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Host Plant Chemistry and Preferences in Egg-laying *Trioza apicalis* (Homoptera, Psylloidea)

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Abstract—Sixteen species belonging to the family Apiaceae were examined for their acceptance as host plants by *Trioza apicalis* in non-choice tests. The number of eggs laid per day varied from 18 on *Daucus carota* subsp. *sativus* to zero on *Aegopodium podagraria*. In a comparative test, the psyllids landed significantly faster and started egg-laying earlier on carrots (*D. carota* subsp. *sativus*) than on dill (*Anethum graveolens*). In a study of shelter plants for *T. apicalis*, the psyllids survived on spruce, *Picea abies*, for more than 30 weeks, but they died on grass, *Phleum pratense* and *Brachypodium sylvaticum*, within 2 weeks. The length of the day is one of the factors regulating hibernation. At 20°C, light regimes shorter than 17 h induced hibernation, while longer light periods led to reproduction. Both the shelter plants and the summer hosts, including the Apiaceae species, released large amounts of monoterpene hydrocarbons, with great differences among the species. The most preferred host plants (carrots) were found to contain (+)- and (−)-α-pinene and (+)-sabinene, while large amounts (>20%) of either (+)- or (−)-limonene were released by the species of low preference. (−)-α-Pinene, (−)-β-pinene, and (−)-limonene were the main components of the spruce odour. A multivariate data analysis of the chemical results showed clearly the significant similarities of the summer host and shelter plants (*Daucus carota*, *Picea abies*, and *Juniperus communis*). © 1997 Elsevier Science Ltd

Introduction

Development in the Psylloidea follows different types of life cycles (Hodkinsson and White, 1979). *Trioza apicalis* Förster, one of the 93 psyllids found in Sweden, hibernates as an adult on a shelter plant and migrates to its host plant in early summer. Both males and females gather on carrot plants (*Daucus carota* L.) shortly after the carrot seedlings have emerged. They feed and mate and after oviposition both sexes die. Only one generation per year is formed. The eggs hatch into nymphs in about 10 days. The nymphal period lasts for about six weeks. During this period, the nymphs live rather sedentarily on the underside of the carrot leaves. One to three days after the last moult, they leave the carrots and start migrating to their hibernation sites, conifers (Láska, 1976; Rygg, 1977).

Three species among the Apiaceae have been reported as summer host plants: carrot (*Daucus carota*), parsley (*Petroselinum crispum*), and caraway (*Carum carvi*) (Burckhardt, 1986). Eggs have been found on other species of Apiaceae (Láska, 1976; Rygg, 1977), but the resulting nymphs failed to develop into adults. Norway spruce (*Picea abies* L.) is known as the winter host or the shelter plant (Rygg, 1977).

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The carrot psyllid, *Trioza apicalis*, is a pest that attacks carrots especially in the northern parts of Europe. The damage to the carrots is done mainly during the oviposition period. Both adults and nymphs cause damage to the carrot (Láska, 1964; Markkula *et al.*, 1976). The saliva injected by adults during feeding causes curling of the green parts and nymphal feeding causes reduction of the root growth. Feeding by the adults is usually considered to be the most serious. The chemical structure of the active salivary substance is still unknown (Markkula and Laurema, 1971; Laurema, 1989). The plant damage is systemic and appears on the newly formed leaves growing after the psyllid suction (Láska, 1964). Very young seedlings are more badly damaged than older ones and the damage becomes obvious about 2 days after infestation. If the infestation is very light, the plant can recover and undamaged leaves will develop. However, even small field populations of the carrot psyllid have been found to cause great damage; one psyllid per plant can cause a total loss of yield (Markkula *et al.*, 1976).

The main volatile compounds released from carrot roots were identified as terpinolene and caryophyllene (Buttery *et al.*, 1968; Cronin and Stanton, 1976; Simon *et al.*, 1980). Simon and co-workers have made several studies on the variation of components between plants and within a plant, as well as on the inheritance of specific volatiles in the carrot roots (Simon, 1982a,b; Senalik and Simon, 1986, 1987). The main components of the carrot foliage odour perceived by *Papilio polyxenes* females were identified by Baur *et al.* (1993) as sabinene and myrcene.

Several substances in carrots, both volatile and non-volatile ones, have been shown to be important for insect–carrot relationships in the families Lepidoptera and Diptera (Guerin *et al.*, 1983; Feeney *et al.*, 1989; Baur and Feeney, 1992; Baur *et al.*, 1993). The polar fraction as well as the total mixture of volatiles were found to increase the number of eggs laid by the black swallowtail butterfly, *Papilio polyxenes* (Baur *et al.*, 1993). Sabinene hydrate, 4-terpineol, bornyl acetate, and (*Z*)-3-hexenyl acetate were identified from the active fraction by GC–EAD and GC–MS techniques. The carrot fly, *Psila rosae*, has received considerable attention in this respect. Beside the general green leaf volatiles (aliphatic aldehydes and alcohols), substituted propylbenzenes, *E*-methylisoeugenol, and *E*-asarone are the most attractive to *Psila rosae* (Guerin *et al.*, 1983). Thus, quite different chemical cues seem to act on the insect taxa of different families that use carrots as hosts.

The aim of the present study was to investigate mechanisms in the seasonal host-shift and some factors affecting the summer and winter host range of *Trioza apicalis*. In the chemical part of this paper, we have focused on the volatile monoterpene fraction of the leaf emission from Apiaceae plants. The enantiomeric compositions of the chiral monoterpenes in small seedlings have not yet been reported for any species belonging to this family.

Materials and Methods

Insects. Trioza apicalis females, to be used for tests 1 and 2 (see below), were collected from a natural population in a carrot field during the oviposition period. Insects of mixed sexes for tests 3–5 were collected in the carrot field at the nymphal stage and kept in a greenhouse at 20°C under the natural light/dark conditions (9/15 h). After the last eclosion, adults at the beginning of the migration period to hibernation sites were used for the experiments.

Plants. Apiaceae plants were grown from seeds in the greenhouse at the same spring period as carrots in the field. The seedlings were kept at 20°C. At the development stage (with cotyledons and 1–2 true leaves) they were planted one by one in pots and used for experiments 1 and 2. Shelter plants (spruce and two grass species) to be used in experiment 3 were taken from a forest edge near an infested carrot field.

