Appl. Entomol. Zool. 43 (3): 315–321 (2008)
http://odokon.org/

Mini Review

Chemical stimuli supporting foraging behaviour of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae): volatiles and allelobiosis

Jan Pettersson,[1,*] Velemir Ninkovic,[1] Robert Glinwood,[1] Sate Al Abassi,[1] Michael Birkett,[2] John Pickett[2] and Lester Wadhams[2]

[1] Department of Ecology, Swedish University of Agricultural Sciences; Box 7044, SE 750 07 Uppsala, Sweden
[2] Biological Chemistry Division, Rothamsted Research; Harpenden, Herts, AL5 2JQ, UK

(Received 6 February 2007; Accepted 11 April 2008)

Abstract
This mini review focuses on ladybird foraging behaviour with special reference to *Coccinella septempunctata* (L.) and chemical stimuli. Cues related to aphid finding, such as aphid alarm pheromone, honeydew, and chemical messengers released by aphid-attacked plants are described. Stimuli related to searching behaviour for high quality habitats are reviewed with special reference to the effects of botanical diversity and plant/plant communication.

Key words: Ladybirds; allelobiosis; aphids; habitat preferences; semiochemicals

INTRODUCTION

Seasonal migrations to and from hibernating sites are key elements in the population biology of the sevenspotted ladybird, *Coccinella septempunctata* L. This dynamic redistribution of adults in the landscape has inspired investigations of both principle and mechanistic aspects of foraging behaviour and food sources (Kareiva, 1987; Ives et al., 1993).

Stimuli of most categories are involved in mechanisms regulating behavioural processes during different phases of the annual cycle. Adults hibernate in well-recognisable sites such as ridges, hills, mountains, etc. The distribution of ladybirds within such a hibernating site is patchy, and the density of ladybirds in an aggregation can be high, sometimes exceeding 200 individuals per m^2 (Majerus, 1994; Hodek and Honek, 1996). Several steps in the behaviour of adults are supported by pheromones (Pettersson et al., 2005). Thus, aggregation behaviour may be supported by a putative aggregation pheromone, pyrazine (Al Abassi et al., 1998). There is evidence for an oviposition-deterring pheromone affecting ovipositing ladybird females at sites with favourable food sources (Evans, 2003), which would minimize risks of cannibalism. Semiochemicals produced in footprints have been identified and there is more to understand about their ecological function (Kosaki and Yamaoka, 1996).

C. septempunctata is polyphagous and can survive on a broad range of food. Gut dissections of field-collected adults (Triltsch, 1999) show that food choice varies during the season and encompasses aphids, pollen and fungal spores; however, for successful survival and reproduction, a diet that contains a fraction of aphids is optimal. Aphids have been ranked as the highest priority 'essential food' and other items such as pollen, fungal mycelia and organic matter as a lower priority 'less optimal food' (Hodek and Honek, 1996). Even the limited addition of 'essential food' (aphids) to a diet of less optimal food increased the reproductive capacity of *C. septempunctata* and *Coccinella transversalis* (Evans et al., 1999; Evans, 2000). A valuable contribution to this discussion is given by Rana et al. (2002) showing laboratory evidence that habituation to one aphid species leads to a diminished capacity to use another as optimal food.

Depending on food availability and the physiological status of the insect, the priority of food

* To whom correspondence should be addressed at: E-mail: jan.pettersson@ekol.slu.se
DOI: 10.1303/aez.2008.315

sources may change; thus, it has been suggested that during the start of the season when conditions are dry and migration is intensive, the preference of *C. septempunctata* for pollen and nectar from flowers is related both to its value as a food source and also the insect's need for water (Hodek and Honek, 1996).

Different principal aspects of foraging behaviour have been studied in relation to general ecological theories focussed on predator prey interactions (Kareiva, 1987; Ives et al., 1993). In a recent review with bearing on habitat parameters, the general principle for the foraging behaviour of *C. septempunctata* is described as a 'journey through the landscape', during which different food sources are used when found (Evans, 2003). To be successful, this searching strategy presupposes a capacity to perceive and process a broad set of information on different food sources and adapt to them. Mechanistic aspects for the efficient use of different food sources have been discussed earlier (Vet and Dicke, 1992; Majerus, 1994; Dicke, 1999; Dixon, 2000) stressing adaptive learning and the balance of reliability–detectability with regards to stimuli.

