

CAN SEMIOCHEMICALS ALTER THE USE OF PARASITES IN IPM PROGRAMS?¹

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ABSTRACT - Semiochemicals are increasingly found to play a significant role in host location and acceptance by parasitic hymenoptera. The roles of these chemicals range from stimulating parasites to search for hosts to influencing the species of hosts attacked. The source of these compounds also ranges from plants, hosts and associated organisms. In plants they comprise an important part of a plant's resistance to pests that may be overlooked. These semiochemicals can attract and retain parasites in select environments and can influence the levels of parasitism that occur. The result is that one of the major problems in the use of parasitic insects for biological control in IPM (Integrated Pest Management) systems, that is the lag in response of parasites to a host population increase can be overcome. Although the premise is that semiochemicals can attract, retain and stimulate parasites to function in cropping systems before the pest population begins to increase, what is our state of knowledge and where do we stand in the use of semiochemicals for biological pest management? This issue will be discussed, however, significant progress towards the practical use of semiochemicals may well depend on the availability of mass produced parasitic species. Rapid progress in *in vitro* production of parasitic insects is also being made. The status of *in vitro* production and how the combined efforts of these two areas (*in vitro* production and behavioral manipulation) provide the technology to significantly alter our use of parasitic insects for IPM will be presented.

Index terms: Hymenoptera, hosts, plant resistance, *in vitro* production, behaviour manipulation.

PODEM SUBSTÂNCIAS SEMIOQUÍMICAS ALTERAR O USO DE PARASITAS EM PROGRAMAS DE MANEJO DE INSETO-PRAGAS?

RESUMO - Os semioquímicos estão sendo cada vez mais fadados a desempenhar um papel importante na localização e aceitação de hospedeiros pelos himenópteros parasitas. Os papéis dessas substâncias variam desde o estímulo aos parasitas a procurarem hospedeiros, até a influência em espécies de hospedeiros atacados. A fonte desses compostos varia em relação a plantas, hospedeiros, e organismos associados. Em plantas, os compostos semioquímicos compreendem uma parte importante da resistência vegetal a pragas, a qual pode ser injustamente, desprezada. Esses compostos podem atrair e reter parasitas em ambientes selecionados, e podem influir no nível de parasitismo. O resultado é que um dos maiores problemas no uso de insetos parasitas em sistemas de manejo de insetos-pragas (MIP), que é a demora na resposta de parasitas ao crescimento da população hospedeira, pode ser superado. Embora a premissa seja de que as substâncias semioquímicas podem atrair, reter e estimular, parasitas a agirem em sistemas de cultivo antes que a população de pragas comece a crescer, perguntamos: Qual é o nosso estado de conhecimento, e onde estamos, no tocante ao uso de compostos semioquímicos em manejo de pragas? Este assunto é aqui discutido; porém, o progresso significativo na direção do uso prático desses compostos pode bem depender da viabilidade de produção, em massa, de espécies parasitas. Está sendo alcançado progresso rápido na produção *in vitro* de insetos-parasitas. É apresentado, aqui, o estado da produção *in vitro* e o modo pelo qual os esforços combinados das duas áreas (produção *in vitro* e manipulação de comportamento) fornecem à tecnologia meios para alterar significativamente o nosso uso de insetos-parasitas para o manejo de insetos-pragas.

Termos para indexação: Hymenoptera, hospedeiros, resistência vegetal, produção *in vitro*, manipulação de comportamento.

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INTRODUCTION

The control of pest insects has utilized many approaches including toxic chemicals, host plant resistance, ecological manipulation, and biological control. Presently, these methods of insect control are being used in various combinations to form part of what is called integrated pest management (Flint & Bosch 1981). Biological control forms an integral part of the integrated pest management strategy and itself relies on a number of approaches including the utilization of parasitic insects (parasitoids). Parasitoid utilization involves: a) assessing the natural parasitoid population, b) conservation, c) augmentation, d) introduction of exotics, and e) management (Vinson 1988a). Of these techniques the introduction of exotic's or "the classical approach" (Caltagirone 1981, Sailer 1976), has received most attention. While management of beneficials in the past has not received consideration separate from other approaches, recent advances (Greany et al. 1984, Vinson 1986, Thompson 1986) are beginning to provide researchers and practitioners with the ability to manipulate the behavior of adult parasitoids and to inexpensively rear large numbers of adults for use in new and exciting ways. These advances are providing new approaches to biological control that will allow for the aggressive management of parasitoids for pest control.