Oviposition range experiment (1). Sixteen Apiaceae species, both wild and cultivated ones, were studied for their oviposition acceptance by *Trioza apicalis*. The following species were examined: *Daucus carota* L. subsp. *sativus* (Hoffm.) Schübl. et Martens (carrot), *Daucus carota* subsp. *carota* (wild carrot), *Coriandrum sativum* L. (coriander), *Petroselinum crispum* (Mill.) A.W. Hill (parsley), *Pimpinella saxifraga* L. (burnet saxifrage or black carroway), *Pastinaca sativa* L. (parsnip), *Foeniculum vulgare* Mill. (fennel), *Anthriscus cerefolium* (L.) Hoffm. (garden chervil), *Angelica archangelica* L. (angelica), *Levisticum officinale* Koch (garden lovage or bladder seed), *Aethusa cynapium* L. (wild parsley), *Pimpinella anisum* L. (anise), *Anthriscus sylvestris* (L.) Hoffm. (wild chervil), *Anethum graveolens* L. (dill), *Carum carvi* L. (caraway), and *Aegopodium podagraria* L. (goutweed). For comparison, *Trifolium pratense* L., red clover (Fabaceae) was included in the experiment. Each seedling was covered by a small cage. The cage was a Plexiglas cylinder, 10 cm high and 7 cm in diameter, with a net on top of it. The cages were changed to a bigger size during the growth period. Overwintered small plants of *Levisticum* were used in this test instead of the seedlings described above.

In non-choice test, one female of the carrot psyllid was put in a cage. The number of eggs laid on the host plant was recorded after 24 h. The typical symptom of damage, curled leaves, was also noted. Plant species, on which the completed development of eggs into adults had taken place, were recorded. There were 17–30 replicates for every plant species. The mean numbers of eggs laid on each plant species were compared using one-way analysis of variance, $P = 0.05$. Differences between plant species were tested, using the Tukey HSD multiple range test.

Timing of oviposition on plants of high and low preference (2). The oviposition rhythm of *T. apicalis* on the highly preferred carrot (*D. carota* subsp. *sativus*) was compared with the rhythm on the less preferred dill (*Anethum graveolens*). Small plants of carrots and dill, planted in separate pots and covered with small cages of the type described above, were used. One female was placed inside each cage on the net surface. The numbers of females settling and laying eggs on the two species studied were recorded. The behaviour of the females was recorded six times, at 30 min intervals, between 10.00 and 12.30, and again after 24 h. There were 24 replicates of each plant species.

Investigation of shelter plants (3). The test was carried out in August, at the beginning of the natural period for psyllids to migrate to their hibernation sites. Small hillocks of grass, *Phleum pratense* and *Brachypodium silvaticum*, 2 cm in diameter at the soil surface and 10–12 cm high, were planted in plastic pots (15 cm diameter). Small spruce seedlings of the same heights were also planted in separate pots. Ten pots with plants of each species were covered with small cages of the type described above and kept in the greenhouse at 20°C with the natural dark/light period of August. Ten psyllids were introduced into each cage, i.e. 100 insects per plant species. The number of psyllids alive was counted on each plant species eight times over the following 33 weeks. Mean values and standard deviations of the numbers of surviving insects were calculated.

Influence of conifer volatiles on insect behaviour (4). Plants: carrot seedlings at the developmental stage described for experiments 1 and 2 were grown in groups of four plants per pot (size 7×7 cm). Fresh spruce sawdust (20 ml) was spread on the soil surface around the seedlings in every second pot. The pots were then covered with cages (11×7 cm) as described above. Paired comparisons were made between untreated and sawdust-treated plants. Pots with untreated and sawdust-treated carrots were placed 30 cm apart in the greenhouse. Ten psyllids were introduced into each cage. The number of psyllids sitting on untreated and sawdust-treated carrots, respectively, was registered every hour between 11 a.m. and 5 p.m. The test was made in September, light/dark period 13/11 h.

Influence of photoperiod on insect behaviour (5). Plants: carrot seedlings of the type used in experiments 1, 2, and 4, covered with cages. One female and one male were placed in each cage. Ten pots with carrots were used in each photoperiod test. The number of days needed for the start of the oviposition was determined at different photoperiods. The ratios light/dark 17/7, 16/8, 15/9, and 13/11 were investigated. The temperature was constant in all photoperiods, 20°C.

Collection of volatiles. An entrainment technique was used for trapping the volatile compounds released from the above-mentioned species of Apiaceae plants and from twigs of *Picea abies* (L.) Karst. and *Juniperus communis* L. Seedlings with one to three true leaves and roots (about 100 individuals; 6 g wet weight, 0.25 g dry weight) were kept in water in a glass container or the green parts were enclosed in a heat resistant plastic bag (Melitta®). The volatiles released from the small plants were collected on the organic polymer Porapak Q (100 mg; 80–100 mesh) through entrainment. The air used, 100 ml min^{-1} for 24 or 48 h, was filtered through charcoal. The volatiles were eluted from the sorption material with 2 ml of redistilled pentane (Merck, p.a.). Three to five samples of each species were prepared by this procedure. In some cases, the same plants (6 g) were extracted with pentane (5 ml) after the sorption period, to compare the compounds present in both samples. The green parts of the plants were extracted at room temperature for 16 h, the extract was filtered through a small column of silica gel (0.5 g; Matrex silica, Amicon) and the solution was concentrated at 40°C in a water bath to the volume of 0.2 ml.

