Chapter 9

COCCINELLIDS AND SEMIOCHEMICALS

Jan Pettersson
Department of Ecology, Swedish University of Agricultural Sciences, Box 7044,
SE-750 07 Uppsala, Sweden

Ecology and Behaviour of the Ladybird Beetles (Coccinellidae), First Edition. Edited by I. Hodek, H.F. van Emden, A. Honěk.

9.1 INTRODUCTION

Coccinellids are friendly, colourful insects, serving as valuable supporters of biological control of pests such as aphids and scales in important crops. However, they have developed a set of unpleasant and poisonous defence chemicals which together with striking colouration constitute an aposematic enemy barrier. The unique aposematic chemistry forms a basis for several prominent features of coccinellid population biology and behavioural ecology. Furthermore the ecological adaptability of coccinellids and their capacity to sense and respond to a broad set of information carried by stimuli from the environment is an important contribution to their ecological success (Hodek & Michaud 2008). Information mediated by semiochemicals contributes not only to different aspects of food and food search but also to social and ecological behavioural processes such as competition, reproduction and other important traits in behavioural ecology. Recently a valuable summary of coccinellid chemistry has been published by Durieux et al. (2010). This chapter summarizes semiochemical-supported mechanisms related to the main features of the population biology of coccinellids, their interaction with foes and friends, foraging and prey discrimination and social interaction.

9.2 APOSEMATISM AND REFLEX BLEEDING CHEMISTRY

9.2.1 Reflex bleeding

Coccinellids provide a typical case of aposematism i.e. striking colouration and, when provoked, promptly release of repellent and aggressive **defence substances** (Majerus 1994). Adults bleed from the tibiofemoral joints and larvae from dorsal glands. The **amount of reflex fluid** emitted by ladybirds in response to an attack can be very high (up to 20% of body fresh weight), and the alkaloid component can constitute several per cent of the weight of the fluid (Holloway et al. 1991, 1993). The exudates are yellowish/orange and are mostly toxic to other organisms and sometimes also distasteful with a strong flavour. Several studies have demonstrated the importance of these substances as a defence barrier against enemies (Marples 1993a, Majerus & Majerus 1997).

The aposematic chemicals play an important and complex role in the interaction between coccinellids and their enemies and other competitors. This relationship may involve finely tuned interactions as in the competition that occurs in the ant–coccinellid relationship.

9.2.2 Reflex bleeding substances

9.2.2.1 Experiments

The efficiency of the multiple-component defence secretion of *C. septempunctata* has been investigated in **feeding experiments** with Japanese quail, *Coturnix japonicus* (Marples et al. 1994). Even if the interaction between colour and taste was also important, colour pattern was the most significant deterrent for experienced birds. The birds detected the insect's smell but rarely used it as a cue to toxicity. No single element was sufficient to maintain avoidance comparable to that caused by the whole insect.

9.2.2.2 Identification

Aposematically active compounds have aroused a considerable amount of interest and a broad range from different coccinellid species have been **chemically identified**. So far 50 different **alkaloids** have been identified from 43 species (Daloze et al. 1994, Pasteels 2007). The **chemistry of** the **defensive substances** forms a specific framework for the semiochemistry of coccinellids (Schroeder et al. 1998, Laurent et al. 2005). Examples of aposematic substances are shown in Fig. 9.1. Most of them have negative effects on other organisms in that they are repellent and/or toxic. However, the insect pathogenic fungus, *Beauveria bassiana*, seems to overcome or tolerate them. *Beauveria bassiana* is a common mortality factor attacking hibernating coccinellids (Roy & Cottrell 2008; Chapter 8).

9.2.2.3 Sources

The **synthetic pathway** for most of the **autogenous** aposematic substances follows a common pattern, beginning with a hydrocarbon chain to which nitrogen from amino acids is added. The **site of synthesis** of coccinelline and adaline has been localized to cells in the **fat body** (Laurent et al. 2005)**.** The alkaloid content in the reflex bleeding is similar to that in the haemolymph (Holloway et al. 1991). Experimental results showing the occurrence of **haemocytes** in the

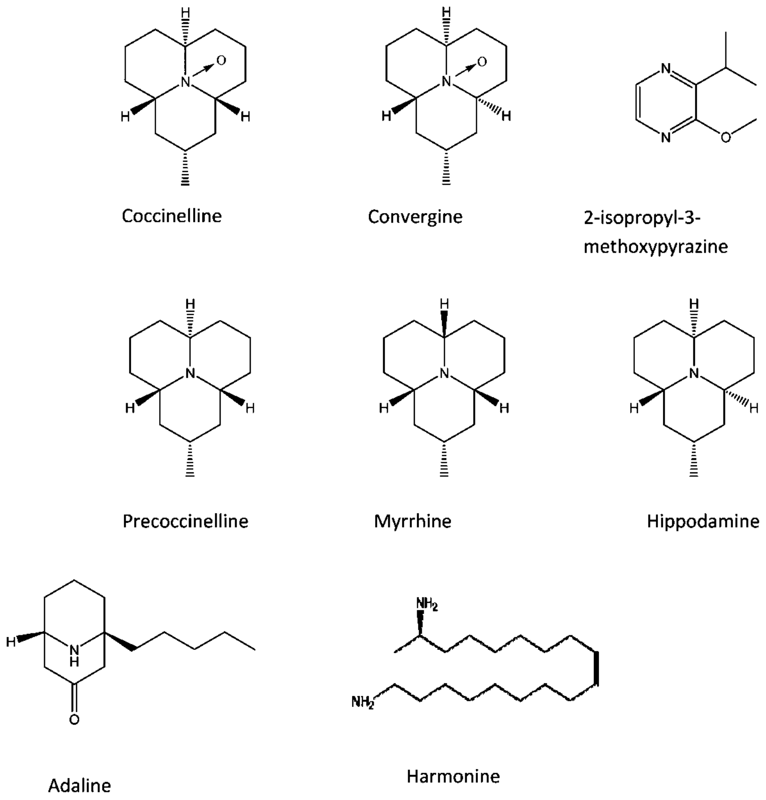


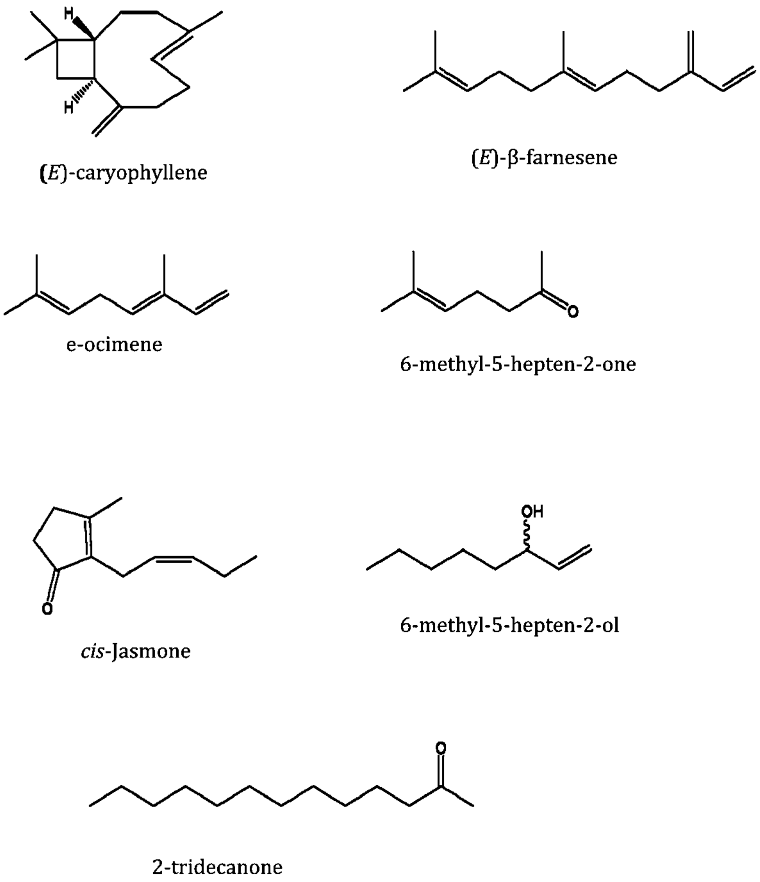
Figure 9.1 Chemical components in coccinellid aposematism and reflex bleeding systems.

reflex bleeding fluid may indicate shared origin of both the bleeding liquid and the haemolymph (Karystinou et al. 2004). Although most of the defensive alkaloids are synthesized by the coccinellids themselves, several cases have been reported where coccinellids **sequester toxins from** their aphid **prey**; the toxins originate from the host plant of the prey. Thus *C. undecimpunctata* sequester **cardenolides** from *Aphis nerii*, which in turn gets these by feeding on *Nerium oleander* (Rothschild et al. 1973). **Pyrrolizidines** are sequestered by *C. septempunctata* preying on *Aphis jacobaeae* feeding on *Senecio* (Witte et al. 1990).

In *C. septempunctata*, the fluid that is emitted at the tibio-femoral joints contains highly toxic alkaloids. One of them, **coccinelline** (Fig. 9.1), the N-oxide of the free base **precoccinelline**, has extremely high mammalian toxicity (Marples 1993b). Both compounds are released along with the volatile **pyrazine** (Fig. 9.1), which seems to serve a dual role in the chemical ecology of *C. septempunctata* as an enemy repellent and a putative aggregation pheromone (Al Abassi et al. 1998).

9.2.2.4 Production cost

The production of aposematic compounds means **a cost for the coccinellid individual**. In a trade-off study with *Menochilus sexmaculatus*, the concentration of alkaloids present in reflex bleeding exudates in the larvae and adult females of different ages were determined and the cost of chemical defence to life-history parameters, viz. body weight, fecundity, egg weight, hatching success of eggs and longevity, was measured (Agarwala & Bhowmik 2007). The results showed that females which had been provoked to release chemicals had shorter longevity and produced smaller eggs by weight, and that the hatching success of their eggs was significantly reduced compared to eggs of unprovoked



(*E*)-caryophyllene

(*E*)-β-farnesene

e-ocimene

6-methyl-5-hepten-2-one

cis-Jasmone

6-methyl-5-hepten-2-ol

2-tridecanone

Figure 9.2 Semiochemicals related to foraging and food searching behaviour in coccinellids.

control females. However, no effect was found on body weight, reproductive age and fecundity. Larvae that had been provoked developed into smaller females than unprovoked larvae. Results of exudate collection from individuals of different ages suggested that there was an **age-related variation** in the amount of defence fluid produced and the concentration of alkaloids, in line with what has been described for *Epilachna paenulata* mentioned above (Camarano et al. 2006).

