• Conclusion

The growers have 2 effective chemical tools to control BYDVs vectors on barley and wheat, sprayings of insecticides and seed treatment. The decision to use one or the other of these 2 strategies is depending on parameters such as local risk situation, the opportunity or not to use sprayings equipment according to the soil conditions in autumn. There is also a today's tendency to carry out earlier drillings in order to realise potential yields, spread workloads and use lower seed rates. In that context the use of a seed treatment with imidacloprid to control BYDVs is especially advisable because of the higher exposure risk to aphids flight.

Without seed treatment, in high risks situations there might be a need for 2 sprayings of insecticides and in low-medium risk, one application, in order to safeguard potential yields. The program seed treatment/foliar spraying can be of interest in situations such as very early drilling, combined with a prolonged flight of the aphids.

Anonymous., 1982. *Deltamethrin monograph.* Roussel-UCLAF, 352 p.

Babe.S., 1998. Les outils de prévisions des risques de la jaunisse nanisante de l'orge en Champagne Ardenne. *Proc. 1st colloque transnational sur les luttes biologique, intégrée et raisonnée,* Lille, 259-267.

Beuve M., Lapierre H., Fouchard M., Van Waetermeulen X., Astruc E., 1999. Recherche d'un seuil dynamique d'intervention JNO associé à l'estimation rapide des populations virulifères des ailès de *Rhopalosiphum padi* capturés vivants dans les jeunes semis. *Proc. 5th international conference on pests in agriculture*, Montpellier, **2**, 441-451.

De Proft M., Latteur G., Steyer S., 1998. 10 années de suivi de la jaunisse nanisante de l'orge en Belgique. *Proc. 1st colloque transnational sur les luttes biologique, intégrée et raisonnée*, Lille, 249-258.

Fabre F., Pierre J.S., Plantagenest M., Hulle M., Van Waetermeulen X., 1999. Développement d'un système d'aide à la décision pour le raisonnement des interventions dirigées contre la jaunisse nanisante de l'orge à l'automne. *Proc. 5th international conference on pests in agriculture*, Montpellier, **2**, 495-502.

Krohn J., Hellpointer E., 2002. Environmental fate of imidacloprid. *Pflanzenschutz-Nachrichten Bayer*, **55**. 26 p.

Miles E.J., Bluett D.J., Mann D.H., 2001. The influence of seed rate on the efficacy of imidacloprid seed treatment in winter cereals. *Proc. Symposium Seed treatment: challenges and opportunities*, Wishaw, 47-52.

Pflüger W., Schmuck R., 1991. Ecotoxicological profile of imidacloprid. *Pflanzenschutz-Nachrichten Bayer*, **44**, 145-158

Rose P.W., Oades L., 2001. Effect of imidacloprid seed treatment against wireworms and slugs. *Proc. Symposium Seed treatment: challenges and opportunities*, Wishaw, 191-196.

The natural enemies of grass aphids and their role as biological control agents

Jean-Louis Hemptinne

• Introduction

Aphids of cultivated grasses constitute an abundant and geographically concentrated food source for many predators and parasitoids. Field observations in the United Kingdom during the serious cereal aphid infestations in the late 1960s and 1970s revealed that there could be up to 400 species feeding on aphids of winter wheat (Wratten and Powell, 1991). However, individuals of many of these species were probably occasional visitors to the fields or opportunistic consumers of aphids. Far fewer species are considered as having a role in the suppression of these aphids. They belong to three categories: aphid parasitoids, aphid-specific predators and polyphagous predators (Carter *et al.*, 1980). Impressive aggregations of these natural enemies in fields heavily infested by

"Viruses and virus diseases of Poaceae (Gamineae)".
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aphids led many people to believe that they have an important potential for biological control. As a consequence, much effort has been devoted to determining whether the number of aphids killed per natural enemy per day compensates for aphid rate of increase (Chambers and Adams, 1986; Chambers, 1988; Iperti *et al.*, 1988; Wratten and Powell, 1991; Dixon, 2000).

Today biological control is far from being established as the dominant strategy for regulating aphid abundance (Dixon, 1998; 2000). One objective of this paper is to find explanations of why this is so. Cereal aphids have been intensively studied because they have a strong economic impact in Europe and are therefore an ideal case study into the role of natural enemies as biological control agents.

