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ABSTRACT

The physiological and ecological effects of two plant-derived insecticidal compounds - berberine and α-terthienyl (α-t) - were investigated in a model food chain, using the lepidopteran Ostrinia nubilalis and its solitary endoparasitoid Diadegma terebrans. O. nubilalis larvae were reared on meridic diets containing sublethal concentrations (10, 31 and 100 ug/g) of the compounds. Effects on growth and development of O. nubilalis were monitored. Larval growth rates were reduced with both compounds at 100 ug/g in the diet. Berberine produced few effects on duration of preimaginal stages and pupal and adult weights. However, mortality was quite high with 100 ug/g in the diet. α-t produced some sublethal effects at 31 and 100 ug/g in the diet, and decreased survival was observed, particularly at 100 ug/g. The adverse effects of α-t towards O. nubilalis were not as severe as those incurred with berberine.

O. nubilalis larvae reared on the different test diets were parasitized by O. terebrans, and the development and survivorship of parasitoids reared from these hosts were observed. Berberine did not significantly affect duration of the immature stages or pupal and adult weights. Survival to pupation and adult emergence declined with all concentrations of berberine, but the degree of mortality did not correspond to the concentrations administered in the diet. α-t did not significantly affect growth

parameters of D. terebrans except in the 100 ug/g treatment. No females were produced at this concentration, and male pupal and adult weights were significantly reduced. Survival to pupation and adult emergence were severely reduced with this treatment. Survival was also reduced, albeit less severely, with the 31 ug/g α-t treatment. However, 10 ug/g α-t in the diet somewhat improved the survivorship of parasitoids compared to the control diet.

Treated and control larvae were exposed to D. terebrans in a number of dual-choice and no-choice experiments. Dual-choice tests with treated and control larvae of the same chronological age were performed, and the ratios of Treated / Control progeny (T/C) were calculated. Berberine in the diet conferred an advantage to the developing parasitoids, especially with the 100 ug/g treatment. α-t was not beneficial at any of the concentrations tested.

Dual-choice tests with treated and control larvae of the same physiological age revealed that percent parasitization was significantly increased in the 100 ug/g berberine treatment compared to the controls. This was also apparent for the 10 ug/g α-t treatment. However, percent parasitization was significantly reduced with 100 ug/g α-t in the diet of the host.

For no-choice tests between treated and control larvae of the same physiological age, percent parasitization was significantly decreased for the 100 ug/g α-t group

compared to the controls. T/C ratios revealed that no advantage was conferred to the parasitoids by allelochemicals in the diet, except for a slight enhancement for the 10 ug/g α-t treatment.

HPLC analyses of the body burden of allelochemicals were performed for second to third instar O. nubilalis larvae reared on the various diets. Analyses were also performed for adult parasitoids reared from hosts fed treated diets and their pupal cases. Berberine was not detected in any of the samples analyzed. However, α-t and a polar metabolite of α-t were present in samples of host larvae, emerged wasps and pupal cases.

The physical properties of allelochemicals, and their bearing on parasitoids are discussed with regard to agricultural implications.

RÉSUME

Les effets physiologiques et écologiques de deux phytochimiques aux propriétés insecticides - le berbérine et l'α-terthiényl (α-t) - furent etudiése dans une chaîne trophique modèle en utilisant le lépidoptère Ostrinia nubilalis et son endoparasitoïde solitaire Diadegma terebrans. Les larves d'O. nubilalis furent nourries d'une diète méridique contenant les deux composés en concentrations sublétales (10, 31 et 100 ug/g). Les effets sur la croissance et le développement d'O. nubilalis furent notés. Le taux de croissance larvaire fut réduit par les deux composés lorsqu'incorporés au taux de 100 ug/g de nourriture. Le berbérine exerça peu d'effets sur la durée du développement préimaginal et le poids des pupes et des adultes. Cependant, le taux de mortalité fut très élevé pour les larves nourries avec 100 ug/g. L'α-t a exerça quelques effets lorsqu'utilisé en concentrations de 31 et 100 ug/g dans la nourriture, et le taux de survie fut réduit, surtout lorsque l'α-t fut utilisé au taux de 100 ug/g. Les effets néfastes de l'α-t sur la croissance d'O. nubilalis n'étaient pas aussi marqués que ceux du berbérine.

Les larves d'O. nubilalis élevées avec les nourritures différentes ont été parasitées par le D. terebrans, et le développement et la survie de ces parasitoïdes furent observés. Le berbérine n'affecta pas de façon significative la durée du développement préimaginal et le

poids des pupes et des adultes. La survie jusqu'aux stages de pupe et d'adulte diminua pour chacune des trois concentrations de berbérine, mais le taux de mortalité ne dépendait pas directement des concentrations. L'α-t n'exerça pas d'effets significatifs sur la croissance de D. terebrans, sauf au taux de 100 ug/g. Aucune femelle ne fut obtenu à cette concentration, et les poids des pupes et des adultes mâles furent réduits. La survie jusqu'aux stages de pupe et d'adulte fut réduite avec le traitement de 100 ug/g. La survie fut réduite dans le groupe traité avec 31 ug/g d'α-t, mais pas de façon aussi marquée. Au taux de 10 ug/g, l'α-t incorporée à la nourriture a amélioré le taux de survie des parasitoïdes.

Les larves d'O. nubilalis qui ont été élevées avec de la nourriture contenant ou pas du berbérine ou de l'α-t furent exposées au D. terebrans dans des expériences à choix simple ou sans choix. Pour les expériences à choix, des larves traitées et des larves témoins du même âge chronologique furent utilisées, et les rapports des progénitures Traitement / Contrôle (T/C) furent calculés. Un plus grand nombre d'adultes de D. terebrans fut obtenu à portu de larves d'O. nubilalis exposées au berbérine que des larves témoins. Aux concentrations utilisées, l'α-t n'affecta pas le nombre de progénitures.

Les expériences à choix révélèrent que le berbérine à 100 ug/g même à un accroissement du taux de parasitisme. Alors que le même effet fut obtenu pour l'α-t a 10 ug/g,

le pourcentage de parasitisme fut réduit pour l'α-t a 100 ug/g.

Pour les expériences sans choix avec des larves de même âge physiologique, le pourcentage de parasitisme fut plus bas pour la groupe traité avec 100 ug/g d'α-t, comparé au groupe témoin. Les rapports T/C révélèrent que les phytochimiques avaient peu d'effets autre qu'une légère augmentation du nombre de progénitures pour les parasites sur les larves traitées avec 10 ug/g d'α-t.

Des analyses chromatographiques (HPLC) déterminèrent les concentrations de berbérine et d'α-t dans le corps des larves d'O. nubilalis du deuxième et troisième stade, ainsi que dans les cocons et le corps des parasites adultes issus de larves traitées avec les phytochimiques. Le berbérine ne fut retrouvé dans aucun des échantillons analysés. Par contre, l'α-t et un de ses métabolites polaires étaient présents dans les larves hôtes et les parasites adultes et leurs cocons.

Les propriétés physico-chimiques des composés allélochimiques et leur effets sur les parasitoïdes sont discutés en relation aux applications agricoles.

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1.0 INTRODUCTION

Modern agriculture depends heavily on the use of synthetic pesticides to maintain high yields and the quality of produce. However, the benefits of insecticides do not come without environmental and biological problems created by their usage. These are now well established: resistance in pest organisms, environmental contamination and adverse effects on non-target organisms, and residues in food and their consequences on human health (Pimentel and Perkins, 1979).

Two of the most serious problems associated with insecticide usage are the phenomena of pest insect resurgence, and the creation of new pests from previously innocuous species. This occurs when the natural enemies of herbivores are eliminated by the indiscriminate application of pesticide (DeBach, 1974; Van den Bosch et al, 1982).

The detrimental effects of pesticides on beneficial insects have been documented since the 1940s. Essentially, these effects may be separated into the following potential problems:

1. Predators and adult parasitoids may be killed directly by the chemicals (Doutt, 1964b; Croft, 1977). In fact, this was demonstrated in the laboratory by Bartlett (1963) with 61 pesticides and five species of hymenopteran parasitoids and six coccinellid predators.
2. If the pesticide affects the temporal patterns of the host's developmental stages, host-parasitoid synchrony may

be lost, and the parasitoid's reproductive success is greatly reduced (Doutt, 1964b). Even the microbial insecticide Bacillus thuringiensis increased the developmental time of Apanteles melanoscelus within gypsy moth (Lumantria dispar) hosts by three days (Ahmad et al, 1978).

3. Sublethal effects of pesticides on the behavior of natural enemies may profoundly affect their performance in the field (Croft, 1977).

4. The insecticide may eliminate or reduce populations of alternate hosts or prey, or honeydew producers necessary for proteinaceous food for adult parasitoids (Doutt, 1964b).

5. Parasitoids and predators which do locate hosts or prey may be intoxicated by pesticide residues in these insects (Ahmed et al, 1954; Croft, 1977). Unfortunately, this has been observed with some of the third generation insecticides (insect growth regulators) (Beckage, 1985 and references cited therein).

6. The insecticide-treated hosts may not be acceptable for oviposition by adult parasitoids, resulting in reduced parasitization rates (Root and Gowan, 1978).

In the search for more efficient and less dangerous methods for pest management, agricultural researchers are increasingly directing their efforts towards 'natural', ecologically sound strategies for plant protection. Two principal directions have been taken: improving biological control by manipulation of natural enemies via

semiochemicals (Jones et al, 1976; Lewis et al, 1980; Gross, 1981; Lewis, 1981; Strand and Vinson, 1982; Chiri and Legner, 1982; Greany et al, 1984), and using the natural defences of plants for resistance breeding (Philogène, 1984) and as a source for new botanical insecticides (Arnason et al, 1983).

Ideally, biological control and naturally occurring plant defences should be compatible. However, these defensive compounds are insecticidal, and, in some cases, they are comparable to conventional pesticides regarding toxicity (Arnason et al, 1981; Philogène et al, 1985). This presents a question as to the fate of natural enemies taking nourishment from phytophages which ingest these compounds: could similar problems occur with allelochemicals as was seen with applied synthetic pesticides?

Brader (1973) described several potential problems of resistance breeding with respect to natural enemies. Since host plant resistance reduces the numbers of herbivores present, host finding by natural enemies may be hampered. As well, the quality of host insects may be altered by the physiology of the plant, and this may affect the development of natural enemies. The plants themselves may also be unattractive as ovipositional sites for predators. On the other hand, allelochemicals may, in fact, enhance the effectiveness of natural enemies through their growth inhibiting effects on phytophagous insects. The susceptible stages of hosts or prey to natural enemies

would be prolonged, leading to increased parasitism or predation (Feeny, 1976; Price et al, 1980).

It is reasonable to assume that the physical properties of plant defence compounds, and their biological sites of action can provide clues as to their ability to affect organisms of one or more trophic levels removed from the source plant. The present research was undertaken to test this assumption with a host-parasitoid association, and to develop a system for future assessment of potentially useful allelochemicals.

1.1 LITERATURE REVIEW

Plants, Herbivores and Parasitoids

Secondary plant substances are recognized to be the key factors mediating the feeding habits of herbivorous insects. This was first suggested by the work of Verschaffelt (1910), but neglected until Fraenkel (1959) published the famous "Raison d'être" paper. Since then, the field of insect-plant interactions has developed rapidly, and the elegant theories of allelochemically-mediated plant-herbivore coevolution were generated (Beck, 1965; Ehrlich and Raven, 1965; Schoonhoven, 1972a; 1972b; Feeny, 1975; Seigler and Price, 1976; Rhoades and Cates, 1976; Levin, 1976; Swain, 1977 and numerous other reviews).

The study of chemical interactions between plants and insects is much more complex when considering three, rather than two trophic levels (see review by Price et al, 1980). This is a rather new research area in plant-insect chemical ecology, and future work will undoubtedly reveal further complexity. Price et al (1980) proposed that the natural enemies of herbivores should be considered as mutualists with the plant, and part of its defence system. In order to appreciate fully the possible consequences of allelochemical changes in the environment, it is important to review the process of host selection by parasitoids, and in particular, where plants fit into this scheme.

The sequence of events in a parasitoid attack has been

compartmentalized by Doutt (1964a) into four distinct stages: (1) Host habitat finding, which refers to the environment, or crop in which the host is located; (2) Host finding, or the location of the host within the habitat; (3) Host acceptance, when the parasitoid makes the choice to oviposit once the host is found; and (4) Host suitability, which determines whether or not the immature parasitoid will survive in, or on the host. Vinson (1975a) added a fifth step to this scheme: Host regulation, which refers to the physiological and ethological changes effected in the host by the parasitoid, in order to ensure optimal developmental conditions. As knowledge of the semiochemicals involved in host selection increased, a detailed scheme of the first three stages in Doutt's sequence was proposed by Lewis et al (1975) involving eight behavioral activities mediated by various types of cues.

The subject of host selection by parasitoids, particularly with regard to semiochemicals, has been extensively reviewed (see Vinson, 1975a; 1976; Vinson and Iwantsch, 1980; Arthur, 1981; Price, 1981; Vinson, 1981; Weseloh, 1981), and the role of semiochemicals in host-parasitoid coevolution is analagous to that of secondary plant substances in plant-herbivore coevolution (Vinson, 1975; Price, 1981). The present review of the literature will approximately follow the format of Doutt's host selection sequence, and the influence of the host plant will be highlighted. Information regarding specific semiochemicals (identified or implied) is presented in

tabular form (Tables 1 to 3). In the cases where chemical cues elicit more than one mode of behavior in the host selection process, the citation appears in more than one table. Because the subject of this research is plant-insect interactions, parasitoids of non-herbivorous hosts (for example, Muscidae) will not be considered.

1.1.1 The Host Environment

The influence of plants in host selection is very apparent in host habitat finding. A wealth of literature has been generated throughout this century regarding the significance of the host plant in host-parasitoid specificity. In many cases, the host plant species, rather than the host itself, is responsible for observed host-parasitoid associations. This is especially true of parasitoids with host ranges that extend over several taxonomic groups (Picard and Rabaud, 1914), or whose hosts are normally concealed within the host plant (Cushman, 1926). In the case of the European pine shoot moth, Rvacionа buoliana, the parasitoid Itoplectis conquisitor is preferentially attracted to Scots pine over red pine trees, even though the host burrows into the buds of both species. However, the bud size and needle coverage of Scots pine is more suited to ovipositor probing by the wasp, and so this association with the tree developed (Arthur, 1962). Numerous examples of these plant-parasitoid associations have been reported (Seamans and McMillan, 1935; Knight, 1944; Streams et al, 1968; Rabb and Bradley, 1968; Bottrell

et al, 1968; Graham et al, 1972; Katanyukul and Thurston, 1973; Mueller, 1983). In all of these cases, the host insects occur on a variety of plant species, but parasitization rates are much higher on certain plants preferred by the parasitoids.

Certain parasitoids are attracted to particular environments (Flanders, 1937; Laing, 1937) or food plants (Monteith, 1955; Nishida, 1956) irrespective of the presence of hosts. Parasitoid complexes associated with different tree species within the same environment have been reported to be very different, even though suitable hosts were ubiquitous (Zwolfer and Kraus, 1957; Ball and Dahlsten, 1973; Askew and Shaw, 1978). Native entomophages have been known to attack exotic herbivores because they were feeding on plant species normally searched for hosts (Goeden and Louda, 1976). The braconid Monoctonus paulensis was observed to parasitize an unsuitable aphid host because it was feeding on a preferred host plant (Calvert, 1973).

Food plant specificity is implicated in the evolution of strains and races of parasitoid species (Inayutullah, 1983). This is understandable, considering how rapidly some parasitoids can become conditioned to respond to chemicals associated with their hosts and host's food (Arthur, 1971; Vinson et al, 1976; Vinson et al, 1977).

Long-range attraction to the host habitat is mediated by visual and olfactory stimuli. However, olfaction is the most important mode of attraction, and numerous studies

have been published which attest to this (summarized in Table 1). The majority of these volatile chemicals are synomones emanating from the host plants preferred by the parasitoid, although many are host insect pheromones.

Table 1

Chemical Cues Mediating Host Habitat Finding

Parasitoids	Hosts	Active Compounds (if known); Source	Reference
Tachinidae			
tachinid flies	Rhagoletis pomonella	ammonium acetate - protein hydrolysate; synthetic lure for apple maggot adults	Moore, 1960.
Bessa harveyi	tenthredinid sawfly larvae	volatile; odours of unhealthy host trees	Monteith, 1964.
Drino bohemica			
Cuzenis albicans	Operopthera brunata	sugars; sap of damaged host tree leaves	Hassell, 1968.
Eucarcelatoria sp.	Heliothis virescens	volatile; odours of cotton and okra and host larvae fed okra leaves	Nettles, 1979; 1980.
	Spodoptera eridania		
	Estigmene acrea		
Eucarcelia rutilla	Bupalus piniarius	volatile; odours of oak attract immature females and repel mature females; odours of pine repel immature females and attract mature females	Herrebout, 1969; Herrebout and van den Veer, 1969.
	Semiothisa liturata		
Trichopoda pennipes	Nezara viridula	sex pheromones of male hosts	Mitchell and Mau, 1970.
Braconidae			
Apanteles flavipes (Pakistan strain)	Chilo partellus	volatile; maize stems and frass of hosts fed maize, sorghum and Johnson grass stems	Mohyuddin et al, 1981.
	Acigona steniellus		
(U.S.A. strain)	Diatraea saccharalis	volatile; frass of hosts fed sugarcane	

Table 1 (cont.)

Biosteres longicaudatus	tephritid fruit fly larvae	acetaldehyde, ethanol, acetic acid; fungal fermentation products of rotting fruit	Greany et al, 1977.
Diaeretiella rapae	Myzus persicae	allyl isothiocyanate; cruciferous host plants	Read et al, 1970.
Peristenus pseudopallipes	Lygus lineolaris	volatile; odours of Erigeron flowers; attraction increases with increasing number of eggs in ovaries	Shahjahan, 1974.
Trioxys indicus	Aphis craccivora	volatile; host plants and aqueous extracts of host plants: Cajanus cajun, Dolichos lablab, Vigna sinensis and Solanum melongena	Singh and Sinha, 1982.
Ichneumonidae			
Campoletis sonorensis	H. virescens	ethyl ether extractable; sorghum panicles; also odours of sorghum, cotton, tobacco and bluebonnet	Elzen et al, 1983.
Heydenia unica	Dendroctonus frontalis	α-pinene + frontalin + verbenone; host tree terpene + aggregation pheromones of host	Camors and Payne, 1971.
Itoplectis conquisitor	Rhyacionia buoliana	volatile; odours of Scots pine are more attractive than odours of red pine	Arthur, 1962.
Pimpla ruficollis	Rhyacionia buoliana	volatile; oil of Pinus sylvestris; repels immature females and attracts mature females	Thorpe and Caudle, 1938.
Aphelinidae			
Aphytis spp.	Aonidiella aurantii	sex pheromones of female hosts	Sternlicht, 1973.