9.2.2.5 Age and stage modifications

The composition of **toxins** (including autogenous aposematic compounds) may vary between developmental stages **in** some **phytophagous species**. The defensive chemistry of *Epilachna paenulata* was shown to be a mixture of **piperidine**, **homotropane** and **pyrrolidine** alkaloids. Whole body extracts of adult beetles contain four major alkaloids, 1-(6-methyl-2,3,4,5-tetrahydro-pyridin-2-yl)-propan-2-one, 1-(6-methyl-2-piperidyl)-propan-2-one, 9-aza-1-methyl-bicyclo [3.3.1]nonan-3-one and 1- (2″- hydroxyethyl)-2-(12′-aminotridecyl)-pyrolidine. Comparisons of the composition of alkaloids in eggs, larvae, pupae and adults showed both qualitative and quantitative differences between the four life stages, and also varied during the adult stage, with optimum content during the oviposition period. Laboratory predation bioassays showed that **adults are better protected** than larvae and pupae against wolf spiders and, in field tests, the adult alkaloid extract also was deterrent to ants (Camarano et al. 2006).

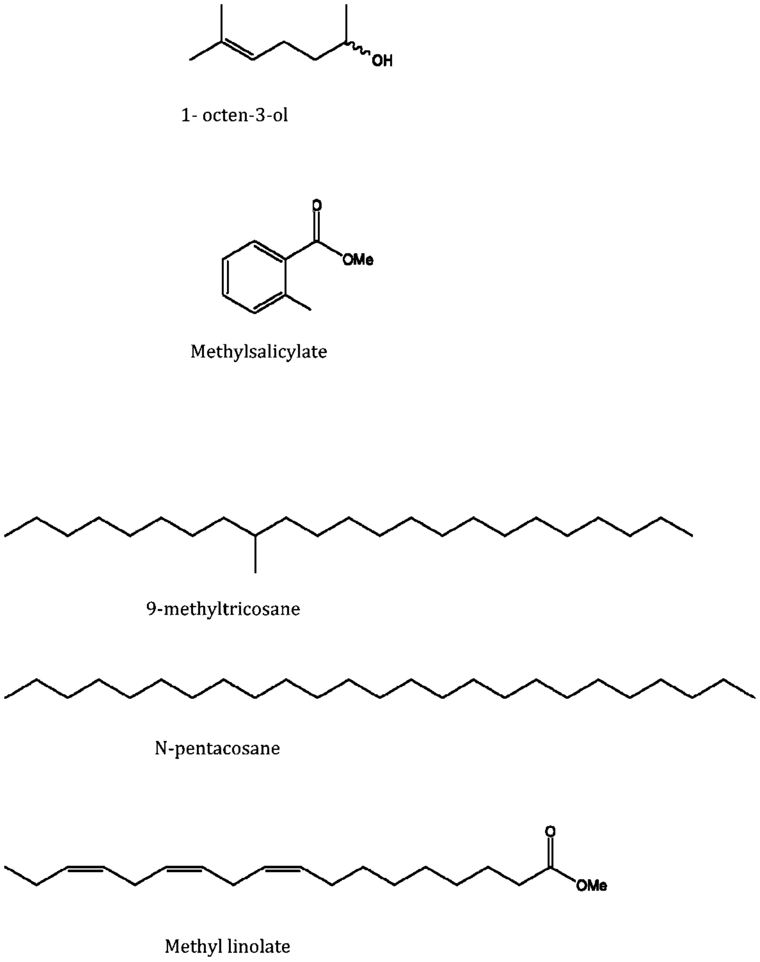


Figure 9.3 Examples of semiochemicals involved in kin recognition and mobility of coccinellids.

9.2.2.6 Species specific chemistry

Generally the composition of the reflex bleeding exudates for most coccinellid species seems to be species-specific and to contain only one or a few main components (review by Laurent et al. 2005). Thus it has been suggested that these alkaloids could be used as a monitoring **tool for estimation of intraguild predation** (IGP, Ch. 7; Hautier et al. 2008). Sloggett et al. (2009) used a gas chromatography-mass spectrometry (GC-MS) based approach for studies of predation of *Har. axyridis*. The alkaloid hippodamine from a single egg of *Hip. convergens* was detected in all 10 third instar larvae of another ladybird, *Har. axyridis*, for 12 hours after consumption. A comparison of the alkaloids of five ladybird species that co-occurred in the field study found that, in general, the alkaloids were sufficiently distinct to allow species identification of ladybirds that had been consumed by predators, although there was some overlap between species in alkaloid content. With the same analytical method, Kajita et al. (2010) found intraspecific variation of alkaloid content in egg clusters of *Har. axyridis* and *C. septempunctata*. The alkaloids affected egg consumption rates of adults and it was also found that *C. septempunctata* was more affected by alkaloids than

Har. axyridis. It was shown that this difference could be attributed to differences in alkaloid metabolism by the two species.

9.2.3 Relation to enemies and competitors

9.2.3.1 Parasitoids

The parasitoid, ***Dinocampus coccinellae*** (Ch. 8.3) causes mortality in adult *C. septempunctata* (9–72% in East Anglia) (Barron & Wilson 1998). The oviposition process is very rapid and seems to be initiated by a specific set of stimuli (Richerson & DeLoach 1972). Orr et al. (1992) compared the attack patterns and specificity of *D. coccinellae* with respect to four coccinellid species and concluded that orientation towards the host preceding final attack is an important step. It is suggested that volatile semiochemicals play a key role in this **location of adult** *C. septempunctata* by a *D. coccinellae* female. In laboratory experiments, it was demonstrated that the free base **precoccinelline** is attractive to the parasitoid and is highly active at the electrophysiological level (Al Abassi et al. 2001). Other naturally occurring ladybird alkaloids with similar structures e.g. **myrrhine** from the 18-spot ladybird, *Myrrha octodecimguttata*, and **hippodamine** from the convergent ladybird, *Hip. convergens*, showed significant biological activity on the parasitoid's behaviour. However, it remains to be seen to what extent other stimuli such as visual cues contribute to orientation of the wasp towards its host for the final attack and under natural conditions.

9.2.3.2 Ants

Ants compete with coccinellids for the **exploitation of aphids** and aphid products (honeydew) as food sources (5.4.1.6 and 8.2.4). Based on studies of aposematism and the interaction between *Lasius niger* and *C. septempunctata*, it has been suggested that alkaloids may also protect the ladybird from ant attack and thus increase its chances of consuming aphid prey (Marples 1993b). This form of protection seems to be better developed for *C. septempunctata* than for *A. bipunctata*, and is in agreement with the observation that *C. septempunctata* appears to use the trail pheromones of *Formica polyctena* in foraging (Bhatkar 1982). The specific relationship between ants and *C. septempunctata*, compared to that between ants and *Har. quadripunctata*, has also been observed for ant-attended aphid colonies on Scots pine, *Pinus sylvestris* (Sloggett & Majerus 2000). The results indicate that ant attendance prolongs the survival of aphid colonies, thus stabilizing the food supply for the ladybirds. Aqueous solutions of **convergine** (from *Hip. convergens*) and **coccinelline** (from *C. septempunctata*) have been tested for repellence to ants (*Formica rufa*) and quails (*Coturnix coturnix*) (Pasteels et al. 1973). Repellence to ants was consistent, while responses from individual quails showed variation. In a review of defensive chemistry in insects, Laurent et al. (2005) stress a wider ecological perspective on alkaloids, which are the most frequently encountered defensive compounds not only in coccinellids but also in other insects. This is also stressed by Majerus et al. (2007). Studies of the ovipositing behaviour of *A. bipunctata* showed that the presence of *L. niger* reduced (via semiochemicals) the number of eggs laid (Oliver et al. 2008). It was also found that the survival of eggs was reduced due to ants attacking but not consuming the coccinellid eggs.

Few cases of myrmecophily are known in coccinellids (8.2.4). However, Vantaux et al. (2010) showed that larvae of the coccinellid *Diomus thoracicus* live safely inside the nests of the ant *Wasmannia auropunctata* and prey exclusively on the ant larvae. In contrast adults are always attacked. The tolerance of ants to the larvae in the ant nest is based on chemical mimicry of the ant cuticular chemistry.

9.2.3.3 Spiders

Coccinellids fall prey to spiders especially during the autumn migration to the hibernating sites. In feeding experiments, the European orb-web spider, *Araneus diadematus*, was offered *C. septempunctata* and *Har. axyridis* as prey (Sloggett 2010). Spiders were not deterred by the coccinellid alkaloids and no significant effect on spider development was observed. Several investigations on selectivity of spider foraging showed, with variable results (Nentwig 1983, 1986), that predator–prey combinations are important.

9.3 SEMIOCHEMICALS RELATED TO FOOD

9.3.1 Plant volatiles

9.3.1.1 Herbivore-induced plant volatiles

Informative volatile cues from herbivores and/or herbivore-infested plants shorten the searching time for the predator and increase foraging efficiency. There is experimental evidence for behavioural effects also of volatiles from plants on coccinellid food search having a short active range (Pasteels 2007) and they may be seen as part of the final step in foraging behaviour (9.3.4 and 5.4.1).

Semiochemicals indicating the presence of food can be produced directly by the prey/food and produced as plant responses to herbivore attack. Most coccinellids prey on a broad range of herbivores, and semiochemicals carrying information on **plant status,** i.e. **whether attacked or unattacked**, can be expected to be one of the leads in dispersal and foraging. The ecological importance of this kind of information has been well documented in mite predator–prey systems on lima bean where it was shown that predatory mites intensified their searching behaviour in contact with lima bean plants that had been attacked by mites (Dicke et al. 1998; Dicke 2000). Similar preferential responses have been shown in olfactometer experiments with *C. septempunctata* exposed to barley plants previously attacked by aphids, *Rhopalosiphum padi* (Ninkovic et al. 2001). Tea shoots attacked by aphids or mechanically damaged were shown to be more attractive to natural enemies and this was interpreted as a combined response to **volatiles produced by plants** (synomones) and by herbivores (kairomones) from the tea aphids (*Toxoptera aurantii*; Han & Chen 2002, 2005).