Identifications of the volatile constituents. The components of the monoterpene fraction were identified on a Finnigan 4500 GC–MS instrument, connected to a Varian 3400 GC, using a DB-WAX fused silica capillary column (J. and W. Scientific, 30 m, 0.25 mm i.d., 0.25 μm film thickness). The temperature programme was 40°C for 4 min, followed by 4°C min^{-1} up to 200°C. The mass spectra were compared with those of authentic samples or with literature data. A multi-dimensional GC system (for details see Borg-Karlson *et al.* (1993)) equipped with one DB-WAX (J. and W. Scientific, 30 m, 0.25 mm i.d., 0.25 µm film thickness) and two chiral capillary columns, Cyclodex B (J. and W. Scientific, 30 m, 0.25 mm i.d., 0.25 µm film thickness), and Lipodex E (Macherey–Nagel, 30 m, 0.25 mm i.d., 0.25 µm film thickness) were used for the determination of the enantiomeric composition of the main chiral monoterpene hydrocarbons. The temperature programme on the DB-WAX column started at 40°C for 1 min, followed by 50°C min^{-1} up to 65°C (11 min) while eluting the monoterpene hydrocarbons, and thereafter 20°C min^{-1} up to 130°C. For the chiral columns, the temperature programme started with 30°C isothermally for 30 min, followed by an increase of 3°C min^{-1} up to 75°C.

The monoterpene enantiomers were identified by means of their GC-retention times, using natural or synthetic reference compounds. Pure (+)-β-phellandrene was prepared as described earlier (Valterová *et al.*, 1991). A sample of the flower fragrance of *Laserpitium latifolium* was used as a reference for (−)-sabinene (Borg-Karlson *et al.*, 1994).

Multivariate data analysis. The gas chromatographic data were subjected to a multivariate data analysis (Sjödin *et al.*, 1989; Wold *et al.*, 1989). Two statistical methods were used—PCA (principal component analysis) and PLS–DA (projection to latent structures–discriminant analysis). In both methods (program CODEX® version 5.2, product of SumIT System AB, Solna, Sweden), (+)- and (−)-enantiomers of the chiral monoterpenes were treated as separate compounds (Valterová *et al.*, 1995; Persson *et al.*, 1996). The group of summer and winter hosts (both subspecies of *Daucus carota*, *Picea abies*, and *Juniperus communis*) were compared with the rest of the Apiaceae species in a PLS–DA statistical treatment.

Results

Biological tests

Trioza apicalis laid eggs on all plant species except the non-host plant, *Trifolium pratense* (Fabaceae). *Daucus carota* subsp. *sativus*, *Daucus carota* subsp. *carota*, and *Coriandrum sativum* received the highest numbers of eggs per female (14–18, see Table 1). The average number of eggs on *Petroselinum crispum* was somewhat lower, about 9. Only very few eggs were deposited on the other plants. *Carum carvi*, one of the hosts reported earlier, belonged to this less favoured group in our experiment. The absence of curled leaves on some species (*Aegopodium podagraria*, *Aethusa cynapium*, *Anethum graveolens*, and *Angelica archangelica*) indicated that the psyllids had not fed on these plants. The eggs laid developed into adults on all species except the four above-mentioned ones. Thus, these plants cannot be regarded as hosts. They had not been accepted as

TABLE 1. MEAN NUMBERS OF EGGS LAID ON DIFFERENT SPECIES OF APIACEAE BY *Trioza apicalis* DURING 24 h; SD = STANDARD DEVIATIONS. Means are compared using analysis of variance. Figures followed by different letters are significantly different. The x-mark in a column indicates that adults developed on this plant species and/or that the plant showed curled leaves as a symptom of injury

Species	Number of eggs	SD	Adults	Curled leaves	Number of females
Daucus carota subsp. *sativus*	17.7 e	2.2	x	x	*n* = 17
Daucus carota subsp. *carota*	16.1 e	3.0	x	x	*n* = 21
Coriandrum sativum	13.6 de	1.8	x	x	*n* = 30
Petroselinum crispum	8.9 cd	1.7	x	x	*n* = 21
Pimpinella saxifraga	4.8 abc	1.4	x	x	*n* = 21
Pastinaca sativa	4.1 abc	1.8	x	x	*n* = 21
Foeniculum vulgare	4.0 abc	1.4	x	x	*n* = 21
Anthriscus cerefolium	3.2 ab	1.1	x	x	*n* = 21
Angelica archangelica	2.8 ab	0.6	—	—	*n* = 30
Levisticum officinale	2.7 ab	0.9	x	x	*n* = 21
Aethusa cynapium	1.9 ab	0.8	—	—	*n* = 21
Pimpinella anisum	1.5 a	0.6	x	x	*n* = 21
Anthriscus sylvestris	1.3 a	0.7	x	x	*n* = 21
Anethum graveolens	1.0 a	0.5	—	—	*n* = 30
Carum carvi	0.6 a	0.3	x	x	*n* = 21
Aegopodium podagraria	0.4 a	0.4	—	—	*n* = 21
Trifolium pratense	0.0 a	0	—	—	*n* = 30

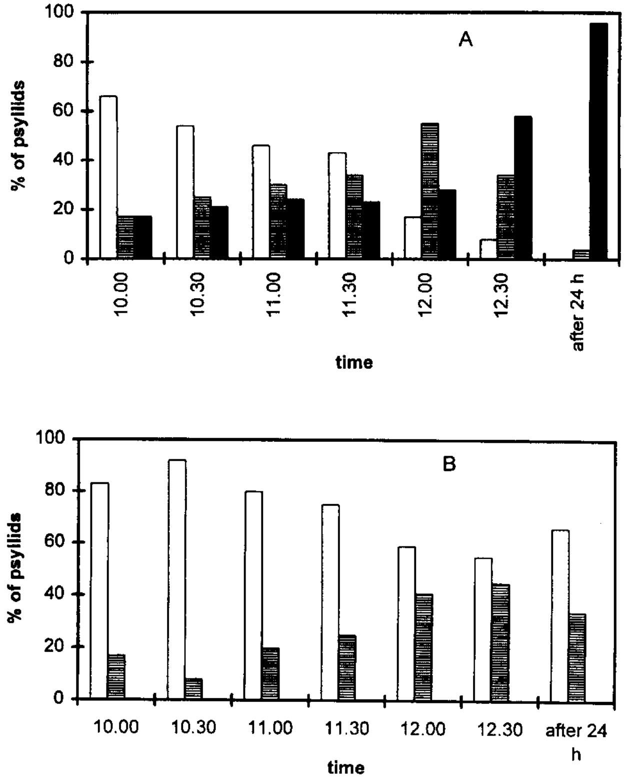

FIG. 1. BEHAVIOUR OF FEMALE *Trioza apicalis* ON CARROT (A) AND DILL (B) DURING OVIPOSITION. Per cents of insects sucking on the respective plant species at different times, and per cents of insects ovipositing on the respective plant.

food-plants and only few eggs were deposited on them. *Trifolium pratense* was included in the test to determine whether *T. apicalis* females with a heavy eggload would also oviposit on non-host plant species. This was not the case as all females in the cages with *Trifolium pratense* died within 3 days without egg-laying.