Table 1 (cont.)

Trichogrammatidae			
Trichogramma spp.	*H. zea*	hexadecanal, (Z)-7-hexadecenal, (Z)-9-hexadecenal, (Z)-11-hexadecenal; sex pheromones of female hosts	Lewis *et al*, 1982.
T. evanescens	*Mamestra brassicae*	sex pheromones of female hosts	Noldus and Van Lenteren, 1983.
T. pretiosum	*H. zea*	hexane extracts of tomato leaves	Nordlund *et al*, 1985.
Pteromalidae			
Tomicobia tibialis	*Ips* spp.	volatile; aggregation pheromones of host; male host frass	Rice, 1968; 1969.

1.1.2 Vegetational Diversity and the Chemical Environment

The discussion of host habitat has so far been almost entirely focussed on single-plant associations with parasitoids. As most agricultural concerns in developed countries practice monoculture, this information is highly relevent. However, in natural ecosystems, and in most tropical agricultural systems, a variety of plant species may be found within the same immediate environment, and plants other than the host's food plant can influence habitat finding by parasitoids. Atsatt and O'Dowd (1976) recognized that naturally-occurring groups of plants cooperated, in an ecological sense, as plant defence guilds. Certain species attracted parasitoids and predators with nectaries, while other species harboured alternate hosts or prey.

Altieri and Todd (1981) reported that Trichogramma sp. wasps parasitized Heliothis zea eggs more efficiently in corn-soybean polycultures than in soybean monocultures. Parasitism by Trichogramma was also increased in soybean plots interspersed with weeds (Desmodium, Croton, and Cassia spp.) compared to weed-free soybean plots (Altieri et al, 1981). In this same study, increased rates of parasitization were observed in soybean, cowpea, tomato and cotton plots sprayed with aqueous extracts of Amaranthus sp. and corn stems and leaves. Plant extracts applied to cotton wicks also improved parasitization efficiency in soybean plots. In okra, this was observed with the

Amaranthus extract only. In a greenhouse study, Altieri et al (1982) found that extracts of A. retroflexus sprayed on fava bean plants increased rates of parasitization of Anagasta kuehniella eggs by T. pretiosum, and this activity was apparently dose-dependent.

In spite of these remarkable observations with Trichogramma spp., a chemically diverse environment is not necessarily beneficial for all parasitoids. Monteith (1960) observed that parasitism of the sawfly Pristophora erichsonii on larch trees by the tachinid Bessa harveyi was diminished in host trees in close proximity of Picea glauca. Olfactometer studies with another tachinid (Drino bohemica) demonstrated that non-food plants tended to mask the odours of hosts and their host plants. Shahjahan and Streams (1973) observed similar effects with the braconid Leiophron pseudopallipes, which parasitizes the tarnished plant bug Lygus lineolaris on Erigeron plants. The occurrence of parasitism was greater in pure stands of the host plant than in stands of mixed herbs.

1.1.3 Searching Behavior

Once the parasitoids are inside the host habitat, appropriate chemical stimuli must be present to incite them to search for their hosts. The identified searching kairomones to date (Table 2) include host pheromones, host-produced kairomones, plant-produced synomones and chemicals which originate from the host plant, but are concentrated as kairomones within the host (Hendry et al,

Table 2

Chemical Cues Mediating Searching Behavior

Parasitoids	Hosts	Active Compounds (if known); Source	References
Braconidae			
Cardiochiles nigriceps	Heliothis virescens	13-methyltritriacontane, (11-methyl-hentriacontane, 12-methyldotriacontane, 16-methyltritriacontane; mandibular glands of host	Vinson et al, 1975.
Chelonus texanus	H. virescens	water-soluble, heat stable component in host eggs and ovariole tissue	Vinson, 1975b.
Microplitis croceipes	H. zea	13-methylhentriacontane + unknown synergists; host frass, haemolymph and salivary secretions	Lewis and Jones, 1971; Jones et al, 1971; Gross et al, 1975.
Orgilus lepidus	Phthorimaea operculella	n-heptanoic acid; frass of hosts fed potatoes	Hendry et al, 1973; Hendry et al, 1976b.
Ichneumonidae			
Campoletis sonorensis	H. virescens	α-humelene, γ-bisabolene, β-caryophyllene oxide, spathulenol, β-bisabolol, gossonorol; essential oil of flowers, terminals, and buds of cotton, cotton-fed host larvae and frass of these larvae	Elzen et al, 1984a; 1984b.
Phaeogenes cynarae	Platyptilia carduidactyla	volatile; odours of wounded host host plants: Cirsium vulgare and Cynara scolymus	Bragg, 1974.
Scelionidae			
Telenomus remus	Spodoptera frugiperda	(Z)-9-tetradecene-1-ol acetate and (Z)-9-dodecene-1-ol acetate; sex pheromones of female hosts	Nordlund et al, 1983.

Table 2 (cont.)

Encyrtidae			
Microterys flavus	*Coccus hesperidum*	fructose, sucrose and an unidentified ninhydrin-active compound; host honeydew	Vinson *et al*, 1978.
Trichogrammatidae			
Trichogramma achaeae	*H. zea*	tricosane; moth scales	Lewis *et al*, 1975.
T. evanescens	*H. zea*	tricosane, (docosane, tetracosane, pentacosane); moth scales, corn tissue	Jones *et al*, 1973; Hendry *et al*, 1976b.
T. pretiosum	*H. zea*	tricosane; moth scales	Lewis *et al*, 1975.

1976a). Of the latter category, only three plant-host-parasitoid systems have been experimentally shown, with techniques of analytical chemistry, to display this sequestration mechanism (Hendry et al, 1976b; Elzen et al, 1984b). The hydrocarbon tricosane from corn is sequestered within Heliothis zea moth scales, and their dispersal in the field incites searching by Trichogramma evanescens. Heptanoic acid from potatoes is concentrated within the frass of Pthoromaea operculella and as such induces searching by Orgilus lepidus. A group of sesquiterpenes from cotton flowers and buds was found in H. virescens larvae and frass from larvae fed cotton, but not in samples of artificial diet-reared insects or frass. These allelochemicals act both as kairomones with respect to the larvae, and as synomones emanating from the plants.

It is highly probable that sequestration of allelochemicals and other plant chemicals in herbivorous insects occurs for reasons other than to attract natural enemies. However, parasitoids have adapted to these substances because it is a profitable arrangement. It is also very likely that many more of such systems exist, but are yet to be discovered (Hendry et al, 1976a).

1.1.4 Host Recognition and Acceptance

A diverse range of host recognition kairomones have been identified (Table 3). Those which originate in the host insect may occur exclusively in the haemolymph, cuticle, accessory glands, mandibular glands or silk glands of larvae, or in the wing scales of adult lepidopterans. Often, these substances occur in several regions of the host's anatomy, or throughout the organism. Several are host oviposition-deterrent or epidietic pheromones. There are also examples where chemicals of host plant origin may be concentrated in the host and host frass, although cause-and-effect relationships have not been demonstrated by analytical chemistry techniques.

In one case, plant chemicals alone (from tomato leaves) have been shown to induce oviposition responses in Trichogramma pretiosum (Nordlund et al, 1985), but the active compound has not yet been identified. Fungal fermentation products are important ovipositor probing stimulants for ichneumonid parasitoids of wood-boring wasps (Madden, 1968; Spradberry, 1970). A mutualistic association exists between siricid wasps and parasitic fungi (Amylostereum spp.), where the siricid inoculates the tree upon oviposition, and the fungus subsequently invades the tree, creating a more suitable environment for siricid development. The ichneumonids which parasitize Siricidae take advantage of this mutualism in host finding and recognition.

Table 3

Chemical Cues Mediating Host Recognition or Acceptance

Parasitoid	Hosts	Active Compounds (if known); Source; Biological Activity	References
Tachinidae			
Archytas marmoratus	Heliothis virescens	protein, molecular weight 30.000 +/- 5,000, soluble in water, 0.1 N HCl and 0.1 N acetic acid; frass, haemolymph and whole body extracts of host; larviposition	Nettles and Burks, 1975.
Lexophaga diatraeae	Diatraea grandiosella	methanol soluble; frass of hosts fed sugarcane; larviposition	Roth et al, 1978.
Ludella grisescens	Ostrinia nubilalis	ethanol and water soluble; frass of hosts fed corn; larviposition	Hsiao et al, 1966.
Braconidae			
Apanteles flavipes (Pakistan strain)	Chilo partellus	contact chemical; frass of hosts fed maize, sorghum and Johnson grass; examination and ovipositor probing	Mohyuddin et al, 1981.
	Acigona steniellus		
(U.S.A. strain)	Diatraea saccharalis	contact chemical; frass of hosts fed sugarcane; examination and ovipositor probing	
A. melanoscelus	Lymantria dispar	proteinacious, soluble in water, methylene chloride and n-hexane; exuvaiae of hosts, silk and silk glands; examination and ovipositor probing	Weseloh, 1974; 1977.
Bracon mellitor	Anthonomus grandis	long chain fatty acids of cholesterol; frass of hosts fed cotton squares; ovipositor probing	Hensen et al, 1977.
Chelonus texensis	H. virescens	water soluble, heat stable component in host eggs and ovariole tissue; examination and ovipositor probing	Vinson, 1975b.

Table 3 (cont.)

Microplitis croceipes	H. zea	water soluble; frass of hosts fed cotton, soybeans or pea cotyledons; examination and ovipositor probing	Sauls et al, 1979; Nordlund and Sauls, 1981.
Opius lectus	Rhagoletis pomonella	contact oviposition deterrent pheromones of hosts; examination and ovipositor probing	Prokopy and Webster, 1978.
Orgilus lepidus	Phthorimaea operculella	contact chemical; host cuticle; oviposition	Greany and Oatman, 1972.
Ichneumonidae			
Campoletis sonorensis	H. virescens	acetone and methanol soluble; host cuticle, salivary secretions and frass; oviposition	Wilson et al, 1974.
	H. zea	volatile after extraction with diethyl ether; host tissues; oviposition	Schmidt, 1974.
Ibalia leucospoides	Sirex noctilio	acetaldehyde; product of symbiotic fungus (Amylostereum sp.) invading host tree, Pinus radiata; drilling (ovipositor probing)	Madden, 1968.
Itoplectis conquisitor	Galleria mellonella	hexoses and 19 common amino acids, Mg++, pH 7; host haemolymph (concentration specific); oviposition	Hegdekar and Arthur, 1973.
	Celerio euphorbiae		
Megarhyssa nortoni	S. noctilio	water, ethanol, methanol and acetone extracts of host frass and symbiotic fungal cultures (Amylostereum sp.); drilling (ovipositor probing)	Madden, 1968.
Rhyssa persuasoria	Siricidae	same as above	Madden, 1968; Spradberry, 1970.
Nemeritis canescens	Ephestia kuehniella	epidietic pheromone; mandibular glands of host; ovipositor probing	Corbet, 1971.
	Plodia interpunctella	unknown; host mandibular gland secretions; arrestment, ovipositor probing	Waage, 1978.

Table 3 (cont.)

Phaeogenes cynarae	*Platyptilia cardui dactyla*	volatile; odours of wounded host plants: *Cirsium vulgare* and *Cynara scolymus*; must be present throughout host selection and oviposition	Bragg, 1974.
Scelionidae			
Telenomus heliothidis	*H. virescens*	proteinacious; accessory glands of adult female hosts; oviposition	Strand and Vinson, 1982.
Chalcididae			
Brachymeria intermedia	*L. dispar*	dimethylpentatricontane, (heptacosane, nonacosane and several dimethyl compounds in the pentatriacontane to tetracontane range); host cuticle; oviposition	Tucker and Leonard, 1977.
Encyrtidae			
Cheiloneurus noxius	*Coccus hespiridum*	proteinacious, molecular weight > 150,000; host cuticle; oviposition	Weseloh and Bartlett, 1971.
Trichogrammatidae			
Trichogramma evanescens	*Pieris brassicae*	contact chemicals in host wing scales and oviposition deterrent pheromone produced by female *P. brassicae*; arrestment	Noldus and Van Lenteren, 1983.
	P. rapae		
	Mamestra brassicae		
T. pretiosum	*H. zea*	hexane extractable; tomato leaves; oviposition	Nordlund *et al*, 1985.

From the survey of host recognition and acceptance kairomones, the role of the host plant at this stage of the host selection process appears to be minor. Most of the semiochemicals involved in host recognition and acceptance are host-synthesized biomolecules. However, it should be acknowledged that changes in host plant quality can hypothetically affect the synthesis or metabolism of these compounds by effecting changes in the physiology of the herbivore. This may partially explain why it is possible to rear parasitoids on factitious hosts, a procedure successfully accomplished by rearing the hosts on relatively 'inert' plants, or artificial media (Simmonds, 1944; Fedde et al, 1982).

1.1.5 Host Plant Chemistry and Host Suitability

According to Vinson and Iwantsch (1980), host suitability is primarily concerned with factors affecting the preimaginal stages of parasitoid life. These authors have reviewed the subject in terms of four main elements involved in successful parasitoid development: (1) Avoidance of, or defence against the host's immune system; (2) Competition with other parasitoids; (3) The presence of toxins; and (4) Host nutritional adequacy. The literature concerning host plant effects on host suitability relates to all but the second of these categories, which may also be classified as direct effects of allelochemicals toward the developing parasitoid, and indirect effects *via* effects on the host.

The first documented suggestion of direct allelochemical interference on parasitoid development was proposed by Morgan (1910), who remarked that the lack of parasitism of *Phlegethontius* (*Manduca*) *sexta* by *Apanteles* (*Cotesia*) *congregatus* in tobacco fields was likely due to the toxic effect of nicotine. Gilmore (1938) investigated this same host-parasitoid relationship in the laboratory, and found that hosts fed dark-fired tobacco became unsuitable for parasitoid development. Narayanan and Subba Rao (1955) also reported the toxic effects of tobacco fed to the gram caterpillar, *Plusia orichalcea*, towards the braconid *Microbracon gelechiae*. Mortality was 100 percent in preimaginal parasitoids within mature hosts fed tobacco,

compared to 40 percent within gram-fed hosts. However, when younger larvae fed tobacco were parasitized, parasitoid mortality was 59 percent, which suggests that the host's age when parasitized influenced the toxicity of nicotine towards the parasitoids.

Thurston and Fox (1972) established that nicotine in the host diet impaired the emergence of C. congregatus from M. sexta. Concentrations of 0.5, 1.0 and 1.5 percent nicotine in artificial diet, as well as topical application of nicotine to parasitized hosts reduced the number of emerging C. congregatus.

The suitability of California red scale, Aonidiella aurantii, reared on different food plants, for several hymenopteran parasitoids was investigated by Smith (1957). Hosts reared on Yucca filipendula were more suitable for the encyrtids Comperiella bifaciata and Habrolepis rouxi, producing larger, longer-lived and more prolific adults (predominantly female), than hosts on orange, lemon, grapefruit, agave, and sago palm. In fact, mortality increased markedly for both parasitoids developing within hosts on sago palm, and was 100 percent for H. rouxi. Similar results were observed with H. rouxi and the oleander scale, Aspidiotus nerii (Blumberg and DeBach, 1979). Scales reared on lemons were less suitable for parasitoid development than those reared on potato tubers.

Altahawy et al (1976) found that the food plant of Spodoptera littoralis affected both the percent

parasitization of Microplitis rufiventris and the fitness of the emerged parasitoids. Castor-oil leaves were preferred by the parasitoids over cotton or sweet potato. The diet of castor-oil leaves conferred lower mortality in parasitoid pupae and increased adult longevity compared to the other food plants tested.

Smith (1978) reported that Danus chrysippus was less susceptible to parasitism by tachinid flies when feeding on plants containing high levels of cardiac glycosides than on plants with low levels or no cardiac glycosides. Although parasitoid intoxication was not demonstrated in the laboratory, the author acknowledged that the attractiveness of the host plant is not exclusive of host suitability in the ecological sense. This is corroborated by the work of Brower et al (1967), which demonstrated that Monarch butterfly larvae (Danaus plexippus) fed nonpoisonous plants were palatable to blue jays, whereas insects fed plants containing cardenolides caused the birds to vomit.

Carotenoids (Rothschild et al, 1977) and pyrrolizidine alkaloids (Benn et al, 1979) from food plants were found to persist through herbivorous insects and into their parasitoids. Nicotine was found in C. congregatus wasps and pupal cases, reared from M. sexta fed nicotine-containing diets (Barbosa et al, 1982). Pasteels (1978) observed wing deformities in progeny of the coccinellid predator Adonia variegata feeding on aphids (Aphis nerii) occurring on Cionura erecta. When deformed predators fed on aphids occurring on different host plants, their progeny

developed normally. Unknown toxins from C. erecta were suggested as the cause of these deformities.

The effects of the glyco-alkaloid α-tomatine (from tomato foliage) on the ichneumonid Hyposoter exiguae was investigated by Campbell and Duffy (1979a). The alkaloid persisted through Heliothis zea larvae fed diets containing the compound, and was detectable in the adult parasitoids. Although parasitization rates were not affected by the presence of the compound in the host's diet, the larval period of H. exiguae was significantly prolonged with 0.3 and 0.5 percent α-tomatine (wet weight). The pupal period was also significantly prolonged for parasitoids reared from hosts fed 0.5 percent α-tomatine diets. Pupal eclosion and adult weight and longevity were significantly reduced at both concentrations, compared to controls.

Because α-tomatine impairs sterol utilization, the augmentation of ß-cholesterol to diets treated with α-tomatine attenuated some of the observed effects for the 0.3 percent treatment. In a subsequent study (Campbell and Duffy, 1981), deformities in antennal, abdominal and genital structures were observed in 20 percent of the wasps reared from H. zea fed diets containing 5.0 percent α-tomatine (dry weight). However, the adverse effects of the alkaloid were supressed when equimolar or supramolar augmentations of 3-ß-hydroxy-sterols were included in the diets. Extracts of foliage from different tomato cultivars were tested for comparable toxicity, and it was shown that toxicity to H. exiguae depended on the relative proportions

of α-tomatine and sterols within the plants, rather than levels of α-tomatine as such.

