (Renwick, 1990), mainly with the view of using deterrents in pest control programs (Renwick, 1988). Polar extracts are known to be the most effective compounds that deter oviposition of lepidopterans (Renwick, 1990). Though nonpolar extracts are known to be less effective as oviposition deterrents, it is possible that the lipid material making up the bulk of such extracts may form a layer over polar stimulants at the leaf surface, thus preventing the insects from detecting a stimulant or a deterrent compound. If a nonpolar extract masks the effect

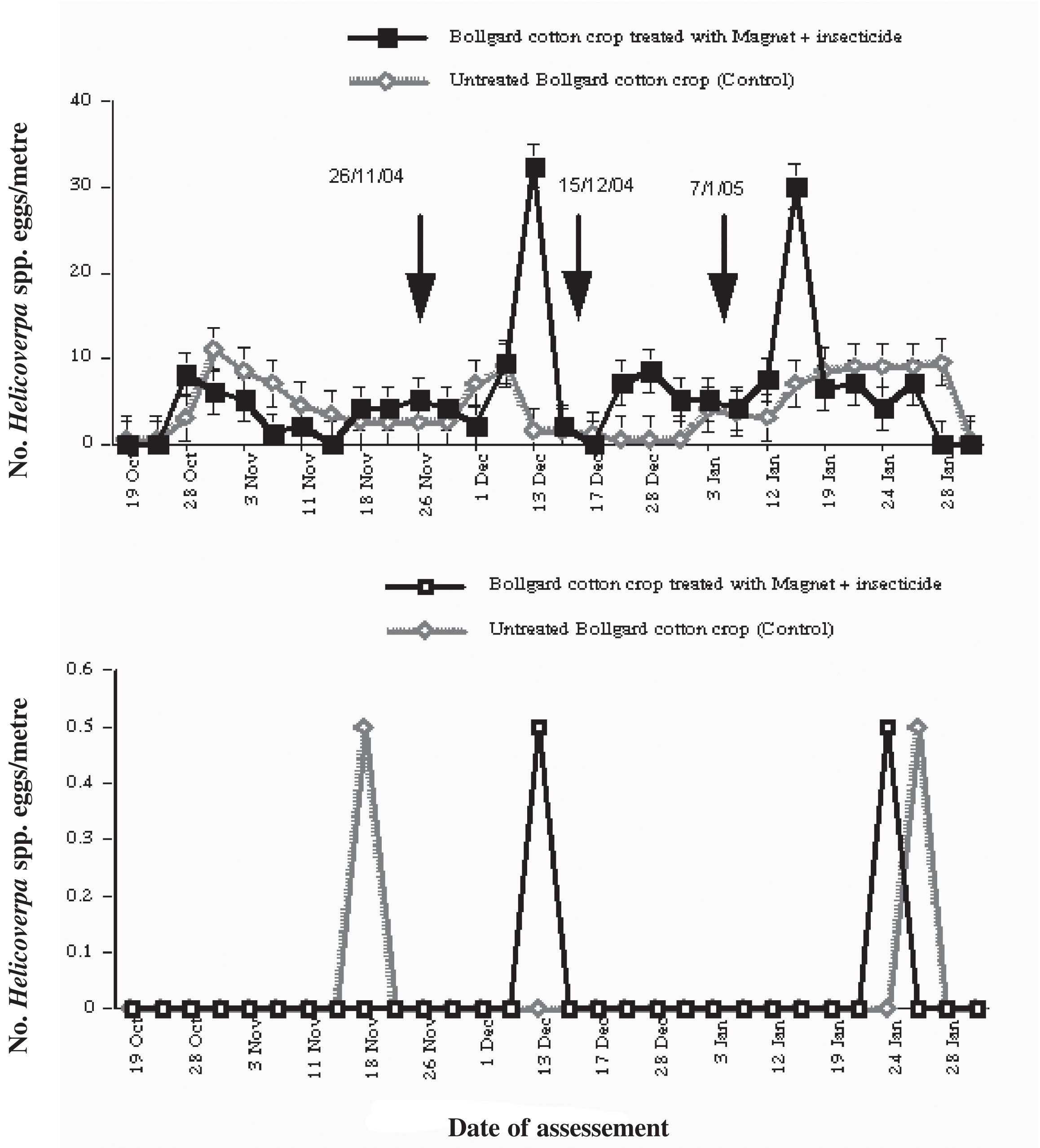

Fig. 1. Effect of application of Magnet® mixed with insecticide on BollgardII® cotton crops on oviposition and larval survival of *Helicoverpa* spp. at Carbucky near Goondiwindi in 2004-05 (Source: Mensah and Macpherson, 2010).

of an oviposition stimulant, then it will act as a deterrent because it will prevent the insect from recognizing the resource as a host. For example, applying Envirofeast or petroleum spray oils to cotton may have a deterrent effect, suppressing oviposition of *Helicoverpa* spp. on these plants (Mensah, 1996). Because deterrents suppress feeding and oviposition behaviours of insect pests, they often found by studying the chemistry of non-host plants of a particular pest species (Bernays, 1983).

There is a general view that the efficacy of a deterrent based method may be increased if used in combination with another method that attracts the pest to a non-valued resource in a stimulo-deterrent diversion (Miller and Cowles, 1990) or push-pull (Pyke *et al.,* 1987) strategy. The stimulo-deterrent strategy was suggested for insect herbivores but is applicable to many pests and any resource type (Foster and Harris, 1997). In the cotton industry, it seems likely that such combined behavioural manipulation methods may reduce the size of *Helicoverpa* spp. population in cotton, provided that suitable deterrents or stimulants can be identified.