• The most important natural enemies of cereal aphids

Aphid parasitoids

The parasitoids of aphids belong to two families of *Hymenoptera*, the *Aphidinae* and the *Aphelinidae* (Carter *et al.*, 1980; Wratten and Powell, 1991). They are solitary endoparasites, which means that each female inserts one egg into an aphid. As a result, a single parasitoid larva develops inside its host. At the end of the development of the parasitoid the aphids die and their body becomes mummified. Mummies are inflated aphid bodies and have a rather metallic colour. On becoming adult, the parasitoid cuts a circular hole in the mummy and departs.

The life cycle of these parasitoids takes place in cereal fields and habitats where wild grasses are infested by aphids. Parasitoids hibernate in mummified aphids in grasslands emerge in the spring and eventually start to reproduce. The next generation colonizes cereal fields as adults or immature stages inside winged aphids (Carter *et al.*, 1980). Although it is not easy to follow these rather tiny insects throughout their life, it is thought that they disperse over relatively great distances as many of them are caught in 12 m suction traps that sample high flying insects (Wratten and Powell, 1990).

The parasitoids of cereal aphids are in turn attacked by several species of hyperparasitoids belonging to five *Hymenopteran* families (Carter *et al.*, 1980; Wratten and Powell, 1991).

Aphid-specific predators

Ladybird beetles (Coleoptera, Coccinellidae)

They are on average the most abundant and probably the most well known predators of cereal aphids. Up to six species are recorded in cereal fields in Europe. One or two small species belonging to the tribe Scymnini and four to five bigger species of the sub-family *Coccinellinae* are recorded. The most frequent and numerous ladybird beetles in European cereal fields are *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.) (Hodek and Honek, 1996).

These ladybirds only spend a part of their life cycle in cereal fields. They hibernate in forest litter (Hodek and Honek, 1996) and begin to leave their hibernation sites in early spring. Then, the adults are on the move and will successively feed and lay eggs on different aphids. Aphids on nettles generally constitute the first opportunity to lay eggs (Hodek and Honek, 1996). In their search for optimal oviposition sites, females will eventually leave nettle beds and enter cereal fields. New adults will emerge there at the time of harvest. Those that escape combine harvesters will exploit nectar, pollen and aphids and finally end up in their hibernation sites. Adult ladybirds probably travel distances of an order of magnitude of 10 km between their feeding grounds and hibernation places. Both adults and larvae prey on aphids but the latter are more voracious than the former.

Hoverflies (Diptera, Syrphidae):

Hoverflies are generally second to ladybirds in terms of abundance in cereal fields. Entomologists record up to six species but *Episyrphus balteatus* (De Geer) and *Metasyrphus corollae* (F.) are the most frequent throughout Europe (Carter et al., 1980). Unlike ladybird beetles, hoverfly adults do not eat aphids but pollen. Therefore, females need flowers in order to mature their eggs. Their life cycle is similar to that of ladybird beetles although is has been less studied. It should be noted that hoverflies probably travel greater distances and *E. balteatus* probably migrates between Northern Europe and Africa (Gilbert, 1993).

Lacewings (Neuroptera, Chrysopidae)

The genus *Chrysoperla* is widespread in cultivated areas. The genus is actually divided into four distinct groups. One of them, the *carnea* group, contains species considered as enemies of field crop pests and is present throughout Europe. Once referred to as a single species, *C. carnea*, the *carnea* group contains at least 20 more or less cryptic sibling species (Duelli, 2001). The larvae are predatory and the adults feed on honeydew produced by Homoptera and on pollen. Their life cycle is characterized by three distinct phases. Firstly, lacewings perform long migratory flights to their overwintering sites after diapause induction in late summer. They leave these sites in the spring. Secondly, adults born in the spring undergo an obligatory migration flight for about two days before they start to react to habitat kairomones. Then females copulate and will soon begin to lay eggs. Thirdly, and similarly to ladybird beetles, lacewings are continuously on the move throughout their reproductive period (Duelli, 2001). Females do not appear to stay more than two days in the same field even if there is plenty of food. In Switzerland, an immigration rate of 1500 lacewings per hectare and per night has been measured (Duelli, 2001). Eggs are laid singly and not necessarily close to aphid colonies (Duelli, 2001).