Presently, many species of parasitoids are difficult and expensive to rear, often in insufficient numbers to do much more than conduct general biological studies or inoculative releases. However, this situation is changing with the development of *in vitro* rearing techniques (Thompson 1986, Lu 1988, Li et al. 1988, Greany 1986, Grenier & Bonnot 1988, Xie et al. 1986, Rotundo et al. 1988, Strand et al. 1988). As the development of *in vitro* rearing is perfected and gains

acceptance, its use will become an essential component of beneficial insect management. However, more immediate beneficial insect management can involve the use of the behavioral chemicals.

The potential of utilizing behavioral chemicals to manage parasitic hymenoptera has been discussed by several authors (Gross Junior 1981, Lewis & Nordlund 1985, Lewis et al. 1976, Nordlund et al. 1986, Vinson 1977, 1988a). I will review the unique opportunities that behavioral chemicals offer to biological control, address some of the concerns, and provide some insight into those concerns. Background concerning the behavioral aspects of host selection (Arthur 1981, Doult 1959, Alphen & Vet 1986, Vinson 1981, 1984a, b, 1985), the sources of these chemicals (Vinson 1976, 1988b), and the types of chemicals involved (Jones 1981, Vinson 1985) will not be covered here.

Potential implications of semiochemicals in biological control

The isolation and identification of parasitoid behavioral chemicals over the last decade offer the opportunity to manipulate the behavior of parasitoids in ways that can lead to new opportunities in biological control. This potential depends not only on their isolation and identification, the parasitoid behavior these chemicals elicit, and the level of the host selection chain in which these chemicals are involved; but research in regard to their use in the field. Few studies investigating the use of behavioral chemicals in the field have been conducted (Takabayashi & Takahashi 1988, Gross 1981; Altieri et al. 1981). Such chemicals include pheromones, synomones and kairomones, each of which may be used to attract and retain parasitoids in select locations, stimulate them to search, and influence the particular hosts for which they search (Table 1).

TABLE 1. Potential of allelochemicals for beneficial insect management

| Behavior | Potential allelochemicals | Method of use: crops |
|---|---|--|
| Attract parasitoid to crops (habitat) | synomones | Application to: Genetic incorporation in: |
| | Volatile kairomones Aggregation pheromones | Application to: Application to: |
| Stimulate and retain parasitoids in crop | Kairomones | Application to: |
| Prerelease stimulation and learning (imprinting, conditioning, associative learning). | Synomones Kairomones Pheromones | Influence behavior prior to release of parasitoids to: |
| Stimulate oviposition to obtain eggs for <i>in vitro</i> rearing | Contact kairomones and physical factors | Provide parasitoids for release to: |

Attractants

a) Synomones - Plants play a pivotal role in influencing the physiology and behavior of third trophic level organisms (predators, parasitoids, and parasites) (Price 1986), but attention to what the plants role is and the identification of the stimuli involved has received relatively little concern until now. Such a lack of information is a surprise since the mutual beneficial interaction between plants and insects that gather pollen and nectar is well recognized (Kevan & Baker 1983). Further it has also been recognized that plants and insects have coevolved mutual relationships where the insect (ants) obtains food and shelter and the plant (Acacca) is protected from herbivores (Janzen 1966). Data has accumulated to demonstrate that plants release volatiles that are attractive to parasitoids (Elzen et al. 1984, Nettles 1979, Lecomte & Thibout 1984, 1988, Reed et al. 1970, Williams et al. 1988) and within a few

species the attractive volatiles are known to differ from the volatiles that attract the pest species (Auger et al. 1987). Further, there is increasing evidence that the plant may be induced to release different chemicals when attacked (Nadel & Alphen 1987) and that the nature of the chemicals can depend on the herbivore (Turlings et al. 1990). The literature also suggests that plant synomones are wide spread (Vinson 1981) and, as found in cotton (Elzen et al. 1987), consist of a blend of attractive compounds that differ among different cultivars. Different cultivars not only differ in their attractiveness to parasitoids (Elzen et al. 1986) but may lack attractive compounds. Such information is essential to host plant resistance programs to insure that plant cultivars remain attractive or to increase their attractiveness to beneficials (Boethel & Eikenbary 1986, Williams et al. 1988). Understanding the role of volatile chemicals as parasitoid attractants can be of value in

explaining why some herbivores are under control (attacked) by a parasitoid on one plant but not another.

As the isolation, identification, and role played by synomones in parasitoid biology becomes better understood these compounds will be used to increase the attractiveness of plants to predators and parasitoids. This can be accomplished in several ways. One is by the direct application of these chemicals to plants (Altieri et al. 1981, Nordlund et al. 1985). Selective plant breeding is another way the levels of these attractants can be increased in various cultivars. In the future, bioengineering may prove ways to insert genes into certain cultivars that result in the production of attractive compounds.