A **common volatile** released **from herbivore-stressed plants** is **methyl salicylate** (Walling 2000). However, Bi et al. (2007) showed that allelopathic responses in rice also included the production of methyl salicylate. Several investigations have shown that methyl salicylate is a messenger substance for coccinellids, releasing an **arresting behaviour**. Both in field and laboratory experiments, James and colleagues (James & Price 2004, James 2005) recorded such an arresting response in adult *C. septempunctata*. Similar results have been reported for other coccinellids (Zhu & Park 2005). Using sticky traps baited with herbivore-induced volatiles, James and colleagues (James & Price 2004, James 2005) showed that *Stethorus punctum picipes* was significantly attracted to sticky traps baited with a more complex mixture of volatiles, namely methyl salicylate, ***cis*-3-hexen-1-ol** and **benzaldehyde**.

So far only a few active substances have been identified that are exclusively linked to plant responses to herbivory. **cis-jasmone** ((Z)-jasmone) is a common plant volatile involved in a switch-on mechanism for **defence** metabolism **in plants**. In wind tunnel tests *C. septempunctata* adults demonstrated attraction to (Z)-jasmone. When applied in the vapour phase to intact bean plants, (Z)-jasmone induced the production of volatile compounds, including the monoterpene (*E*)-ocimene, an attractant to the aphid parasitoid *Aphidius ervi* (Birkett et al. 2000, Bruce et al. 2008). Possibly, this is support for a general mechanism whereby predators and parasitoids of herbivores can trace plants under stress.

9.3.1.2 Adult receptors for food semiochemicals

Experiments with adult *Hip. convergens* indicate that receptor centres for food- related volatiles are located on the **antennal tips** (Hamilton et al. 1999). Responses of beetles whose antennae, maxillary palps or antennal tips had been amputated were compared in olfactometer experiments with non-injured beetles. Only beetles with their antennae or antennal tips intact responded positively both to the odour of radish leaves infested with peach–potato aphids, *Myzus persicae*, and to clean radish leaves. Scanning electron microscope studies of the distribution of different receptor types suggested that the primary function is executed by **trichoid sensilla** located **on the terminal antennal segment**. The synergistic effects of plant and prey volatiles have so far only been given moderate attention.

9.3.1.3 Responses of larvae

Most experiments on semiochemicals and food finding by coccinellids have been made with adults, but several reports also include the behaviour of larval stages. A common technique for laboratory studies of adult responses to semiochemicals is olfactometry, whilst experiments with **larvae** are usually based on recording **arresting responses** induced by volatiles in an arena. The searching behaviour of *Hip. convergens* larvae was studied as affected by volatile chemicals from tobacco aphids, *Myzus persicae nicotianae* (Jamal et al. 2001). Larvae (second, third and fourth instars) were exposed to three volatile sources: aphids alone, aphids on tobacco leaves and tobacco leaves previously exposed to aphids. The search path of larvae was traced in an arena and the different angles and velocities of movement were recorded. In general, older larvae were more efficient at searching than younger ones. In most cases significant effects attributable to olfactory cues were obtained. The results support the potential of olfactory cues to modify the behaviour of coccinellid larvae and call for more research on the semiochemicals involved.

9.3.1.4 Prey sex pheromones: predator kairomones

Rhyzobius spp. larvae responded to **sex pheromones** of pine bast scales *Matsucoccus*. The response of coccinellid larvae was tested in field trials using pine tree arenas baited with the sex pheromones of *M. josephi*, *M. feytaudi* and *M. matsumurae*. Both field and laboratory tests demonstrated a significant positive response to the sex pheromones of *M. feytaudi* and *M. matsumurae* (Branco et al. 2006).

It has been suggested that the foraging activity of coccinellids feeding/searching in aphid colonies also promotes formation of alate aphids (Dixon & Agarwala 1999). However, it is still open as to whether this is only due to disturbance of aphid feeding, or whether repellence of the volatile semiochemistry of the aggressive coccinellid also contributes to increasing the mobility of aphids that would promote alate offspring.

9.3.2 Prey alarm pheromones

9.3.2.1 Aphid alarm pheromone

When attacked by predators many aphids release a **secretion from the cornicles** that contains an alarm pheromone. Aphids that are nearby respond to the pheromone by pulling out their mouthparts and falling from the plant to escape (Nault et al. 1973). Similar observations on the behaviour of treehoppers (Membracidae) attacked by coccinellids have been reported (Nault et al. 1974). Since the main component of the aphid alarm pheromone, the sesquiterpene hydrocarbon **(*E*)-β-farnesene** (EBF), was identified (Nault et al. 1973) it has been given considerable attention both as an aphid repellent and as a **coccinellid attractant**. Experimental studies have shown that adult *C. septempunctata* and larvae of *A. bipunctata* are arrested/attracted by EBF and the odour of crushed aphids (Nakamuta 1991, Hemptinne et al. 2001b, Hatano et al. 2008).

9.3.2.2 Mechanism for modified responses

EBF is also a common substance in nature, occurring in several plants. This represents a problem, since a rigid positive response by ladybirds to EBF may cause them to stay longer in environments that are less favourable through being devoid of prey. Experiments have shown that the response of *C. septempunctata* to EBF is modified by another common plant substance, **(-)-β-caryophyllene** (Al Abassi et al. 2000). As long as the amount of EBF does not exceed a specific ratio that is maintained between it and the caryophyllene, no behavioural response of the coccinellids is elicited. Such is the case when a walking ladybird passes an undisturbed aphid colony on a plant that naturally manufactures EBF. However, if one of the aphid individuals in the colony responds to the threat of a predator and releases alarm pheromone, the proportion of EBF exceeds the critical ratio between the two active substances and the behaviour of the ladybird becomes aggressive. How far this mechanism also operates for other coccinellids is still unknown.

(-)-β-caryophyllene on its own elicited a positive **aggregation response** of adults of *Har. axyridis* in laboratory experiments by Verheggen et al. (2007), indicating that a certain semiochemical may have multiple roles depending on conditions and species involved.

9.3.2.3 EBF release: aphid individual risks

The release of alarm pheromone by an attacked aphid makes this individual more easily detectable. Thus the question has been raised as to whether it is a risk for aphids to reveal their presence by producing EBF. This topic has been studied for the *Har. axyridis–Acyrthosiphon pisum* relationship. However, the results did not show that this apparent **altruistic behaviour** would be costly for the individuals releasing the alarm pheromone. Its release did not have any negative effect for the producer (Mondor & Roitberg 2000).

Myzus persicae habituated to EBF had an increased reproduction rate compared to EBF sensitive aphids. However, predation by *Hip. convergens* significantly reduced the habituated aphid population and outweighed the initial increase in reproduction (de Vos et al. 2010).

9.3.3 Toxic substances in prey

The cabbage aphid, *Brevicoryne brassicae,* accumulates **glucosinolates** such as **sinigrin,** from its host plants (brassicas) and has an enzyme system, myrosinase (β-thioglucoside glucohydrolase), that breaks them down to behaviourally active compounds such as **isothiocyanates** (Kazana et al. 2007). When uptake of sinigrin from an artificial diet was studied, it was found that there was a significant **difference between winged and wingless** aphid morphs with regards to sequestration. Winged aphids excreted significantly higher amounts of glucosinolate in the honeydew than wingless aphids and the higher level of sinigrin in wingless aphids had a significantly stronger negative impact on survival of a ladybird predator. Larvae of *A. bipunctata* were unable to survive when fed on apterous aphids from a diet with 1% sinigrin. However, the larvae survived successfully when fed on winged aphids from the same diet.

Different coccinellid species may handle plant secondary metabolites in prey differently. In experiments with sinigrin, *B. brassicae* and larval stages of *A. bipunctata* and *C. septempunctata*, it was found that the first instar of *A. bipunctata* was unable to survive when fed with *B. brassicae* reared on *Brassica nigra* or artificial diets containing 0.2% **sinigrin**. By contrast, first instars of *C. septempunctata* were able to survive when fed with aphids reared on *B. nigra* or artificial diets containing up to 1% sinigrin, although the presence of sinigrin in the aphid diet reduced nymphal growth and increased the time the larvae took to reach second instar (Pratt et al. 2008).

Similar results were obtained in a series of experiments with *A. bipunctata* in which the effect of different aphid food plants was compared with special reference to **glucosinolates (GLS)** (Francis et al. 2001). The polyphagous aphid *M. persicae* was fed on broad bean (*Vicia faba*; GLS free), oilseed rape (*Brassica napus* subsp. *oleifera*; low GLS level) and white mustard (*Sinapis alba*; high GLS level). Both rape and mustard shortened the developmental time and increased the adult weight of *A. bipunctata*. No significant differences in mortality were observed, but rape-fed *M. persicae* caused higher egg production and larval emergence in the ladybird, while mustard-fed *M. persicae* caused lower fecundity and egg viability. A possible explanation for the differences in the effects on the coccinellids between the experiments with *B. brassicae* (Kazana et al. 2007) and *M. persicae* (Francis et al. 2001) may be that GLS metabolism differs between the polyphagous *M. persicae* and the cabbage feeder *B. brassicae*. (See also 5.2.6.)

9.3.4 Feeding stimulants for phytophagous coccinellids

Feeding experiments with *Epilachna admirabilis*, which mainly feeds on plants of the genus *Trichosanthes* (Cucurbitaceae), showed that the **cucurbitacins**, especially cucurbitacin E-glucoside, strongly stimulated both adults and larvae to feed (Abe & Matsuda 2000). In further studies of **phagostimulants** for *Henospilachna vigintioctomaculata* with potato *Solanum tuberosum*, an interesting synergism between different components from the host plant was shown. The feeding stimulants were isolated and identified as **methyl linolenate** from a lipid-soluble fraction, and glucose and fructose from an aqueous fraction. Although methyl linolenate alone was inactive, it acted positively synergistically with sugars. Methyl linolenate maximized the feeding activity on sugars at the concentration occurring in potato leaves. It is suggested that methyl linolenate plays an important role in host selection by *H. vigintioctomaculata* (Endo et al. 2004). The results indicate that host plant discrimination and feeding site acceptance have a semiochemically complex structure where a mix of specific and trivial plant compounds contribute to a complete message/cue.

9.3.5 Learning

Ladybirds use different sets of stimuli for food localization, and it has been suggested that **associative learning** may play an important role in increasing efficiency (Vet & Dicke 1992). However, conclusive experimental support for this hypothesis is as yet limited. Learned responses in terms of selectivity for prey were recorded in *A. decempunctata* in predation on *Hyalopterus pruni* (Dixon 1959). After previous feeding on *H. pruni*, *A. decempunctata* rejected this aphid when it was touched with the palps.

Adaptive changes in prey handling behaviour have been observed in the coccinellid *Anisolemnia tetrasticta* feeding on a plataspid heteropteran, *Caternaultiella rugosa*. It was found that the efficiency of attack behaviour improved with increasing experience of the prey (Dejean et al. 2003).