Polyphagous predators

The polyphagous predators are a huge group of several species of insects belonging to two families of the *Coleoptera*, the *Carabidae* and the *Staphylinidae*. Spiders of the family *Araneae* are also included in this group (Carter *et al.*, 1980; Wratten and Powell, 1991). They are all generalist predators, which means that they feed on many different species of prey. As a consequence they respond less strongly to fluctuations in abundance of a particular prey (Snyder and Ives, 2001). In addition, carabids and staphylinids are ground predators. That means that they are awkward plant climbers and are therefore unable to efficiently hunt aphids at the apex of herbaceous plants except when the plants are still small (Losey and Denno, 1999; Snyder and Ives, 2001). They prey on aphids that fall to the ground in an attempt to avoid their specific predators. When they succeed in climbing, it appears that these predators mainly eat immobile mummified aphids (Snyder and Ives, 2001). Compared to the specific predators, the life cycle of carabids and staphylinids in field crops is dominated by shorter scale migrations to and from hibernation sites. They hibernate in grass tussocks or under mats of dried grasses at field boundaries. In the spring they progressively invade the neighbouring fields. For those species that do not fly, colonization of the field is rather slow (Wratten and Powell, 1991).

• Regulation of aphid populations by natural enemies: a theoretical perspective

The **ladybird beetle** *Rodolia cardinalis* (Mulsant), a highly specific voracious predator, was an outstanding success in the biological control of *Icerya purchasi* Maskell, a coccid that devastated the Californian citrus orchards at the end of the XIXth Century. This encouraged people to believe that they could repeat the Californian story and control aphids. After more than a century, it is clear that ladybird beetles are not as successful as was expected. A detailed analysis reveals that they are quite efficient agents of biological control of coccids but poor regulators of the abundance of aphids (Dixon, 2000). A knowledge of the oviposition behaviour of the ladybird beetles is essential in understanding this difference.

The developmental time from egg to adult of a ladybird beetle is about 4 to 5 weeks in the field. This is similar to the life span of aphid colonies, which lasts for 6 to 8 weeks (Hemptinne *et al.*, 1992). These colonies grow exponentially, reach a peak in abundance and then decline suddenly when the winged aphids become dominant in the colony (Fig. 2.28a). The migration of the winged aphids, the proportion of which increases with the age of the colony, provokes this rapid decline (Dixon, 1998). After hatching, neonate larvae of ladybirds can survive for 24 h without eating (Dixon, 1959). That is, they can forage for a day but need to have eaten at least one aphid at the end of the day in order to survive. With this information in mind, let us consider three scenarios.

a - Ladybird females always lay their batches of eggs at the very beginning of the development of an aphid colony (Fig. 2.28b). At this time, the density of prey is extremely low. The probability that neonate larvae catch a prey in the first critical 24 h is close to zero. In this scenario, most neonate larvae will starve to death. These batches of eggs will have a weak contribution to the fitness of the female. Therefore, such a strategy is unlikely to have been selected for and favoured by natural selection.

b - Females lay their eggs when aphids reach their peak in abundance (Fig. 2.28c). The larvae will begin their life in optimal conditions and grow quickly because food is plentiful. Suddenly winged aphids appear in the colony and fly away. The larvae that are now in their second or third instar of development are left without prey. As hunger increases so does the risk of cannibalism. Because of their limited dispersal ability, the majority of the larvae will die from bites inflicted by other similar sized starving larvae and from cannibalism. This second scenario is no better than the first.

c - The successful strategy lies somewhere between these two extremes (Fig. 2.28d). Females have to start laying eggs when aphid density reaches a threshold at which larvae are likely to catch an aphid in the first 24 h of their life. This threshold has to be crossed rather early in the development of aphid colonies in order to give enough time to the ladybird larvae to complete their development before the disappearance of their prey. Figure 2.28d shows that these conditions are met in a narrow reproductive window.