The nutritional quality of the host's food can significantly affect parasitoids which take sustenance from these insects (Flanders, 1942; House and Barlow, 1961; Zohdy, 1976). The physical size and developmental rate of many parasitoids is correlated with that of the host (Salt, 1941), and, therefore, if the quality of the food plant affects host physiology, this will be manifested in parasitoid fitness. Two separate cases where the host plant was shown to affect host nutritional suitability were reported by Greenblatt and Barbosa (1981). Although allelochemicals were not implicated in the suitability of gypsy moth (Lymantria dispar) and fall webworm (Hyphantria cunea) pupae for the pupal parasitoids Brachymeria intermedia and Coccygomimus turionellae, the foliage diets of the hosts affected their nutritional quality, and hence the growth and development of the parasitoids. Gypsy moth hosts reared on red oak (Quercus rubra) produced larger and heavier B. intermedia females than those reared on grey birch (Betula populifolia), white oak (Q. alba), red maple (Acer rubrum) or synthetic diet. Wasp weight was not dependent on host weight. Rather, nutritional indices revealed that red oak-reared L. dispar female pupae were the most digestible of the host types, and red oak-reared male pupae were most efficiently converted to wasp biomass. In the case of C. turionellae, wasp weight was correlated with the weight of gypsy moth pupal hosts, and not dependent on

the host tree. However, in the association of C. turionellae with fall webworm, the host tree was found to be more important. Hosts reared on black cherry (Prunus serotina) produced heavier wasps than those reared on pin cherry (P. pensulvanica), shagbark hickory (Carya ovata) or white ash (Fraxinus americana).

Food plants may affect host suitability by conferring to the host immunity from the developing parasitoid. Cheng (1970) investigated parasitism by the tachinid Lypha dubia of the winter moth, Operophthera brunata. In this case, the relationship of the host tree to parasitoid encapsulation is somewhat indirect. The developmental rate of O. brunata was found to be accelerated by feeding on oak leaves compared to hawthorn, blackthorn and hazel. L. dubia attacks fifth instar host larvae, and in order for the parasitoid to avoid encapsulation, it must develop to the second instar before the host enters the prepupal stage. Because host development is accelerated on oak leaves, the larvae are parasitized later in the fifth instar, and the prepupal stage is reached before the parasitoid has ecdysed to the second instar. For this reason, a higher percentage of L. dubia are encapsulated by hosts feeding on oak leaves compared to concurrent parasitization on other food plants.

1.1.6 Resistant Varieties and Biological Control

The use of resistant crop varieties may not be advantageous in the long term if the natural enemies of phytophagous insects are adversely affected (Philogène, 1984). The literature is sparse for studies regarding the effects of resistant varieties on the third trophic level, and many of these studies are concerned with physical (or mechanical) resistance, such as leaf pubescence or glandular trichomes (Casagrande and Haynes, 1976; Elsey and Chaplin, 1978; Obrycki et al, 1983; Turner, 1983; Obrycki and Tauber, 1985).

Crop cultivars which differ biochemically have been shown in some cases to affect significantly the performance of natural enemies. Franklin and Holdaway (1966) found that the tachinid Lydella thompsoni (grisescens) was preferentially attracted to the corn hybrid A332 x A334 over the hybrid W22 x A73, even though both were equally susceptible to feeding by European corn borer. Subsequently, Sandlan et al (1983) investigated parasitism by L. thompsoni on resistant and susceptible corn varieties. Although parasitization rates were found to be dependent on host density, rather than the cultivars as such, the susceptible variety (W22 x A73) produced heavier parasitoid pupae and more fecund adult females than the other cultivars tested (Mn 5302 - resistant, M14 - susceptible and OH-43 - resistant). These differences were not statistically significant. However, a biologically

significant three-fold increase was observed in the number of eggs produced per female per day from W22 x A73, relative to the other varieties.

In a study concerning the greenbug parasitoid Aphelinus asychis, Esmaili and Wilde (1971) found that mummies produced on resistant KS 30 sorghum were significantly smaller in size than those produced on Arkwin oats (susceptible) and Diktoo barley (resistant). Numbers of mummies and percent pupal eclosion were not significantly different between the crop lines, but fecundity was reduced on KS 30 sorghum. In this case, one resistant cultivar (KS 30 sorghum) adversely affected the parasitoid, while the other (Diktoo barley) exerted no detrimental effects. In fact, more mummies were produced on Diktoo barley compared to the susceptible Reno barley cultivar.

Starks et al (1972) also reported reduced mummy size for the greenbug parasitoid Lysiphlebus testaceipes on resistant barley and sorghum varieties. However, as the number of parasitoid mummies produced was considerably less than the reduction observed in the greenbug population, the integration of resistant varieties and biological control was judged to be successful. Salto et al (1983) observed no adverse effects towards L. testaceipes with resistant oat varieties. Fecundity was not significantly different in females reared from hosts on CI4888 (resistant) and Nora (susceptible) oat cultivars.

Another example of host plant resistance compatibility

with biological control agents was reported by Pimentel and Wheeler (1973). Resistant alfalfa varieties did not hinder the activity of parasitoids and predators towards pea aphids. Wyatt (1970) found that parasitization by Aphidius matricariae was actually increased on resistant chrysanthemum cultivars compared to susceptible varieties, regardless of host (aphid) population density.

However, Orr et al (1985) found that stink bug eggs oviposited on the resistant sorghum cultivar PI 17444 were less suitable for the egg parasitoid Telenomus choropus than those on the susceptible Davis variety. Parasitoid emergence was significantly reduced, as was the fecundity and duration of the ovipositional period in females.

It is apparent from the studies reviewed that resistance breeding may or may not be compatible with biological control. Individual cropping systems should be carefully examined before such strategies are implemented.

1.2 Objectives

The principal objectives of the present research were to investigate the physiological and ecological effects of secondary plant substances on the third trophic level, using an economically important host-parasitoid association, Ostrinia nubilalis and Diadegma terebrans. Two different plant derived compounds, berberine and α-terthienyl - chosen for their different physical and biological properties - were used to demonstrate the possible consequences of secondary plant substances on the natural

enemies of phytophagous insects. The effects under study included:

1. Physiological effects on the host insect, O. nubilalis, and the parasitoid, D. terebrans;
2. The influence of treated hosts on host selection by D. terebrans; and,
3. The persistence of naturally occurring insecticidal compounds through the food chain.

1.3 The Experimental Insects

1.3.1 Ostrinia nubilalis (Hübner)

(Lepidoptera: Pyralidae)

The European corn borer is a well-known international pest of corn and many other crops. Since it was introduced to the United States on broom corn in 1909 (Caffrey and Worthley, 1927), over one thousand studies have been devoted to the biology and control of this destructive lepidopteran. These will not be completely reviewed here. Rather, the aspects of this insect pertinent to this research will be highlighted.

The general biology of O. nubilalis has been described by Guthrie et al (1971). Eggs are deposited in masses on the underside of the host plant leaves. Prior to eclosion, the cephalic capsules of the embryos melanize and become visible through the chorion - a condition known as the black head stage. Under the rearing conditions of this laboratory (2.1.1), hatching occurred within six hours of the appearance of black heads.

There are normally five larval instars. The first and second instar larvae feed on leaf tissue; third instar larvae feed within the whorl of the plant and subsequently burrow into the stalk. The fourth and fifth instars are passed within the plant, feeding and excavating vertical tunnels through the stalk. These are the most destructive instars, causing 'lodging' in corn (the weakened stalks fall over) when the number of borers per plant exceeds the economic threshold for the particular cultivar. If the fifth instar larvae do not enter diapause, pupation will occur within the stalks, and adults emerge and escape through the burrows to begin a new generation during the same season. Otherwise, winter is spent as mature larvae in diapause within the corn stalks.

The number of generations per year varies with location and latitude (Davidson and Lyon, 1979). In Ontario and Quebec, there are two strains of O. nubilalis: a univoltine strain and a bivoltine strain (McLeod and Nagai, 1979; Foott and Timmins, 1981). However, diapause in this insect is primarily controlled by photoperiod and temperature regime (Beck, 1977). Although the colony in the Ottawa laboratory originated from a nucleus of the bivoltine strain, the proportion of larvae entering diapause was kept very low by the use of a non-diapause-inducing photoperiod and temperature schedule (2.1.1).

The principal host plants of O. nubilalis in Europe were reportedly corn, hemp, hops and millet, and, in addition, there is a variety of minor food plants (Vinal

and Caffrey, 1919). However, the insect is clearly capable of adapting to new food plants. Caffrey and Worthley (1927) reported it feeding on 152 plant species in the United States. A more complete host plant list ws published by Hodgson (1928) which includes over 200 species representing 40 families. As well, infestations of O. nubilalis in crops previously untouched or rarely attacked by the pest have been recorded in recent years (Willson, 1980; Tedders et al, 1981; Weires and Straub, 1982).

1.3.2 Diadegma terebrans (Gravenhorst)
(Ichneumonidae: Campopleginae)

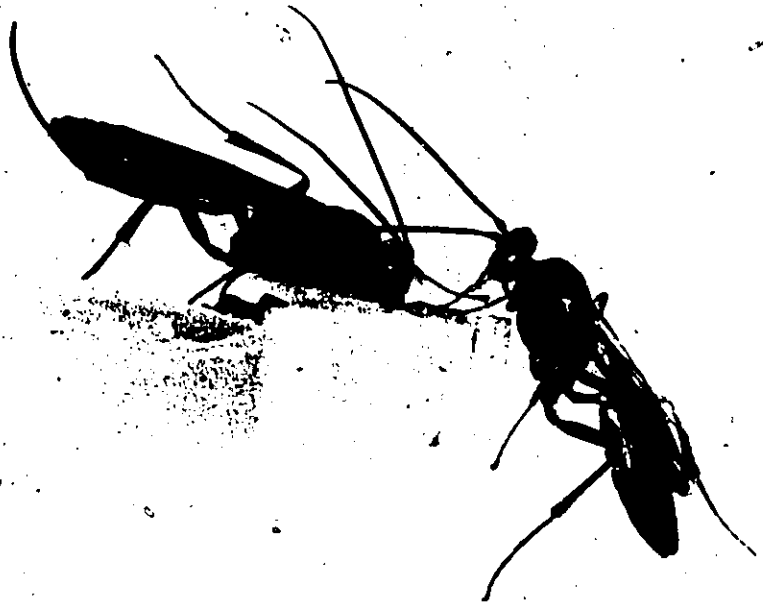
Diadegma terebrans (Plates 1 and 2), native to Europe and Asia, is one of 17 exotic parasitoids imported from 1927 to 1940 for biological control of European corn borer (Baker et al, 1949, as Horogenes punctorius [Roman]), and is one of the four larval parasitoids which have become established in North America. However, parasitization rates of this ichneumonid in the field have been consistently low (Peairs and Lilly, 1975; Hill et al, 1978; Winnie and Chiang, 1978; Andreadis, 1980; 1982; Lewis, 1982). The parasitoid has become established in southern Ontario, most probably as a result of migration from Ohio (Wressell, 1973).

D. terebrans was chosen for this study primarily because of its availability and relatively simple culture method. In addition, it is a solitary parasitoid, and therefore uniform food availablity for developing larvae

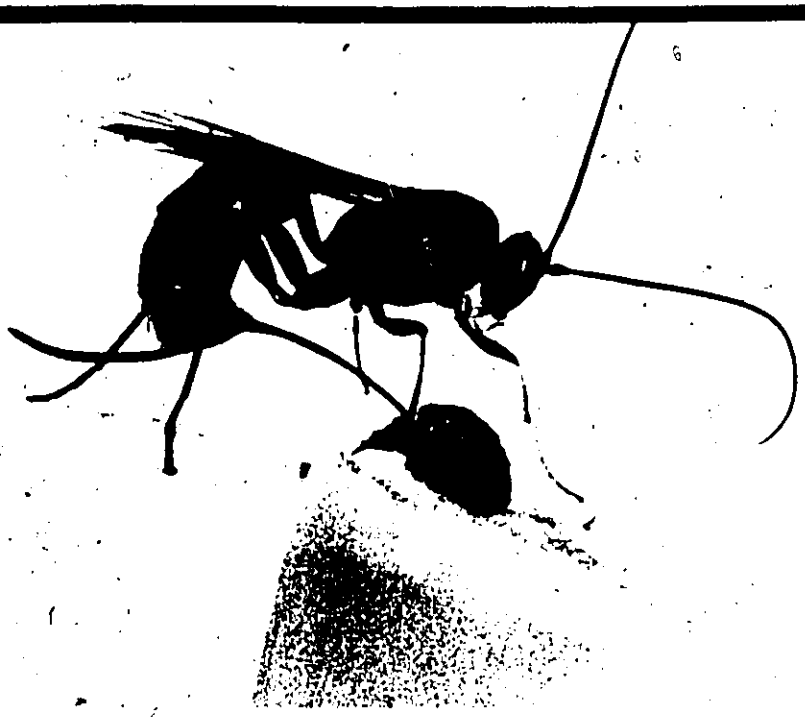
Plates 1 and 2

1. Female (left) and male (right) Diadegma terebrans.
2. Female D. terebrans parasitizing an Ostrinia nubilalis larva feeding on a piece of corn stalk.

1



2



was a gratis condition of these experiments. As well, it is an endoparasitoid, residing in the host's haemolymph, and as such is maximally exposed to toxic compounds ingested by the host.

The biology of this ichneumonid has been described in detail by Baker et al (1949). Eggs are deposited singly in the haemolymph and hatch in 32 hours at 26.5 C. If a female oviposits more than once in a single host, only one larva survives; supernumary first instar larvae become encapsulated. Unfertilized eggs give rise to male progeny, but fertilized eggs may produce offspring of either sex (they are arrhenotokous).

There are three larval instars, but the major part of D. terebrans' developmental time is spent in the first instar. The parasitoid does not ecdyse to the second instar until its host reaches the fifth instar, and the second and third instars last only a few days. Mature larvae exit from the anterior third of their hosts. However, feeding continues until the host is completely consumed except for the cephalic capsule and possibly some desiccated larval cuticle. Baker et al (1949) found that the average duration of the internal stages was 14.9 days at a constant temperature of 26.5 C.

Upon completion of feeding, the parasitoid spins a cocoon - a silken structure lined with secretinous material. The pupal stage lasts 9.4 days, on average, at 26.5 C (Baker et al, 1949). Adults emerge after gnawing an exit hole at the end of the cocoon. The males normally

precede the females by at least one day. A fluid meconium is left inside the empty cocoons.

The diapause physiology of D. terebrans is intimately connected with that of its host. The parasitoid will overwinter as a first instar larva within a fifth instar host in diapause, which suggests that the physiological changes associated with prepupal D. nubilalis are necessary for D. terebrans ecdysis to the second instar (Baker et al, 1949). In nature, the parasitoid is well-synchronized with the univoltine strain of its host (Manojlovic, 1984b), and the first generation of the bivoltine strain (Winnie and Chiang, 1982). However, the second generation of D. terebrans associated with the second generation of the bivoltine strain of D. nubilalis does not coincide with peak host abundance (Winnie and Chiang, 1982). This may partially explain the observed low levels of parasitization in the field with D. terebrans.

Apart from corn, D. terebrans has been recovered from D. nubilalis on common burdock, common mugwort, hemp and hops (Manojlovic, 1984a). It is not known to parasitize other insect species, probably because of the specificity of the symbiotic virus associated with the ovaries of this parasitoid (Stoltz et al, 1981). The virus is injected into the host upon oviposition, making the host environment suitable for parasitoid development. In effect, the immune system of the host is altered, such that encapsulation of the parasitoid is prevented (Stoltz and Vinson, 1979).

1.4 The Experimental Compcunds

1.4.1 Berberine

Berberine (umbellatine; 5,6-dihydro-9,10-dimethoxybenzo[g]-1,3-benzodioxolo [5,6-a] quinolizinium) (Figure 1) is an isoquinoline alkaloid which occurs in at least 26 genera of ten plant families (Suffness and Cordell, 1985). A great deal of literature has been published regarding its antitumor activity (reviewed by Suffness and Cordell, 1985). It is also known to be fungitoxic (Greathouse and Watkins, 1938) and antimicrobial (Yoshikazu, 1976).

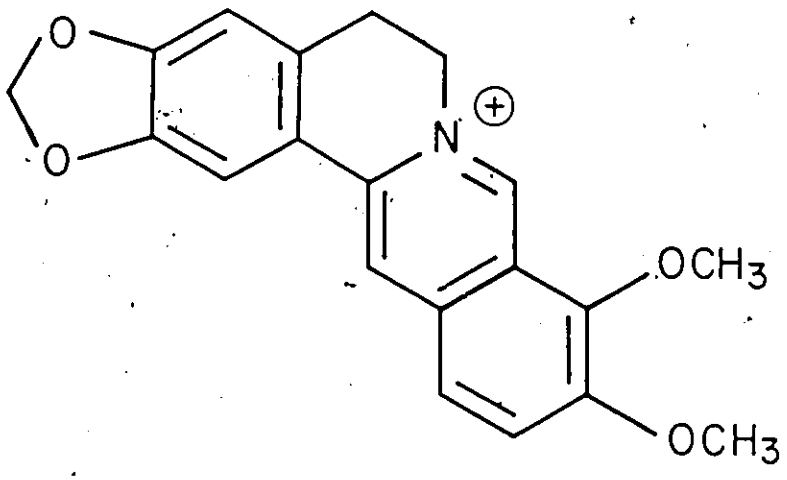
Berberine's insecticidal activity is well-documented. It has been shown to be toxic to the Colorado potato beetle, Leptinotarsa decemliniata (Buhr et al, 1958) and to the silkworm, Bombyx mori (Isogai et al, 1973). Chronic effects on growth and developmental parameters were reported by Devitt et al, (1980) for the dark-sided cutworm, Euxoa messoria, fed larval diets containing 3 mg/g berberine. Severe mortality in the larval stages resulted with berberine at a concentration of 10 mg/g in the diet. The phototoxic activity of berberine towards insects was demonstrated with the rock hole breeding mosquito Aedes atropalpus by Philogène et al (1984). In the presence of near ultraviolet radiation, the acute (24 hour) LC_{50} was found to be 8.8 ppm, compared to 250 ppm in darkness.

Berberine is known to have two principal sites of

Figure 1

Molecular Structure of Berberine

1.



