

Chemical communication with volatile semiochemicals in *Phyllotreta* species (Coleoptera, Chrysomelidae): a minireview

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Summary: *Phyllotreta* species (Coleoptera, Chrysomelidae, Halticinae) rank among the most important horticultural pests in the Northern Hemisphere. Leaf damage caused by flea beetles upsets the water balance, blocks plant growth and sometimes causes a high level of mortality of seedlings. Several species are known to act as vectors of numerous pathogens as well. Chemical communication plays an important role in the host finding, feeding and oviposition behaviour of flea beetles. In the first phase volatile mustard oils (isothiocyanates and thiocyanates) are released from the host plants through the decomposition of non-volatile glucosinolates (chemicals specific to Cruciferae) by myrosinase, and beetles are attracted to the source of release from a distance. Among the isothiocyanates, allyl isothiocyanate is the longest known and widespread compound utilized in the host-plant location of *Phyllotreta* species, but some species may have a stronger preference to other isothiocyanates or thiocyanates. The attractive effect of the plant volatiles is enhanced by the emission of a male-produced aggregation pheromone. The presence of such a pheromone was first demonstrated in *Phyllotreta cruciferae* Goeze. In this species [(5*R*,5*aS*)-1,1,5,8-tetramethyl-1,2,3,4,5,6,5*a*-heptahydrobenzo[1,2-*a*][7]annulene] was found to be the main pheromone component. Significant attraction by the pheromone was recorded only in the presence of ALLYL ITCN. The biological activity of the pheromone compound was connected to the *plus* (+) chirality. The same component seems to be occurring also in the pheromones of several other *Phyllotreta* spp. as well, suggesting a wider occurrence in the genus. Once attracted by the joint effect of plant volatiles and aggregation pheromone, the presence of the non-volatile glucosinolates in the plant tissues is necessary for continuous feeding. Aggregations of flea beetles on suitable host plants, which result from the joint effects of plant-derived and pheromonal chemical cues detailed above may also be good rendez-vous occasions, increasing the probability of encounters with the opposite sex and mating in the vicinity of the optimal oviposition site. Due to the horticultural importance of *Phyllotreta* spp., deciphering details of their chemical communication has considerable significance in the development of new methods of integrated control.

Key words: *Phyllotreta*, flea beetle, Chrysomelidae, chemical communication, attractant, isothiocyanate, aggregation pheromone, himachalene, trapping

Introduction

Flea beetles (Coleoptera, Chrysomelidae, Halticinae) rank among the most important horticultural pests in the Northern Hemisphere. Improving our knowledge on their chemical communication may lead to the development of improved and more selective ways of environmentally harmless new control methods. In the present minireview we aimed at summarizing results in the literature concerning volatile semiochemicals playing a role in the chemical communication of flea beetles living on cruciferous plants. Earlier literature data are complemented with the most recent findings of our laboratory on *Phyllotreta* spp.

General life habits of flea beetles and their importance as pests

The economically most important flea beetle species mostly belong to the genus *Phyllotreta*, which feed on

cruciferous plants. They are important pests of several cruciferous cultures both in Eurasia (Chen & Kung, 1955; Varma, 1961; Jourdeuil, 1966; Vig, 1992, 1998a; Sáringer, 1998) and in North America, where most species are univoltine (Feeny et al., 1970; Lamb, 1989; Soroka, 2005). In other areas, i.e. in India, as many as 8 generations per year were reported (Varma, 1961). In the Carpathian Basin, of the total of ca 250 Halticinae species ca. 10% belong to the genus *Phyllotreta* (Kaszab, 1962, Vig, 1992).

The importance of this insect group is, on the one hand due to the wide range of cultivated cruciferous plant species in horticulture, and on the other hand, due to their capability of damaging several plant cultures (cabbage varieties, radish, rape, mustard species etc.) (Dobson, 1956; Vig, 1992; Balázs et al., 1998; Vörös & Garamvölgyi, 1998). In North America, costs of damage caused by the most important flea beetle species and of control measures exceed 300 million dollars annually (Knodel & Olson, 2002).