The aim of this paper is to review the foraging behaviour of polyphagous adults of *C. septempunctata* with special reference to the effects of volatile stimuli supporting food search, habitat choice and tritrophic effects of plant/plant communication-allelobiosis (sensu Pettersson et al., 2003; Ninkovic et al., 2006).

PRESENCE OF APHIDS-HONEYDEW

Some of the first experimental evidence that ladybirds use traces of aphids in finding food sources was given by Hagen (1971) who showed that deposition of aphid honeydew components promote ladybird presence. In later studies, it has been claimed that the amino acid tryptophan occurring in honeydew plays an important role (Ben Saad and Bishop, 1976). Honeydew is a lead for finding aphids and as it represents a complex mixture of carbohydrates, amino acids and secondary metabolites (Wiedemann et al., 2004; Kazana et al., 2007), it may give further information on qualitative value. It has been shown that host plant choice of the excreting aphid is important for ant attendance (Fischer et al., 2005) and there is experimental evidence that the nutritional value of the same aphid species for preimaginal ladybird development may vary according to the host plant on which the aphids have been feeding (Giles et al., 2002; Francis et al., 2001; Rice and Wilde, 1989). To what extent this is also of importance as informative value to ladybirds about honeydew excreted by the aphids is still an open question.

Recent investigations have shown that plots treated with sucrose are significantly more attractive to *C. septempunctata* than untreated plots (Evans and Gunther, 2005). This may indicate that the role of honeydew for foraging ladybirds can be complex. Obviously it may constitute a message about aphid presence similar to honeydew but there are other possible effects as a result of the response of plant-associated microorganisms. Honeydew deposition on plant leaves offers an excellent substrate for fungal epiphytes that can serve as a food source for adult ladybirds. These sooty moulds sometimes cover the leaf surface to the extent that there is a significant reduction of plant photosynthesis (Vereijken, 1979). If this stress is similar to aphid attack, the induced effects on the plant could be a lead for ladybirds to identify stressed plants (see below). The cited experimental results may indicate that honeydew may not exclusively be seen as an aphid presence stimulus but also as a cue of other potential food sources.

APHID PHEROMONES

Aphids respond to disturbance by raising and waving their abdomen and release an alarm pheromone that makes the colony leave the feeding site. The alarm pheromone substance, (*E*)-beta-farnesene (EBF), should be an excellent searching stimulus for ladybirds to locate aphids. Two factors affect these expectations.

Firstly, aphids produce EBF from the cornicles when disturbed (Nault et al., 1973). This means that EBF is not produced by undisturbed aphids, which will escape attention by ladybirds. This explains why ladybirds sometimes walk straight through an undisturbed aphid colony feeding on a leaf (Pettersson, unpublished). Secondly EBF is a common substance in nature and, without a modifying mechanism, the searching efficiency of ladybirds would be considerably reduced. It has been shown that beta-caryophyllene, a common plant chemical, modifies the ladybird response to EBF

(Al Abassi et al., 2000). Only when there is an excess of EBF in relation to beta-caryophyllene does the former act as a positive stimulus, but below a threshold ratio it releases no ladybird behavioural response. Whether there is a natural variation in the ratio between these substances in certain plant stages/species, and to what extent such differences may affect the foraging behaviour of *C. septempunctata* is still an open question.

Aphid population dynamics has a key influence on the ecological success of *C. septempunctata*. The overall regulator of aphid density in a colony is the development of winged forms (alatae) as a response to colony density, intermittent feeding and photoperiod (Dixon, 1998); however, it has also been shown that chemical cues are involved in the regulation of mobility among wingless aphids (apterae) at lower population densities. These substances act as aphid spacing pheromones and are behaviourally active when the colony size exceeds a certain threshold value (Pettersson et al., 1995; Quiroz et al., 1997). Obviously cues indicating high population densities would be valuable to ladybirds in their search for aphid colonies. Olfactometer experiments with key components in density-related substances reported by Quiroz et al. (1997) and Quiroz and Niemeyer (1998) indicate that these substances have an arresting effect on the walking of ladybird adults (Ninkovic et al., unpublished).

HERBIVORE STRESS ON PLANTS

Recent investigations have shown that plant stress responses to herbivory may cause changes in the volatile profile that makes the plant more attractive to predators. There is experimental evidence that changes of the volatile profile of an attacked plant may induce changes in neighbouring plants, making them less attractive to aphids (Pettersson et al., 1996). Olfactometer experiments with adult *C. septempunctata* show that ladybirds prefer plants previously attacked by the bird cherry-oat aphid, *Rhopalosiphum padi* compared to non-attacked plants (Ninkovic et al., 2001). This indicates that the aphid attack induces changes in the plant volatile profile that can be a lead for the searching behaviour of the ladybird.