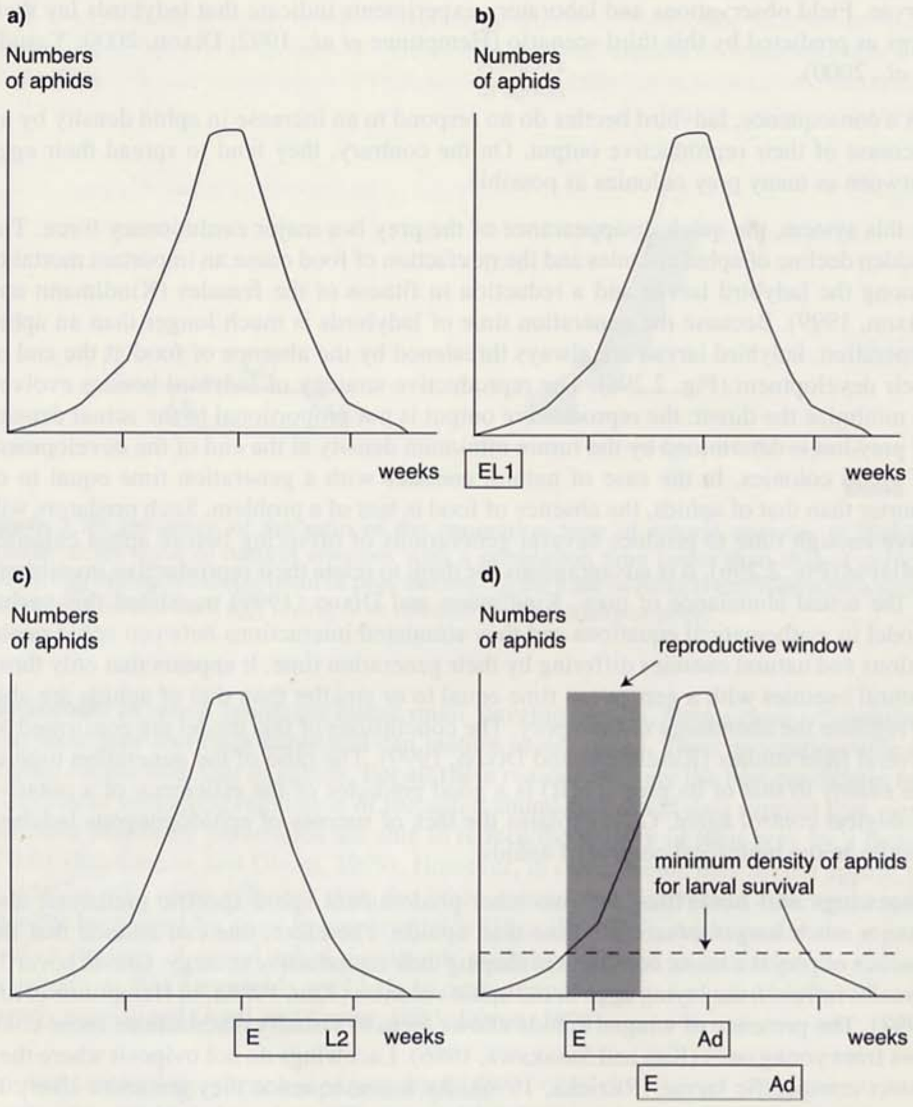

Figure 2.28 The reproductive strategy of ladybird beetles: a) the development of an aphid colony; b) eggs (E) laid at the beginning of the colony give birth to first instar larvae (L1) that die from starvation; c) eggs laid at the peak of the colony give birth to larvae that die from starvation in their second instar (L2); d) eggs laid at the beginning of the reproductive window produce adults (Ad).

Eggs laid in that window will significantly contribute to female fitness. In addition, the number of eggs per reproductive window should be small, about one or two batches (Kindlmann and Dixon, 1993) otherwise, there will be too many predators that will hasten the collapse of the colony. Once again cannibalism will decimate the population of larvae. Field observations and laboratory experiments indicate that ladybirds lay their eggs as predicted by this third scenario (Hemptinne *et al.*, 1992; Dixon, 2000; Yasuda *et al.*, 2000).

As a consequence, ladybird beetles do no respond to an increase in aphid density by an increase of their reproductive output. On the contrary, they tend to spread their eggs between as many prey colonies as possible.