How effective the use of synomones may be in reducing pest populations and the impact of synomone use on beneficial insect populations is unknown. We can speculate that these compounds will attract beneficials to treated plants, but whether the parasitoid remains for a short or long period within the plant habitat is at present unknown but likely the retention of the beneficial within the plant assemblage will be different for certain species groups. If synomones attract and retain the beneficial in a "less-than-optimal" habitat for reproduction, these compounds could have a negative impact on the long range fitness of the beneficial insect population (Vinson 1977, 1988b). If synomones only attract beneficials to the habitat for a short period of time, unless host traces are encountered, then the use of synomones may not seriously impact the beneficial insect population. In the later case the use of synomones could have a major impact on the pest population, particularly in cases where the pest is escaping parasitic mortality because the crop is not attractive (Vinson 1981).

b) Kairomones - Some parasitoids are attracted over meter distances by volatile kairomones (Camors Junior & Payne 1971, Aldrich et al. 1984). These compounds are often host sex attractants or aggregation pheromones which attract parasitoids that

attack stages other than those that release the kairomone (Aldrich et al. 1984, Vinson 1988b). Exceptions do occur of which the best known involves the attraction of the parasitoid to the sound of calling male crickets and cicadas (Cade 1975, Soper 1976, Mangold 1978), although chemical exceptions also occur (Aldrich et al. 1984). These compounds, like synomones, may attract certain parasitoids to treated locations, but how long the parasitoid will be retained in such an area is unknown. Because kairomones indicate the presence of a host population and because the long range volatile kairomones are often released from stages preceding the stage to be utilized (Vinson 1988b), these compounds may cause parasitoids to allocate a significant proportion of their reproductive life to such a habitat. While this behavior, if true, would likely be counter productive in the manipulation of natural parasitoid populations (Vinson 1977), it could be of significant value in the manipulation of parasitoids in an inundative release program.

The use of attractive semiochemicals, particularly kairomones could also be of use in attracting parasitoids to an area prior to a host outbreak if accurate predictions are possible. Thus, one of the major problems in biological control, the lag in the parasitoids response to pest populations (Huffaker et al. 1977) could be overcome.

c) Pheromones - Like most insects, pheromones play an important role in the biology of parasitic hymenoptera. These include the epideictic pheromones (Prokopy 1981, Roitberg & Prokopy 1987, Roitberg & Mangel 1989), the sex pheromones (Jones 1989, Tanaka 1985), and aggregation pheromones (Roelofs 1981). While the sex pheromones of parasitic hymenoptera (Robacker & Hendry 1977, Eller et al. 1984) may someday play an important role in evaluating the density and determining the location of parasitoid populations in the field (Elzen & Powell 1989), they do not presently appear to be useful in the direct manipulation of parasitoids for biological control. The

aggregation pheromones (Lewis et al. 1970, Mohamed & Coppel 1987), however, may be useful in attracting and retaining parasitoids in certain crops, although very little work has been done on such compounds.

The potential of using the epideictic pheromones is more speculative. Since these compounds result in dispersal they could prove useful in repelling hyperparasitoids (Vinson 1977), but such a use would probably be impractical unless the hyperparasitoids were a serious limiting factor to the success of the primary parasitoid. Yet these compounds could become very useful in weed control by repelling or dispersing parasitoids that would protect the phytophagous weed controlling species from attack.

Searching stimulants

Once a parasitoid has been attracted to a habitat or community that may harbor hosts, the encounter of host traces (fecal, feeding, defensive, or other secretions that are left in the environment but are important to the functioning of the host) indicate that hosts are present (Lewis et al. 1975b, Vinson 1988b). When encountering such compounds the parasitoid allocates a certain amount of time to search the area for hosts (Waage 1979). These stimuli also generally release an intense searching of the microhabitat by the parasitoid that often results in increased movement of the parasitoid and an increased frequency of turning (Strand & Vinson 1982). These host traces or "spore" kairomones result not only in an increased investment of time in the microhabitat, but an increased coverage of the habitat.

If a female is successful in locating a host she often allocates additional time to the habitat (increases her giving up time - Waage 1979). This reallocation of time to the habitat is similar to the behavior referred to as the "find and attack cycle" (Lewis et al. 1976). The find and attack cycle is particularly important for species that attack aggregated hosts, being less important or even absent

from the host selection process of species attacking highly dispersed hosts. The importance of the find and attack cycle for reasonably aggregated species is demonstrated in the application of searching stimulant kairomones to crops which results in increasing the parasitism of the host insects present (Lewis et al. 1975a, b, Takabayaski & Takahaski 1988). These searching stimulants work because they retain and stimulate the parasitoid to search (Gross et al. 1975). The increased allocation of searching time increases the chance that a host present in the search area will be discovered.