This is in line with studies of mites on lima beans where it has been shown that beans attacked by herbivorous mites are attractive to predatory mites and that an attacked plant may induce effects in neighbouring non-attacked plants (Bruin et al., 1995; Dicke, 1999; Bruin and Dicke, 2001). Similar results have also been reported in relation to the searching behaviour of parasitoids of *Cotesia* spp., for which plant responses to herbivore attack have a decisive importance for prey localisation (Turlings et al., 1995). In this experiment, the stress condition of a maize plant is induced by armyworm larvae on which the adult parasitoid oviposits. It has been claimed that a substance, volicitin, in the saliva of the caterpillar induces a change in the volatile profile of the attacked maize, which is then detected by the parasitoid during its search for oviposition sites (Alborn et al., 1997).

Some chemicals related to herbivore damage have been shown to release a positive response in adult *C. septempunctata*. Exposure of plants to volatile *cis*-jasmone, a common plant volatile, induces airborne release of defence compounds that make the plants less acceptable to herbivores such as aphids. The effect also promotes the recruitment of natural enemies such as *C. septempunctata* and aphid parasitoids (Birkett et al., 2000). Studies with methyl salicylate have shown a similar pattern (Zhu and Park, 2005).

IDENTIFYING HIGH QUALITY HABITATS

C. septempunctata is a polyphagous insect with high adaptive capacity to different food sources (Majerus, 1994; Hodek and Honek, 1996) and it is clear that parameters constituting high quality change during the annual life cycle. A favourable foraging habitat can be described as an environment where behavioural cues elicit intensified food-searching behaviour. A favourable foraging habitat could be a site where optimal food-aphids-is present. A crop field heavily attacked by aphids is definitely in a short time perspective a high quality habitat; however, in the absence of aphids, a favourable habitat could also be a site where it is likely that alternative suitable food sources can be found.

In studies of outdoor microcosms with two levels of soil fertility and a tritrophic system with grasses (Fraser and Grime, 1998), aphid and plant biomass responded dramatically to increased fertility as did ladybird feeding. This preference for fast-growing plants invites speculation on how different plant stand parameters can contribute to preferred ladybird habitats.

Experimental results indicate that botanical diversity may be of importance for habitat preferences potentially offering both a diversity of prey and/or pollen or other organic matter for survival. Elliott et al. (2002) found a correlation between the structure of the landscape matrix and the plant community in a field of aphid predators and that these effects sometimes overshadow the direct numerical response by predators to aphids.

Although volatile cues representing favourable plant species could play an important role, knowledge about such mechanisms is still fragmented. Species-specific plant substances can act directly on insects. Schaller and Nentwig (2000) made olfactometer experiments with ethanol extracts of 22 different plants and found extracts of *Berberis vulgaris* and *Tripleurospermum inodoratum* to be attractive. Other influential factors contributing to the value of a monocrop/aphid situation are host plant species or genotypes that combine soil fertility and water regime.

PLANT/PLANT CHEMICAL INTERACTION

The importance of increased botanical diversity has frequently been discovered in connection with mixed cropping and effects on herbivore natural enemies (Vandermeer, 1992). A recent review of mixed cropping (Norris and Kogan, 2005) states that factors such as microclimate and food diversity have general importance for the positive effects that have been found in field experiments.

However, messenger substances could also act indirectly by inducing responses in neighbouring plants that affect insects that are living on and around these plants. Experiments with adult *C. septempunctata*, barley and two common weeds, *Elytrigia repens* L. Bauv. and *Cirsium arvense* (L.) have led to discussions of plant olfactory cues as factors that contribute to the aggregated distribution and habitat preferences of *C. septempunctata* adults in barley fields (Ninkovic and Pettersson, 2003). A series of ladybird inventories were made in a commercial barley field at the two-leaf stage where no aphids, flowering weeds or other ladybird food sources were present. Estimates of the distribution of *C. septempunctata* showed that the number of adult ladybirds was higher in barley plots containing one of the two weeds than in weed-free barley plots with comparable plant biomass.