Ferrer et al. (2008) studied effects on fitness of adaptive food preferences (learning) in an experiment with *A. bipunctata* testing the effects on food preferences of feeding larvae on different food sources. One group of larvae were fed throughout their development on pea aphids, *A. pisum*, which is a high quality prey. The other group was fed on cowpea aphids (*Aphis craccivora*), considered a suboptimal prey on the basis that adults developing from larvae fed on this aphid were lighter and had fewer ovarioles and a lower overall fitness than individuals reared on pea aphid. When offered a choice, naïve first instar larvae of *A. bipunctata* from the cowpea aphid group more frequently attacked cowpea than pea aphids. However, older larvae did not show this preference and attacked the two species of prey irrespective of the aphids that were previously fed. This is different from what has been shown for parasitoids (van Emden et al. 2008) where the **selectivity** for prey **can develop late** during the larval–pupation phase and even not till emergence from the aphid mummy.

In laboratory experiments with fourth instar larvae of *Col. maculata* ssp. *lengi* Boivin et al. (2010) tested how previous experience affected prey rejection behaviour. It was found that the initial contact and prey discrimination was affected by previous experience but prey representing good food quality were always finally accepted. After 48 hours the learned behaviour appeared to be partially forgotten.

Finding food sources can be seen as a **two-step procedure** in which an initial patch or site preference phase is followed by a close range search process where several semiochemicals directly related to the food source change coccinellid behaviour from dispersal to feeding/attacking behaviour. This feeding response can be modified in an associative learning process by the presence of unique semiochemicals or specific ratios between trivial chemicals indicating presence of food sources. Olfactorily mediated associative learning has been demonstrated in experiments with adults of *C. septempunctata* and four cultivars of barley (Glinwood et al. 2011). *Coccinella septempunctata* did not prefer the odour of one aphid-infested barley cultivar over another. However, after feeding on aphids for 24 hours on a cultivar, adults preferred the odour of that particular cultivar in olfactometer experiments. After feeding experience on a different aphid infested cultivar this preference disappeared.

9.4 MATING AND SEX PHEROMONES

Knowledge about sex pheromones and other semiochemicals promoting coccinellid mating is still limited. However, experimental results indicate the involvement of a **sex pheromone** in the reproductive behaviour of *A. bipunctata* (Hemptinne et al. 1996). A putative **aggregation pheromone** identified in *C. septempunctata* (Al Abassi et al. 1998) also seems to be used by *A. bipunctata* (Hemptinne & Dixon 2000). Possibly the mating cue is separate from the set of volatiles involved in species discrimination where the pattern of aposematic substances may play a role (9.5.1).

9.4.1 Chemoreceptors on the antennae

Studies on *Cer. undecimnotata* showed a **difference** in terms of the presence of antennal receptors **between males and females** (Jourdan et al. 1995). Of 12 different types of antennal sensilla, two **cheatiform sensilla** on the male antenna are missing in the female antenna and one type is specific for the female antenna. Different responses to food and the opposite sex were shown by adult males and females of *A. bipunctata* (Hemptinne et al. 1996). While females mainly respond to prey density (aphids), the males primarily respond to females and mating opportunities. The suggested explanation for this difference in searching behaviour is that a **sexual difference in receptor presence** can be a complement to odour discrimination at the receptor level of the two sexes.

A significant **sexual difference in electroantennogram (EAG) responses** of male and female antennae was shown by Baker et al. (2003). The **male antennae** of *Col. maculata* responded to females but not to males, indicating that chemicals from females are involved in sexual communication. Hexane extracts from conspecific females but not those from males produced significant electrophysiological responses (EAG) from male antennae. The only identified chemical that corresponded to this pattern was **1-octen-3-ol**. A significant EAG response was also recorded to the extracts of fluids produced during ‘reflex bleeding’ and it may be hypothesized that these substances are part of a complex blend constituting the sex pheromone. Female *Col. maculata* antennae exhibited high thresholds in response to several compounds including **α-terpineol**, (Z)-3-**hexenol** and (4aS,7S,7aR)-**nepetalactone**. Field traps baited with **2-phenylethanol** and α-terpineol were highly attractive to adult *Col. maculata*.

9.4.2 Hydrocarbons on elytra

Bioassays indicated that the **female elytra** of *A. bipunctata* could be the source of the active semiochemicals (Hemptinne et al. 1996; Burns et al. 1998). The mating behaviour of *A. bipunctata* proceeds in steps: a male first palpates the female elytra with his maxillary palps, then mounts her and mates. **Elytra washed** in chloroform **failed to stimulate mating**. Analysis of the chloroform extracts of the elytra revealed that male and female ladybirds are coated with the same blend of hydrocarbons among which 9- and 7-**methyl tricosane** are dominant. It was suggested that visual stimuli, in particular movement, are necessary for a male to discriminate males from females while so far unidentified olfactory cues are important for species recognition. It may be hypothesized that again the set of species-specific aposematic compounds mentioned above play an active role.

9.4.3 Ultrastructure of the integumentary glands

Studies of adult *Cer. undecimnotata* showed that glands **with and without secretory ducts** are distributed over the head, thorax and abdomen. Glands without ducts are thought to release **volatile pheromones**. Such glands consist of a single cell and a secretory apparatus located within the thickness of the cuticle and equipped with a **cuticular cribriform plate**. This cribriform plate separates two superimposed cavities, and epicuticular filaments fill the lower cavity. The secretory products from glands with a duct are abundant and released on the surface of the cuticle in the shape of twisted cylinders, which are resistant to acetone treatment. However, their role in modifying behaviour is not yet known (Barbier et al. 1992).

To conclude, there is considerable evidence that sex attractants support mating of coccinellids. Although some active substances that may be components in a complex pheromone blend have been identified, conclusive information on the composition and role of the pheromones is still lacking. Behavioural experiments show that males and females can respond differently to mating partners. Sexual differences in the occurrence of olfactory receptors and behavioural responses to mating-related semiochemicals in behavioural responses to semiochemicals may explain the difference in behaviour between females and males.

9.5 OVIPOSITION

9.5.1 Oviposition deterrence: oviposition deterrence pheromones

Aphids constitute an unstable food supply and **cannibalism** on immobile/less mobile stages (eggs and young larvae) is a common trait in coccinellid biology. Unravelling the mechanistic regulation of this cannibalism via semiochemicals is an exciting ecological challenge as it deals with a complex contribution to the decisive importance of cannibalism for ecological fitness. (See also 5.4.1.3.)

An important requirement for the ovipositing female is to identify a site free from competitors and potential predators on her offspring. Hemptinne et al. (1993) suggested that contacts with coccinellid larvae by the female act as an oviposition inhibiting cue. In later work by Ruzicka (1994, 1997), the general mechanism of an oviposition deterrence pheromone (ODP) was described and defined in *C. septempunctata.* He demonstrated that gravid females utilized semiochemicals in **larval tracks to avoid oviposition** on the sites where conspecific larvae had already walked. ODPs have been shown to occur among coccinellids and are primarily a means for an ovipositing female to avoid sites where her offspring may later be exposed to predation by offspring from other females which had used the same site.

9.5.2 Species-specificity of oviposition deterrence pheromone substances

Species-specificity is illustrated by the fact that female *A. bipunctata* do not avoid tracks deposited by larvae of two other species, *A. decempunctata* and *C. septempunctata* (Hemptinne & Dixon 2000). The results of a study, in which the antennae and maxillary palps were amputated, indicate that females exclusively use contact chemoreceptors on their maxillary palps to detect oviposition-deterring tracks of conspecific larvae (Ruzicka 2003). Females of *Cer. undecimnotata* laid significantly smaller egg batches on paper strips with conspecific tracks than on clean paper strips. However, females of *Cycloneda limbifer* laid significantly larger batches of eggs on paper strips with **conspecific larval tracks** than on clean paper strips. This is the first evidence of an opposite effect in different species of conspecific oviposition-deterring larval tracks on egg clustering in aphidophagous coccinellids (Ruzicka 2003). The ecological background to these different behavioural responses is still an open question.

It has been suggested that **egg-surface** chemicals act as semiochemicals for the avoidance of intraguild (egg) predation between *C. septempunctata* and *A. bipunctata* (Hemptinne et al. 2001a). Behavioural experiments showing an interspecific relationship between *Har. axyridis* and *Calvia quatuordecimguttata* based on ODP are reported (Ware et al. 2008). The experiments are based on previous observations showing that eggs of *C. quatuordecimguttata* escape attack by *Har. axyridis*. The relationship between the deterring effects on *Har. axyridis* is discussed in relation to the palatability of the eggs as food and whether or not the semiochemicals located on the egg surface are really honest signals conveying information to the attacker.

The **persistence** of oviposition-deterring effects is variable and limited in time as shown in a series of experiments with different coccinellid species by Ruzicka (2001, 2002, 2006). Although the response to 10 day old conspecific larval tracks remained significant (see also Hemptinne et al. 2001a) it was considerably lower than the response to fresh tracks. In choice tests with fresh tracks of conspecifics, *Cycloneda limbifer, Cer. undecimnotata* and *Har. dimidiata* larvae, and 10 day old tracks of conspecific larvae, clutch sizes were smaller in the blank test without larval tracks than in tests with fresh tracks. Similarly, semiochemicals in the tracks of conspecific and heterospecific coccinellid larvae can contribute considerably to the spacing of *Menochilus sexmaculatus* offspring among prey of differing quality and that conspecific as well as heterospecific larval tracks can influence the **distribution of larvae. The persistence of intra- and interspecific** effects on the response of *M. sexmaculatus* to larval tracks has also been investigated. Fresh tracks of *M. sexmaculatus*, *Cycloneda limbifer* and *Cer. undecimnotata* larvae effectively deterred *M. sexmaculatus* females from ovipositing; larval tracks from two other ladybird species have also been shown to deter oviposition by females of *M. sexmaculatus*.

9.5.3 Active substances in oviposition deterrence pheromone tracks

The chemical nature of *A. bipunctata* semiochemicals has been investigated in relation to reproduction, oviposition deterrence and intraguild prey avoidance. **Alkanes** with chemical and structural similarity have been identified in each case, indicating that ladybirds exploit their natural product chemistry with parsimonious versatility (Hemptinne & Dixon 2000), similar to that described above for **pyrazine** (Al Abassi et al. 1998). Intraguild interactions between *Har. axyridis* and *P. japonica* are mediated by odour substances from the **faeces** (Agarwala et al. 2003). This mechanism is an interspecific complement to the intraspecific communication and reduces competition between these two coccinellid species.