Many studies have been conducted in cotton cropping systems using a strategy that involves application of a semiochemical product on the host plant to deter oviposition of *Helicoverpa* spp. adults and feeding of 1/3rd instar larvae (Mensah, 1996; Mensah, 2000). Studies by Mensah and Moore (2005-unpublished) showed that application of a fractionated extract formulation of a plant code-named Plant X on cotton plants reduced *Helicoverpa* spp. eggs (Table 2) and showed a strong antifeedant effect to *Helicoverpa* spp. second instar larvae (Figure 2).

Table 2. No-choice oviposition test of *Helicoverpa armigera* females on filter papers treated with Plant X fractions 1-3 at ACRI in Narrabri, 2004-05 (Mensah and Moore, 2004, 2005 – unpublished)

Treatments	No. eggs/ plant ± SE	[1] Oviposition Deterrent Index (ODI)
Fraction 1	32.75 ± 25.39 a	20.1 a
Fraction 2	41.00 ±14.41 a	9.1 a
Fraction 3	17.50 ± 7.84 b	47.6 b
Fraction 4	6.50 ± 1.19 a	42.2 a
Fraction 5	58.25 ± 22.96 b	-56.9 b
Fraction 6	35.00 ± 10.40 b	-37.3 b
Control (water)	49.25 ± 17.21 a	0.0 a

Means within columns followed by the same letter are not significantly different (P>0.05) (Tukey-Kramer Multiple comparison test).

3.1.4 Oviposition and feeding stimulants with insecticides

The technique involves the use of synthetic insecticides combined with semiochemical lures that attract the pest to another crop to lay and also encourages the larvae hatching from the eggs to increase their feeding and ingest a lethal dose of the insecticides. Potential uses of stimulant chemicals include increasing an insect's ingestion of toxins