When the behaviour on carrot and dill was compared, differences were found in both the time before settling/feeding and the time before starting oviposition (see Fig. 1). After 24 h, 100% of the females tested in carrot cages were sitting/ovipositing on the carrots, while just 33% of the females inserted in the dill cages were sitting on the dill. After 24 h, no eggs had been laid on dill, whereas 23 out of 24 females had deposited eggs on carrot seedlings. The oviposition on carrots had already started after 30 min and continued through the whole experiment.

Trioza apicalis lives longer on spruce than on the grasses *Phleum pratense* and *Brachypodium silvaticum* (Table 2). Some psyllids still survived on spruce after 30 weeks, while none was alive on grasses even after 3 weeks. This result shows that the carrot psyllids feed on their shelter plants during the period preceding the diapause.

The spruce sawdust enhanced the attractiveness of the carrot plants for the autumn population of the psyllids tested. A significantly higher number of psyllids landed on the

TABLE 2. MEAN NUMBERS OF CARROT PSYLLIDS, *Trioza apicalis*, SURVIVING ON DIFFERENT SHELTER PLANTS AFTER DIFFERENT PERIODS IN THE GREENHOUSE. The total number of psyllids per cage was 10 ($n = 10$)

	Number of weeks in greenhouse							
Plant species	1	2	3	4	9	13	29	33
Picea abies	8.1	6.6	5.9	5.6	5.4	4.4	1.1	1.0
Phleum pratense	2.4	0.3	0	0	0	0	0	0
Brachynopodium sylvaticum	1.8	0.3	0	0	0	0	0	0

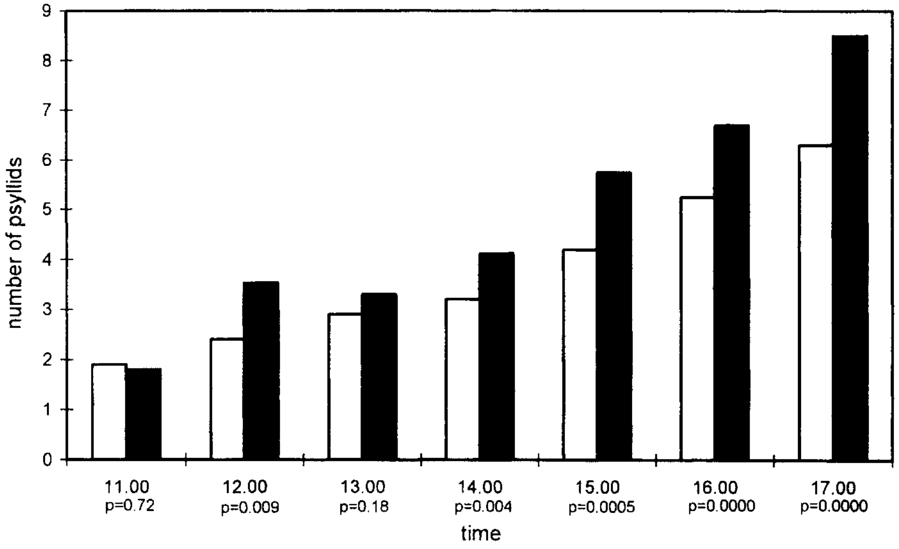

FIG. 2. INFLUENCE OF THE SPRUCE VOLATILES ON THE BEHAVIOUR OF *T. apicalis*. Numbers of psyllids settled on carrot plants (open bars) and on sawdust-treated carrots (dark bars).

sawdust-treated plants than on the untreated ones (Fig. 2). The photoperiod was shown to be of great importance for the insect status. The critical daylight period for oviposition is 17 h, while shorter days lead to hibernation behaviour by the insect females (Table 3).

TABLE 3. NUMBER OF *Trioza apicalis* FEMALES STARTING OVIPOSITION AT DIFFERENT PHOTOPERIODS AT 20°C. Recordings after different periods of time

	Oviposition after			
Photoperiod (h) (day:night)	7 days	15 days	17 days	Number of psyllids
17:7	2	6	8	$n = 8$
16:8	0	0	1	$n = 10$
15:9	0	1	1	$n = 8$
13:11	0	0	0	$n = 8$

Plant volatiles

The compositions of the volatile fractions released by the 16 Apiaceae taxa were species specific. Pentane extracts and entrainment samples obtained from the seedlings contained large amounts of monoterpene hydrocarbons. Almost all of the monoterpenes were present in all species, although in different proportions. The relative amounts of the monoterpenes, regardless of their enantiomeric compositions, are summarized in Table 4. Table 5 shows the enantiomeric compositions of the chiral monoterpene hydrocarbons, while the proportions of the components of the volatile fractions, considering (−)- and (+)-enantiomers as separate compounds, are shown in Figs 3 and 4 in a graphic form.

When several samples of one species were analysed, differences in both proportions and enantiomeric compositions were observed to some extent. On the other hand, each entrainment sample of volatiles, when compared with the sample obtained by the following pentane extraction of the same group of plants, gave the same quantitative composition of monoterpenes both with respect to relative amounts and enantiomeric proportions. To exclude the influence of individual variations, a mean value derived from 3 to 5 samples was calculated for each species.