In this system, the quick disappearance of the prey is a major evolutionary force. The sudden decline of aphid colonies and the rarefaction of food cause an important mortality among the ladybird larvae and a reduction in fitness of the females (Kindlmann and Dixon, 1999). Because the generation time of ladybirds is much longer than an aphid generation, ladybird larvae are always threatened by the absence of food at the end of their development (Fig. 2.29a). The reproductive strategy of ladybird beetles evolved to minimize the threat: the reproductive output is not proportional to the actual density of prey but is determined by the future minimum density at the end of the development of aphid colonies. In the case of natural enemies with a generation time equal to or shorter than that of aphids, the absence of food is less of a problem. Such predators will have enough time to produce several generations of offspring before aphid colonies collapse (Fig. 2.29b). It is advantageous for them to relate their reproductive investment to the actual abundance of prey. Kindlmann and Dixon (1999) translated this verbal model in mathematical equations and they simulated interactions between aphid populations and natural enemies differing by their generation time. It appears that only those natural enemies with a generation time equal to or smaller than that of aphids are able to regulate the abundance of their prey. The conclusions of this model are confirmed by several field studies (Kindlmann and Dixon, 1999). The ratio of the generation time of the enemy to that of its prey (GTR) is a good predictor of the efficiency of a putative biological control agent. GTR explains the lack of success of aphidophagous ladybird beetles in the biological control of aphids.

Lacewings and hoverflies, the two other predominant aphid-specific predators, also have a much longer generation time than aphids. Therefore, one can assume that the absence of prey is a major constraint in shaping their reproductive strategy. Gravid hoverfly females refrain from laying eggs in old aphid colonies (Kan, 1988a, b; Hemptinne *et al.*, 1993). The presence of winged aphids allows them to visually discriminate these colonies from young ones (Kan and Sasakawa, 1986). Lacewings do not oviposit where they detect conspecific larvae (Ruzicka, 1996). As a consequence they are more likely to choose young than old colonies as oviposition sites. Similarly to ladybird beetles these predators tend to distribute their eggs between many colonies of prey and they only weakly respond to the actual density of prey. The GTR model predicts that these natural enemies will be unable to regulate aphid numbers and in the case of hoverflies, this is supported by field data (Kindlmann and Dixon, 1999).

Polyphagous predators by definition feed on many species of prey. Therefore, they respond less strongly to fluctuations of abundance of any single species (Snyder and Ives, 2001). This may limit their ability to control aphid populations. Moreover, their generation time is much longer than that of aphids. According to theory, they are therefore not good biological control agents of aphids.

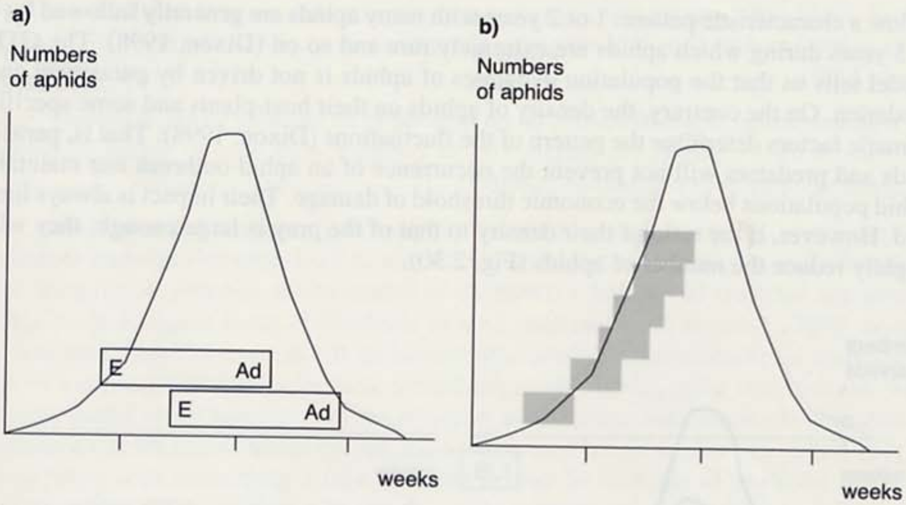

Figure 2.29 Influence of the ratio of the generation time of natural enemies to that of aphids: a) the case of natural enemies with a generation time larger than that of aphids where egg laying is independent of prey density; b) the case of natural enemies with a short generation time where egg laying is in relation to the density of prey.