Berberine

action. It has been shown *in vitro* to intercalate with DNA (Krey and Hahn, 1969; Faddejeva *et al*, 1980; Rungsiliyakorn *et al*, 1981; Maiti and Chaudhuri, 1981). In addition, Faddejeva *et al* (1980) found that berberine uncoupled respiration and oxidative phosphorylation in intact rat liver mitochondria. Berberine's phototoxic (in the presence of near u.v.) mechanism is singlet oxygen generation ($^1O_2$ is produced when O_2 reacts with the photoexcited alkaloid). Because berberine intercalates with DNA, the photooxidative damage caused by $^1O_2$ takes the form of chromosomal aberrations (Philogène *et al*, 1984).

Berberine was chosen as a model compound for this study for several reasons: As a quaternary ammonium compound, it may be transported across the blood-brain barrier if converted to its dihydro derivative (Bodor *et al*, 1981). However, because it is hydrophilic, it may also be rapidly excreted at sublethal concentrations. In addition, the compound is fairly heat and light stable. Finally, synthetic berberine is available is quantity, and this is an important consideration for a detailed study of third trophic level interations.

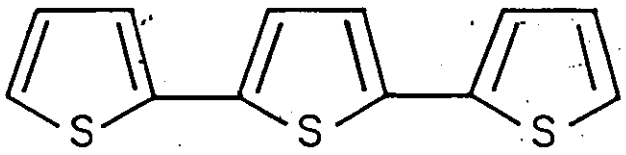
1.4.2 α-terthienyl

α-terthienyl (α-t) (Figure 2) is a thiophene which occurs in numerous genera of the Asteraceae (Bohlmann *et al*, 1973). It has long been recognized as one of the nematicidal principals in marigold roots (*Tagetes* spp.) (Uhlenbroek and Bijloo, 1958). Recently, the phototoxic

Figure 2

Molecular Structure of α-terthienyl

2.



α-terthienyl

properties of this compound have been demonstrated (Towers, 1984 and references cited therein). It has been shown to cause cell lysis and enzyme damage in human erythrocytes (Yamamoto et al, 1979; MacRae et al, 1980; Wat et al, 1980) and, additionally, is bacteriocidal (Downum et al, 1982), fungitoxic (DiCosmo et al, 1982), allelopathic (Campbell et al, 1982) and insecticidal (Arnason et al, 1981; Champagne, 1984; Champagne et al, 1984; Downum et al, 1984; Philogène et al, 1985).

The enhanced toxicity of α-t in the presence of near ultraviolet radiation was shown to be photodynamic, or oxygen dependent (Arnason et al, 1981; Downum et al, 1982; McLachlan et al, 1984; Garcia et al, 1984). Physiological damage occurs at cell membranes when cell membrane components are oxidized by singlet oxygen. α-t is also toxic to insects in the absence of u.v. radiation. Champagne (1984) demonstrated the potent feeding deterrent and growth inhibiting effects of 100 ug/g α-t in larval diets towards the dark-sided cutworm, Euxoa messoria, the tobacco hornworm, Manduca sexta, as well as the European corn borer. The biochemical mechanism of this insecticidal / insectistatic activity is not precisely known. However, a reduction in nutrient assimilation was revealed by a series of nutrient utilization indices.

α-t was chosen as the second model compound for the present study because it is highly lipophilic (log p = 5.6, where p = the octanol / water coefficient) (McLachlan, 1984). In contrast to berberine, the site of action is at the

membrane level (Towers, 1984). α-t would likely have to be modified by the insect's detoxification enzyme systems prior to excretion. Additionally, the compound is practically suited to this type of study. It is fairly heat stable, and not readily photodegraded. Synthetic α-t was also available in decagram quantities.

1.5 Plan of Study

An immediate problem arises in executing a study of the effects of insecticidal compounds from plants on entomophagous insects: an endoparasitoid must be exposed to the toxic substance via the host, in contrast to conventional insecticides, which can be sprayed. It is necessary to intoxicate the host insect, yet keep it alive to support the development of the parasitoid. Therefore, it was essential for these experiments to determine a concentration range for berberine and α-t which would be sublethal to O. nubilalis. After preliminary experiments, it was decided that three concentrations would be sufficient to demonstrate the various effects of these compounds on O. nubilalis, and to simultaneously investigate if similar effects could be seen in O. terebrans. Further, the study was restricted to the 'dark' toxicity of these compounds, and there are two reasons for ignoring phototoxicity in this research. First, O. nubilalis larvae habitually burrow into their food medium, and so exposing them to an ultraviolet light source is a difficult technical problem in itself. Second, the

phototoxic properties of these compounds towards immature D. terebrans would not be manifested under natural field conditions. Since the host instars parasitized are the second and third, which burrow into the stalk of the host plant, the parasitoid is practically shielded from sunlight during its preimaginal life.

In an attempt to investigate the effects of these compounds on D. terebrans, dual-choice tests (treated hosts versus controls) were conducted using 12-day-old larvae. A dual-choice system was preferred over a multiple choice system for the following reasons. The parasitization rate obtained with these insects in this laboratory was considerably less than 100 percent. As well, the female wasps normally probe into their potential hosts with their ovipositors, and so many of the larvae offered for parasitization die from severe mutilation. Therefore, it was necessary to expose large numbers of larvae of each treatment group to obtain a reasonable number of surviving, parasitized larvae for statistical purposes. This was greatly facilitated by exposing the groups in pairs of treatment plus control, rather than all of the treatments at one time.

It was observed that in some cases the female wasps were preferentially attracted to one group of hosts over the other in some of the pairs of groups presented for parasitization. This made comparisons of growth parameters statistically unreliable. Therefore, the developmental effects and survivorship rates were studied

in a no-choice system using host insects of a uniform physiological status. Further dual-choice tests using physiologically similar host insects were conducted to elucidate whether or not the presence of the compound within the host's diet could have an effect on parasitization rates, irrespective of physiological age. A dual-choice test was also performed between untreated second and third instar O. nubilalis, to check for differences in successful parasitism by O. terebrans due to host instar.

Finally, the body burden of these compounds in potential hosts, and residue in parasitoid adults were analyzed quantitatively by HPLC. Body burden studies on second and third instar O. nubilalis would provide information as to whether or not some of the observed ovipositional preferences on the part of female wasps could be linked to the presence or absence of xenobiotics in host tissues. Residue analysis in parasitoid adults, and cocoons with meconia, could provide at least a partial explanation for the observed physiological effects and mortality. Additionally, this information could provide a basis for predictions regarding the fate of adult wasps exposed to ultraviolet radiation after emerging from hosts reared on diets containing phototoxins.

2.0 METHODS AND MATERIALS

2.1 Rearing Methods

2.1.1 Ostrinia nubilalis

A laboratory colony of Ostrinia nubilalis was initiated using eggs supplied by M. Hudon (Agriculture Canada, St. Jean, P.Q.) and periodically boosted with eggs supplied by G. McLeod (Agriculture Canada, London, Ont.). The culture was maintained according to the method of Guthrie et al (1971), except that corn cob grits were added as a supplement to the meridic diet fed to the larvae.

Larvae were reared within a controlled environment chamber (Conviron model E7), with a photoperiod of 16/8 (L/D), at 26.5 C during the photophase, and 19 C during the scotophase. Relative humidity was kept constant at 80%. Lighting was provided by four 20 W solar simulating fluorescent lamps (Vitalight® 48T12 U.H.O.) separated from the chamber by a 3 mm sheet of plexiglass. The resultant light intensity in the chamber was measured to be 7.6 W/m^2 with a Yellow Springs Radiometer with a u.v. cut-off at 390 nm.

Adults were maintained in a plexiglass and aluminium screen cage (inner dimensions 45 x 45 x 61 cm in height), in a controlled environment chamber (Conviron model E7), with a photoperiod of 18/6 (L/D) at 26.5 C (photophase) and 19 C (scotophase), and a constant relative humidity of 85%. Lighting was provided by four 60 W fluorescent lamps (Coolwhite F48T12/CW/HO) and one 40 W incandescent bulb,

separated from the chamber by a 3 mm sheet of plexiglass. The resultant light intensity inside the cage was 3.6 W/m^2.

The moths were provided with distilled water sprayed into the cage several times daily with a hand-held plant mister. In addition, a portable cool-spray vaporizer was positioned in the chamber adjacent to the cage, with the outlet port facing one side of the screen cage. In this way, drinking water was accessible while the culture was unattended.

2.1.2 Diadegma terebrans

Diadegma terebrans pupae were obtained from R. L. Jones (University of Minnesota, St. Paul, Minn.), and reared according to methods in that laboratory (Chiang and Palmer, 1978). Adults were maintained in a plexiglass and steel screen cage (inner dimensions 51 x 51 x 59 cm in height), in a controlled environment chamber (Conviron), equipped with a humidity regulator. Lighting was provided by six 20 W solar simulating fluorescent lamps (Vitalight ® 48T12 U.H.O.) separated from the chamber by 5 mm glass. The resultant light intensity was 8 W/m^2. Rearing conditions were: photoperiod 16/8 (L/D), temperature 25 C (8 hours) and 15 C (16 hours), with the thermophase occurring one hour after the commencement of the photophase. A constant relative humidity of 70% was maintained within the chamber.

Adults were provided with distilled water from a

bottle with a wick of cotton wool. Honey was supplied from a cotton wool pad soaked with distilled water, on the screen ceiling of the rearing cage. Additional honey was available from a 5 cm (diameter) crystallization dish filled with cotton wool and soaked with distilled water, on the floor of the cage.

Routine parasitization was accomplished as follows. Between 100 and 200 second and third instar O. nubilalis larvae were removed from the mass culture boxes and placed in an empty rearing box with chopped corn stalks (approximately 1 cm long). The presence of corn provided an essential stimulus for host recognition by these wasps. The sweet corn hybrid, Silver Queen (Stokes), was used in all rearing and experimental procedures because of its susceptibility to corn borer feeding (Mason, 1984, personal communication). Most of the corn used for routine rearing was freshly harvested, but occasionally frozen and thawed corn stalks were substituted when the supply of fresh corn was limited. All of the corn was greenhouse-grown.

The rearing boxes with the corn and larvae were covered, and the larvae allowed to feed and burrow into the corn overnight. The following day, during the thermophase, the box was uncovered and placed into the ichneumonid cage, raised 45 cm above the floor by a retort stand with a support ring. Larvae were exposed to the parasitoids for approximately one hour, and then removed from the cage. The larvae were then dissected from the corn, and placed into a 1 litre mason jar filled to approximately 5 cm with

the meridic (wheat germ-based) diet, and capped with a ring top and a fitted disk of brass or copper screen.

After seven to ten days, 40 to 50 cm of paper towelling were crumpled and placed into the mason jar above the diet. Parasitized larvae and prepupal unparasitized larvae would crawl into the paper, and the parasitoids would emerge and pupate in the paper. The jars of larvae were kept in the same chamber as the mass-reared O. nubilalis larvae. Pupae were harvested weekly by searching through the paper. The pupae were held in 10 cm glass petri dishes, lined on the bottom with a moist filter paper disk (Whatman no. 4). When the first adults emerged, the dish was transferred to the adult cage and the cover removed.

2.2 Preparation of Test Compounds

Commercially available berberine hydrochoride (Sigma) was recrystallized twice in 99% ethanol (Philogène et al, 1984), and its purity verified by HPLC (see 2.8). The chromatogram obtained by monitoring at lambda = 254 nm yielded one peak, and the u.v. scan of this peak produced the characteristic berberine spectrum (lambda $_{max}$ at 265 and 343 nm).

Synthetic α-terthienyl was obtained from Dr. P. Morand (Department of Chemistry, University of Ottawa). The synthesis of the particular supply of α-t used is described as synthesis b. in Philogène et al (1985). The purity of the batch was verified by HPLC (see 2.8). By

monitoring at lambda = 254 nm, the chromatogram yielded one peak, and the u.v. scan of this peak produced the α-t spectrum. ($lambda_{max}$ at 265 and 350 nm).

2.3 Preparation of Test Diets

The meridic diet used for all tests was prepared as described by Guthrie et al (1971). However, the antimicrosporidial agent, bicyclohexylammonium fumagillin (Fumadil B) was omitted from the test diets for the Ostrinia nubilalis growth studies, due to limitations in the supply of the additive at the time they were done. For all experiments, the concentrations of berberine and α-t in the meridic diets were 10, 31 and 100 ug/g wet weight.

For the preparation of the berberine diets, the compound was premixed with distilled water. A stock solution of 0.5 mg/ml berberine was used to prepare the 10 ug/g diets. For the 31 and 100 ug/g concentrations, berberine crystals were weighed out on an analytical balance (Mettler AE 163), and mixed with a small quanitity of water to form a slurry. The additional water for all of the berberine diets, including the control, constituted 2% of the wet weight.

For the α-t tests, a stock solution of 5 mg/ml in 95% ethanol was used in the preparation of all treated diets. Because of the high mortality observed with concentrations of ethanol greater than 1% in the diet, α-cellulose powder (Alphacel, Bioserve) was used as an inert carrier. Appropriate aliquots of α-t stock solution were pipetted

into beakers containing a measured amount of α-cellulose powder. The ethanol was allowed to evaporate overnight in darkness, or in a darkened vacuum desiccator for several hours. The amount of α-cellulose powder added to the α-t° diets, including the control, constituted 2% of the wet weight.

Quantities of warm, unsolidified meridic diet were weighed in beakers using an electronic balance. The test compounds in their inert carriers were then added to the liquid media with vigourous stirring with a glass rod. The treated diets were then poured into 1 x 1 x 1 cm cuboidal moulds and allowed to cool and set. Each of these diet cubes weighed approximately 2 grams.

2.4 Ostrinia nubilalis - Growth and Developmental Studies with Berberine and α-terthienyl

Thirty to fifty neonate larvae of uniform age (within six hours of eclosion) were placed on 2-gram cubes of the variously treated and control meridic diets in 20 ml glass scintillation vials plugged with cotton wool. After eight days, survivors were randomly chosen, weighed on an analytical balance, and individually placed on one gram (one half of a cube) of the appropriate diet. Subsequently, the larvae were weighed, and diets and vials changed at four day intervals. These experimental subjects were observed daily for metamorphosis, and the dates of these events were recorded.

Pupae were weighed one day following their formation,

in order to allow the cuticle to harden and thereby prevent unnecessary stress. Each pupa was placed in a fresh vial with a strip of moistened filter paper to maintain high humidity within the vials. The filter paper strips were remoistened daily.

Adults were weighed and sexed on the day of emergence. Mortality was noted when it occurred; escaped subjects and accidental deaths were not included in the statistical analysis.

Experiments were set up as three replicates of 10 insects per treatment for each compound. Analysis of variance with Duncan's Multiple Range Test was performed on weight data using the SAS General Linear Models Procedure. The time measurements were subjected to the Kruskal-Wallis Test (SAS NPAR1WAY Procedure), as this data was not of the form of a normal distribution. In all analyses, the level of significance was taken to be 0.05. Because of the natural differences between the sexes in weight and developmental rates, growth parameters were analyzed separately for males and females.

2.5 Diadegma terebrans - Dual-choice Tests with Hosts of the Same Chronological Age

Neonate O. nubilalis larvae were reared on test diets as described for the growth studies (2.4) until they were 11 days old. At this time, 50 insects of each of the treated and control groups were placed in designated round plastic boxes (18.5 cm diam. x 7.5 cm high) containing 25

to 30 pieces of chopped corn stalks (necessary as a host recognition cue). The boxes were covered and left overnight as described previously (2.1.2). The following morning, the two groups of larvae were uncovered and placed into the O. terebrans rearing cage, supported above the floor by two inverted glass jars (20 cm high). As these tests were performed in an open laboratory (light intensity approximately = 4 W/m^2), the larvae were left exposed to the parasitoids for five hours. However, subsequently it was observed that the searching behavior and frequency of ovipositor probing was greatly enhanced by high light intensity. For this reason, later experimental parasitizations (2.6 - 2.7) were executed within the controlled environment chamber (light intensity = 8 W/m^2).

After exposure, the larvae were removed from the corn and returned to vials containing the correct diet. Diet and vials were changed every four days until the emergence of parasitoids from their hosts, or the pupation of unparasitized O. nubilalis. The gross effects of the test compounds on parasitoid production were evaluated by taking the following ratio:

$$\frac{\text{number of parasitoids produced in the treated group}}{\text{number of parasitoids produced in the control group}}$$

This index includes only those individuals capable of procreating (adults).

2.6 *Diadegma terebrans* - No-choice Tests with Hosts of the Same Physiological Age

O. nubilalis egg masses in the black head stage were placed on test diet cubes in vials, and the neonates reared as described (2.4). The control larvae were reared until they were nine days old. At this time, 100 second instar larvae, selected within a weight range of two to seven mg, were placed on chopped corn stalks in a plastic rearing box and confined overnight to feed. The following morning, the box was uncovered and placed into the *O. terebrans* cage within the controlled environment chamber (2.1.2) and left for one hour. Following this, the larvae were removed from the corn tissue and returned to fresh vials containing the appropriate diet. No more than three larvae were placed into each vial.

For the groups of larvae treated with berberine or α-t, the age of the larvae when parasitized was chosen based on information obtained from the *O. nubilalis* growth studies. That is, the physiological status of the treated groups resembled that of the control groups at 10 days:

All controls		- 10 days
Berberine	10 ug/g	- 9 days
	31 ug/g	- 10 days
	100 ug/g	- 12 days
α-t	10 ug/g	- 10 days
	31 ug/g	- 10 days
	100 ug/g	- 14 days

Because of fluctuations in numbers, and possible physiological differences in the ichneumonid population from week to week, a separate control group was parasitized

along with each treatment group. Only one experimental group with its complementary control was parasitized each week, and the sequence for all of these experiments was as follows:

Day 1 - no parasitization
Day 2 - routine parasitization for culture
Day 3 - control group parasitized
Day 4 - treated group parasitized
Day 5 - routine parasitization for culture
Day 6 - routine parasitization for culture
Day 7 - no parasitization

A full day was left between experimental parasitizations in order to allow the female wasps to feed (they are syn-ovigenic). Thus, their ovarioles would contain mature eggs for adequate parasitization of each group of larvae.