The field observations were followed by laboratory olfactometer experiments; the plant combinations were tested for ladybird preference. Neither of the weeds was shown to be directly attractive to adult ladybirds; however, when odour blends of volatiles from barley and either of the two weeds was presented, both were preferred to the odour of barley only. When the weeds themselves were removed from the odour blend, ladybirds still showed a preference for barley plants previously exposed to *C. arvense* compared to unexposed barley plants; however, the same preference was not shown for barley plants exposed to *E. repens*. The results of the experiments can be taken to support the hypothesis that plant volatiles can contribute to aggregation in weedy field plots by acting as an arresting factor. The effects of *E. repens* may represent ladybird recognition of ‘broader plant diversity’, while those to *C. arvense* invite discussion on how plant interaction via volatiles affect insects living on and around them. Field data supporting host plant-defined habitat preference are presented by Leather et al. (1999) and Elliott et al. (2002).

Plant interaction with the environment is mediated by a wide range of stimuli, of which chemical messenger substances represent one category. So far, most experimental evidence for the ecological effects of chemically-mediated plant/plant communication (allelopathy; Rice, 1984) is limited to how one plant affects another plant. The most common biotic challenge to a plant individual is sharing available resources with neighbouring plants. It may be speculated that plant/plant communication induces a condition similar to general plant stress that can be recognised by adult ladybirds, leading to similarities with herbivore-induced effects that are used in a more precise search. This would mean that, under certain conditions, undamaged plants can affect the behaviour of herbivores and their natural enemies (allelobiosis; Pettersson et al., 2003; Ninkovic et al., 2006). These results support the hypothesis that allelobiosis may contribute to arresting behaviour, and that mixed plant species odours may do the same under certain conditions. This may contribute to a mechanistic explanation of the results obtained by Honek and Martinkova (1991) in experiments with a combination of maize and *Echinochloa crusgalli*.

The time taken for searching/foraging means energy and time lost for feeding and digestion. A challenge for further studies is the balance between migratory behaviour and adaptive capacity to discriminate and evaluate a broad set of potential food sources, as discussed in several papers (Kareiva, 1987; Ives et al., 1993; Hodek and Michaud, 2008). Recent studies on the effects of plant/plant communication on the behaviour of the seven-spotted ladybird indicate that allelobiosis is a mechanism that should be considered in future studies of foraging behaviour of *C. septempunctata*.

CONCLUSION

The foraging behaviour of ladybirds can be considered on different spatial scales, as discussed by Dixon (2000) and illustrated by examples of active mechanisms given above. One obvious set of stimuli and mechanisms is directly related to available essential food sources-aphids. The aphid alarm pheromone represents such a stimulus that leads the ladybird to prey over short distances. Its potential as a tool for the recognition of aphids is modified by aphid behaviour and interfering semiochemicals. Honeydew is an immediate lead to aphid colonies but it is not understood to what extent it can also carry important information on aphid species and host plants to be used by predators.

The next spatial level-the high quality habitat-is represented by cues that may be related to food sources; however, active cues can also perform the role of primers for receiving and responding to close-range information for different food sources. A typical informative source of this kind would be volatile blends from herbivore (aphid)-attacked plants. This represents a plant individual in a specific condition, caused by aphids or possibly other organisms (fungal epiphytes) that may serve as food sources.

C. septempunctata preference for a certain plant community can be a response to botanical diversity or to plant status as affected by allelobiosis. So far, knowledge on allelobiosis has been gained mainly from examples of barley cultivars and some weeds; however, if the results of these experiments (Ninkovic and Pettersson, 2003; Pettersson et al., 2003) can be shown to represent a generally occurring mechanism, it is an aspect that should be considered in future studies of *C. septempunctata* foraging behaviour.

The allelobiotic condition of *C. septempunctata* reported in the *Hordeum*/*Cirsium* interaction (Ninkovic and Pettersson, 2003) could possibly be a general plant stress condition with similarity to the volatile message from herbivore attacks. If so, the combination of certain plant species communities would be more attractive to *C. septempunctata* than others, but the message would not always be beneficial to the ladybird as it is based on ecological traits for plant competitiveness.

The examples given above illustrate the capacity of *C. septempunctata* and other coccinellids to use information on essential food sources. Current knowledge is far from complete and there is a challenge to seek further knowledge of the mechanisms of adaptive capacity and foraging strategies of coccinellids. This possibly adds a new perspective as to whether polyphagous feeding and seasonal migration are offensive strategies in evolution.