Bioassays with larvae of *A. bipunctata* have shown that the anal disc of the 10th abdominal segment deposits ODP substances onto the substrate leaving tracks of these semiochemicals (Laubertie et al. 2006). The **chemical composition** of the larval tracks of *A. bipunctata* has been investigated (Hemptinne et al. 2001b) and found to be a complex mixture of around 40 chemically distinguishable alkanes. N-pentacosane is a major component (15.1%). The alkanes are likely to spread easily on the hydrophobic cuticle of plants and so leave a large signal. They are not quickly oxidized and can be long lasting. Observation showed that 10 day old larval tracks still significantly deterred oviposition. Klewer et al. (2007) identified **(Z)-pentacos-12-ene** as a key compound in the larval tracks of *Menochilus sexmaculatus* and **proved** its **oviposition deterring effects in bioassays**. Other compounds found in the tracks were tested in bioassays for oviposition deterrence but were not found to have a significant behavioural effect.

9.5.4 Relation to other aphid enemies

Elegant studies have shown that, to avoid **intraguild predation** (IGP; 7.8), females of the aphid parasitoid *Aphidius ervi* detect semiochemicals in fresh **adult and larval footprints** of *C. septempunctata*, thereby avoiding aphid colonies under attack from ladybirds (Nakashima et al. 2004, Nakashima & Akashi 2005). The response of three aphid parasitoid species, *Aphidius eadyi, A. ervi* and *Praon volucre* to footprint semiochemicals from adult *C. septempunctata* and *A. bipunctata* was investigated by Nakashima et al. (2006). Females of all three parasitoid species avoided leaves previously visited by *C. septempunctata* or *A. bipunctata* adults. *Praon volucre* avoided trails of both ladybird species to a similar degree but the avoidance of the *Aphidius* species was stronger to trails of *C. septempunctata* than to those of *A. bipunctata*. The footprint semiochemicals were identified and quantified. **n-pentacosane** and **n-heptacosane** occurred in significantly greater amounts in *C. septempunctata* trails than in those of *A. bipunctata* and the trails of the two species differed qualitatively in the other hydrocarbons present. The response of the three aphid parasitoids females was tested to three **footprint semiochemicals** occurring in both coccinellid species, n-tricosane ($C_{23}H_{48}$), n-pentacosane ($C_{25}H_{52}$), and n-heptacosane ($C_{27}H_{56}$). It was found that *A. eadyi* was more sensitive to **n-tricosane** than the other two species, only *Praon volucre* showed avoidance responses to n-heptacosane. All three species responded to n-pentacosane.

A similar mechanism has been described for the relationship between the aphid parasitoid, *Aphidius colemani* and *C. septempunctata*, *Har. axyridis* and *P. japonica*, where the number of eggs deposited in aphid colonies with coccinellid larvae was reduced in the presence of semiochemicals from the **larval tracks** of *C. septempunctata* (Takizawa et al. 2000). An important member of the aphidophagous guild *Chrysopa oculata* utilizes the footprint semiochemicals for intraspecific oviposition deterrence; these semiochemicals also have a similar role in *C. septempunctata* (Ruzicka 1997).

The examples given indicate that semiochemicals play a significant role in intraguild interactions between *C. septempunctata* and other aphid natural enemies (7.8).

9.5.5 Aphid abundance

So far most of the positive oviposition semiochemical mechanisms demonstrated for coccinellids in experiments are related to different aspects of food resources, and it has been shown experimentally that oviposition activity is positively affected by **aphid density itself** (Elliot 2000; Frechette et al. 2004). Investigations on the changes in volatiles that occur in aphid-attacked plants have shown that levels of **common plant volatiles** are elevated as discussed in the previous section. An interesting investigation by Oliver et al. (2006) shows that the trade-off between the repellence of larval tracks and increased quality of a certain oviposition site in favour of acceptance is positively related to aphid density, i.e. higher aphid density reduces the repellent effect of the larval tracks. Although three volatiles related to aphid density have been identified (9.3.3) further messenger substances expressing aphid density, either from the aphids themselves or from the attacked plants, seem to be of importance in coccinellid feeding behaviour.

9.6 EGG AND PUPA PROTECTION

9.6.1 Protection of eggs

Cannibalism and interspecific predation are common coccinellid traits that are discussed in 5.2.7 and 5.2.8. The importance of eggs as a first food source for neonate larvae has been observed and discussed by several authors (Gagné et al. 2002; Santi et al. 2003; Michaud & Grant 2004; Michaud & Jyoti 2008). The level and ecological significance of cannibalism vary between species, but it seems common that **conspecific eggs are** identified and **preferred** to those of other coccinellid species and even to some preferred foods such as aphids.

The aposematic substances of coccinellids (9.2) show a species-specific pattern and so constitute a basis for discrimination between the eggs of different species. Thus Sloggett et al. (2009), in an elegant study, demonstrated the possibilities of gas chromatography–mass spectrometry (GC–MS) analysis of **prey alkaloids** to trace IGP in coccinellids. The amount of the alkaloid hippodamine in a single egg of *Hip. convergens* was enough for detection with this method in third instar larvae of *Har. axyridis* after 12 hours (and occasionally even after 36 hours) after consumption. Using an internal standard enabled this method to be used to make estimates of the number of eggs consumed.

9.6.2 Protection of pupae

Generally the pupal stage of holometabolous insects is a vulnerable phase in development, and **chemical defence** of coccinellid pupae has been reported. The pupal surface of *Subcoccinella vigintiquatuorpunctata* bears glandular hairs that produce a secretion consisting principally of three **polyazamacrolide alkaloids** that serve as a potent anti-predator defence; contact with it elicited pronounced cleaning activity by the predatory ant *Crematogaster lineolata*. Application of the secretion to palatable food items rendered them unacceptable to the ant (Smedley et al. 2002).

9.7 HIBERNATION AND AGGREGATION

Aggregation behaviour is discussed in detail in 6.3.1.4. The **intrinsic preference** to join conspecifics is an important mechanism in the formation of aggregations. The formation of denser aggregations seems to be a process affected by prevailing climatic conditions such as temperature and rainfall (Klausnitzer 1989). In the context of the specific conditions during the late autumn, any pheromone would need to have potent olfactory activity even if temperatures are low. To be active over a longer time it should also be chemically very stable. Indeed, a pheromone fulfilling these requirements was isolated and identified for *C. septempunctata* as **2-isopropyl-3-methoxypyrazine** (Al Abassi et al. 1997). In terms of properties, this compound is well suited for its expected functions i.e. high olfactory activity and low volatility and chemical stability under field conditions. Thus, it may function as a messenger substance even if aggregation itself is a slow process that is accentuated only on days with favourable temperatures.

9.8 HABITAT PREFERENCES: RESPONSES TO PLANTS AND PLANT VOLATILES

9.8.1 Habitat selection

Two different plant-derived semiochemical messages can be expected to contribute to **habitat/patch arrestment** of polyphagous coccinellids. One is information on **botanical composition** and possibly the presence of preferred plants (Schmid 1992). The second type of message would carry information on **plants under stress**, either from the presence of herbivores or caused by interaction on the plant–plant level. In summary there is experimental evidence that plant volatiles contribute to the patch preferences of several coccinellid species. Several of the recorded compounds are trivial plant volatiles, but some of them may also represent a stressed plant status, and there may be similarities between effects of herbivore (coccinellid prey) attacks and plant stress caused by plant–plant interactions. (See also Chapter 4 and 5.4.1)

Information related to both **prey density** and **plant status** contributes to the switch of an individual coccinellid from extensive foraging and dispersal to patch identification with intensified food-searching behaviour, and here a range of semiochemicals play an active role (Pettersson et al. 2008). The ecological importance of species-specific differences in the balance between the two types of behaviour is illustrated by a study comparing the searching behaviour efficiency of *Har. axyridis* and *Col. maculata* in **fragmented versus clumped landscapes** with clover patches infested with the pea aphid, *Acyrthosiphon pisum* (With et al. 2002). The two coccinellids did not differ in their search success within fragmented landscapes. It was only in clumped landscapes that *Har. axyridis* maximized search success and foraged within clover patches that had 2.5–3 times more aphids than those in which *Col. maculata* occurred. *Harmonia axyridis* was more efficient in finding aphid-infested clover cells, while *Col. maculata* made more efficient use of the aphids in such infested clover cells. A key factor for the difference between the two species seemed to be their difference in mobility and, therefore, different dependence on cues in the switch from dispersal to searching mode.

9.8.2 Plant stand traits

Coccinellid food can be classified as **essential food** that promotes development and propagation, and lower quality (**alternative**) **foods** that **only supports survival** (Hodek & Michaud 2008; 5.2.2. and 5.2.11). Thus volatile messenger substances carrying information on prey/food quality in terms of essential food and possibly longevity of the food source are important. Field investigations have shown a correlation between **increased botanical diversity** and the frequency of polyphagous predators (coccinellids), and different factors are suggested as contributing to this, including **microclimate** and **increased prey density** (Andow 1991; Vandermeer 1992). In a field site inventory study, *C. septempunctata* and *A. bipunctata* were dominating species and their distribution was significantly correlated with the percentage of ground cover of certain weed species (Leather et al. 1999). This is in line with studies by Schmid (1992) on plant discrimination by coccinellids. Of 73 plant species, most of which were common agricultural weeds, at least 20 were found to be highly attractive to coccinellids. Even moderate manipulations of the genetic homogeneity of a barley crop may be important in relation to habitat preferences. In a field experiment with pair-wise mixed and pure stands of different barley genotypes, it was found that, in the absence of prey, adult *C. septempunctata* preferred a specific genotype-pair mix (Ninkovic et al. 2011).

9.8.3 Avoided plants

Coccinellids have been shown to respond to species-specific **plant volatiles**. In laboratory experiments with **terpenoids** from catnip oil and from grapefruit seeds (Riddick et al. 2008), *Z,E*-dihydronepetalactone or *E,Z*-dihydronepetalactone caused a concentration-dependent avoidance behaviour in adult males and females of *Har. axyridi*s. The avoidance behaviour was expressed by trying to fly, jumping back or turning away from the odour source. Other tested compounds, *E,Z*-iridomyrmecine and *Z,E*-**myrmecine**, were less effective. Finally, **nootkatone** and tetrahydronootkatone were least effective. Based on the behavioural responses of the beetles, it is suggested that the substances should be tested as repellents to prevent aggregates of *Har. axyridis* at sites where they are unwanted. To what extent these preferences represent a permanent pattern of species-specific plant preference or an adaptive response remains to be tested. Investigations on effects of plant volatiles on coccinellid foraging responses have focussed on consumption patterns in *Aphidecta obliterata*, which as a conifer specialist was better adapted to spruce than the generalist *A. bipunctata* (Timms et al. 2008).