Treated groups were parasitized in the same manner as the controls. For all groups, the rearing vials were changed weekly and fresh diet was added biweekly. Approximately 10 days after the larvae were exposed to D. terebrans, a square (25 cm^2) of paper towelling was crumpled and placed into each vial, just above, but not touching the meridic diet. This was accomplished by pinning a corner of the paper between the cotton plug and the interior neck of the vial. Parasitized larvae, and prepupal D. nubilalis would crawl into the darkness, and D. terebrans would pupate in the paper. The vials were checked daily for pupae and dead larvae. When dead D. nubilalis larvae were found, they were dissected to search for parasitoids.

D. terebrans pupae were weighed the day following their formation, to allow the cocoons to harden. Gelatin

capsules (Parke-Davis, no. 0) were used to contain the individual pupae until adult emergence, when the wasps were weighed and sexed.

Although each treatment group consisted of 100 host larvae, the number of individuals surviving exposure to D. terebrans fluctuated between experimental runs, as did the number of insects actually parasitized. Therefore, the following statistics were calculated for each treated group and compared with that for its control group:

$$\% \text{ Parasitization} = \frac{\text{total number of hosts parasitized} \times 100}{\text{number of hosts surviving experiment}};$$

$$\% \text{ Survivorship to Pupation} = \frac{\text{number of pupae} \times 100}{\text{number of hosts parasitized}}$$

$$\% \text{ Survivorship to Adult Emergence} = \frac{\text{number of adults emerged} \times 100}{\text{number of hosts parasitized}}$$

As well, the ratio of parasitoids produced in treated / control was calculated to compare with the results of the dual-choice test (2.5). This would provide information as to whether or not the absence of host choice (controls) influenced the overall success of D. terebrans with treated hosts.

For growth parameters, statistical analysis was performed separately for males and females, and each of the treatment groups was compared to its control. Pupal and adult weights were subjected to t-tests (SAS TTEST Procedure). The Kruskal-Wallis test (SAS NPAR1WAY Procedure) was used to evaluate the differences in the duration of the immature stages. Significant differences

were claimed if confidence limits exceeded 0.95. Percent parasitization data were subjected to Chi Square tests (α = 0.05).

2.7 *Diadegma terebrans* - Dual-choice Tests with Hosts of the Same Physiological Age

Ostrinia nubilalis egg masses in the black head stage were placed on test diet cubes in vials, and the neonates reared as described (2.4). The differences in days required to develop to the second instar were again taken into account when setting up the different experimental parasitisms, such that the treated group reached the physiological status of the 10-day-old control larvae on the same day (2.6). Fifty second instar larvae (2 to 7 mg) from each group (treated and control) were placed on 25 to 30 pieces of chopped corn in rearing boxes, covered, and left overnight as described previously (2.12, 2.5). The following day, the boxes were uncovered and placed into the *D. terebrans* cage within the controlled environment chamber (2.1.2). A second support ring was mounted on the retort stand inside the cage, close to the first ring, so that both the control and treated boxes were raised above the floor, adjacent to each other, but not touching. The larvae were exposed to the parasitoids for one hour, and then removed from the cage.

Larvae from both of these groups were removed from the corn and placed into mason jars on regular culture diet and reared as described (2.1.2). The jars were checked

weekly for pupae by searching through the paper towelling. Percent parasitization was calculated as follows:

$$\frac{\text{Number of parasitoids produced}}{\text{Number of parasitoids + Number of surviving hosts}} \times 100$$

These results were subjected to Chi Square tests ($\alpha = 0.05$) to determine if treatments were significantly different from controls.

2.8 Dual-choice Tests Between Untreated Second and Third Instar *Ostrinia nubilalis*

A dual-choice test was set up in which *D. terebrans* were offered a choice between 50 second instar and 50 third instar *O. nubilalis* larvae which had been reared on untreated diet. The details of the experimental design are identical to those which are described in 2.7.

2.9 HPLC Analysis for Body Burden in *Ostrinia nubilalis* and Residue in *Diadegma terebrans*

The analysis for body burdens of berberine and α-t was performed on second to third instar *O. nubilalis* larvae which had been reared from eclosion on treated diets. Before being sacrificed, the larvae were allowed to feed on fresh corn stalks for approximately 24 hours, in order to clear their guts of the treated diet. In this way, artificially high results could be avoided, and the condition of the larvae at the time of exposure to the parasitoids could be more accurately simulated. Three samples of each treatment were analyzed, with each sample

consisting of three individual larvae. The larvae were weighed, and then preserved as sample groups in 2 ml methanol.

D. terebrans adults and cocoons with meconia, reared from treated hosts, were collected on the day of adult emergence. Immediately following weighing, they were preserved in groups of three in 2 ml methanol and placed in a freezer at -4 to -6 C pending extraction. Three of such samples of wasps, and their cocoons containing meconia, were processed for each treatment.

Preliminary trials with insects injected with a known amount of berberine or α-t had shown that a fairly high efficiency (80%) could be obtained using a simple methanol extraction for both berberine and α-t. At the low concentrations expected in these samples, both of these compounds were observed to dissolve readily in solvents of moderate polarity such as methanol and acetonitrile.

The extraction protocol was as follows. Each 2 ml methanolic sample was ground to a paste using a 15 ml Wheaton homogenizer. An additional 3 ml of methanol was added, and the slurry was further homogenized. The suspension was transferred to a vial and refrigerated for 2 days at 4 C to allow the compounds to dissociate from the insect material. After this time, the samples were vortexed and centrifuged for 10 minutes at 2000 rpm to remove the solids. The supernatant was transferred to a 7 ml glass vial and evaporated to dryness under vacuum using a rotary evaporator equipped with a Wheaton adapter modified

for small vials. HPLC grade acetonitrile (0.5 ml) was then added to the dried samples, and the vials were sonicated for approximately one minute to ensure that the compounds adsorbed to the interior of the vials would be solubilized. The samples were then filtered using a millipore filter (Schleicher and Schuell, 0.45 um), and 20 ul aliquots were analyzed by HPLC.

HPLC was performed using a Beckman Series 332 gradient liquid chromatograph, equipped with a model 165 variable wavelength u.v. - vis. detector, 2 model 110A solvent delivery pumps, a model 420 system controller and a model 210 sample injection valve. The analytical columns used for both compounds were 25 cm x 4 mm (internal diameter), packed with Ultrasphere® octadecylsilicate (ODS) (reversed phase, C_{18}, pore size 5 um). A guard column preceded the analytical column in the system, and this was packed with Ultrapack® ODS (pore size 10 um).

The HPLC method employed for berberine was an ion-pairing technique modified from Asmus and Freed (1979) for catacholamines. The solvents consisted of 50% 0.1 M tricholoroacetic acid (in HPLC grade water), buffered to pH 2.15 with saturated NaOH, and 50% HPLC grade acetonitrile. Solvents were run isocratically, and the retention time for berberine with this system was 11.2 minutes. A standard curve of peak height versus berberine concentration gave a correlation coefficient of 0.987, with slope = 0.94 and y intercept = 0. Therefore, peak height was judged as an acceptable measure of concentration for experimental work.

By monitoring at lambda = 343 nm, the minimum level of detection for berberine was 0.09 ug/ml (1.8 ng in a 20 ul injection).

α-t was run isocratically with 85% HPLC grade acetonitrile and 15% water, monitored at lambda = 350 nm. The retention time was 7.0 minutes with this solvent system. A standard curve of peak height versus α-t concentration gave a correlation coefficient of 0.9997, with slope = 0.76 and y-intercept = -1.2. Therefore, peak height was an accurate measure of concentration for this compound as well. The minimum level of detection for α-t was 0.008 ug/ml (0.16 ng in a 20 ul injection), which was approximately 11 times better than that for berberine.

Insect extracts run in both solvent systems yielded very clean chromatograms (no more than two peaks), and the compounds were readily distinguishable. However, control larvae, wasps and pupal cases were also extracted and analyzed in both solvent systems, to ensure that peaks in experimental samples corresponding to the compounds' retention times were indeed phytochemicals, and not artifacts.

3.0 RESULTS

3.1 Ostrinia nubilalis - Growth and Developmental Studies

3.1.1 Berberine

Concentrations of 31 and 100 ug/g berberine in larval diets reduced growth rates, and larval weights were significantly lower than the controls in the 100 ug/g group throughout much of the larval period (Figure 3). In addition, there was notable enhancement of the growth rate in the 10 ug/g group, which was significantly different from the controls on day 20. The 31 ug/g curve falls slightly beneath the control curve, but larval weights at any particular time interval were not significantly different from controls.

The growth parameters recorded for the berberine treatments are summarized in Table 4. With 31 and 100 ug/g berberine in the diet, there were corresponding increases in the number of days to pupation for both males and females, but these observations were not significantly different from the control group. Similar trends were observed in the number of days to adult emergence with 31 and 100 ug/g berberine. However, in the 10 ug/g treatment group, there appeared to be a hastening effect in days to pupation and adult emergence.

Pupal weights were not markedly affected by berberine in the diet. However, the mean pupal weight of the females, but not males, in the 100 ug/g group (85.3 mg) was significantly lower than that of the controls (100.4

Figure 3

Larval growth curves for Ostrinia nubilalis fed diets containing 0 (●), 10 (▲), 31 (■) and 100 (O) ug/g berberine. Log mean weight (mg) is plotted against time (days). Males and females were grouped together for these plots. Measurements ended when the number of larvae not pupated in one or more of the treatment groups was too low to provide reliable information.

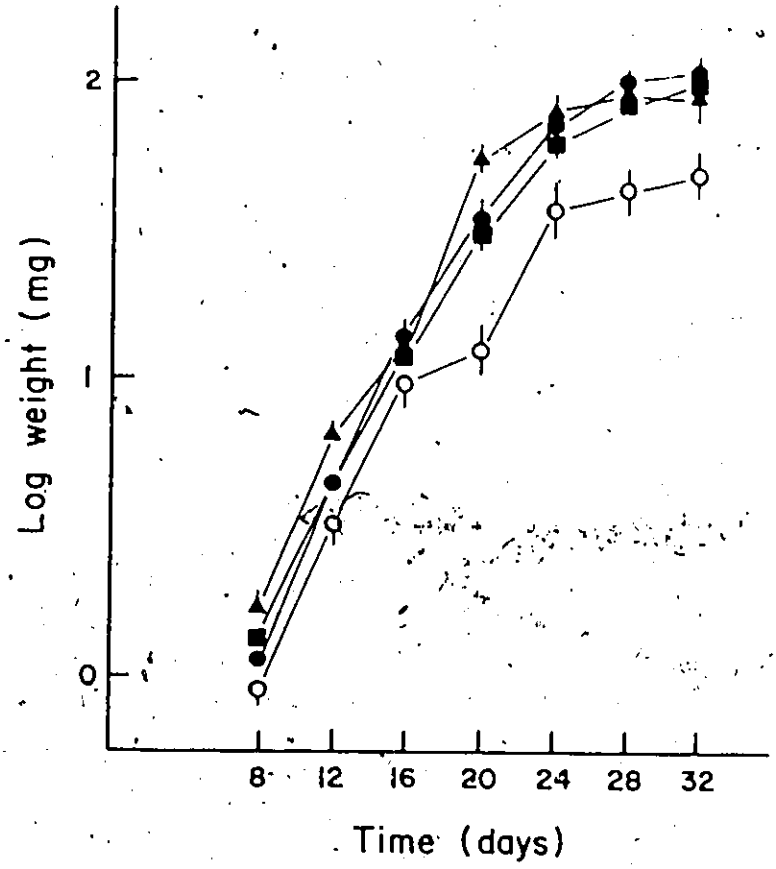

Log weight (mg)
2
1
0
8
12
16
20
24
28
32
Time (days)

Table 4

Effects of Dietary Berberine on Growth Parameters of Ostrinia nubilalis

Berberine Concentration (ug/g)	Mean Time (days) to Pupation		Mean Pupal Weight (mg)		Mean Time (days) to Adult Emergence		Mean Adult Weight (mg)	
	M	F	M	F	M	F	M	F
0	31.9	35.3	77.2a	100.4a	41.7	44.1	40.8a	53.3a
10	30.9	31.4	77.3a	93.6ab	41.6	40.9	40.8a	58.2a
31	34.9	36.8	74.8a	96.3ab	45.3	45.9	41.4a	60.2a
100	39.3	40.0	70.4a	85.3b	49.7	49.4	39.8a	52.8a

Time measurements were subjected to the Kruskal-Wallis test. Underlined values would indicate that treatments values are significantly different from control values ($p = 0.05$). Weight measurements were subjected to Duncan's Multiple Range test. Means in columns followed by the same letter are not significantly different at $p = 0.05$.

mg). Data for adult weights did not yield significantly different results with berberine treatments.

When survivorship statistics were considered (Table 5), adverse effects were apparent only with 100 ug/g berberine in the diet. At this concentration, only 61% (corrected as percent of control) of the larvae developed to the pupal stage. A subsequent decrease was seen in survival to adult emergence, with just 56% of the 100 ug/g group successfully reaching adulthood. Surprisingly, survivorship was somewhat improved in the larvae exposed to 10 and 31 ug/g berberine in the diet. Five percent and nine percent more of the 10 and 31 ug/g larvae, respectively, pupated successfully, but survival to adult emergence was approximately equal to that in the controls. The sex ratio of the surviving adults in most groups was roughly 50% female. However, an exception was seen in the 31 ug/g group, with a sex ratio biased in favour of females (F/T = 0.71). This may have influenced the position of the larval growth curve for this treatment concentration (Figure 3), as females are normally heavier than males.

Table 5

Survival of Ostrinia nubilalis Larvae Fed Berberine-treated Diets

Berberine Concentration (ug/g)	Survival to Pupation %	Survival to Pupation % of Control	Survival to Adult Emergence %	Survival to Adult Emergence % of Control	Sex Ratio (F/T) of Surviving Adults
0	85	100	81	100	0.48
10	89	105	82	101	0.52
31	93	109	83	102	0.71
100	52	61	45	56	0.54

3.1.2 α-terthienyl

As was the case for berberine, the effect of α-t in reducing larval development was made clearly evident by the larval growth curves (Figure 4). At 100 ug/g α-t, larval weights throughout the developmental period were significantly lower than the controls. The 10 and 31 ug/g groups did not show significant differences from the controls, although slight stimulation was visible in the 10 ug/g group, as was slight growth inhibition in the 31 ug/g larvae.

Growth parameters for the α-t treatments are presented in Table 6. Sublethal effects were more apparent with this compound as compared to berberine. The preimaginal development of O. nubilalis was significantly prolonged with 100 ug/g α-t in the diet. At this dosage, the mean number of days to pupation was 30.7 for the males and 37.7 for the females, compared to the controls, with 23.7 and 24.8 days for males and females, respectively. With the 10 and 31 ug/g α-t diets, no significant differences were observed in time to pupation.

The number of days to adult emergence yielded similar results in the 100 ug/g treatments. Both males and females required significantly more time to reach adulthood - 39.9 and 46.0 days for males and females, respectively, compared to 32.9 and 31.2 days for the controls. Again, with 10 ug/g α-t, there were no significant differences from the controls. However, in the 31 ug/g group, the

Figure 4

Larval growth curves for Ostrinia nubilalis treated with 0 (●), 10 (▲), 31 (■) and 100 (◘) ug/g α-terthienyl in the diet. Log mean weight is plotted against time (days). Males and females were grouped together for these plots. Measurements ended when the number of larvae not pupated in one or more of the treatment groups was too low to provide reliable information.

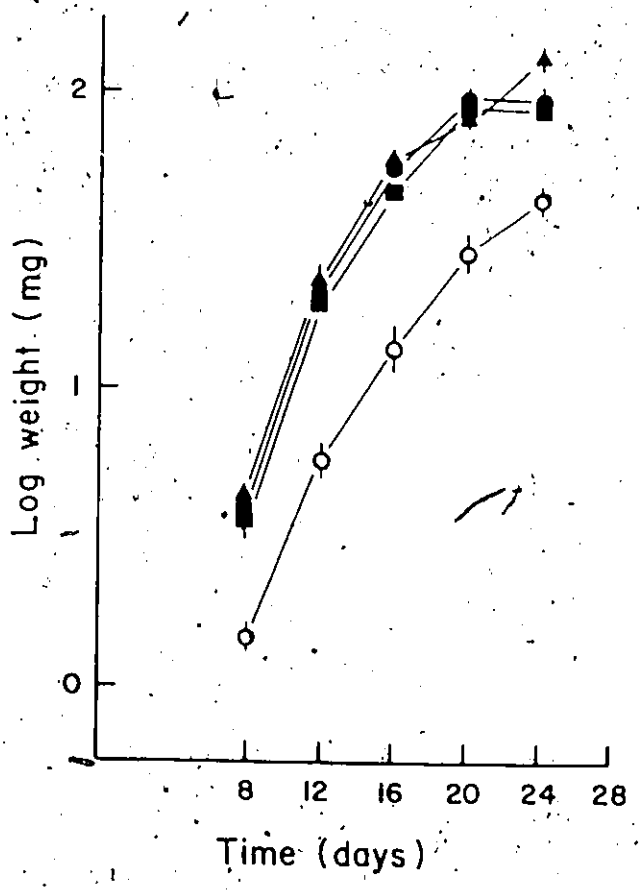

Log weight (mg)
2
1
0
8
12
16
20
24
28
Time (days)

Table 6

Effect of Dietary α-terthienyl on Growth Parameters of Ostrinia nubilalis

α-t Concentration (ug/g)	Mean Time to Pupation (days)		Mean Pupal Weight (mg)		Mean Time to Adult Emergence (days)		Mean Adult Weight (mg)	
	M	F	M	F	M	F	M	F
0	23.7	24.8	77.7a	98.3a	32.9	31.2	36.7a	60.3a
10	22.2	23.5	76.0a	100.1a	30.9	31.9	35.8a	60.2a
31	22.7	24.7	71.9a	95.2a	31.3	33.3	34.8a	54.9a
100	30.7	37.7	62.2b	65.5b	39.9	46.0	27.7b	27.7b

Time values were subjected to the Kruskal-Wallis test. Underlined values are significantly different from controls at p = 0.05. Weight values were subjected to Duncan's Multiple Range Test. Means in columns followed by the same letter are not significantly different at p = 0.05.

number of days to adult emergence for the females (3.3.3) was significantly increased compared to that for control females (31.2).

Pupal weights were not significantly affected by 10 and 31 ug/g α-t in the diet, although they decreased slightly with increasing concentration. At 100 ug/g α-t, the mean pupal weights were significantly reduced (62.2 mg for males and 65.5 mg for females) compared to the controls (77.7 and 98.3 mg for males and females respectively). The same trends were observed for mean adult weights. At 10 and 31 ug/g, there were gradual reductions in weight with increasing concentration. However, these were not significant with respect to the controls until the 100 ug/g treatment, where mean adult weights of both males and females were 27.7 mg, compared to control means of 36.7 mg for males and 60.3 mg for females.