Overwintering adult *Phyllotreta* emerging from overwintering sites (leaf litter, hedgerows, and other available

shelter) cause the most severe damage to the seedlings in the spring, near the field damaged in the previous year (Vincent & Stewart, 1983; Balázs et al., 1998; Vig, 1998a).

In Hungary, they appear usually in the first part of April and attack cruciferous crops causing many feeding-holes on the leaves. This upsets the water balance, blocks plant growth and sometimes causes a high level of mortality of seedlings (Vig, 1992; Sáringner, 1998; Vörös & Garamvölgyi, 1998; Spilák et al., 1998).

Weather conditions evidently have critical effects on the flea beetles, the highest numbers can be observed on warm, sunny and calm days and only very low numbers on cold, rainy, or very windy days (Vig, 1998a, b).

In July and August, adults of the new generation may cause a second period of damage, before the migration to overwintering sites. This is characterized by unequal ripening of the crop (Feeny et al., 1970; Vincent & Stewart, 1983; Vig, 1998a, 1992; Sáringner, 1998; Spilák et al., 1998).

The importance of flea beetles as pests is aggravated by the fact that several species are known to act as vectors of numerous pathogens as well. These pathogens include *Alternaria brassicola* Wiltshire (Dillard et al., 1998), and from the viruses the radish mosaic virus (RMV) (Campbell & Colt, 1967; Glits, 2000), the turnip yellow mosaic virus (TYMV) (Markham & Smith, 1949; Hill, 1983; Walkey et al., 1986; Stobbs et al., 1998) and the brome mosaic virus (BMV) (Ryden, 1989).

Dillard et al. (1998) confirmed the propagation of the spores of *Alternaria brassicola* not only on the body surface of the beetles, but also through their frass. Markham & Smith (1949) observed the symptoms of turnip yellow mosaic virus within 10–14 days after the feeding of infected beetles on the plants. Among *Phyllotreta* spp., *Ph. undulata* Kutsch., *Ph. cruciferae* Goeze, *Ph. nemorum*, L., and *Ph. atra* Fabr. have been confirmed as vectors. It is likely that flea beetles propagate viruses not only through simply mechanically damaging plant tissues while feeding. In the course of feeding, beetles regurgitate part of the contents of the foregut to aid digestion of the leaf tissue, and this regurgitation process may also assist in the virus infection (Markham & Smith, 1949).

Host plant – insect relationships

The host-finding, feeding and oviposition behaviour of flea beetles is widely assisted by chemical communication. In several field and laboratory tests, it was observed that non-volatile glucosinolates (which can be found characteristically in cruciferous plants) were feeding arrestants and oviposition stimulants in the case of several *Phyllotreta* species (Feeny et al., 1970; Hick, 1974; Nielsen, 1978; Pivnick et al., 1992) (Figure 1). This effect can be enhanced by the presence of mustard oils (volatile degradation products of glucosinolates) (Hick, 1974).

A feeding response could be elicited by non-host plants, cultured in an aqueous solution of several glucosinolates (i.e. sinigrin). For the feeding stimuli a 0.01% sinigrin

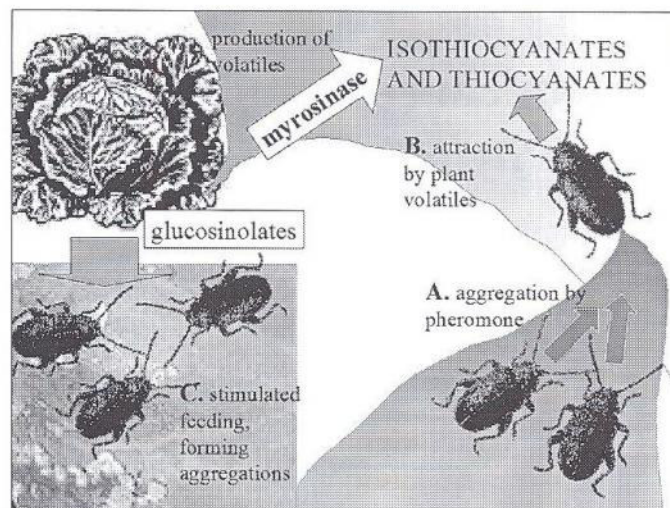


Figure 1 General scheme of chemical communication connected to host plant–insect and pheromonal relationships in flea beetles

concentration [= allyl glucosinolate of which decomposition product is allyl isothiocyanate (ALLYL ITCN)] was needed (Hicks, 1974).