The practical use of searching stimulants may be counter productive unless used in combination with other approaches. When used in the field to increase parasitism of pest populations by the retention of natural parasitoid populations, these compounds may cause difficulties by reducing the retained parasitoids reproductive success (Vinson 1977). The searching stimulants in effect indicate to the parasitoid that the habitat contains many hosts and, therefore, a high reproductive potential. However, the treated habitat contains fewer hosts than the applied kairomone indicates and even though these hosts are attacked, the reduced total number of hosts attacked is at the expense of future parasitoid generations. These problems can be circumvented by the release and retention of mass produced parasitoids. The release of reared parasitoids would insure that parasitoids were present thus reducing the dependence on the attraction of parasitoids from near by environments. Further, the presence of released parasitoid in the managed area should result in an increased level of epideictic pheromones which should reduce the immigration of parasitoids from the surrounding environment thus further reducing the impact on the natural population.

We may also predict that many released females will disperse from these high conspecific female concentrations (Roitberg & Prokopy 1987) due to epideictic pheromone buildup. If true, the potential of released

parasitoids to effect control could be further enhanced if the response of mass released parasitoids to epideictic pheromones could be reduced. This may be possible through selective breeding and would have the advantage of reducing the fitness of the laboratory produced females in competition with the natural population. Such an approach could be extended to some other biological characteristics that might increase mass reared parasitoid effectiveness and reduce their impact on the gene pool of the naturally produced population.

Host attack and oviposition stimulants:

The identification of kairomones that release host examination, ovipositional probing, drilling and oviposition do not appear to have a direct role to play in the field manipulation of parasitoids. However, these compounds will play a central role in the development of *in vitro* rearing and parasitoid mass production (Vinson 1986, 1988a) by providing methods to obtain large numbers of eggs needed for mass production programs. As discussed (Vinson 1988a), the identification of ovipositional stimuli for *Itopectus conquisitor*, *Trichogramma pretiosum* and *Telenomus heliothidis* (Arthur et al. 1972, Nettles et al. 1982, Strand & Vinson 1983a) provided eggs that helped lead to the subsequent rearing of these species on an artificial diet (House 1978, Strand et al. 1988, Xie et al. 1986).

Few studies have dealt with host attack and oviposition. Both shape and chemicals are often important synergistic ovipositional factors (Strand & Vinson 1983b, Vinson &

Piper 1986), but the identification of all the interacting factors may not be essential in obtaining parasitoid eggs for rearing. Hegdekar & Arthur (1973) were able to induce *Itopectus* to oviposit in Petri dishes containing several amino acids and sugars. Morrison et al. (1983) induced *Trichogramma* to oviposit through a flat membrane over an oviposition stimulating salt solution even though shape is important in *Trichogramma* oviposition (Schmidt & Smith 1985). Even if parasitoids can not be induced to lay eggs there are other options; eggs may be removed from the female and activated (Vinson & Jang 1987) or large numbers of activated eggs can sometimes be removed from the host (Burks & Nettles 1978). The ability to obtain viable eggs is a prerequisite to *in vitro* rearing.

The development of the technology for the inexpensive *in vitro* rearing of parasitoids has the potential to revolutionize the field of biological control. As outlined in Table 2, the ability to mass rear parasitoids free of their host will provide for approaches to develop improved, and inexpensive parasitoids consistently for mass release and manipulation. The development of *in vitro* rearing technology will also provide biological control practitioners with the ability to rear some species presently unavailable, whether exotic or native, in sufficient numbers to study and evaluate. *In vitro* rearing will also provide for the development of quality control, the application of genetics to "improve" - the quality of beneficials, optimize the nutritional quality of the food for the developing stages, and provide increased control over the timing and availability of adults. Also, the ability to

TABLE 2. *In vitro* rearing may lead to parasitoid husbandry that will provide for.

| |
|------------------------------------|
| Mass production |
| Consistent and predictable numbers |
| Quality control |
| Genetic improvement |
| Nutritional improvement |

rear parasitoids *in vitro* will open new avenues to the study of their physiology and biochemistry.

However, it will be the ability to consistently produce a large number of a particular parasitoid species that can be released when needed (even prior to a pest outbreak) that, in conjunction with the behavioral chemicals, will offer new opportunities in the biological control of pest insects.