9.8.4 Plant–plant interactions/ attractive plants

A detectable plant stress indicator would be an important predator tool. The most common biotic challenge for a growing plant is sharing available resources with other plants and this has, in some cases, led to the development of advanced systems of plant–plant communication via semiochemicals. **Suppression of plant competitors** via semiochemicals defined as **allelopathy** by Molisch (1937) was later redefined by Rice (1984) as also involving effects related to microorganisms associated with plants. Advances in methods of chemical analysis and improved understanding of plant ecology have resulted in an increased scientific interest in allelopathy and its ecological importance.

However, as yet, the **intertrophic effects** of allelopathy (**allelobiosis** *sensu* Pettersson et al. 2003; Ninkovic et al. 2011), i.e. the effects upon herbivores and their natural enemies of plant responses in **plant–plant interactions**, have not been extensively studied. The efficiency of the searching behaviour of a polyphagous predator would benefit from a volatile cue allowing identification of plants stressed by herbivores.

Investigations of behavioural responses of adult *C. septempunctata* to barley and two common weeds have contributed to this topic. The distribution of *C. septempunctata* in a commercial barley crop with weeds indicates the importance of odour stimuli (Ninkovic & Pettersson 2003). Adults were significantly aggregated to patches with *Elytrigia repens* and *Cirsium arvense*, although no obvious food resource such as pollen, aphids or other small prey insects was abundant there. In olfactometer experiments, adult ladybirds showed no difference in orientation to either of the weeds. However, when barley and one of the two weeds were used together as the odour source, this was preferred compared to the odour of barley alone. Barley plants exposed to volatiles from *C. arvense* remained attractive even when the weed was taken away, whereas those exposed to *E. repens* lost their attractiveness in the absence of barley. This indicates that the positive effect of the barley–*E. repens* combination may merely be an effect of mixed volatiles, whereas the barley–*C. arvense* mixture is likely to represent a more complex mechanism involving **allelobiosis**.

A conclusion from these results is that **mixed plant stands** may have a stronger arresting effect on adult ladybirds than pure stands, if proximity of a different plant species makes a plant emit the volatile signature characteristic of general plant stress that would include herbivore-attacked plants. Hypothetically, an increased arresting effect could be a response merely to a complexity of plant volatiles. This would fit well with the *E. repens*–barley combination. However, the results from the tests of the *C. arvense*-barley combination suggest another possibility. Barley plants exposed to allelobiotic provocation from thistle volatiles become significantly less acceptable to aphids (Glinwood et al. 2004). Thus the positive ladybird response to *C. arvense*-exposed barley plants could be a response to a **plant-stress condition** upon herbivores and their natural enemies, which is similar whether induced by plant–plant interaction or aphid attack. This would be in line with the positive response of ladybirds to aphid-attacked barley plants (Ninkovic et al. 2001).

9.9 CONCLUSIONS AND FUTURE CHALLENGES

This chapter has summarized information on the chemical ecology of coccinellids. A considerable amount of experimentation has shown that coccinellids depend on semiochemical-mediated information to complete several of the important steps in their population ecology. However, so far there is only a limited understanding of the mechanisms involved and of how chemical ecology profoundly interacts with other stimuli regulating life processes.

Most of the behavioural responses of coccinellids to semiochemicals reported are related to major events in the life cycle. Thus the response to certain stimuli may vary depending on where in the **annual life cycle** the specific individual is. Several of the chemical cues related to mobility and foraging are commonly occurring substances, and one of the future challenges is to understand the subtle mechanisms that contribute to give this trivial set of information a precise meaning for the individual coccinellid. The integration of external information to be expressed in subsequent action is picked up by **chemoreceptors**, then processed at different sensory system levels and finally modified as a function of the status of the individual coccinellid. This status can be looked upon as an **endogenous response filter** that regulates the capability of the **coccinellid to respond to external stimuli**. Factors such as adaptive learning, mating and feeding status or different stages in the annual population cycle will modify the selectivity of this behaviour modifying filter (BMF). Basic elements controlling the dynamic variability of coccinellid behaviour such as **adaptive responses** and **learning** affected by a broad set of multiple blends of trivial chemicals such as green leaf volatiles and semiochemicals from other organisms are exciting fields where further research is needed.

The considerable knowledge on the chemical compounds that constitute the **aposematic chemistry** of coccinellids has created a challenging source for future studies on the behaviour of coccinellids in an ecological perspective. The metabolic costs of the powerful aposematic chemistry are high and further links to general ecological functions could be searched for. Increasing information of the aposematic chemistry in intra- and interspecific recognition stimulates further studies of the contributions of semiochemicals involved in aspects of the behavioural ecology of coccinellids such as territorial behaviour, cannibalism/foraging and interaction with other behavioural stimuli such as colouration and tactile stimuli, where so far only very little is known for coccinellids. Some of the aposematic compounds are chemically complex and some of them (such as pyrazine) are behaviourally active in such small amounts that they challenge conventional methods for entrainment and chemical identification. Improved methods of chemical analysis will reduce these problems but also enable more sophisticated methods in studies of how coccinellids respond to semiochemicals. Further development of improved bioassay methods for studying coccinellid behaviour is needed in relation to processes such as kin recognition, aggressivity between individuals, courtship and mating and cues involved in migration.

Studies of the **olfactory receptor** systems on the antennae have shown sexual dimorphism. However, the behavioural consequences of this for different behavioural responses between males and females to different stimuli have so far not received much attention. Present knowledge on identified semiochemicals indicates that several biologically trivial compounds common both in several potential prey herbivores and their host plants convey important information to coccinellids. Responses to the same chemical can differ depending on time and place and the influence of the BMF mentioned above. Good examples of cues where these common **volatiles** may be behaviourally active are those **related to plant damage/stress**. Such volatiles form a vast set of active compounds that must be recognized by the olfactory receptors of coccinellids and, although the topic has often been discussed, there is only limited knowledge on how this challenge is met by different coccinellid species. Further studies of the principles for receptor function of coccinellids and its potential as a priming factor for specific chemical cues is therefore an interesting challenge.

With regards to foraging and feeding behaviour, the focus has been on **herbivore-induced volatiles** and other stress induced substances. Thus the borderline between stimuli expressed in food search and arresting responses in favourable patches is diffuse. Efficient use of a broad range of food sources means that identification of favourable habitats can be more profitable than searching for specific food sources. This creates a dynamic balance between investments in **localizing optimal habitats** where food is likely to be available, and in **finding specific** preferred food **resources**. This presupposes a pronounced adaptive capacity to meet a variable set of food sources.

Few insects can compete with coccinellids with regard to scientific challenges within the field of chemical ecology. Their own chemistry is expressed in complex aposematic compounds. They show an outstanding capacity to cope with different ecological requirements such as foraging, mating and responses to IGP, as well as to conspecific density. It is difficult to find another group of insects that is so close to human activities, and yet it must be admitted that conclusive data on the **identity and importance of semiochemicals** under natural conditions are still limited. It is to be expected that future studies will not only give results of general scientific value but also contribute to improved options for the different roles of coccinellids in human activities in biological production and nature conservation.

REFERENCES

Abe, M. and K. Matsuda. 2000. Feeding responses of four phytophagous lady beetle species (Coleoptera: Coccinellidae) to cucurbitacins and alkaloids. *Appl. Entomol. Zool.* 35: 257–264.

Agarwala, B. K. and P. J. Bhowmik. 2007. Effect of chemical defence on fitness of ladybird predator, Cheilomenes sexmaculata (Fabricius). *J. Biol. Control.* 21: 89–96.

Agarwala, B. K., H. Yasuda and Y. Kajita. 2003. Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: Role of fecal cues in predator avoidance. *J. Chem. Ecol.* 29: 357–376.

Al Abassi, S., M. A. Birkett, J. Pettersson, J. A. Pickett, L. J. Wadhams and C. M. Woodcock. 1997. Ladybird beetle odour identified and found to be responsible for attraction between adults. *Cell. Mol. Life Sci.* 54: 876–879.

Al Abassi, S., M. A. Birkett, J. Pettersson et al. 1998. Ladybird beetle odour identified and found to be responsible for attraction between adults. *Cell. Mol. Life Sci.* 54: 876–879.

Al Abassi, S., M. A. Birkett, J. Pettersson et al. 2000. Response of the seven-spot ladybird to an aphid alarm pheromone and an alarm pheromone inhibitor is mediated by paired olfactory cells. *J. Chem. Ecol.* 26: 1765–1771.

Al Abassi, S., M. A. Birkett, J. Pettersson et al. 2001. Response of the ladybird parasitoid *Dinocampus coccinellae* to toxic alkaloids from the seven-spot ladybird, *Coccinella septempunctata*. *J. Chem. Ecol.* 27: 33–43.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* 36: 561–86.

Baker, T. C., J. J. Obrycki and J. W. Zhu. 2003. US Patent 6562332: *Attractants of Beneficial Insects*, issued 2003.

Barbier, R., A. Ferran, J. Le Lannic and M. R. Allo. 1992. Morphology and ultrastructure of integumentary glands of *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae). *Int. J. Insect Morphol. Embryol.* 21: 223–234.

Barron, A. and K. Wilson. 1998. Overwintering survival in the seven spot ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 95: 639–642.

Bhatkar A. P. (1982. Orientation and defence of ladybeetles (Coleoptera, Coccinellidae) following ant trail in search of aphids. *Folia Entomol. Mexicana* 53: 75–85.

Bi, H. H., R. S. Zeng, L. M. Su, M. An and S. M. Luo. 2007. Rice allelopathy induced by methyl jasmonate and methyl salicylate. *J. Chem. Ecol.* 33: 1089–103.

Birkett, M. A., C. A. M. Campbell, K. Chamberlain et al. 2000. New roles for cis-jasmone as an insect semiochemical and in plant defence. *Proc. Natl Acad. Sci. USA* 97: 9329–9334.

Boivin, G., C. Roger, D. Coderre and E. Wajnberg. 2010. Learning affects prey selection in larvae of a generalist coccinellid predator. *Entomol. Exp. Appl.* 135: 48–55.

Branco, M., J. C. Franco, E. Dunkelblum et al. 2006. A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bull. Entomol. Res.* 96: 179–185.