Parasitoids of cereal aphids are rather small, develop rapidly, have a close relationship with their prey and each parasitoid can mature in one aphid. Their generation time is slightly longer than that of aphids. For all these reasons they are the best candidates for a successful biological regulation of the aphid abundance. Field data support that view and show that some parasitoids are able to reduce the density of their prey by a factor of 0.01 (Kindlmann and Dixon, 1999). However, in cereal fields they do not appear to be consistently more efficient than the other natural enemies. Their effectiveness is strongly hampered by their hyperparasitoids (Hassell, 1978). Additionally the reproductive strategy of cereal aphid parasitoids probably evolved to minimize the risk of parasitism so that parasitoids are likely to cease ovipositing in a patch of aphids that is already parasitized (Ayal and Green, 1993; Dixon, 1998).

• Prospects for biological control of cereal aphids

According to the theoretical framework provided by the GTR model, none of the natural enemies introduced at the beginning of this chapter is a good candidate for the biological control of cereal aphids, and of grass aphids by extension. Parasitoids lose the benefit of a rather favourable developmental time in a high rate of hyperparasitoid attack. This is confirmed by laboratory experiments: in controlled conditions with no hyperparasitoids, the parasitoid *Aphidius rhopalosiphi* de Stefani Perez significantly reduces the spread of Barley yellow dwarf viruses (Smyrnioudis *et al.*, 2001).

However the above predictions of the GTR model do not mean that biological control of cereal is impossible. Firstly, the model just indicates that **natural** populations of predators and parasitoids will not do a good job. The fluctuations of abundance of aphids follow a characteristic pattern: 1 or 2 years with many aphids are generally followed by 4 to 5 years during which aphids are extremely rare and so on (Dixon, 1998). The GTR model tells us that the population dynamics of aphids is not driven by parasitism and predation. On the contrary, the density of aphids on their host-plants and some specific climatic factors determine the pattern of the fluctuations (Dixon, 1998). That is, parasitoids and predators will not prevent the occurrence of an aphid outbreak nor maintain aphid populations below the economic threshold of damage. Their impact is always limited. However, if the ratio of their density to that of the prey is large enough, they will slightly reduce the number of aphids (Fig. 2.30).

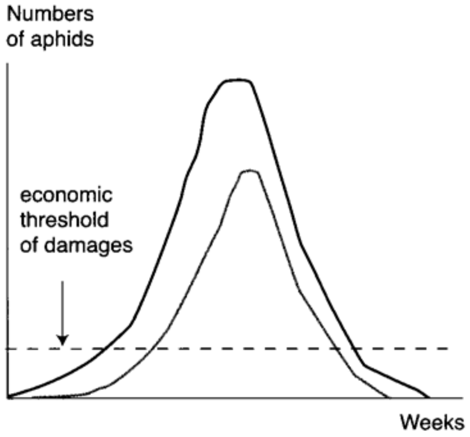

Figure 2.30 The impact of natural enemies on the abundance of aphids. The curve showing the fluctuation in abundance of aphids is shown in the absence (black curve) or presence (grey curve) of natural enemies.

Secondly, the conclusions of the GTR model are an invitation to search for other solutions. They also remind us that eating or killing do not necessarily mean regulation. This point in the ecological theory is still largely ignored in practice. As a consequence, biological control should never be founded exclusively on the existence of antagonistic relationships but take note of the evolutionary ecology of both prey and natural enemies.

As an example, farmers can try to compensate for the innate tendency of natural enemies of aphids to distribute their eggs between many aphid patches. For that, they will have to introduce larvae in their fields when forecasting models predict a serious risk of outbreak. Such an inundative strategy will only work if natural enemies are cheap. There is therefore a need of improving our knowledge of the feeding ecology of natural enemies to reduce the cost of their rearing. One also needs to know how immature instars of natural enemies distribute themselves in the field.

Ayal Y., Green R.F., 1993. Optimal egg distribution among host patches for parasitoids subject to attack by hyperparasitoids. *American Naturalist*, **141**, 120-139.

Carter N., McLean I.F.G., Watt A. D., Dixon A.F.G., 1980. Cereal aphids: a case study and review. *Applied biology*, **5**, 271-384.

Chambers R.J., 1988. A re-appraisal of the Bombosh model for quantifying predation on an aphid population. *In: Ecology and effectiveness of Aphidophaga*, Niemczyk E., Dixon A.F.G. eds., SPB Academic Publishing, 199-202.