REFERENCES

Al Abassi, S., M. A. Birkett, J. Pettersson, J. A. Pickett, L. J. Wadhams and C. M. Woodcock (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, J. A. Pickett, L. J. Wadhams and C. M. Woodcock (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.

Alborn, H. T., T. C. J. Turlings, T. H. Jones, G. Stenhagen, J. H. Loughrin and J. H. Tumlinson (1997) An elicitor of plant volatiles from beet armyworm oral secretion. *Science* 276: 945–949.

Ben Saad, A. A. and G. W. Bishop (1976) Attraction of insects to potato plants through use of artificial honeydews and aphid juice. *Entomophaga* 21: 49–57.

Birkett, M. A., C. A. M. Campbell, K. Chamberlain, E. Guerrieri, A. J. Hick, J. L. Martin, M. Matthes, J. A. Napier, J. Pettersson, J. A. Pickett, G. M. Poppy, E. M. Pow, B. J. Pye, L. E. Smart, G. H. Wadhams, L. J. Wadhams and C. M. Woodcock (2000) New roles for *cis*-jasmone as an insect semiochemical and in plant defense. *Proc. Natl. Acad. Sci. USA* 97: 9329–9334.

Bruin, J. and M. Dicke (2001) Chemical information transfer between wounded and unwounded plants: backing up future. *Biochem. Syst. Ecol.* 29: 1103–1113.

Bruin, J., M. W. Sabelis and M. Dicke (1995) Do plants tap SOS signals from their infested neighbours? *Trends Ecol. Evol.* 10: 167–170.