Behavioral chemicals and learning

Over the past several decades there has been increasing evidence that insects can "learn" to respond to certain stimuli (Timbergen 1951, Alloway 1972, 1973) and parasitoids have been in the fore-front if these studies (Thorpe 1938, Vet 1983). While the exposure and associative learning of parasitoids enabling them to respond to novel stimuli may prove useful, it is the ability of parasitoids to continue to recognize and respond to their innate set of stimuli that may prove equally important (McAuslane 1990). Although the exposure of parasitoids to host selection cues may become important in the release of *in vitro* reared parasitoids to insure they have encountered the proper host cues, the limited data indicate that *in vitro* reared parasitoids continue to respond to their natural host (Lu 1988, Karjia et al. 1988). Once these behavioral plasticities and limitations are understood they can be used to improve the effectiveness of biological control agents. As shown by Gross et al. (1975), exposure of laboratory reared parasitoids to natural host selection cues prior to release places the parasitoids in the find and attack cycle. Thus, upon release they begin to search for hosts rather than initiating an escape response. But there are even additional opportunities that can be realized by adding cues that the parasitoids can learn through association and that can be used to direct females before release to a particular potential host community. For example, Gross et al. (1975) also observed that if the parasitoid was

exposed to the host and plant-complex before releasing, the released parasitoid would tend to orient to and search the same variety of plant in the host-plant-complex the parasitoid was exposed to. These observations have been confirmed with other species (Vet 1983, Vet Opzeeland 1984, Lewis & Tumlinson 1988, Lewis et al. 1990).

The results of studies such as described above suggest that if parasitoids can be reared, there are many opportunities to manipulate their behavior in a positive way prior to release. Such Knowledge not only has potential for the management of beneficial insects in an inundative release approach but may benefit an inoculative release program.

SUMMARY

The technology for the *in vitro* rearing of parasitoids and their behavioral manipulation is rapidly developing. As the behavioral chemicals for more species are identified and made available, and as more species are reared on artificial diets, opportunities for the management of beneficials, whether native or exotic, will rapidly increase. Many opportunities exist. For example, in beneficial insect rearing the ability to *in vitro* rear will allow for the production and study of some species that, for various reasons, are presently unavailable. *In vitro* rearing will also allow for the development of quality control, mass and consistent production of some species. Such production capabilities will allow for the planning necessary to have large numbers available when and where needed. In addition, *in vitro* rearing will open up other avenues of research. One of these is the identification of parasitoid produced products that regulate various host biochemical processes that may be exploited for alternative control approaches. Another is the development of parasitoid insect husbandry. The area of parasitoid husbandry could grow to include genetic improvement through selective breeding, genetic engineering and nutritional improvement. Lastly, *in vitro* rearing will

provide the numbers of beneficials needed to expand the use and potential of semiochemical manipulation of beneficial organisms (particularly mass released, but will include inoculative releases and natural agents) for pest management.

The availability of large numbers of beneficials that could be released in sufficient numbers prior to or simultaneously with the occurrence of a pest population, could eliminate the typical lag in control of pests by beneficials. Second, through pre-release stimulation the released parasitoids could be placed in a find and attack cycle thus reducing the loss of released adults through an escape response. Further, through the use of associative learning, pre-exposure and knowledge of attractant compounds, the types of habitat (crop) and possibly even the types of hosts that the female initially searches for could be influenced.

Synomones and other attractant chemicals may also be used to increase the attractiveness of crops to both released (exotic and native) and natural populations of beneficials. This increased attractiveness could be obtained through application to the crop and by genetic incorporation either through traditional or biotechnological approaches. Also knowledge of attractant synomones may aid plant breeders and those interested in host plant resistance to increase, retain or at least not reduce the attractiveness of the plants to beneficials.

Searching stimulants may be used to retain and stimulate host search in areas applied, although there is yet much to be learned about how to best apply these materials for results (Gross 1981). Also, because compounds from various parasitoid-host relationships influence the behavior of the parasitoid in specific ways, some thought must be given to the use of these compounds for control. Some compounds may stimulate searching of the immediate area by the particular parasitoid involved. In other parasitoid species the isolated stimulants may stimulate the parasitoid to search the highest leaves on the plant or locations on the ground

below.

The proper use for crop plant synomones, host kairomones, and aggregation pheromones not only offers promise for the manipulation of beneficials in the field for insect pest management, but confining the use of behavioral chemicals to certain limited areas and the release of beneficials to these limited areas may offer new approaches to the management of pest problems in urban, industrial, and other less traditional situations. Lastly, the behavioral chemicals are playing an important role through the development of artificial hosts in which parasitoids deposit eggs for *in vitro* rearing use.

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