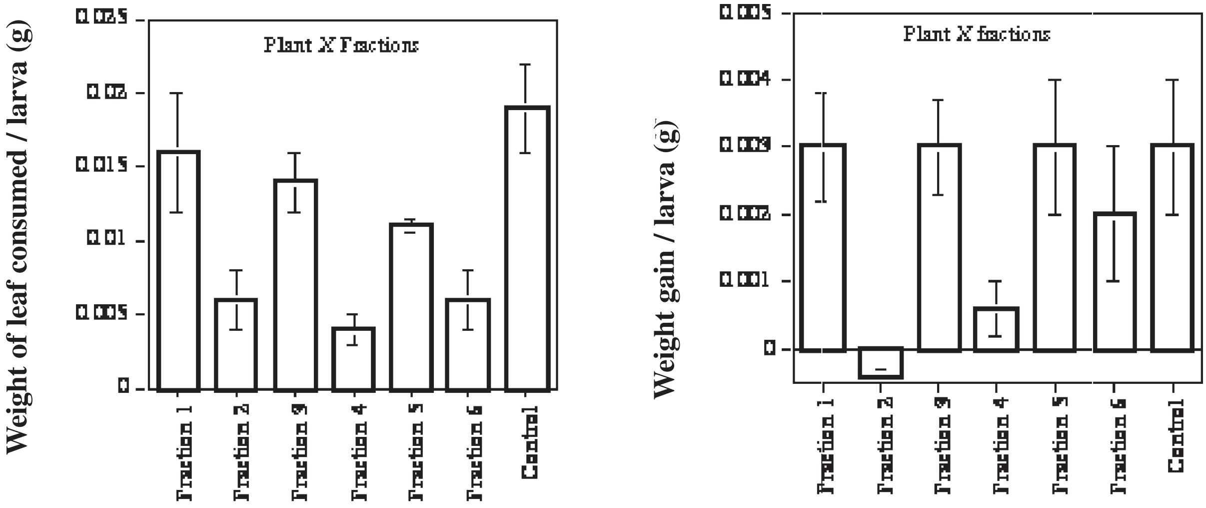

Fig. 2. Feeding response of *Helicoverpa armigera* 3rd instar larvae on cotton leaves treated with Plant X fractions (no-choice tests) at ACRI in Narrabri, 2004-05

and pathogens etc., and stimulating egg lay by a pest on a refuge or trap crop in order to reduce the size of the population developing in the primary crop or resource. Feeding stimulants are especially useful in conjunction with toxins (Ave, 1995) because they can increase the pest's contact with the toxin so that a lethal dose of the toxin is picked up by the pest. Oviposition stimulants have the potential to be used in combination with moth attractants to ensure that the moths lay their eggs on a less preferred host plant, where both moths and larvae will be destroyed. Thus, oviposition stimulants could be used to divert oviposition from cotton (a protected resource) to an alternative crop (trap or refuge crops) to reduce the size of the population.

With respect to oviposition stimulants, there is evidence that sesquiterpenes which are detected by moths on the leaf surface of pigeon pea, which is now being used as trap and refuge crop for *Helicoverpa* spp. in both normal and transgenic cotton, influence the moths' acceptance or rejection of the crop as an oviposition site in a concentration-dependent manner. Higher concentrations of sesquiterpenes can act as oviposition deterrents and lower concentrations as oviposition stimulants. Such compounds are sufficiently volatile to function as attractants as well. Aliphatic short chain alcohols and monoterpenes are more common ovipositional stimulants whereas sesquiterpenes have rarely been found as ovipositional stimulants (Metcalf, 1988). Soluble carbohydrates leaching onto the plant surface have also been identified as oviposition stimulant for moths (Derridj and Fiala, 1983). In *H. virescens* high levels of duvane triterpenes were found to stimulate the insect's egg lay on tobacco plants (Jackson *et al.,* 1984). In the case of *H. zea*, sesquiterpene carboxylic acids stimulate oviposition and *H. subflexa* oviposited in response to methanolic extracts of groundcherry. (Mitchell and Heath, 1987)

4.1.5 Synergism of semiochemical mix with synthetic insecticides

This is a strategy that involves mixing a semiochemical product with reduced label rates of synthetic insecticides to increase the efficacy of the mixture equivalent to the efficacy caused by the full label rate. This strategy reduces the quantity of insecticides used.