Dicke, M. (1999) Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivo-

rous arthropods? *Entomol. Exp. Appl.* 91: 131–142.
Dixon, A. F. G. (1998) *Aphid Ecology*. 2nd ed. Chapman & Hall, London.
Dixon, A. F. G. (2000) *Insect Predator–Prey Dynamics—Ladybird Beetles and Biological Control*. Cambridge University Press, Cambridge. pp. 268.
Elliott, N. C., R. W. Kieckhefer, G. J. Michels, Jr. and K. L. Giles (2002) Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. *Environ. Entomol.* 31: 253–260.
Evans, E. W. (2000) Egg production in response to combined alternative foods by the predator *Coccinella transversalis*. *Entomol. Exp. Appl*. 94: 141–147.
Evans, E. W. (2003) Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *Eur. J. Entomol.* 100: 1–10.
Evans, E. W. and D. I. Gunther (2005) The link between food and reproduction in aphidophagous predators: a case study with *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 102: 423–430.
Evans, E. W., A. T. Stevenson and D. R. Richards (1999) Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia* 121: 107–112.
Fischer, M. K., W. Volkl and K. H. Hoffmann (2005) Honeydew production and honeydew sugar composition of polyphagous black bean aphid, *Aphis fabae* (Hemiptera: Aphididae) on various host plants and implications for ant-attendance. *Eur. J. Entomol.* 102: 155–160.
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.
Fraser, L. H. and J. P. Grime (1998) Top-down control and its effect on the biomass and composition of three grasses at high and low soil fertility in outdoor microcosms. *Oecologia* 113: 239–246.
Giles, K. L., R. D. Madden, R. Stockland, M. E. Payton and J. W. Dillwith (2002) Host plants affect predator fitness via the nutritional value of herbivore prey: investigation of a plant-aphid-ladybeetle system. *Biocontrol* 47: 1–21.
Hagen, K. S., R. L. Tassan and E. F. Sawall, Jr. (1971) The use of food sprays to increase effectiveness of entomophagous insects. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manag*. 3: 59–81.
Hodek, I. and A. Honek (1996) *Ecology of Coccinellidae*. Kluwer Academic Publishers, Dordrecht. pp. 480.
Hodek, I. and J. P. Michaud (2008) Why is *Coccinella septempunctata* so successful? (A point-of-view). *Eur. J. Entomol.* 105: 1–12.
Honek, A. and Z. Martinkova (1991) Competition between maize and barnyard grass *Echinochloa crus-galli*, and its effect on aphids and their predators. *Acta Oecol.* 12: 741–751.
Ives, A. R., P. Kareiva and R. Perry (1993) Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74: 1929–1938.
Kareiva, P. (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326: 388–390.
Kazana, E., T. W. Pope, L. Tibbles, M. Bridges, J. A. Pickett, A. M. Bones, G. Powell and J. T. Rossiter (2007) The cabbage aphid: a walking mustard oil bomb. *Proc. Royal Soc. Lond. B* 274: 2271–2277.
Kosaki, A. and R. Yamaoka (1996) Chemical composition of footprints and cuticular lipids of three species of lady beetles. *Appl. Entomol. Zool.* 40: 47–53.
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. (1994) *Ladybirds*. Harper Collins, London. pp. 368.
Nault, L. R., L. J. Edwards and W. E. Styer (1973) Aphid alarm pheromones: secretion and reception. *Environ. Entomol.* 2: 101–105.
Ninkovic, V. and J. Pettersson (2003) Plant/plant communication supports searching behaviour of the seven-spotted 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 sevenspot ladybird, *Coccinella septempunctata*. *Biol. Control* 21: 191–195.
Ninkovic, V., R. Glinwood and J. Pettersson (2006) Communication between undamaged plants by volatiles: the role of allelobiosis. In *Communication in Plants: Neuronal Aspects of Plant Life*. Vol. 28 (F. Baluška, S. Mancuso and D. Volkmann, eds.). Springer-Verlag, Berlin, pp. 421–434.
Norris, R. and M. Kogan (2005) Ecology of interactions between weeds and arthropods. *Ann. Rev. Entomol.* 50: 479–503.
Pettersson, J., A. Quiroz, D. Stephansson and H. Niemeyer (1995) Odour communication of *Rhopalosiphum padi* on grasses. *Ent. Exp. Appl.* 76: 325–328.
Pettersson, J., A. Quiroz and E. F. Ahmed (1996) Aphid antixenosis mediated by volatiles in cereals. *Acta Agric. Scand. B Soil Plant Sci*. 46: 135–140.
Pettersson, J., V. Ninkovic and R. Glinwood (2003) Plant activation of barley by intercropped conspecifics and weeds: allelobiosis. The BCPC International Congress-Crops Science & Technology, pp. 1135–1144.
Pettersson, J., V. Ninkovic, R. Glinwood, M. A. Birkett and J. A. Pickett (2005) Foraging in a complex environment-semiochemicals support searching behaviour of the seven spot ladybird. *Eur. J. Entomol.* 102: 365–370.
Quiroz, A. and H. M. Niemeyer (1998) Activity of enantiomers of sulcatol on apterae of *Rhopalosiphum padi*. *J. Chem. Ecol.* 24: 361–370.
Quiroz, A., J. Pettersson, J. A. Pickett, L. Wadhams and H. M. Niemeyer (1997) Key compounds in a spacing pheromone in the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera, Aphididae). *J. Chem. Ecol*. 23: 2599–2607.
Rana, J. S., A. F. G. Dixon and V. Jarosik (2002) Costs and benefits of prey specialization in a generalist insect preda-

tor. *J. Anim. Ecol*. 71: 15–22.

Rice, E. L. (1984) *Allelopathy*. 2nd ed. Academic Press, Orlando, Florida, USA. pp. 421.

Rice, M. E. and G. E. Wilde (1989) Antibiosis effect of sorghum on the convergent lady beetle (Coleoptera: Coccinellidae), a third-trophic level predator of the greenbug (Homoptera: Aphididae). *J. Econ. Entomol.* 82: 570–573.

Schaller, M. and W. Nentwig (2000) Olfactory orientation of the seven-spot ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae): attraction of adults to plants and conspecific females. *Eur. J. Entomol*. 97: 155–159.

Triltsch, H. (1999) Food remains in the guts of *Coccinella septempunctata* (Coleoptera: Coccinellidae) adults and larvae. *Eur. J. Entomol.* 96: 355–364.

Turlings, T. C. J., J. H. Loughrin, P. J. McCall, U. S. R. Rose, W. J. Lewis and J. H. Tumlinson (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proc. Natl. Acad. Sci. USA* 92: 4169–4174.

Vandermeer, J. (1992) *The Ecology of Intercropping*. 2nd ed. Cambridge University Press, Cambridge, UK. pp. 249.

Vereijken, P. H. (1979) Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands. pp. 58.

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

Wiedemann, R., J. Woodring, W. Volkl and K. H. Hoffmann (2004) Amino acid composition of honeydew from aphid species feeding on tansy, *Tanacetum vulgare*. *Mitt. Deutschen Gesellschaft Allgemeine Angewandte Entomol.* 14: 459–462.

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.