To date, about one hundred glucosinolates are known to occur in nature, and their occurrence is restricted to the members of the plant family Cruciferae (= Brassicaceae) (and some other smaller families such as Capparaceae and Resedaceae) (Kjaer, 1960; Vig, 1992).

Myrosinase can be found isolated in special 'myrosine cells' in the plant tissues. The enzyme is released after damaging or injuring these cells and it causes the hydrolysis of glucosinolates. This hydrolysis in the cruciferous plants is also a part of the natural decomposition (Bones & Iversen, 1985; Chew, 1988; Pivnick et al., 1992).

The decomposition of non-volatile glucosinolates by myrosinase yields the volatile mustard oils (isothiocyanates and thiocyanates), which were found to be attractive to several flea beetle species. *Brassica* species may contain isothiocyanates in a concentration as high as 410 ppm (Görnitz, 1956; Josefsson, 1967; Pivnick et al., 1992).

Among the isothiocyanates ALLYL ITCN is the longest known chemical which was found to be attractive to flea beetles (Görnitz, 1956; Matsumoto, 1970; Blight et al., 1989; Pivnick et al., 1992; Liblikas et al., 2003; Tóth et al., 2003).

The ALLYL ITCN content of a cabbage leaf (*Brassica oleracea* var. *capitata* L.) was 2.9 ppm, while that of indian mustard (*B. nigra* L.) was 82.9 ppm, respectively (Hicks, 1974). Pivnick et al. (1992) found in a field trapping experiment that at least a 0.4 mg/day release rate of ALLYL ITCN was necessary for the attraction to *Ph. cruciferae* and *Ph. striolata* Fabricius., which equals to the release from 2000 brown mustard (*B. juncea* Czern.) plants.

Görnitz (1956) found that the extract of rape seeds had an attractive effect to *Ph. cruciferae* and *Ph. striolata*, and he attributed this to the presence of the mustard oils. Later Feeny et al. (1970) demonstrated that the same two species were attracted by a 1% aqueous solution of ALLYL ITCN by itself. In the experiments of Matsumoto (1970) and

Burgless & Wiens (1980) the attractive effect of ALLYL ITCN was confirmed.

ALLYL ITCN appears to be a very widely used compound in the host plant location of *Phyllotreta* spp., as in other field tests ALLYL ITCN proved to be attractive also for *Ph. undulata* (Foster 1984, Tóth et al., 2003), *Ph. vittula* Redtb., *Ph. procera* Redtb., *Ph. balcanica* Heikert, and *Ph. nodicornis* Marsham (Tóth et al., 2003).

In the case of the close relative *Psylliodes chrysocephala* L. (Coleoptera, Chrysomelidae, Halticinae) Blight et al. (1989) reported that ALLYL ITCN (together with 3 other isothiocyanates) evoked strong electrophysiological responses from the antennae, and this species was also captured in significant numbers in ALLYL ITCN-baited traps (Tóth et al., 2003). *P. chrysocephala* is recorded as a pest of rape (Vig, 2003).

Other studies suggested that besides ALLYL ITCN some other related compounds may have some attractive effect on certain flea beetles, such as benzyl isothiocyanate, ethyl isothiocyanate, the mixture of ethyl and methyl 4-isothiocyanatobutyrate, 3-methylthiopropyl isothiocyanate, n-butyl isothiocyanate, 3-butenyl isothiocyanate and 3-butenyl thiocyanate (among others) (Matsumoto, 1970; Pivnick et al., 1992; Liblikas et al., 2003). Different compounds evoked responses of differing intensity, thus the conclusion was that flea beetles were able to discriminate between the different glucosinolate hydrolysis products. Generally nitriles were the least effective, and isothiocyanates which are released from the injured cruciferous plant tissue in larger quantities were more attractive (Cole, 1976; Pivnick et al., 1992).