Bruce, T. J. A., M. C. Matthes, K. Chamberlain et al. 2008. cis-Jasmone induces *Arabidopsis* genes that affect the chemical ecology of multitrophic interactions with aphids and their parasitoids. *Proc. Natl Acad. Sci. USA* 105: 4553–4558.

Burns, D. A., J. J. McDonnell, J. L. Hemptinne, G. Lognay and A. F. G. Dixon. 1998. Mate recognition in the two-spot ladybird beetle, *Adalia bipunctata*: role of chemical and behavioural cues. *J. Insect Physiol.* 44: 1163–1171.

Camarano, S., A. Gonzalez and C. Rossini. 2006. Chemical defence of the ladybird beetle *Epilachna paenulata*. *Chemoecology.* 16: 179–184.

Daloze, D., J. C. Braekman and J. M. Pasteels 1994. Ladybird defence alkaloids: structural, chemotaxonomic and biosynthetic aspects (Col.: Coccinellidae). *Chemoecology.* 5: 3–4.

Dejean, A., M. Gibernau, J. Lauga and J. Orivel. 2003. Coccinellid learning during capture of alternative prey. *J. Insect Behav.* 16: 859–864.

Dicke, M. 2000. Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perspective. *Biochem. Syst. Ecol.* 28: 601–617.

Dicke, M., J. Takabayashi, M. A. Posthumus, C. Schütte and O. Krips. 1998. Plant–phytoseiidd interactions mediated by herbivore induced plant volatiles: variation in production of cues and in responses of predatory mites. *Exp. Appl. Acarol.* 22: 311–333.

Dixon, A. F. G. 1959. An experimental study of the searching behaviour of the predatory Coccinellid beetle *Adalia decempunctata*. *J. Anim. Ecol.* 28: 259–281.

Dixon, A. F. G. and B. K. Agarwala 1999. Ladybird-induced life-history changes in aphids. *Proc. R. Soc. Lond.* (B) 266: 1549–1553.

Durieux, D., F. Verheggen, A. Vandereycken, E. Joie and E. Haubruge. 2010. Chemical ecology of ladybird beetles. *Biotechnologie, Agronomie, Société et Environnement* 14: 351–367.

Elliot, N. C. and R. W. Kieckhefer. 2000. Response by coccinellids to spatial variation in cereal aphid density. *Popul. Ecol.* 42: 81–90.

van Emden, H. F., A. P. Storeck, S. Douloumpaka et al. 2008. Plant chemistry and aphid parasitoids (Hymenoptera: Braconidae): Imprinting and memory. *Eur. J. Entomol.* 105: 477–483.

Endo, N., M. Abe, T. Sekine and K. Matsuda. 2004. *Appl. Entomol. Zool.* 39: 411–416.

Ferrer, A., A. F. G. Dixon and J. L. Hemptinne. 2008. Prey preference of ladybird larvae and its impact on larval mortality, some life-history traits of adults and female fitness. *Bull. Insect Ecol.* 61: 5–10.

Francis, F., E. Haubruge, P. Hastir and C. Gaspar. 2001. Effect of aphid host plant on development and reproduction of the third trophic level, the predator Adalia bipunctata (Coleoptera: Coccinellidae). *Environ. Entomol.* 30: 947–952.

Frechette, B., A. F. G. Dixon, H. Alauzet and J. L. Hemptinne. 2004. Age and experience influence patch assessment for oviposition by an insect predator. *Ecol. Entomol.* 29: 578– 583.

Gagné, I., D. Coderre and Y. Mauffette. 2002. Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecol. Entomol.* 27: 285–291.

Glinwood, R., V. Ninkovic, E. Ahmed and J. Pettersson. 2004. Barley exposed to aerial allelopathy from thistles (*Cirsium* spp.) becomes less acceptable to aphids. *Ecol. Entomol.* 29: 188–195.

Glinwood, R., E. Ahmed, E. Qvarfordt and V. Ninkovic. 2011. Olfactory learning of plant genotypes by a polyphagous insect predator. Oecologia DOI 10.1007/s00442-010-1892-x.

Hamilton, R. M., E. B. Dogane, G. B. Schaalje and G. M. Booth. 1999. Olfactory response of the lady beetle *Hippodamia convergens* (Coleoptera: Coccinellidae) to prey related odors, including a scanning electron microscopy study of the antennal sensilla. *Environ. Entomol.* 28: 812–822.

Han, B. Y. and Z. M. Chen. 2002. Behavioral and electrophysiological responses of natural enemies to synomones from tea shoots and kairomones from tea aphids, *Toxoptera aurantii*. *J. Chem. Ecol.* 28: 2203–2219.

Han, B. Y. and Z. M. Chen. 2005. Composition of the volatiles from intact and mechanically pierced tea aphid–tea shoot complexes and their attraction to natural enemies of the tea aphid. *J. Agric. Food Chem.* 50: 2571–2575.

Hatano, E., G. Kunert, J. P. Michaud and W. W. Weisser. 2008. Chemical cues mediating aphid location by natural enemies. *Eur. J. Entomol.* 105: 797–806.

Hautier, L., J. C. Gregoire, J. de Schauwers et al. 2008. Intraguild predation by *Harmonia axyridis* on coccinellids revealed by exogenous alkaloid sequestration. *Chemoecology.* 18: 191–196.

Hemptinne, J. L. and A. F. G. Dixon. 2000. Defence, oviposition and sex: Semiochemical parsimony in two species of ladybird beetles (Coleoptera, Coccinellidae)? A short review. *Eur. J. Entomol.* 97: 443–447.

Hemptinne J. L., A. F. G. Dixon, J. L. Doucet and J. E. Petersen 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms. *Eur. J. Entomol.* 90: 451–455.

Hemptinne, J. L., A. F. G. Dixon and G. Lognay. 1996. Searching behaviour and mate recognition by males of the two-spot ladybird beetle, *Adalia bipunctata*. *Ecol. Entomol.* 21, 165–170.

Hemptinne, J. L., G. Lognay , C. Gauthier and A. F. G. Dixon. 2001a. Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera: Coccinellidae). *Chemoecology.* 10: 123–128.

Hemptinne, J. L., G. Lognay, M. Doumbia and A. F. G. Dixon. 2001b. Chemical nature and persistence of the oviposition deterring pheromone in the tracks of the larvae of the two spot ladybird, *Adalia bipunctata* (Coleoptera, Coccinellidae). *Chemoecology.* 11: 43–47.

Hodek, I. and J. P. Michaud. 2008. Why is *Coccinella septempunctata* so successful? (A point-of-view). *Eur. J. Entomol.* 105: 1–12.

Holloway, G. J., P. W. De Jong, P. M. Brakefield, P. W. De Jong and H. De Vose. 1991. Chemical defense in ladybird beetles (Coccinellidae). I. Distribution of coccinelline and individual variation in defence in 7-spot ladybirds (*Coccinella septempunctata*). *Chemoecology.* 2: 7–14.

Holloway, G. J., P. W. De Jong and M. Ottenheim. 1993. The genetics and cost of chemical defence in the two-spot ladybird (*Adalia bipunctata* L.). *Evolution* 47: 1229–1239.

Jamal, E., C. Brown and C. Grayson. 2001. Orientation of *Hippodamia convergens* (Coleoptera: Coccinellidae) larvae to volatile chemicals associated with *Myzus nicotianae* (Homoptera: Aphidiidae). *Environ. Entomol.* 30: 1012–1016.

James, D. G. 2005. Further field evaluation of synthetic herbivore-induced plant volatiles as attractants for beneficial insects. *J. Chem. Ecol.* 31: 481–495.

James, D. G. and T. S. Price. 2004. Field testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. *J. Chem. Ecol.* 30: 1613–1628.

Jourdan, H., R. Barbier, J. Bernard and A. Ferran. 1995. Antennal sensilla and sexual dimorphism of the adult lady beetle Semiadalia undecimnotata Schn. (Coleoptera, Coccinellidae). *Int. J. Insect Morphol. Embryol.* 24: 307–322.

Kajita, Y., J. J. Obrycki, J. J. Sloggett and K.F. Haynes. 2010 Intraspecific alkaloid variation in ladybird eggs and its effects on con- and hetero-specific intraguild predators. *Oecologia* 163: 313–322.

Kazana, E., T. W. Pope, L. Tibbles et al. 2007. The cabbage aphid: a walking mustard oil bomb. *Proc. Biol. Sci.* 274: 2271–2277.

Karystinou, A., A. P. M. Thomas and H. E. Roy 2004. Presence of haemocyte-like cells in coccinellid reflex blood. *Physiol. Entomol.* 29: 94–96.

Klausnitzer, B. 1989. Aggregations of ladybirds on the Baltic coast (Col., Coccinellidae). *Entomol. Nachr. Ber.* 33: 189–195.

Klewer, N., Z. Ruzicka and S. Schulz. 2007. Z-pentacos-12-ene, an oviposition-deterring pheromone of *Cheilomenes sexmaculata*. *J. Chem. Ecol.* 33: 2167–2170.

Laurent, P., J. C. Braekman and S. Daloze. 2005. Insect chemical defense. *Topics Curr. Chem.* 240: 167–229.

Laubertie, E., X. Martini, C. Cadena et al. 2006. The immediate source of the oviposition-deterring pheromone produced by larvae of *Adalia bipunctata* (L.) (Coleoptera, Coccinellidae). *J. Insect Behav.* 19: 231–240.

Leather, S. R., R. C. A. Cooke, M. D. E. Fellowes and R. Rombe .1999. Distribution and abundance of ladybirds (Coleoptera: Coccinellidae) in non-crop habitats. *Eur. J. Entomol.* 96: 23–27.

Majerus, M. E. N. 1994. *Ladybirds*. Harper Collins, London. 367 pp.

Majerus, M. E. N. and T. M. O. Majerus, 1997. Predation of ladybirds by birds in the wild. *Entomol. Mon. Mag.* 133: 1592–1595.

Majerus, M. E. N., J. J. Sloggett, J. F. Godeau and J. L. Hemptinne. 2007. Interactions between ants and aphidophagous and coccidophagous ladybirds. *Popul. Ecol.* 49: 15–27.

Marples, N. M. 1993a. Toxicity assays of ladybirds using natural predators. *Chemoecology* 4: 33–28.

Marples, N. M. 1993b. Is the alkaloid in 2spot ladybirds (*Adalia bipunctata*) a defence against ant predation? *Chemoecology* 4: 29–32.