Mortality effects on O. nubilalis treated with α-t (Table 7) were not as variable as that for the berberine treatments. Rather, at 10 ug/g, survival to pupation was identical to that in the controls, and 97% (corrected as percent of control) of this group developed successfully to adulthood. Survivorship declined somewhat with the 31 ug/g treatment, with 97% of the larvae reaching pupation and 89% surviving to adulthood. At 100 ug/g, only 71% of the larvae reached pupation and emerged as adults, but the degree of mortality with α-t at this concentration was still not as severe as that observed with 100 ug/g

Table 7

Survival of Ostrinia nubilalis Larvae, Fed α-terthienyl-treated Diets

α-t Concentration (ug/g)	Survival to Pupation %	Survival to Pupation % of Control	Survival to Adult Emergence %	Survival to Adult Emergence % of Control	Sex Ratio (F/M) of Surviving Adults
0	93	100	93	100	0.52
10	93	100	90	97	0.50
31	90	97	83	89	0.52
100	66	71	66	71	0.47

berberine.

The sex ratio of surviving adults was not affected by any concentration of α-t in the diet. The numbers of males and females were approximately equal in all treatments, and in the controls.

3.2 Diadegma terebrans - Dual-choice Tests with Hosts of the Same Chronological Age

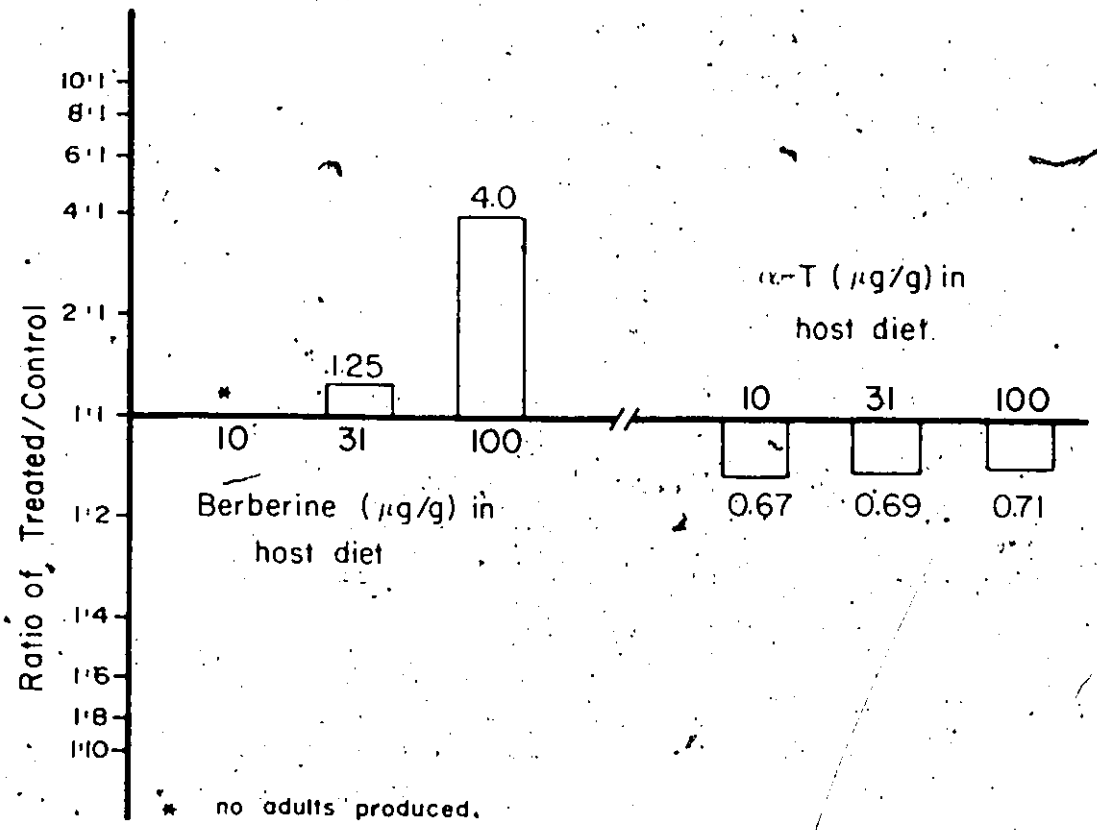
These tests indicated that the presence of berberine in the diet of the hosts generally enhanced parasitism by D. terebrans, while α-t inhibited the overall success of the parasitoids (Figure 5). At 31 and 100 ug/g berberine in the diet, the ratios of treated / control progeny were 1.25 and 4.0, respectively, demonstrating a preference on the part of D. terebrans females for the treated hosts. The T/C ratio of zero for the 10 ug/g berberine experiment suggests that the gravid females preferred the controls when given the choice. Of the few treated larvae that were parasitized, none emerged as adults.

With α-t, all of the T/C ratios obtained were less than one (0.67, 0.69 and 0.71 for the 10, 31 and 100 ug/g experiments, respectively). These ratios would be expected if D. terebrans females were less attracted to the treated hosts, or if they were selectively ovipositing in hosts which proved to be unsuitable in the long term.

Figure 5

Dual-choice Tests - Ratio of Parasitoids Produced in Treatment / Control

Only surviving adults were included in these calculations. Bars represent T/C ratios plotted on log scale. Actual values of ratios appear on the y axis. Positive values indicate that a beneficial effect was conferred by the treatment compared to the control; negative values indicate an adverse effect.


Ratio of Treated/Control
10:1
8:1
6:1
4:1
2:1
1:1
1:2
1:4
1:6
1:8
1:10
4.0
1.25
*
10
31
100
Berberine (μg/g) in host diet
α-T (μg/g) in host diet
10
31
100
0.67
0.69
0.71
* no adults produced.

3.3 *Diadegma terebrans* - No-choice Tests with Hosts of the Same Physiological Age

3.3.1 Effects of Berberine

Berberine in the diet of the host did not markedly affect the developmental parameters of *D. terebrans* (Table 8). This was not unexpected in view of the fact that this compound produced few sublethal effects on growth and development in *D. nubilalis* (3.1.1). In fact, at the 31 ug/g concentration, the mean pupal weight of male wasps (31.0 mg) was significantly higher than that obtained for the control males (25.8 mg). Further, at 31 ug/g, developmental rates (days to pupation and adult emergence) were slightly accelerated compared to the controls, but these differences were not significant. Mean adult weights in the 31 ug/g group were slightly increased as well, but again were not significantly different from controls. In the 10 and 31 ug/g experiments, no significant differences were found between treated and control developmental parameters, and no trends in developmental parameters were apparent.

However, survivorship rates in *D. terebrans* developing within berberine-treated hosts were generally reduced (Table 9). In fact, survivorship to pupation decreased in all treated groups compared to their controls. Survivorship to adult emergence was also diminished with 10 and 100 ug/g berberine in the diet, but at 31 ug/g, survivorship to adult emergence was improved by the

Table 8

Diadegma terebrans - Growth Parameters with Berberine Administered to Host Larvae

Dietary Berberine Concentration	Mean Time (days) to Pupation		Mean Pupal Weight (mg)		Mean Time (days) to Adult Emergence		Mean Adult Weight (mg)	
(ug/g)	M	F	M	F	M	F	M	F
10	17.6	18.2	28.3	28.5	28.1	29.5	9.0	9.6
Control	16.7	16.8	29.2	32.2	27.4	28.4	8.9	10.7
31	16.0	17.2	<u>31.0</u>	31.3	26.5	27.8	9.7	10.3
Control	16.9	18.0	<u>25.8</u>	32.3	27.3	28.6	8.3	10.0
100	18.4	18.8	27.9	31.2	28.9	30.4	8.6	9.6
Control	17.7	19.6	26.6	28.1	28.1	30.1	8.4	9.2

Weight values were subjected to t-tests. Time values were analyzed by the Kruskal-Wallis test. Underlined values indicate significant differences between treatment and control at $p = 0.05$.

Table 9

Diadegma terebrans - Survivorship with Berberine Treatment of Host Larvae

Dietary Berberine Concentration (ug/g)	Survival to Pupation %	% of Control	Survival to Adult Emergence %	% of Control	Sex Ratio (F/T) of Surviving Adults
10	76	93	52	75	0.40
Control	82		69		0.44
31	88	94	81	107	0.39
Control	94		76		0.20
100	77	88	61	75	0.41
Control	88		81		0.36

berberine treatment compared to that in the control group by 7%. A fair amount of mortality normally occurs in the pupal stage, as observed in the three control groups. In the 31 ug/g experiment, the drop in survivorship from pupation to adulthood was much more severe in the control group (94% to 76%) compared to the treated group (88% to 81%).

In all experimental groups, the sex ratio of the surviving adults was fairly close to 40% female, with the exception of the control for the 31 ug/g experiment (F/T = 0.20). It is possible that 31 ug/g berberine in the diet of the host enhanced the growth and survivorship of D. terebrans, as suggested by the significant increase in mean pupal weight of the males, and the other subtle differences in growth parameters discussed previously. However, the rather high mortality in the pupal stages and the unusual sex ratio in the survivors suggest an unusual amount of variability in this particular control group.

3.3.2 Effects of α-terthienyl

Unlike berberine, the effects of α-t in the diet of the host on growth and development of D. terebrans were clearly visible (Table 10). With 100 ug/g α-t, the mean pupal weight of the males was significantly lower than that of the controls (22.1 mg for the 100 ug/g treatment, compared to 31.5 mg for the control group). No females were produced at this concentration. The mean adult weight (of males) was also significantly reduced with 100 ug/g

Table 10

Diadegma terebrans - Growth Parameters with α-terthienyl Administered to Host Larvae

Dietary α-t Concentration (µg/g)	Mean Time (days) to Pupation		Mean Pupal Weight (mg.)		Mean Time (days) to Adult Emergence		Mean Adult Weight (mg.)	
	M	F	M	F	M	F	M	F
10	17.6	19.6	26.8	29.8	28.2	30.6	8.1	9.8
Control	18.1	18.3	29.9	32.9	28.6	29.4	8.9	10.2
31	18.2	17.8	26.0	31.6	28.3	28.6	8.2	10.5
Control	17.5	19.1	26.9	33.3	27.6	29.9	8.4	11.4
100	20.8	Nil	22.1	Nil	30.8	Nil	7.3	Nil
Control	17.8	19.1	31.5	31.6	28.4	30.3	9.5	9.9

Weight values were subjected to t-tests. Time values were analyzed by the Kruskal-Wallis test. Underlined values indicate significant differences between treatment and control at $p = 0.05$. Nil = no females produced in this group.

α-t (7.3 mg) compared to the controls (9.5 mg). At 10 and 31 ug/g, growth parameters were not significantly different between treated and control groups. However, at both of these concentrations, mean pupal and adult weights of both males and females tend to be slightly diminished compared to controls.

The effects of α-t on the incidence of mortality in D. terebrans (Table 11) were much more severe than that observed for the berberine treatment (3.3.1). With 100 ug/g α-t in the diet, survival to pupation was only 43% (corrected as percent of control). Mortality at 31 ug/g α-t was less severe, with 80% of the parasitoids surviving to pupation. However, with α-t at 10 ug/g in the diet, survivorship to pupation was somewhat improved (by 3%). These same trends were also apparent in percent survival to adult emergence.

Sex ratios in most experimental groups were close to 40% female, with two exceptions. The 100 ug/g group produced only males, possibly because the females were more susceptible to the lipophilic toxin. The second exception was, surprisingly, the control group for the 31 ug/g experiment, which yielded a sex ratio of 0.25 (F/T). In this group, the incidence of mortality in the larval and pupal stages was not particularly unusual - 95% of the larvae survived to pupation and 84% emerged as adults. As a reasonable explanation for the low sex ratio cannot be gleaned from the data, it is assumed to be accidental.

Table 11

Diadegma terebrans - Survivorship with α-terthienyl Treatment of Host Larvae

Dietary α-t Concentration (ug/g)	Survival to Pupation %	% of Control	Survival to Adult Emergence %	% of Control	Sex Ratio (F/T) of Surviving Adults
10	92	103	77	104	0.37
Control	89		74		0.46
31	76	80	65	77	0.41
Control	95		84		0.25
100	38	43	25	33	all female
Control	88		76		0.40

3.3.3 Host Selection Effects and Parasitoid Success

The effects of berberine and α-t on host selection by D. terebrans were clearly shown by the parasitization rates obtained in these no-choice experiments (Figure 6). With berberine, there were no significant differences from the control rates at any of the concentrations tested. With α-t, parasitization rates were not significantly different between the 10 and 31 ug/g treatment groups and controls. However, with 100 ug/g α-t, a significant reduction was apparent in the parasitization rate (35%) compared to that of the control group (79%).

The overall success of D. terebrans with hosts reared on diets containing berberine and α-t was measured by the ratio of treated / control progeny reaching adulthood (Figure 7). In contrast to the dual-choice results (3.2), berberine decreased parasitoid production at all concentrations tested. The calculated T/C ratios for 10, 31 and 100 ug/g berberine were 0.56, 0.52, and 0.82, respectively. This suggests that the design of the two experiments (dual-choice and no-choice) revealed different behavioral aspects of D. terebrans with respect to host selection. The control larvae were not attractive to gravid females when berberine-treated hosts were presented at the same time (the dual-choice tests). However, when no alternatives were present (the no-choice tests), control hosts were parasitized at the same rate as the treated hosts, and the toxicity of berberine was manifested as a

Figure 6

Percent Parasitization in No-choice Tests

Separate control groups were run for each treatment. Control larvae were not exposed to Diadegma terebrans concurrently with treated larvae. Bars represent percentages of larvae surviving exposure to D. terebrans which had been parasitized. The asterisk denotes where the treatment is significantly different from control, by the Chi Square test at $\alpha = 0.05$.

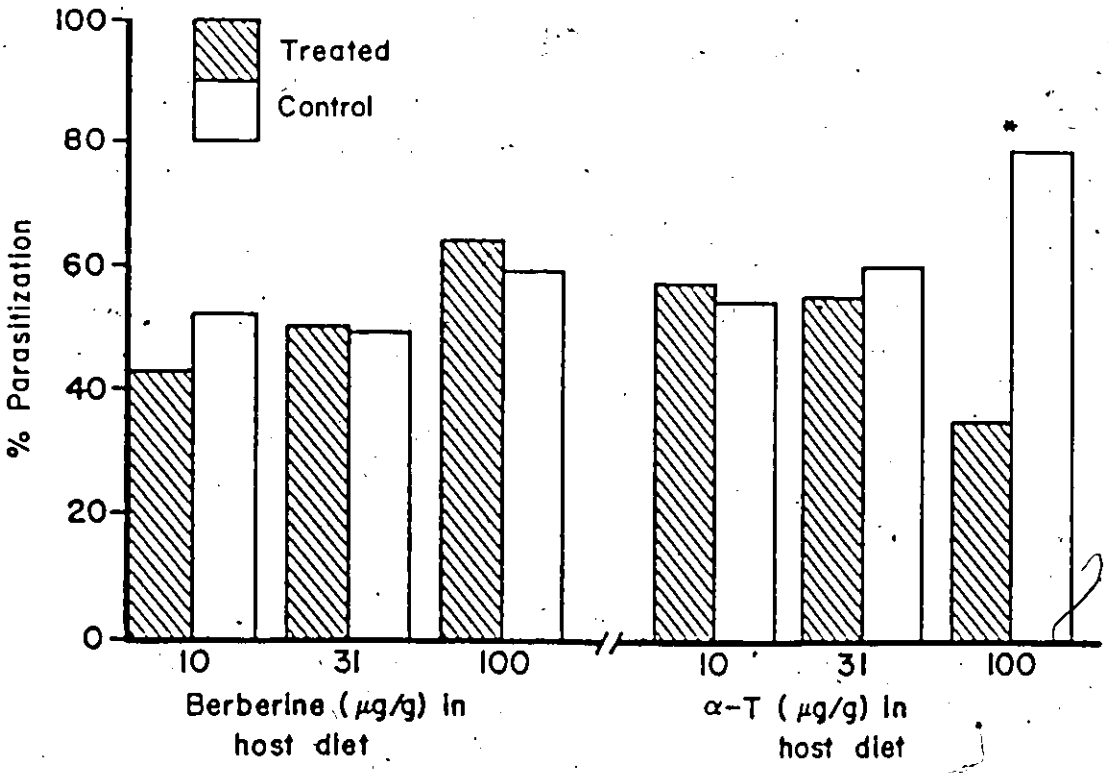
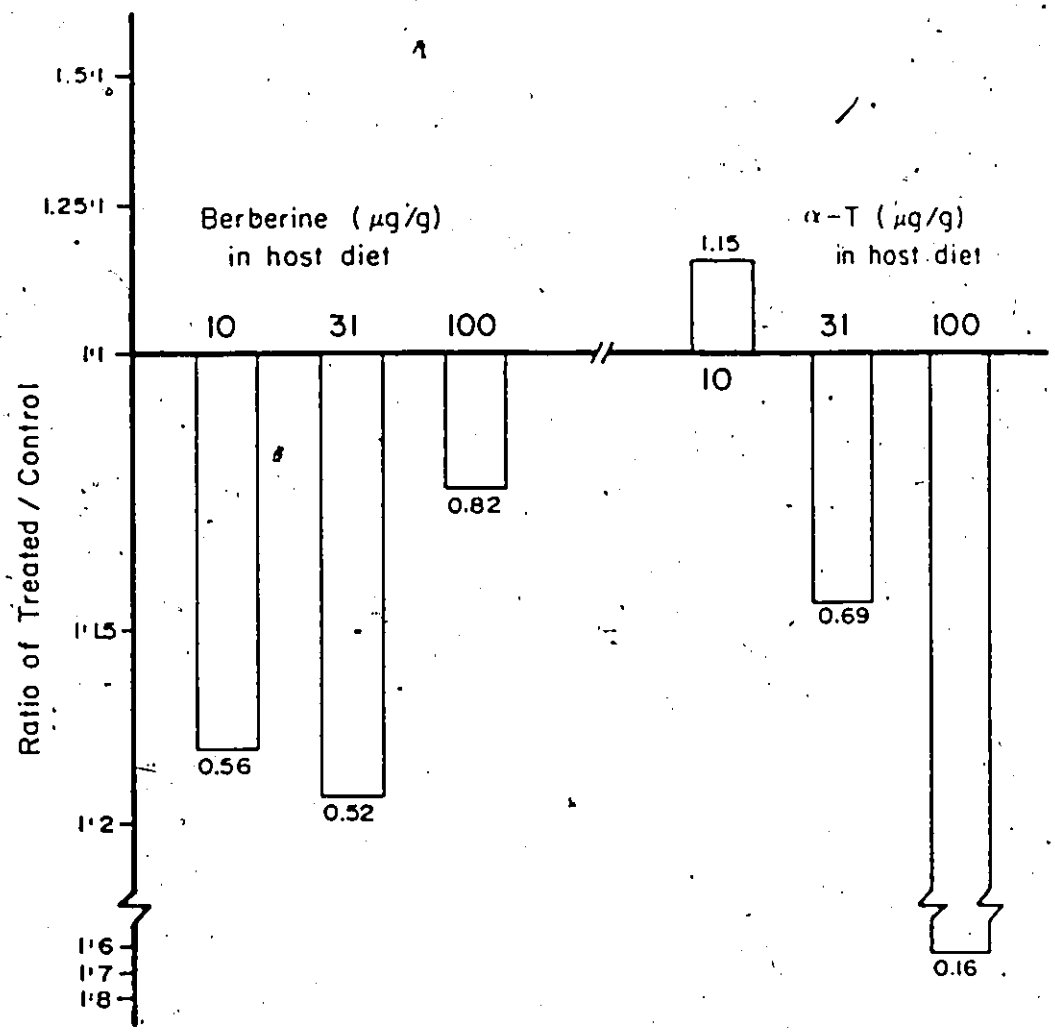

100
80
60
40
20
0
% Parasitization
Treated
Control
10
31
100
10
31
100
Berberine (µg/g) in host diet
α-T (µg/g) in host diet

Figure 7

No-choice Tests - Ratio of Parasitoids Produced in Treatment / Control

Only surviving adults were included in these calculations. Bars represent T/C ratios plotted on log scale. Actual values of ratios appear on the y axis. Positive values indicate that a beneficial effect was conferred by the treatment compared to the control; negative values indicate an adverse effect.