Pheromonal relationships

In a pioneering work, Peng & Weiss (1992) first suggested the existence of an aggregation pheromone in the case of *Ph. cruciferae*. They found in their tests that oilseed rape alone was not attractive, however the hostplant and feeding flea beetles together showed a high level of attraction towards conspecifics (Figure 1). Male and female beetles were attracted in an equal rate (Peng & Weiss, 1992). In the above tests oilseed rape (*B. napus* cv. *Westar*) was used on purpose. Bodnaryk and Palaniswamy (1990) found that in this plant cultivar the major glucosinolate was glucobrassicin which had no hydrolysis products, and in the cotyledon allyl glucosinolate was undetectable. Thus, no interference through the attraction to ALLYL ITCN was to be expected.

Mechanically injured (artificially by scissors) or insect damaged (by flea beetles, or by *Plutella xylostella* L., Lepidoptera, Plutellidae) oilseed rape or when the plants and flea beetles were presented so that the beetles could not get in contact with the plant, were not showing response. This suggested that for the supposed pheromone production feeding on the plants or contact with the host was necessary. The pheromone release may have happened when beetles selected a suitable host plant, or it may have happened through frass excretion (Peng & Weiss, 1992).

Later in a trapping experiment Peng et al. (1999) found that only males of *Ph. cruciferae* produced the supposed aggregation pheromone, and for a detectable attractive effect at least 2 live male insects were needed as baits in a trap.

Through the analysis of volatiles emitted by males of a North American population of *Ph. cruciferae* several pheromone candidate components were identified (Bartelt et al., 2001), and synthesized (Bartelt et al., 2003). The identified compounds included several new himachalene sesquiterpenes, and a new enantiomeric form of a previously known one, the (+)-ar-himachalene. This compound was known to occur in fir trees *Abies alba* Mill. and *Abies normaniana* Spach (Khan & Pentegova, 1988; Khan et al., 1989). One of the identified components, (+)-gamma-cadinene had a different basic structure than the himachalenes. This compound has already been known to occur naturally in several plants (Bartelt et al., 2001).

Csonka et al. (2003) demonstrated the field behavioral activity of a mixture of five from the candidate synthetic pheromone components in a European *Ph. cruciferae* population. This result confirmed results of recent field tests conducted in North America (Soroka et al., 2005) on a North American population of the same species.

In the above field tests the mixture of the candidate pheromone components on their own attracted few *Ph. cruciferae*, while when presented together with ALLYL ITCN catches significantly increased as compared to ALLYL ITCN on its own. Captures showed a tendency of increase with increasing the pheromone dose in the presence of ALLYL ITCN (Csonka et al., 2003; Soroka et al., 2005).

The fact that the supposed pheromone components showed significant activity only in the presence of the host plant-derived attractant ALLYL ITCN corresponded closely with the previous observations that the emission of the pheromone followed the contact with the host, or happened during feeding (Peng & Weiss, 1992).

The similar North American and European results suggest that the pheromone composition of both geographical *Ph. cruciferae* populations may be similar.

Surprisingly, the mixture of the pheromone candidate components identified from *Ph. cruciferae* was attractive also to *Ph. vittula*, and perhaps also to other related *Phyllotreta* spp. (*Ph. nodicornis*, *Ph. ochripes* Curtis, *Ph. nemorum*, *Ph. nigripes* Fabricius) (Csonka et al., 2003; 2005). This may suggest that the tested compounds may have a wider occurrence as possible pheromone components in the genus. This notion is supported by the fact that (+)-ar-himachalene [(5*R*,5*aS*)-1,1,5,8-tetramethyl-1,2,3,4,5,6,5*a*-heptahydrobenzo[1,2-*a*][7]annulene] was previously found to be a common major component in the emissions collected from males of several North American flea beetle species (Bartelt et al., 2001).

The components identified from *Ph. cruciferae* are optically active, so several enantiomers are possible. In nature, the chirality of biologically active compounds usually is of utmost importance. A further example was observed in the case of the flea beetles. In field tests using pure

enantiomers of the pheromone candidate compounds synthesized by Muto et al. (2004), it was found that the biological activity was connected with plus (+) chirality. Consequently this enantiomeric form of the pheromone compounds may be biosynthesized and emitted by the beetles themselves also. The presence of the minus (–) enantiomeric form in synthetic samples did not interfere with the activity of the plus (+) enantiomers (Csonka et al., 2005).