High contents of sabinene (predominantly (+)-enantiomer) and α-pinene (both enantiomers) were found in the subspecies of *D. carota*. These two subspecies are also the ones preferred by the insects. High contents of α-pinene (mostly (+)-enantiomer) were found in *Aegopodium podagraria* and *Aethusa cynapium*, too. Substantial amounts of 3-carene (pure (+)-enantiomer) were also detected in these two species. *Angelica archangelica* and *Foeniculum vulgare* contained high proportions of myrcene. A substantial content of myrcene was also found, besides other compounds, in *Anthriscus sylvestris* and *Anethum graveolens*. β-Phellandrene (predominantly the (+)-enantiomer) was the main component of the volatiles from *Petroselinum crispum* and *Levisticum officinale*, while β-pinene (mostly (+)-enantiomer) was found abundantly in *Anthriscus cerefolium* and *Pastinaca sativa*. Larger amounts of additional compounds such as *cis*- and *trans*-ocimene were found in *P. sativa*. Limonene (the (+)-enantiomer strongly predominating) was present as the main component in two species, *Carum carvi* and *Pimpinella anisum*. These two species also contained a substantial amount of α-terpinene. Two of the 16 species studied differed strongly from the others in the composition of the volatiles. *Coriandrum sativum* contained α-terpinene as the major component, while *Pimpinella saxifraga* had γ-terpinene and alloocimene as the dominant components of the volatile fraction.

The compositions of the volatiles released from the spruce and juniper twigs are shown in Table 6. (−)-α-Pinene, (−)-β-pinene, and (−)-limonene were the main components of the spruce odour. The difference in odour between a twig and the sawdust lays mainly in the presence of large amounts of (+)-3-carene in the sawdust (Nehlin *et al.*, 1994), while 3-carene was only a minor component in the twig odour. (+)-Sabinene was the main component in the juniper sample. α-Pinene, racemic, was also found in abundance.

A multivariate data analysis (PLS–DA) showed a chemical similarity between the summer and winter host (*Daucus carota, Picea abies*, and *Juniperus communis*) and a significant difference between the host-group of species and the non-host group (Fig. 5). Normalized data resulted in a PLS–DA model which explained a minor part of the variance in the data (two significant components, total variance explained by the model

TABLE 4. RELATIVE AMOUNTS OF MONOTERPENE HYDROCARBONS IN SMALL PLANTS OF 16 TAXA OF APIACAE. EACH CONSTITUENT EXPRESSED AS PERCENTAGE OF THE TOTAL MONOTERPENE HYDROCARBON FRACTION ACCORDING TO GC

	D. c. s.	*D. c. c.*	*C. s.*	*P. c.*	*P. sax.*	*P. sat.*	*F. v.*	*A. cer.*	*A. a.*	*L. o.*	*A. c.*	*P. a.*	*A. s.*	*A. g.*	*C. c.*	*A. p.*
α-Pinene	21.4	28.1	23.6	2.6	0.7	4.5	2.4	8.3	6.5	8.2	42.0	13.6	26.3	5.7	8.6	35.3
α-Thujene	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8
Camphene	0.9	0.7	0.0	0.2	0.0	0.1	0.05	0.0	0.2	1.8	0.7	0.0	2.2	0.2	0.0	0.7
β-Pinene	4.3	12.8	11.1	1.7	0.3	28.8	0.3	69.1	2.6	2.8	9.2	6.8	18.3	8.7	0.01	7.3
Sabinene	43.8	28.8	0.0	0.5	0.9	0.8	0.5	0.0	0.0	3.9	1.0	0.9	0.6	0.5	0.2	2.5
3-Carene	0.1	2.2	10.8	0.5	0.04	1.2	0.2	0.7	1.4	1.0	27.7	0.0	4.3	1.5	0.2	14.8
Myrcene	9.9	3.0	0.0	24.4	1.4	1.6	64.4	0.7	51.5	9.3	0.6	0.0	27.1	26.5	0.2	2.3
α-Phellandrene	0.0	0.0	0.0	0.5	0.0	0.03	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.4	0.0	0.0
α-Terpinene	4.7	11.8	44.8	0.3	3.1	6.0	0.2	10.7	17.1	0.3	11.1	30.2	0.0	8.0	18.9	3.7
Limonene	6.6	5.8	5.5	1.8	10.1	1.5	11.0	8.2	2.6	3.0	2.0	34.6	13.1	7.0	59.7	10.7
β-Phellandrene	0.6	0.8	4.3	58.3	10.5	2.1	6.1	1.3	0.8	60.5	1.5	0.9	1.2	8.4	2.8	1.5
cis-Ocimene	0.01	1.2	0.0	0.0	0.1	30.0	0.7	0.0	3.3	6.4	0.0	0.6	1.2	8.0	0.3	2.2
γ-Terpinene	5.5	1.8	0.0	0.4	43.8	0.1	10.5	0.0	0.8	1.2	0.2	0.0	1.5	9.0	0.8	5.4
trans-Ocimene	1.1	1.2	0.0	3.8	2.0	19.7	0.0	0.5	4.9	0.2	2.2	12.4	0.4	2.6	1.8	0.7
p-Cymene	0.5	1.6	0.0	0.8	8.6	0.2	1.9	0.0	0.0	0.7	1.0	0.0	0.8	4.8	1.6	6.6
Terpinolene	0.1	0.1	0.0	0.7	2.5	1.6	0.4	0.0	0.05	0.1	0.4	0.0	3.0	0.3	2.0	0.6
Alloocimene	0.5	0.1	0.0	3.6	16.0	1.8	1.5	0.5	8.2	0.0	0.5	0.0	0.0	8.2	2.8	0.8

D. c. s., *Daucus carota* subsp. *sativus*; *D. c. c.*, *Daucus carota* subsp. *carota*; *C. s.*, *Coriandrum sativum*; *P. c.*, *Petroselinum crispum*; *P. sax.*, *Pimpinella saxifraga*; *P. sat.*, *Pastinaca sativa*; *F. v.*, *Foeniculum vulgare*; *A. cer.*, *Anthriscus cerefolium*; *A. a.*, *Angelica archangelica*; *L. o.*, *Levisticum officinale*; *A. c.*, *Aethusa cynapium*; *P. a.*, *Pimpinella anisum*; *A. s.*, *Anthriscus sylvestris*; *A. g.*, *Anethum graveolens*; *C. c.*, *Carum carvi*; *A. p.*, *Aegopodium podagraria*.