Marples, N. M., W. VanVeelen and P. M. Brakefield. 1994. The relative importance of colour, taste and smell in the protection of an aposematic insect *Coccinella septempunctata*. *Anim. Behav.* 48: 967–974.

Michaud, J. P. and A. K. Grant. 2004. Adaptive significance of sibling egg cannibalism in Coccinellidae: Comparative evidence from three species. *Ann. Entomol. Soc. Am.* 97: 710–719.

Michaud, J. P. and J. L. Jyoti. 2008. Dietary complementation across life stages in the polyphagous lady beetle *Coleomegilla maculata*. *Entomol. Exp. Appl.* 126: 40–45.

Mondor, E. B. and B. D. Roitberg. 2000. Has the attraction of predatory coccinellids to cornicle droplets constrained aphid alarm signalling behaviour? *J. Insect Behav.* 13: 321–329.

Molisch, H. 1937. *Der Einfluss einer Pflanze auf die andere-Allelopathie*. Gustaf Fischer Jena. 106 pp.

Nakashima, Y. and M. Akashi. 2005. Temporal and within-plant distribution of the parasitoid and predator complexes associated with *Acyrthosiphon pisum* and *A. kondoi* (Homoptera : Aphididae) on alfalfa in Japan. *Appl. Entomol. Zool.* 40: 137–144.

Nakashima, Y., M. A. Birkett, B. J. Pye, J. A. Pickett and W. Powell. 2004. The role of semiochemicals in the avoidance of the seven-spot ladybird, *Coccinella septempunctata* by the aphid parasitoid, *Aphidius ervi*. *J. Chem. Ecol.* 30: 1103–1116.

Nakashima, Y., M. A. Birkett, B. J. Pye, W. Powell. 2006. Chemically mediated intraguild predator avoidance by aphid parasitoids: Interspecific variability in sensitivity to semiochemical trails of ladybird predators. *J. Chem. Ecol.* 32(9):1989–1998.

Nakamuta, K. 1991. Aphid alarm pheromone component, (E)-beta-farnesene, and local search by a predatory lady beetle, *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 26: 1–7.

Nault, L. R., L. J. Edwards and W. E. Styer. 1973. Aphid alarm pheromones: secretion and reception. *Environ. Entomol.* 2: 101–105.

Nault ,L. R., T. K. Wood and A. M. Goff. 1974. Treehopper (Membracidae) alarm pheromones. *Nature* 249: 387–388.

Nentwig, W. 1983. The prey of web-building spiders compared with feeding experiments (Araneae: Araneidae, Linyphiidae, Pholcidae, Aegelenidae). *Oecologia* 56: 132–139.

Nentwig, W. 1986. Non web-building spiders: prey specialists or generalists? *Oecologia* 69: 571–576.

Ninkovic, V. and J. Pettersson. 2003. Plant/plant communication supports searching behaviour of the sevenspotted ladybird, *Coccinella septempunctata* (L.). *Oikos* 100: 65–70.

Ninkovic, V., S. Al Abassi and J. Pettersson. 2001. The influence of aphid-induced plant volatiles from barley on the searching behaviour of the seven spot ladybird, *Coccinella septempunctata*. *Biol. Control* 21: 191–195.

Ninkovic, V., S. Al Abassi, E. Ahmed, R. Glinwood and J. Pettersson. 2011. Effect of within-species plant genotype mixing on habitat preference of a polyphagous insect predator. *Oecologia* 166: 391–400.

Oliver, T. H., J. E. L. Timms, A. Taylor and S. Leather. 2006. Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera: Coccinellidae): effects of aphid density, and con- and heterospecific tracks. *Bull. Entomol. Res.* 96: 25–34.

Oliver, T. H., J. M. Cook and S. R. Leather. 2008. Avoidance responses of an aphidophagous ladybird, *Adalia bipunctata*, to aphid-tending ants. *Ecol. Entomol.* 33: 523–528.

Orr, C. J., J. J. Obrycki and R. V. Flanders 1992. Host acceptance behavior of *Dinocampus coccinellae* (Hymenoptera: Braconidae). *Ann. Entomol. Soc. Am.* 85: 722–730.

Pasteels, J. M. 2007. Chemical defence, offence and alliance in ants–aphids–ladybirds relationships. *Popul. Ecol.* 49: 5–14.

Pasteels, J. M., C. Deroe, B. Tursch et al.1973. Distribution and activities of the defensive alkaloids of the Coccinellidae. *J. Insect Physiol.* 19: 1771–1784.

Pratt, C., T. W. Pope, G. Powell and J. T. Rossiter. 2008. Accumulation of glucosinolates by the cabbage aphid *Brevicoryne brassicae* as a defense against two coccinellid species. *J. Chem. Ecol.* 34: 323–329.

Pettersson, J., V. Ninkovic and R. Glinwood. 2003. Plant activation of barley by intercropped conspecifics and weeds: allelobiosis. *The BCPC International Congress: Crops Science and Technology.* 1135–1144.

Pettersson, J., V. Ninkovic, R. Glinwood et al. 2008. Chemical stimuli supporting foraging behaviour of *Coccinella septempunctata* L. (*Coleoptera: Coccinellidae*): volatiles and allelobiosis, *Appl. Entomol. Zool.* 43: 315–321.

Rice, E. L. 1984. *Allelopathy*, 2nd edn. Academic Press, New York.

Richerson, J. V. and C. J. DeLoach. 1972. Some aspects of host selection by *Perilitus coccinellae*. *Ann. Entomol. Soc. Am.* 65: 834–839.

Riddick, E. W., A. E. Brown and K. R. Chauhan. 2008. *Harmonia axyridis* adults avoid catnip and grapefruit-derived terpenoids in laboratory bioassays. *Bull. Insectol.* 61: 81–90.

Rothschild, M., J. V. Euw and T. Reichste. 1973. Cardiac-glycosides in a scale insect (*Aspidiotus*), a ladybird (*Coccinella*) and a lacewing (*Chrysopa*). *J. Entomol. A* 48: 89–90.

Roy, H. and T. E. Cottrell. 2008. Forgotten natural enemies: interactions between coccinellids and insect-parasitic fungi. *Eur. J. Entomol.* 105: 391–398.

Ruzicka, Z. 1994. Oviposition-deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *Eur. J. Entomol.* 91: 361–370.

Ruzicka, Z. 1997. Recognition of oviposition-deterring allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *Eur. J. Entomol.* 94: 431–434.

Ruzicka, Z. 2001. Response of chrysopids (Neuroptera) to larval tracks of aphidophagous coccinellids (Coleoptera). *Eur. J. Entomol.* 98: 283–285.

Ruzicka, Z. 2002. Persistence of deterrent larval tracks in *Coccinella septempunctata*, *Cycloneda limbifer* and *Semiadalia undecimnotata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 99: 471–475.

Ruzicka, Z. 2003. Perception of oviposition-deterring larval tracks in aphidophagous coccinellids *Cycloneda limbifer* and *Ceratomegilla undecimnotata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 100: 345–350.

Ruzicka, Z. 2006. Oviposition-deterring effects of conspecific and heterospecific larval tracks on *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 103: 757– 763.

Santi F, Burgio G and Maini S. 2003. Intra-guild predation and cannibalism of *Harmonia axyridis* and *Adalia bipunctata* in choice conditions. *Bull. Insectol.* 56, 207–210.

Schmid, A. 1992. Investigations on the attractiveness of agricultural weeds to aphidophagous ladybirds (Coleoptera, Coccinellidae). *Agrarökologie* 5: 122.

Schroeder, F. C., S. R. Smedley, L. K. Gibbons et al. 1998. Polyazamacrolides from ladybird beetles: Ring-size selective oligomerization. *Proc. Natl Acad. Sci. USA* 95: 13387–13391.

Sloggett, J. J. 2010. Predation of ladybirds by the orb-web spider *Araneus diadematus*. *BioControl* 55: 631–638.

Sloggett, J. J. and M. E. N. Majerus. 2000. Aphid-mediated coexistence of ladybirds (Coleoptera: Coccinellidae) and the wood ant *Formica rufa*: Seasonal effects, interspecific variability and the evolution of a coccinellid myrmecophile. *Oikos* 89: 345–359.

Sloggett, J. J., J. O. Obrycki and K. F. Haynes. 2009. Identification and quantification of predation: novel use of gas chromatography-mass spectrometric analysis of prey alkaloid markers. *Funct. Ecol.* 23: 416–426.

Smedley, S. R., K. A. Lafleur, L. K. et al. 2002. Glandular hairs: pupal chemical defense in a non-native ladybird beetle (Coleoptera: Coccinellidae). *Northeast. Naturalist* 9: 253–266.

Takizawa, T., H. Yasuda and B. K. Agarwala. 2000. Effect of three species of predatory ladybirds on oviposition of aphid parasitoids. *Entomol. Sci.* 3: 465–469.

Timms, J. E., T. H. Oliver, N. A. Straw and S. R. Leather. 2008. The effects of host plant on the coccinellid functional response: is the conifer specialist *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae) better adapted to spruce than the generalist *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae)? *Biol. Control* 47: 273–281.

Vandermeer, J. 1992. *The Ecology of Intercropping*. Cambridge University Press, Cambridge, UK.

Vantaux, A., O. Roux, A. Magro et al. 2010. Host-specific myrmecophily and myrmecophagy in the tropical coccinellid *Diomus thoracicus* in French Guiana. *Biotropica* 42: 622–629.

Verheggen, F. J., Q. Fagel, S. Heuskin et al. 2007. Electrophysiological and behavioral responses of the multicolored Asian lady beetle, *Harmonia axyridis* Pallas, to sesquiterpene semiochemicals. *J. Chem. Ecol.* 33: 2148–2155.

Vet, L. E. M. and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37: 141–172.

de Vos, M. and G. Jander. 2010. Volatile communication in plant–aphid interactions. *Curr. Opin. Plant Biol.* 13: 366–371.

Walling, L. L. 2000. The myriad of plant responses to herbivores. *J. Plant Growth Regulation* 19: 195–216.

Ware, R. L., F. Ramon-Portugal, A. Magro et al. 2008. Chemical protection of *Calvia quatuordecimguttata* eggs against intraguild predation by the invasive ladybird *Harmonia axyridis*. *BioControl* 53: 189–200.

With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecol. Appl.* 12: 52–65.

Witte, L., A. Ehmke and T. Hartmann. 1990. Interspecific flow of pyrrolizidine alkaloids from plants via aphids to ladybirds. *Naturwissenschaften* 77: 540–543.

Zhu, J. W. and K. C. Park. 2005. Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. *J. Chem. Ecol.* 31: 1733–1746.