In further tests it was revealed that among the five pheromone candidate components tested, only one, the [(5*R*,5*aS*)-1,1,5,8-tetramethyl-1,2,3,4,5,6,5*a*-heptahydrobenzo[1,2-*a*][7]annulene] had a significant attractive effect, so only this compound can be considered to be a pheromone component in the case of *Ph. cruciferae* (Csonka et al., 2005). This single compound had a significant attractive effect also for other *Phyllotreta* spp. (*Ph. vittula*, *Ph. procera*, *Ph. nigripes*, *Ph. undulata*), confirming results of previous tests with the racemic component mixture (Csonka et al., 2005). Some of the other components previously identified from male effluents might be the decomposition products of [(5*R*,5*aS*)-1,1,5,8-tetramethyl-1,2,3,4,5,6,5*a*-heptahydrobenzo[1,2-*a*][7]annulene] with an inferior role.

Chemical communication strategy of *Phyllotreta* flea beetles

In conclusion, it appears that *Phyllotreta* flea beetle species have a complex strategy of chemical communication which can be related to three main levels of activities (Figure 1).

Activity level of host location

Flea beetles use their cruciferous host plants' volatile products, the isothiocyanates and related compounds for the location of their hosts from a distance (Feeny et al., 1970; Hick, 1974; Pivnick et al., 1992; Vig, 1992). The success of this strategy may mainly be due to the fact that these volatile components are specific to Cruciferae (and some other smaller families like Capparaceae and Resedaceae). The strong chemical specificity suggests that in the localization of host plants the main role is played by chemical stimuli and in the host plant-insect relationships only a secondary role is played by plant colour and pubescence. (Fenny et al., 1970).

Isothiocyanates may have toxic properties to birds, insects and monogastric mammals and may have antibacterial, antifungal, allelopathical, repellent and insecticidal effects (Van Eatten & Tookey, 1979; Ahman, 1986; Vig, 1992). Their biosynthesis in response to damage is thought to be at least in part a plant defense mechanism ("first line of chemical defense") (Feeny, 1977; Pivnick et al., 1992; Vig, 1992). This may yield an evolutionary advantage to flea beetles through impeding possible competitor consumers (Vig, 1992; Kjaer, 1960).

Activity level of forming aggregations on suitable hosts

The first pioneering beetles on the host plant attract conspecifics to the suitable feeding site by emitting an aggregation pheromone. First results suggest that these may contain chemically similar components throughout several species of the *Phyllotreta* genus (Bartelt et al., 2001; Csonka et al., 2005). For the pheromone to be effective, the stimulation presence of the host odor is needed (Csonka et al., 2003; Soroka et al., 2005). The strong relationship between the plant-derived attractant and the aggregation pheromone can be explained by their similar roles, which may overlap in the insects' chemical communication.

Based on these observations and results, *Phyllotreta* spp. are probably another example of those Coleoptera, where the relative importance of host-derived and pheromonal cues is similar in their respective chemical communication.

There have been other cases described in the literature where the pheromone produced by the insects is not or hardly active on its own, and the co-emission of host-plant produced substances is necessary for behavioral activity.

Rhynchophorus weevils (Coleoptera, Curculionidae) were not or hardly attracted to their respective aggregation pheromone components presented alone, but the pheromones when presented together with host plant odors significantly increased captures (Jaffé et al., 1993, Giblin-Davis et al., 1994, Oehlschlager et al., 1995, Rochat et al., 1995).

Females of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera, Scolytidae) produce frontalin as their pheromone, which is inactive when released alone, but in the presence of the host tree compound α -pinene it attracts synergistically, predominantly males (Payne et al., 1978)

The main aggregation pheromone component of the scarab, *Oryctes elegans* Prell. (Coleoptera, Scarabaeidae) produced very low catches when presented alone. However, when presented together with host plant odor, it was clearly synergizing activity of the host plant odor (Rochat et al., 2004).

In the case of *Melolontha* scarabs (Coleoptera, Scarabaeidae), males orient towards green leaf volatiles emitted by damaged leaves where female beetles feed (Ruther et al., 2000, 2002). Synthetic green leaf volatiles in fact produce some catches when presented as a bait in a trap (Imrei & Tóth, 2002; Reinecke et al., 2002b), however, the catches increase significantly when the pheromone components are added (Reinecke et al., 2002a, Ruther & Hilker, 2003). The pheromone components on their own show no activity.