TABLE 5. ENANTIOMERIC COMPOSITION (–)/(+) OF MONOTERPENE HYDROCARBONS IN SMALL PLANTS OF 16 TAXA OF APIACEAE

Plant species	α-Pinene (–)/(+)	Camphene (–)/(+)	β-Pinene (–)/(+)	Sabinene (–)/(+)	3-Carene (–)/(+)	Limonene (–)/(+)	β-Phellandrene (–)/(+)
Daucus carota subsp. *sativus*	66/34	71/29	22/78	22/78	low	28/72	low[a]
Daucus carota subsp. *carota*	28/72	47/53	21/79	34/56	0/100	28/72	mostly (–)[b]
Coriandrum sativum	45/55	not present	95/5	not present	0/100	61/39	mostly (–)[b]
Petroselinum crispum	47/53	low[a]	51/49	55/45	low[a]	59/41	1/99
Pimpinella saxifraga	47/53	not present	low[a]	low[a]	low[a]	7/93	67/33
Pastinaca sativa	22/78	low[a]	3/97	low[a]	low[a]	50/50	mostly (–)[b]
Foeniculum vulgare	4/96	low[a]	low[a]	low[a]	low[a]	8/92	1/99
Anthriscus cerefolium	18/82	not present	2/98	not present	low[a]	4/96	mostly (–)[b]
Angelica archangelica	75/25	low[a]	mostly (–)[b]	not present	low[a]	37/63	mostly (–)[b]
Levisticum officinale	27/73	53/47	23/77	30/70	0/100	47/53	1/99
Aethusa cynapium	21/79	low[a]	95/5	low[a]	0/100	76/24	mostly (–)[b]
Pimpinella anisum	25/75	not present	low[a]	low[a]	not present	1/99	low[a]
Anthriscus sylvestris	16/84	93/7	17/83	low[a]	0/100	9/91	mostly (–)[b]
Anethum graveolens	30/70	low[a]	16/84	low[a]	0/100	16/84	5/95
Carum carvi	29/71	not present	low[a]	low[a]	low[a]	2/98	low[a]
Aegopodium podagraria	17/83	49/51	85/15	38/62	0/100	94/6	92/8

[a] A threshold content of monoterpene made it impossible to determine its enantiomeric composition.

[b] A low content of monoterpene made it impossible to determine the exact proportion of enantiomers, the small peak of the (+)-enantiomer being below the detection limit of the column.

in *X*: 11%, variance in *Y*: 91%). The group of *Daucus* ssp. and conifers was resolved on the basis of a combination of (–)-α-pinene and sabinene.

Discussion

Host selection by insects is based on various stimuli released by host plants and consists of a sequence of behavioural responses (Visser, 1986; Pettersson *et al.*, 1994; Städler, 1992). Moran and Brown (1973) studied the citrus psylla, *Trioza erytreae*. They found that antennal chemoreception, mainly olfaction, was more important than previously known for psyllids. The females are stimulated by the citrus scent. Factors received on or in the plant seem to be necessary for eliciting the oviposition of *T. apicalis*. This has been found for the pear psylla, *Cacopsylla pyri*. Plant stimuli perceived before probing affected the discrimination of a host plant, but plant cues perceived during settling and probing were necessary to release the oviposition (Horton and Chrysan, 1991).

Our results showed that a large number of Apiaceae plants could serve as hosts for egg-laying *Trioza apicalis*. However, only few eggs were deposited on most of the plants. The large number of eggs laid on *Coriandrum sativum* was surprising as this plant had not been reported as a host plant for *T. apicalis*. Its attractiveness might be due either to the presence of some favourable compounds or to the lack of unfavourable substances. The volatile substances from dill, registered by the insects in the carrot/dill experiment 2, seem to prevent the psyllids from settling on the dill plants as was shown recently in our preliminary results (Nehlin *et al.*, 1996).

Most of the Apiaceae species studied are probably of minor importance as host plants when carrots are grown in the vicinity at the same time. We observed that some of the cultivated species, such as *Pastinaca sativa*, never received any eggs in the field although they grew close to heavily infested carrots. More accepted plants, such as *Petroselinum crispum*, often receive eggs when growing next to the carrots. In some areas or periods