Ratio of Treated / Control
1·5
1·25
1·1
1·1
1·5
1·2
1·6
1·7
1·8
Berberine (μg/g) in host diet
10
31
100
0.56
0.52
0.82
α-T (μg/g) in host diet
1.15
10
31
100
0.69
0.16

lower yield of new parasitoid adults in the treated groups.

With α-t, the T/C ratios for 10, 31 and 100 ug/g were 1.15, 0.69 and 0.16, respectively, in the no-choice situation. In this case, the 10 ug/g treatment group was at an advantage as compared to the controls, while parasitoid production was reduced in the higher concentration groups (31 and 100 ug/g) as compared to the controls.

3.4 Diadegma terebrans - Dual-choice Tests with Hosts of the Same Physiological Age

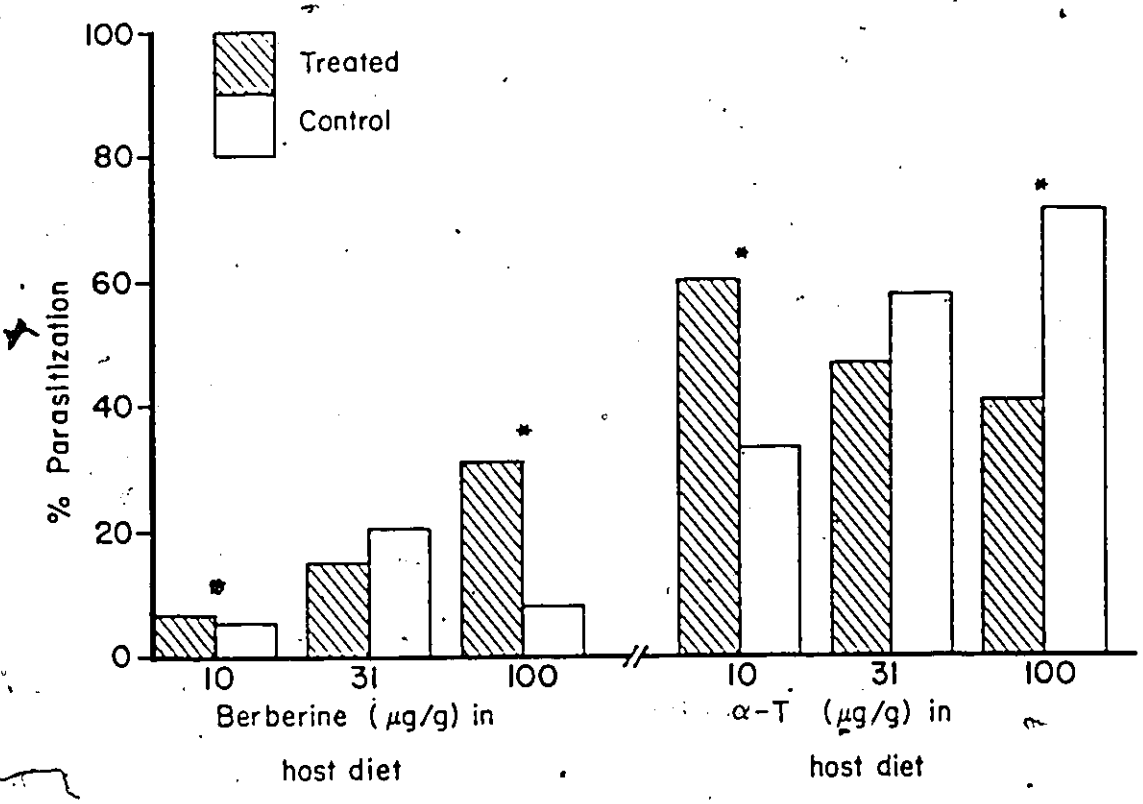
In these tests, unlike the initial dual-choice experiments (3.2), parasitization rate was isolated from both the growth altering aspects of berberine and α-t towards O. nubilalis, and their toxic effects on D. terebrans developing within hosts feeding on diets containing these compounds. The results of these experiments show some marked effects on host selection by female parasitoids (Figure 8). With berberine, percent parasitization was not significantly different with concentrations of 10 and 31 ug/g in the diet, as compared to controls. However, a distinct preference was exhibited for larvae treated with berberine at 100 ug/g over hosts reared on control diets. 31.3% of the 100 ug/g group were parasitized, as compared to 7.9% of the controls.

With α-t, on the other hand, larvae treated with diets containing 10 ug/g of the compound were distinctly preferred over the controls. Parasitization was 60% for

Figure 8

Percent Parasitization in Dual-choice Tests with Hosts of the Same Physiological Age

Separate control groups were run for each treatment. Control larvae were exposed to Diadegma terebrans concurrently with treated larvae. Bars represent percentages of larvae surviving exposure to D. terebrans which had been parasitized. The asterisks denote where treatments are significantly different from controls by the Chi Square test at $\alpha = 0.05$.


100
80
60
40
20
0
% Parasitization
Treated
Control
10
31
100
10
31
100
Berberine (μg/g) in host diet
α-T (μg/g) in host diet

the 10 ug/g α-t-fed larvae, as compared to 40% for the controls. With 31 ug/g α-t, percent parasitization was not significantly different from the control group. However, in the 100 ug/g experiment, a significant preference for the control group was observed: 71.4% in the controls, compared to 40.7% in the group treated with 100 ug/g α-t.

3.5 Dual-choice Test Between Untreated Second and Third Instar *Ostrinia nubilalis*

When 50 second and 50 third instar untreated *O. nubilalis* larvae were exposed for parasitism by *D. terebrans*, a similar number of parasitoid pupae were produced in each group (8 and 7 for second and third instar larvae, respectively). However, the third instar larvae suffered much higher mortality due to mutilation (44%, compared to 16% for second instars), possibly because they were more aggressive and had to be probed or stung repeatedly before oviposition could be accomplished.

The outcome of this test seems to suggest that third instar hosts are somewhat less suitable for parasitism by *D. terebrans* as compared to second instar hosts.

3.6 HPLC Analysis for Body Burden in *Ostrinia nubilalis* and Residue in *Diadegma terebrans*

Berberine was not detected in any of the treated second and third instar host larvae 24 hours after transfer to untreated diet (corn). Neither extracts of adult parasitoids nor pupal cases with meconia contained berberine at the level of detection available (1.8 ng in a 20 ul injection).

The α-t-treated insects yielded very different results (Table 12). After feeding on fresh corn stalks for 24 hours, α-t was still present in second and third instar *O. nubilalis* which had been previously reared on diets containing 31 and 100 ug/g α-t, with 0.31 and 0.05 ug per gram insect, respectively. Larvae of the 10 ug/g group did not contain detectable levels of α-t. The comparatively low levels of α-t in the 100 ug/g larvae relative to the 31 ug/g samples is understandable, considering that α-t at 100 ug/g in the diet is a potent feeding deterrent for *O. nubilalis* (Champagne, 1984): less was accumulating because less was being consumed.

α-t was present in adult wasps reared from hosts fed diets containing 10 and 31 ug/g α-t (0.53 and 0.20 ug/g, respectively), but was not present in the 100 ug/g samples. However, cocoons from all α-t treatments contained detectable levels of α-t. Quantities were highest in the 10 ug/g treatment (4.17 ug α-t per gram pupal case), followed by the 100 ug/g treatment (3.19

Table 12

Quantification of α-terthienyl in Insect Samples

Treatment Concentrations	10 ug/g	31 ug/g	100 ug/g
Host Larvae	n.d.	0.31 (0.257)	0.05 (0.074)
Adult Parasitoids	0.53 (0.335)	0.20 (0.286)	n.d.
Cocoons + Meconia	4.17 (2.97)	0.23 (0.023)	3.19 (1.68)

Units are in ug/g insect material. Values are means of three samples. Standard deviations are in brackets.
n.d. = not detected at lowest level of detection.

ug/g). The 31 ug/g samples contained the least amount of α-t (0.23 ug/g).

In addition, a metabolite of α-t was present in all of the insect samples analyzed. This polar compound (retention time 1.7 minutes) produced a thiophene spectrum (Figure 9). As the structure and extinction coefficient of this metabolite is not yet known, absolute quantification was not possible. However, relative quantities in peak height (mm) per mg insect material have been determined (Table 13). Samples of larvae in the 10 ug/g group contained slightly more of the metabolite (0.07 mm/mg) than the 100 ug/g samples (0.06 mm/mg), while the 31 ug/g samples contained the least amount (0.03 mm/mg). The same trend was visible in the wasps, with 0.14, 0.08 and 0.12 mm/mg insect in the 10, 31 and 100 ug/g groups, respectively. The samples of cocoons with meconia did not follow this trend. The metabolite was in highest quantity in the 31 ug/g samples (0.51 mm/mg), followed by the 10 and 100 ug/g samples (0.39 and 0.33 mm/mg, respectively).

Figure 9

Absorption Spectrum of α-t Metabolite

Relative absorbance is plotted against wavelength (nm).

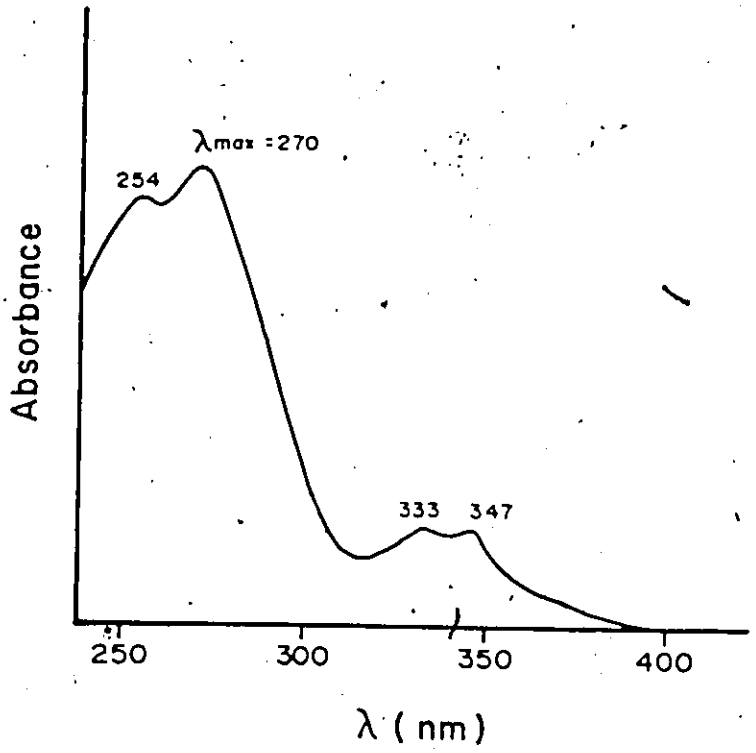

λmax =270
254
333
347
Absorbance
250
300
350
400
λ (nm)

Table 13

Relative Quantities of α-t Metabolite in Insect Samples

Treatment Concentrations	10 ug/g	31 ug/g	100 ug/g
Host Larvae	0.07 (0.033)	0.03 (0.008)	0.06 (0.013)
Adult Parasitoids	0.14 (0.043)	0.08 (0.013)	0.12 (0.112)
Cocoons + Meconia	0.39 (0.269)	0.51 (0.327)	0.33 (0.244)

Units are in peak height (mm)/mg insect material. Values are means of three samples. Standard deviations are in brackets.

4.0 DISCUSSION

The compounds investigated in the present study produced different effects on the host-parasitoid system under study. These effects will be discussed in order of physiological to ecological considerations, followed by their relevance to field applications.

4.1 Physiological Considerations

4.1.1 Gross Effects of Berberine and α-terthienyl

Berberine in the diet of Ostrinia nubilalis had no significant effects on the growth parameters of surviving insects at the concentrations tested (3.1.1). Yet, at the maximum concentration (100 ug/g), survivorship decreased dramatically. A quaternary ammonium salt would be expected to be readily excreted at sublethal concentrations (Bodor et al, 1981), and this is consistent with the absence of detectable levels of berberine in larvae which had been reared on berberine-containing diets, and then allowed to feed for 24 hours on fresh corn (3.6). However, when dosages beyond particular threshold concentrations are administered, the toxicity of berberine is manifested, and mortality is the result.

Diadegma terebrans did not succumb to berberine to the same extent as the unparasitized hosts (3.1.1). Increased mortality was observed with 100 ug/g berberine in the host diet, but this was not nearly as severe as that for O. nubilalis. This may suggest that the compound is removed

from the host environment rapidly enough so as not to affect severely the endoparasitoid. Evidence for this possibility includes the observation that berberine was not detected in emerged adult wasps or their pupal cases (3.6). This may suggest that the mortality observed in D. terebrans was indirect - resulting from host intoxication and the reduction in quality of the host as a food source - rather than a direct effect of the compound on the parasitoid. This type of indirect effect has been observed with the conventional insecticides disulfoton and parathion with the greenbug parasitoid Lysiphlebus testaceipes (Lingappa et al, 1972).

The physiological effects of α-terthienyl were markedly different from those induced by berberine. With 100 ug/g α-t in the diet, sublethal effects were apparent in growth and developmental parameters of D. nubilalis (3.1.2), but mortality was less severe than that which occurred with the berberine treatment. However, for D. terebrans (3.3.2), survivorship decreased with 31 ug/g α-t in the diet of the host, and with 100 ug/g, very few of the parasitoids, none of which were female, survived to adulthood. Of the surviving males, pupal and adult weights were significantly reduced.

It is well known that highly lipophilic compounds tend to accumulate in the fatty tissues of organisms (McEwen and Stephenson, 1979). The lipophilicity of α-t (log p = 5.6) (McLachlan, 1984) is close to that for the organochlorine insecticide DDT (log p = 6.0). α-t would

be expected to accumulate in the fatty tissues of O. nubilalis, and this was in fact observed by the detection of α-t and its metabolite in larvae removed from α-t diets to corn for 24 hours (3.6). Since O. terebrans consumes the entire host insect with the exception of the cephalic capsule prior to pupation, a substantial dose of α-t would be expected to be ingested within a short period of time, resulting in high mortality during the later instars and pupal stage. This is validated by the presence of α-t and its metabolite in adult wasps and their pupal cases derived from α-t-fed host larvae (3.6). Thus, the low survivorship rates obtained for O. terebrans within hosts fed α-t most probably resulted from a combination of direct toxicity to the endoparasitoid, and indirect mortality due to host intoxication.

Examples of differential toxicity towards parasitized and unparasitized host insects have also been reported with conventional insecticides. Oriental fruit moth (Dacus dorsalis) larvae, when parasitized by Opius oophilus, were less susceptible to parathion, but more sensitive to aldrin, dieldrin, endrin, chlordane and lindane (Tamashiro and Sherman, 1955). The alfalfa weevil, Hupera postica, was more susceptible to carbofuran, methyl parathion, Supracide® and methoxychlor when its internal parasitoid Microtonus aethiops was in the larval stages (Dumbre and Hower, 1976).

The information gained from the present study suggests that the toxicity of naturally-occurring insecticidal

compounds towards endoparasitoids is related to their persistence in the host insect. Experience with conventional insecticides reveals that host-parasitoid associations must be examined separately with the compound of interest in order to assess the costs and benefits for biological control agents.

4.1.2 Bioaccumulation and Metabolism

In spite of the differences between the detection efficiencies of berberine and α-t (1.8 and 0.16 ng in a 20 ul injection, respectively), an estimated minimum bioaccumulation of 1.9 ug berberine per gram insect material can still be detected by HPLC. This is not present even in the pupal cases, where hydrophilic wastes are excreted as meconia by the metamorphosing parasitoids. With α-t, the concentrations of the lipophilic parent compound in the pupal cases exceeded this value in the 10 and 100 ug/g sample groups. Therefore, it is reasonable to assume that berberine is excreted by the host insect before it reaches the developing endoparasitoid. The relatively innocuous effects of berberine on parasitoid survivorship (3.3.1) compared to that for Q. nubilalis (3.2.1) provides further validation for this assumption.

The quantities of α-t in the 10 ug/g wasps and pupal cases relative to host body burden after 24 hours not feeding on α-t suggest that the compound bioaccumulated in the parasitoids at this concentration in the diet of the host. Some detoxification occurred, as is evidenced by the

sequential increase in metabolite concentration from hosts to wasps to pupal cases.