Chambers R.J., Adams T.H.L., 1986. Quantification of the impact of hoverflies (Diptera : Syrphidae) on cereal aphids in winter wheat: an analysis of field populations. *J. appl. Ecol.*, **23**, 895-904.
Dixon A.F.G., 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. anim. Ecol.*, **28**, 259-281.
Dixon A.F.G., 1998. *Aphid ecology. An optimization approach*. Chapman & Hall, 300 p.
Dixon A.F.G., 2000. *Insect predator-prey dynamics. Ladybird beetles and biological control*. Cambridge University Press, 257 p.
Duelli P., 2001. Lacewings in field crops. *In*: *Lacewings in the crop environment*, McEwen P.K., New T. R., Whittington. eds., Cambridge University Press, 158-171.
Gilbert F.S., 1993. *Hoverflies*. 2nd edition. Richmond Publishing Co. Ltd, 67 p.
Hassell M.P., 1978. *The dynamics of arthropod predator-prey systems*. Monographs in Population biology, 10, Princeton University Press, 237 p.
Hemptinne J.-L., Dixon A. F G., Coffin J., 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical rresponse. *Œcologia*, **90**, 238-245.
Hemptinne J.-L., Dixon A.F.G., Doucet J.-L., Petersen J.E., 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *Eur. J. Entomol.*, **90**, 451-455.
Hodek I., Honek A., 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers, 464 p.
Iperti G., Lapchin L., Ferran A., Rabasse J.M., Lyon J.P., 1988. Sequential sampling of adult *Coccinella septempunctata* L. in wheat fields. *Can. Entomol.*, **120**, 773-778.
Kan E., 1988a. Assessment of aphid colonies by hoverflies. I. Maple aphids and *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae). *J. Ethol.*, **6**, 39-48.
Kan, E., 1988b. Assessment of aphid colonies by hoverflies. II. Pea aphids and three syrphid species: *Betasyrphus serarius* (Wiedemann), *Metasyrphus frequens* (Matsumara) and *Syrphus vitripennis* (Meigen) (Diptera: Syrphidae). *J. Ethol.*, **6**, 135-142.
Kan E., Sasakawa M., 1986. Assessment of maple aphid colony by the hoverfly *Episurphus balteatus* (de Geer) (Diptera: Syrphidae). *J. Ethol.*, **4**, 121-127.
Kindlmann P., Dixon A.F., G., 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequence for their use in biological control. *Eur. J. Entomol.*, **90**, 443-450.
Kindlmann P., Dixon A.F.G., 1999. Generation time ratios – determinants of prey abundance in insect predator-prey interactions. *Biol. Control*, **16**, 133-138.
Losey J.E., Denno R.F., 1999. Factors facilitating synergistic predation : the central role of synchrony. *Ecol. Appl.*, **9**, 378-386.
Ruzicka Z., 1996. Oviposition-deterring pheromone in chrysopids: intra–and interspecific effects. *Eur. J. Entomol.*, **93**, 161-166.
Smyrnioudis I.N., Harrington R., Clark S. J., Katis N., 2001. The effect of natural enemies on the spread of *Barley yellow dwarf virus* (BYDV) by *Rhopalosiphum padi* (Hemiptera: Aphididae). *Bull. Entomol. Res.*, **91**, 301-306.
Snyder W.E., Ives A.R., 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology*, **82**, 705-716.
Wratten S.D., Powell W., 1991. Cereal aphids and their natural enemies. *In: The Ecology of Temperate Cereal Fields, 32nd Symposium of The British Ecological Society*, Firbank L.G., Carter N., Darbyshire J.F., Potts G.R. eds., Blackwell Scientific Publications, 233-257.
Yasuda H., Takagi T., Kogi K., 2000. Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.*, **97**, 551-553.

Ecological impact of virus-resistant transgenic plants

Mark Tepfer

The first virus-resistant transgenic plants (VRTPs) were described in 1986 (Powell-Abel *et al.*, 1986). Since then, transgenic plants have fully borne out their promise as a theoretically inexhaustible source of virus resistances of several sorts. The vast majority of VRTPs express viral sequences, and constitute a remarkable application of the concept