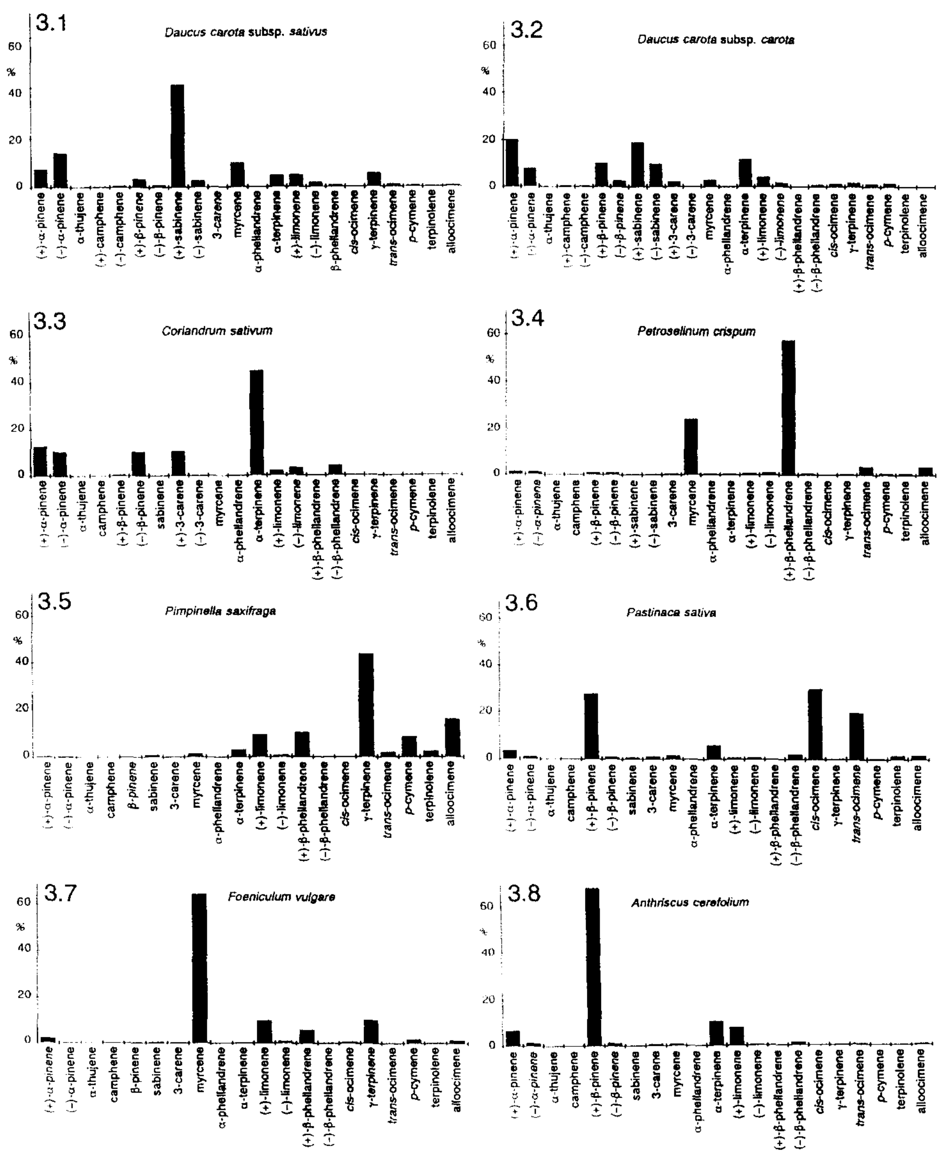

FIG. 3. PROPORTIONS OF SEVEN ENANTIOMERIC PAIRS OF CHIRAL AND TEN NONCHIRAL MONOTERPENE HYDROCARBONS IN SMALL PLANTS OF 8 SPECIES OF APIACEAE. In cases of low contents of some chiral compounds, not allowing the determination of the enantiomeric composition, the sums of the (+)- and (−)-enantiomers are given.

when carrots are not grown, these other plants might be of some importance for maintaining populations of the carrot psyllids.

Our study did not result in finding only one key component being responsible for the host plant attraction. The psyllids do not seem to be specialized to a single specific host compound. Perhaps a specific mixture of volatiles rather than a single compound might be important to guide psyllids to their host. The two most attractive plants (both sub-

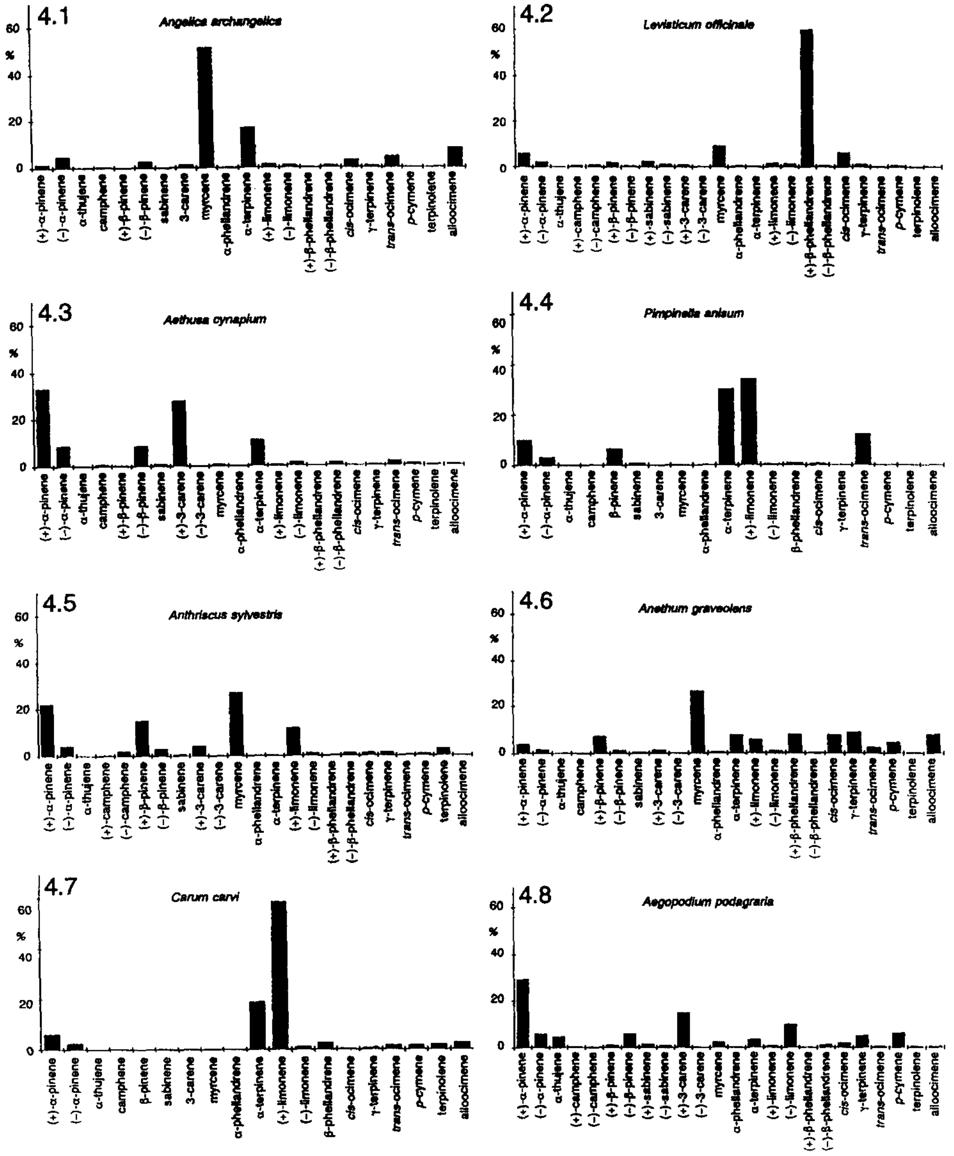

FIG. 4. PROPORTIONS OF SEVEN ENANTIOMERIC PAIRS OF CHIRAL AND TEN NONCHIRAL MONOTERPENE HYDROCARBONS IN SMALL PLANTS OF 8 SPECIES OF APIACEAE. In cases of low contents of some chiral compounds, not allowing the determination of the enantiomeric composition, the sums of the (+)- and (−)-enantiomers are given.