In the parasitoids reared from hosts fed 31 ug/g α-t, there was a decrease in α-t concentration relative to the hosts, which indicates a much higher rate of detoxification during parasitoid development. This is corroborated by the relatively low levels of metabolite found in the hosts and wasps, and the comparatively high levels in the pupal cases - likely excreted by the developing adults. Natural products have been shown to increase the activity of detoxification enzymes in herbivorous insects (Brattsten et al, 1977; Yu et al, 1979; Berry et al, 1980). This type of induction has not yet been reported for endoparasitoids of hosts exposed to insecticidal compounds. However, exposure to insecticides via host feeding would select for parasitoids with increased resistance to the compound in question.

In the 100 ug/g α-t group, the concentration of the parent compound was decreased in the wasps compared to the hosts, yet a marked increase was apparent in the pupal cases. The metabolite concentration with this treatment increased from hosts to wasps, and further increased in the pupal cases. These patterns suggest that the parasitoids surviving this treatment were superior with respect to their detoxification capabilities. Because of the extremely low survivorship in D. terebrans with this treatment (only 25% survived to adult emergence), the ability to detoxify α-t was likely not the result of induction, but was segregated

in this group as a consequence of selection pressure.

4.2 Host Selection Effects of Berberine and α-terthienyl Towards Diadegma terebrans

The system of parasitism used for these experiments obviously eliminates the habitat finding step in host selection by D. terebrans. As with many parasitoids, the presence of the host plant (corn in this case) provides necessary visual and tactile cues for searching and examination behavior. In addition, host haemolymph and frass derived from corn contain necessary chemical stimuli for ovipositor probing (Galeota, 1991). The specific kairomone(s) involved is extractable in hexane, chloroform and chloroform-methanol, but was never identified.

Berberine in the diet of the host did not interfere with the parasitization efficiency of D. terebrans. In the no-choice tests using hosts of the same physiological age (3.3.3), there were no significant differences between the parasitization rates of larvae previously reared on berberine diets and larvae fed control diets. As well, in the dual-choice tests with hosts of the same physiological age (3.4), no significant differences were found between parasitization rates in the 10 and 31 ug/g treatments and respective controls. However, in the 100 ug/g dual-choice experiment, parasitization was significantly increased with the berberine treatment compared to the control.

There is an apparent contradiction between the no-choice and dual-choice results with the 100 ug/g berberine

experiments. However, the explanation for this anomaly is relatively simple. Berberine has been shown to be highly toxic to O. nubilalis at this concentration in the diet, and so the larvae are likely to be weaker and less mobile than the normal controls. Campbell and Duffy (1979b) pointed out that the aggressive behavior of older Heliothis zea larvae could likely interfere with the ability of Hyposoter exiguae to parasitize potential hosts. In the present study, gravid female O. terebrans preferred the less aggressive hosts, and tended to ignore the more vigorous control larvae when presented with a choice. When no alternatives were present, controls were parasitized at the same rate as the treatment groups. It may also be noted that percent parasitization was fairly consistent throughout the treated and control groups in the no-choice experiments. This further suggests that in the absence of choice, O. terebrans parasitizes the same quantity of O. nubilalis of the same physiological age and host density (100 per dish), regardless of subtle behavioural differences.

α-terthienyl in the diet of O. nubilalis exerted more influence on the parasitization efficiency of O. terebrans. In the no-choice experiments (3.3.3), treatments of 10 and 31 ug/g α-t did not significantly affect parasitization rates compared to controls. However, a significant reduction in percent parasitization was observed for hosts reared on diets containing 100 ug/g α-t, relative to the controls. As well, the dual-choice test (3.4) with 100

ug/g α-t yielded a similar result: a significant reduction in the parasitization rate. However, in the dual-choice test with larvae reared on 10 ug/g α-t diets, the opposite effect was observed. Parasitization was increased significantly in the treated group compared to the controls.

The 100 ug/g α-t results are surprising, considering that this concentration would render the larvae less aggressive than the controls. The observed effects of α-t on host acceptance is not correlated with titres of α-t or its metabolite (3.6). Therefore, it is unlikely that α-t could be acting as an oviposition deterrent. Yet, these effects are robust, particularly the consistent reduction in parasitization efficiency in the 100 ug/g treatment groups in both the no-choice and dual-choice tests.

The data obtained in this study do not directly explain differences in parasitization rates with α-t, discussed previously in this section. However, it is not unreasonable to speculate that α-t may have indirectly interfered with the synthesis of certain biomolecules utilized as host recognition and acceptance kairomones by D. terebrans. The ovipositors of hymenopterous parasitoids are extremely sensitive, and highly responsive to stimulation by specific chemicals (Dethier, 1947; Arthur et al, 1969; King and Rafai, 1970; Weseloh, 1971; Greany and Oatman, 1972). For many parasitoids, the response to kairomones is concentration specific (Corbet, 1973; Jones, 1981).

Although host diets containing 10 ug/g α-t did not significantly enhance larval growth and development (3.1.2), metabolic activity was possibly stimulated by this sublethal concentration. This was reflected by the absence of α-t in host larvae in the 10 ug/g group, and the high titre of α-t metabolite compared to the other two treatment groups (31 and 100 ug/g α-t) (3.6). A higher metabolic rate could result in a more rapid synthesis of kairomonal components in the 24 hour period on corn tissue, relative to the controls, and this would make the 10 ug/g group more attractive than the controls in a choice situation.

In the 100 ug/g α-t treatments, the reverse effect likely occurred. Significant adverse effects were observed in the growth rate and developmental parameters of O. nubilalis reared on diets containing 100 ug/g α-t (3.1.2). Since these effects were at least partially due to reduced nutrient assimilation (Champagne, 1984), a reduction in metabolic activity would be the consequence, and hence production of kairomonal components could be retarded. Therefore, the lower levels of parasitization in the 100 ug/g α-t-treated larvae relative to the controls would likely have resulted from poor host recognition or acceptance.

4.3 Allelochemical Effects on Parasitoid Success

Characteristically in natural habitats, plants of different species are found within close proximity to each other. Even in monocropping agricultural systems, weed species occur at the periphery of cultivated fields, and suitable host insects for parasitoids are often found within these weedy areas as well as in the crop. The eggs of phytophages laid on these plants will hatch after a specific number of day-degrees beyond a threshold temperature for development have passed, and the neonates begin to feed. From this time on, the developmental rate of these insects is subject to alteration by the quality of the host plant.

The dual-choice tests with D. terebrans using 12-day-old treated and control larvae (3.2) somewhat resembles this situation. The presence in the diet of allelochemicals may retard or accelerate the growth and development of D. nubilalis, and after 12 days, the physiological age of these larvae may be different from that of larvae not exposed to allelochemicals. This may affect the relative attractiveness of treated and control larvae to D. terebrans. In addition, the physiological effects of these compounds could further enhance or impair the growth and survival of the new parasitoid generation. Therefore, the ultimate success of the parasitoids was measured as the ratio of adults produced in the treated group to adults produced in the controls (T/C). These

ratios were also calculated for the no-choice tests with insects of the same physiological age (3.3.3) to determine if the availability of alternative hosts could affect the success of the parasitoids.

In the dual-choice test (3.2), very few of the larvae reared on 10 ug/g berberine were parasitized, and none of these individuals survived to adulthood. However, 31 and 100 ug/g berberine in the diet of the host appeared to be advantageous to the parasitoids, as evidenced by T/C ratios greater than 1.0.

The T/C ratios (<1.0) obtained for the 10 ug/g berberine experiments require little explanation. As discussed previously (4.2), percent parasitization was not significantly different between 10 ug/g berberine-treated and control larvae in either the no-choice (3.3.3) or dual-choice (3.4) situations. Therefore, the observed T/C ratios are the result of the toxic effects of berberine (3.3.1).

For the 31 ug/g experiments, the dual-choice result (T/C = 1.25) indicates a slight advantage in the berberine treatment group over the controls. Yet, the same treatment proved to be detrimental in the no-choice situation, which is understandable, considering the toxicity of berberine. Parasitization rates were not significantly different in either type of test, and so the presence of 31 ug/g berberine in the host diet cannot be recognized as truly beneficial to parasitoid performance.

With 100 ug/g berberine, the T/C ratios from the

dual-choice (>1.0) and the no-choice (<1.0) tests reflect differences in berberine's influence on parasitization efficiency in the two types of tests. As discussed previously (4.2), the behaviour of the 100 ug/g berberine treated hosts is less aggressive than the normal controls of the same age, and the parasitoids are preferentially attracted to them over the controls when given the choice. Additionally, in the dual-choice tests with insects of the same chronological age, the 100 ug/g berberine group likely included a higher proportion of younger hosts (second instar larvae). Since second instar larvae tend to survive parasitism better than third instar larvae (3.5), the number of parasitized hosts surviving the experiment in the 100 ug/g treatment was improved over that of the controls. These advantages with the 100 ug/g berberine treatment in the dual-choice test compensated for the toxic effects of berberine (3.1.1, 3.3), resulting in a very high T/C ratio compared to any of the other experiments.

With α-t, the T/C ratios in the dual-choice tests with insects of the same chronological age (12 days) (3.2) showed reduced yields of parasitoids with all concentrations tested. However, in the no-choice tests with physiologically similar larvae (3.3.3), the T/C ratio for the 10 ug/g experiment revealed an advantage for D. terebrans with α-t in the diet, although the production of adult parasitoids was reduced with 31 ug/g α-t compared to controls, and even further reduced with 100 ug/g α-t.

It may be recalled that with 10 ug/g α-t in the diet, survivorship was not adversely affected in O. nubilalis (3.1.2), and was slightly improved for D. terebrans (3.3.2). In the no-choice tests, percent parasitization with 10 ug/g α-t was not significantly different from the control groups (3.1.3), and so the slight increase in parasitoid production (T/C = 1.15) was likely due to the enhanced survivorship of D. terebrans with this treatment. In the dual-choice test with physiologically similar hosts, the parasitization rate for the 10 ug/g treatment was significantly greater than the controls. However, with 12-day-old treated and control insects, parasitoid yield was reduced by this concentration of α-t in the diet. Because of the slightly enhanced developmental rate of O. nubilalis with 10 ug/g α-t in the diet (3.1.2), proportionately more physiologically older hosts would be present in the treated group, and, as was observed (3.5), this would lead to decreased survival of hosts exposed for parasitization. Thus, the low T/C ratio in the dual-choice test with 10 ug/g α-t is a consequence of poor host survival.

The 31 ug/g α-t experiments showed fairly consistent results in both no-choice tests and dual-choice tests - T/C ratios were less than 1.0 in both cases. Since parasitization rates of larvae fed 31 ug/g α-t were not significantly different from controls in both the no-choice (3.3.3) and dual-choice (3.4) situations, the reductions in parasitoid yields were likely due to the toxic effects of the compound (3.1.2, 3.3.2).

The T/C ratios for the 100 ug/g α-t experiments were also consistently low in dual-choice and no-choice experiments for obvious reasons. In addition to the toxicity of 100 ug/g α-t (3.1.2, 3.3.2), the parasitization rates observed with this treatment were significantly reduced compared to controls, regardless of the availability of choice (3.3.3, 3.4).

From the comparison of T/C ratios obtained from dual-choice and no-choice experiments with berberine- and α-t-treated hosts, two distinct conclusions may be drawn. First, the two different tests, by design, bring about different host selection behavior in D. terebrans. The parasitoid will reject hosts which are slightly more aggressive in favour of more docile hosts, but the urge to parasitize will overcome them if no alternatives are available. Although these results were obtained in the laboratory (in an enclosed environment), it is not unreasonable to speculate on the relevance to field situations. Resistant crop varieties may retard host development, and even increase mortality in the endoparasitoids of hosts feeding on these plants. However, if the resistant host plant is adjacent to a chemically innocuous plant (such as a weed or an intercrop member), parasitoid performance could hypothetically be improved on the resistant crop. On the other hand, if the titres of resistance factors in the food plants serve only to stimulate host development and possibly kairomone production, the efficiency of the parasitoid may be reduced

because of host mortality due to mutilation. These hypothetical situations would, of course, depend on the timing of host search by the parasitoid, and the use of 12-day-old hosts for the dual-choice tests (2.5) was an arbitrary condition of these experiments.

The second conclusion which may be drawn by inspection of the T/C ratios is that secondary plant substances in the diet of the host generally reduced the number of progeny available for successive procreation (adults). Of the twelve pairs of experimental and control groups, T/C ratios greater than 1.0 were observed only in two instances (discussed previously): the dual-choice test with 100 ug/g berberine (3.2) and the no-choice test with 10 ug/g α-t (3.3.3). Regardless of the persistence in, or biological activity of allelochemicals towards the host - through physiological poisoning or feeding deterrence - the parasitoid was ultimately susceptible to the effects of these compounds, and the significance of this information is not far removed from implications in the field.

4.4 Implications of Allelochemical Changes to Biological Control

The objective of applied biological control is not to eradicate the pest insect - this is impossible even with the most efficient insecticide - but to establish or maintain a balance between hosts and natural enemies such that peak host populations remain below the economic threshold for the particular insect-crop situation. The inclusion of allelochemics in integrated pest management strategies by breeding phytochemical antibiosis factors into crops is an ecologically sound idea, particularly if pesticide application can be avoided. However, as was elucidated in this study, allelochemicals can potentially produce many of the undesirable effects observed with insecticide usage.

With the model compounds investigated in the present study, the mortality incurred in immature D. terebrans was much more severe with the highly lipophilic thiophene, α-terthienyl, than with the more polar alkaloid, berberine. In addition, α-t was shown to persist in host tissues and was detectable in emerged wasps and cocoons reared from α-t-fed hosts, whereas berberine was excreted rapidly. These results suggest that pest management programs which take advantage of persistent secondary plant substances in host plant resistance could run into serious problems with respect to biocontrol. With D. terebrans, the entire host is consumed within a relatively short time interval, and

this proved to be devastating in the case of the 100 ug/g α-t treatment. However, many parasitoids selectively feed on specific host tissues (reviewed by Flanders, 1973), and egg parasitoids and certain larval or pupal parasitoids may be able to escape the direct effects of toxins ingested by the host.

Fortunately, the use of endogenous allelochemicals will not inflict upon natural enemies the severe population crashes seen with biocidal sprays. However, host-parasitoid synchrony could be markedly affected by subtle differences in host developmental time, particularly if the most susceptible host stages are within one or two instars, as is the case with D. terebrans. However, if the ovipositional period of the parasitoid is already out of synchrony with the host - which may occur with new host-parasitoid associations - the inclusion or enhancement of host plant allelochemicals through genetic engineering could hypothetically improve the performance of natural enemies.

Finally, the attractive qualities of potential host insects can be altered by allelochemicals. In this study, reduced host acceptance by D. terebrans was evident with 100 ug/g α-t in the diet of D. nubilalis. From the literature review section of this thesis, it is clear that host plants can profoundly affect all aspects of host selection by parasitoids. The possible effects of allelochemicals on kairomone production is an area which is virtually unresearched.

4.5 Future Research

The present study was an investigation of two dissimilar model compounds with a host-parasitoid association. A myriad of plant defensive compounds occur in nature, having diverse physical properties and biological activity. Potentially useful allelochemicals should be tested not only for efficacy towards herbivorous insects (the pests), but examined in a laboratory system such as this one in order to assess their real usefulness as part of pest management strategies. Some of these novel compounds, such as the triterpenoid azadirachtin, show great promise as botanical insecticides (Arnason et al, 1985). However, as observed with α-t, sublethal quantities of insecticidal compounds in host diets can be lethal to developing parasitoids.

Fairly non-polar allelochemicals may be useful in pest management involving parasitoids which do not consume the entire fat body of the host. The eggs of adult hosts reared on diets containing lipophilic toxins (such as α-t) should be analyzed for traces of the xenobiotic. Egg parasitoids may be able to escape the effects of host-ingested toxins, and therefore would be more suitable for pest control strategies involving this type of allelochemical.

Subtle differences in host quality (behavioral and chemical) should not be ignored, as these effects may profoundly affect parasitoid efficiency. The physiological

mechanisms underlying these effects should be investigated. It may be possible to select for allelochemicals which do not interfere with kairomone production. Perhaps allelochemicals which promote kairomone production could be selected for in certain crop breeding programs.

4.6 Summary

1. Although the isoquinoline alkaloid berberine produces fewer sublethal effects on growth and development of Ostrinia nubilalis than the thiophene α-terthienyl, the mortality imparted by berberine towards O. nubilalis at 100 ug/g in the diet is more severe than that for α-t.

2. In contrast, the endoparasitoid Diadegma terebrans is much more susceptible to α-t than to berberine in the diet of its host.

3. Parasitization rates are affected by host behavior in a choice situation. Allelochemicals in the diet of O. nubilalis may cause larvae to be less vigourous and mobile, facilitating parasitism by D. terebrans.

4. Alpha-terthienyl at 100 ug/g in the diet of O. nubilalis reduced parasitization rates in both choice and no-choice situations. The reason for this phenomenon is not apparent from the data obtained in this study.

5. Berberine does not bioaccumulate in O. nubilalis larvae, and was not detected in adult D. terebrans or the pupal cases of emerged wasps which had been reared on berberine-containing diets.

6. Alpha-terthienyl bioaccumulates in O. nubilalis larvae and was detectable in adult D. terebrans and the pupal cases of emerged wasps which had been reared on α-t-containing diets.

7. A polar metabolite of α-t was found in O. nubilalis larvae and in D. terebrans adults and pupal cases reared

from α-t-fed hosts. This metabolite has not yet been isolated and identified.

8. The overall success of D. terebrans is generally reduced by the inclusion of berberine or α-t in the diet of the host. However, in the dual-choice situation with hosts of the same chronological age, 100 ug/g berberine in the host diet appeared to be advantageous to D. terebrans. This was likely due to the relatively non-aggressive behavior of the treated hosts compared to the controls.

5.0 CONCLUSIONS

The present study suggests that secondary plant substances may adversely affect the parasitoids of herbivorous insects ingesting these compounds. These effects may be manifested as direct toxicity towards the developing parasitoid, particularly if the compound in question bioaccumulates in the host. Secondary plant substances may also be indirectly detrimental to natural enemies. The quality of the host as a food source may be reduced as a consequence of reduced feeding or nutrient assimilation. The attractiveness of the host towards gravid female parasitoids may also be altered due to behavioral or biochemical changes in host larvae.

Studies of allelochemical effects on herbivores do not necessarily reflect the consequences of these substances on the third trophic level. Novel allelochemicals should be examined for effects on natural enemies in order to assess their real usefulness for integrated pest management strategies involving biological control.

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