Although the aggregation pheromone in the case of *Phyllotreta* spp. cause the aggregation of both sexes, presumably it may have a sex pheromonal function also, with increasing the probability of chance meetings with the opposite sex and mating in the vicinity of the optimal oviposition site (Landolt & Phillips, 1997). In any case, the

mutually supportive effect of host plant compound(s) plus pheromone may yield evolutionary benefits first by collecting insects to a good feeding site and then by providing more chances of male-female encounters resulting in mating.

In the *Chrysomelidae* family, pheromones have been identified only for a couple of species. The first chrysomelid pheromones characterized were from the rootworm beetles (*Diabrotica* spp.) which belong to the Galerucinae. These are sex pheromones produced by females and attract only males (Krysan et al., 1989). Recently, chrysomelid pheromone identifications involved male-produced pheromones that attracted both sexes. These include the Colorado potato beetle (*Leptinotarsa decemlineata* Say, Chrysomelinae) (Dickens et al., 2002) and the cereal leaf beetle (*Oulema melanopus* L., Donaciinae) (Cossé et al., 2002; Rao et al., 2003). Although belonging to different subfamilies, the latter two examples may show similar chemical communication strategies involving the synergetic combination of pheromone plus host plant odours as detailed in this review in *Phyllotreta* spp.

Activity level of continuous feeding on suitable hosts

Continuous feeding, of flea beetles on the cruciferous host is maintained through the feeding arrestant or stimulant effect of the non-volatile glucosinolates, which stimulate also oviposition (Hick, 1974; Feeny et al., 1970; Pivnick et al., 1992; Vig, 1992). Glucosinolates are generally thought to be part of the "first line of chemical defense" of cruciferous plants. Evidently the flea beetles exploit this defense mechanism. They feed primarily or exclusively on plants containing glucosinolates, suffer no adverse effects, are stimulated to feed or oviposit in the presence of glucosinolates and are attracted by their volatile products (Chew, 1988; Pivnick et al., 1992).

As a "second line of chemical defense", antifeedant chemicals could be present in certain cruciferous plants (such as cucurbitacine, cardenolide, etc.), which protect the plants against specialised herbivores, evading the "first line of chemical defense". Flea beetles may be insensitive to such antifeedants (Feeny, 1977; Nielsen et al., 1977, 1978).

Practical considerations

Phyllotreta spp. are important pests in horticulture, so the knowledge of their chemical communication has considerable significance in the development of integrated control methods. Traps containing selective and effective attractants would be very useful, for detection of the occurrence of the overwintering adults in springtime, for monitoring their population changes, and for giving an estimate of the population size of the overwintering generation in spring and the next generation which appear later, in summer. Until now, ALLYL ITCN, which attracts a wide range of *Phyllotreta* spp., was used most frequently as a bait in several trapping experiments (Matsumoto, 1970; Feeny et al., 1970; Vincent & Stewart, 1984; Hung &

Hwang, 2000, Tóth et al., 2003; 2004), but other isothio- and thiocyanates were also used as chemical baits in traps (Matsumoto, 1970; Pivnick et al., 1992; Liblikas et al., 2003). These compounds may be to a larger or smaller extent attractive also for several other pest insects of cruciferous plants (Wallbank & Wheatley, 1979; Kostal, 1992; Smart et al., 1997; Blight & Smart, 1999; Han et al., 2001)

Another trapping method based on visual sensitivity of flea beetles was the usage of coloured sticky sheets (mainly different hues of yellow) for trapping, (Vincent & Stewart, 1981; 1986; Laska et al., 1986; Chen & Ko, 1994; Hung & Hwang, 2000). Coloured sticky sheets are not very attractive as compared to chemical baits, and they are considerably less selective capturing a very wide array of flying insects belonging to many insect orders.

More efficient, selective and sensitive plant protection tools can be developed in the future based on our improved knowledge of the chemical communication of flea beetles and through the optimal combination of chemical (host-plant derived and/or pheromonal) and visual cues.

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