species of *D. carota*) contained high proportions of sabinene and α-pinene which might in combination act as the key components for the long-distance attraction. However, high contents of α-pinene were also found in three species of low preference, *Anthriscus sylvestris, Aethusa cynapium*, and *Aegopodium podagraria*. The majority of Apiaceae plants studied in this paper contained less than 11% of limonene. A higher proportion of (+)- or (−)-limonene was found in the least attractive plant species (*Pimpinella anisum*

TABLE 6. RELATIVE AMOUNTS OF MONOTERPENE HYDROCARBONS IN SPRUCE AND JUNIPER TWIGS, THEIR ENANTIOMERIC COMPOSITIONS IN PARENTHESES

	Picea abies % (−/+)		*Juniperus communis* % (−/+)	
α-Pinene	22.4	(75/25)	28.9	(50/50)
Camphene	4.6	(82/18)	0.3	(61/39)
β-Pinene	20.9	(98/2)	1.3	(70/30)
Sabinene	0.5	(28/72)	35.5	(0/100)
3-Carene	0.8	(0/100)	3.5	(0/100)
Myrcene	11.3	—	2.6	—
α-Terpinene	0.2	—	0.6	—
Limonene	21.9	(96/4)	4.5	(7/93)
β-Phellandrene	9.2	(99/1)	2.3	(90/10)
cis-Ocimene	0.02	—	0.3	—
γ-Terpinene	0.04	—	2.2	—
trans-Ocimene	0.2	—	0.2	—
p-Cymene	0.1	—	2.7	—
Terpinolene	0.04	—	3.6	—

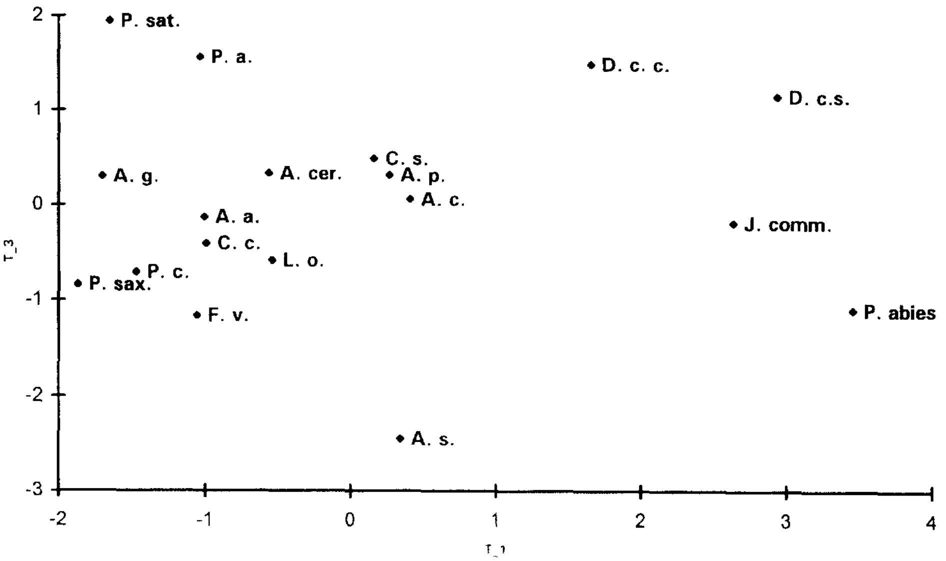

FIG. 5. PLS-DA OF THE GROUP OF SUMMER AND WINTER HOST COMPARED TO THE REST OF THE SPECIES STUDIED, BASED ON THE RELATIVE AMOUNTS OF MONOTERPENES; SCORE PLOT. For the abbreviations of the species names, see Table 4.

and *Carum carvi*). On those species almost no eggs were laid. These results were in agreement with our recent findings that (+)- or (−)-limonene in high concentration is a repellent for *T. apicalis* in a carrot field (Nehlin *et al.*, 1994). Limonene is also known to inhibit the attraction of *Hylobius abietis* to other monoterpenes (Nordlander, 1990, 1991). Karr and Coats (1988) observed a high repelling effect (87%) of (+)-limonene on the German cockroach.

Polar or non-volatile substances, which were not the object of our investigation, could also have been responsible for the differences in attractiveness. That was found for the black swallowtail butterfly, *Papilio polyxenes* (Feeney *et al.*, 1989). The volatile fraction itself was not as active when applied separately, but it increased the landing rate in the oviposition behaviour, as long as the contact chemostimulants (non-volatile components) were also present (Feeney *et al.*, 1989). The defence chemicals in the surface wax of the carrot leaves synergistically stimulated oviposition by *Psila rosae* (Städler and Buser, 1984).

Our investigation of shelter plants (test 3) confirmed the preference of *T. apicalis* for conifers. The results show that the carrot psyllids feed on their shelter plants during the period preceding the diapause. It was not known before whether or not the psyllids feed on shelter plants after the migration to their hibernation sites (Ossiannilsson, 1992). The psyllids did feed on conifers, but the grass species from the same site were unsuitable for feeding, as the psyllids died on them. Observations in the field have shown that *T. apicalis* can survive on *Juniperus communis* too (Nehlin, unpublished). It is of interest to note the high amount of (+)-sabinene in both carrot and juniper samples.

Both the winter and the summer hosts release large amounts of monoterpenes although not in the same proportions. Nevertheless, the taxon specific combination of terpenes is most probably the essential host recognition cue for *T. apicalis*. Guerin *et al.* (1983) came to a similar conclusion in their studies of the attractiveness of carrot volatile components for *Psila rosae* (Diptera). By using a GC–EAD method they found that the most attractive compounds were two substituted propylbenzenes, present in the carrot leaf samples in small proportions. However, individual components did not show as high attraction as the complex mixture itself. The same conclusion was also done by Städler and Buser (1984).

The autumn migration to conifers might be directed by volatiles released from the shelter plants, as shown in experiment 4. The difference in the response to the sawdust odour between the spring and autumn forms of *T. apicalis* is interesting. It was recently shown (Nehlin *et al.*, 1994) that the volatiles from the spruce and pine sawdust reduced the degree of infestation (eggs laid) in carrot crops by *T. apicalis* in the spring. It also seems that the light cycle plays a major role in the regulation of the behaviour. During the insect development there must be a "switch" in behaviour causing the sawdust volatiles to become more attractive to the autumn form of *T. apicalis*.

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