In light of the evidence provided in the literature, exploitation of semiochemicals as stimulants, deterrents, attractants, repellents or synergists in conventional spray programs, either alone or in combination with biopesticides or synthetic insecticides, has the potential to manipulate the behaviour of the pest or cause direct mortality of the pest to protect the resource. Most phytophagous insects, especially lepidopterans, can be managed immediately after landing on a plant when they commence the evaluation of array of sensory or chemical information on the plant surface (Renwick and Chew, 1994; Eigenbrode and Espelie, 1995; Derridj *et al.,* 1996). For ovipositing insects such as *Helicoverpa spp.* that do not contact the inner tissues of the plant (i.e. feed on the plant), recognition and selection of the host plant after landing could be determined by small quantities of many types of chemical substances that come from the inner tissues of the plant that are present on the plant surface (Stadler, 1986; Derridj *et al*., 1996; Fiala *et al.,* 1990). Thus, plant surface cues play a major role in host selection and acceptance for oviposition and feeding of *Helicoverpa spp.* Hence semiochemicals sprayed on host plants can change the behaviour of a pest, particularly *Helicoverpa* spp. which may avoid the host plant or lay fewer eggs, feed less or die from the spray.

5.0 Conclusion

This paper has reviewed some issues regarding the development and exploitation of semiochemicals in managing insect pests on cotton and other agricultural crops. The review has shown that even common plants that can be used to feed animals can act as important chemical signals and display biological activity towards many different species of insects and also can have different functions on different pest species. Plant X is a good representative of this type of semiochemical source. Many chemicals on the plant surface and inner tissues can be used to manipulate the behaviour of beneficial insects and also insect pests such as *Helicoverpa* spp. to protect a resource (i.e. cotton). Such chemicals can include volatile and semi-volatile components, as well as non-volatile (contact) semiochemicals.

Three principal elements of a behavioural manipulation method were identified in the review. They are the behaviour of the pest or beneficial insect, a means by which the behaviour is manipulated appropriately and a method that utilizes the behavioural manipulation for protection of a resource from the pest. The manipulation of pestilential behaviour (e.g feeding on the resource) or a behaviour closely related to the pestilential behaviour (e.g finding the resource) is more likely to be useful for pest management than manipulation of behaviours unrelated to the resource (eg mating disruption). Successful manipulation of the pestilential behaviour will ensure protection of the resource. In contract, successful manipulation of unrelated behaviour may reduce the local population but still not protect the resource because of immigration of outside populations into the area being protected, as can occur in the mating disruption and attractants methods for moths whose larvae are pests on cotton crops. Thus, semiochemicals that produce stimuli that act at close distance (stimulants and deterrents or combination of attractants/stimulants/deterrents) (eg Plant X) could be more useful in pest management than stimuli that act over long distances (attractants, repellents, visual and chemical stimuli (pheromones or pheromone blends).

However, if the stimuli that act over long distances are beneficial insect attractants, then it could be used to attract and conserve natural enemies of pests, enhancing their effectiveness as pest control agents. For example, where a food spray product such as Envirofeast® (beneficial insect attractant) has been applied, changes in the ratio of natural enemies to prey could be mediated by: (1) attraction of natural enemies to the area by volatile compounds emitted by the food spray product; (2) arrestment of natural enemies in the area following contact and subsequent feeding on the food spray; (3) increased searching activity induced by contact with and feeding upon the food spray product with subsequent increase in predation of moth eggs and larvae; and (4) decreased oviposition activity of female moths due to the presence of the food product (Mensah, 1997).

In conclusion, semiochemicals in general have environmental benefits associated with their use, in contrast to conventional insecticides. These semiochemicals are inherently different from synthetic insecticides in terms of their mode of action and subsequent impact on the environment and human health. The United States Environmental Protection Agency (EPA), Office of Pesticide Program (OPP), recognized inherent differences between semiochemicals and synthetic insecticides and so have developed a policy encouraging the development and registration of semiochemicals as safer alternatives to conventional pesticide products.

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