BIOLOGICAL CONTROL OF THE ROSY APPLE APHID, *Dysaphis plantaginea* (PASSERINI) (HOMOPTERA: APHIDIDAE): LEARNING FROM THE ECOLOGY OF LADYBIRD BEETLES.

J.-L. HEMPTINNE, A.F.G. DIXON & E. WYSS

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D. plantaginea is one of the major pests of apple. Technical advisers use empirically derived action thresholds, which depending on the geographic area, vary from 1 to 10 aphids per 100 fruit clusters. Not surprisingly the majority of orchards are sprayed every year. As a consequence, clones of this aphid are now resistant or tolerant to insecticides. There is therefore a need to develop other strategies for controlling this pest. Conservation and enhancement of natural enemies in apple orchards is one of the possible strategies but this technique does not produce consistent results. Releases of larvae of aphidophagous predators are promising but they are still expensive. In the near future, significant improvements in the biological control of *D. plantaginea* require of a threshold of economic damage, a better understanding of the ecology of this aphid and of its natural enemies, and the utilization of more resistant varieties of apple.

Jean-Louis Hemptinne (e-mail: jean-louis.hemptinne@educagri.fr), École Nationale de Formation Agronomique, BP 87, FR-31326 Castanet-Tolosan, France; A.F.G. Dixon, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK & E. Wyss, Research Institute of Organic Agriculture, Ackerstrasse, Postfach, CH-5070 Frick, Switzerland.

INTRODUCTION

Dysaphis plantaginea (Passerini) is one of the major pests of apple in Western Europe and North America (BONNEMAISON 1959; BASSINO 1982; PASQUALINI & BRIOLINI 1982; WHALON & CROFT 1984; CRUZ DE BOELPAEPE et al. 1987; BARONIO et al. 1988; GENDRIER et al. 1989; TOURNEUR et al. 1992; BLOMMERS 1994; SAVINI 2000). It causes the leaves to curl and distorts current year shoots. Heavy infestations, particularly just after flowering, reduce the growth of the fruit and yield by 20 to 30 % (GRAF et al. 1999). However, the aphid is rarely abundant several years running, but tends to reach outbreak levels approximately every 5 to 6 years. Farmers and technical advisers do not seem to be aware of these fluctuations and spray or recommend spraying of orchards every year. The pest status of this aphid has increased over the last decade. Spring infestations have become more severe and last longer. In addition, *D. plantaginea* has become more tolerant and in some cases resistant to the commonly used insecticides (DELORME et al. 1998). Reflecting these trends, the average number of insecticide treatments per growing season in Swiss orchards increased from 1.2 in 1990 to 1.8 in 1995 (HOEHN et al. 1996; GRAF et al. 1999). In South-western France, in 1998 the majority of farmers sprayed 3 to 4 times against *D. plantaginea* (DEDIEU 1998).

Although *D. plantaginea* severely affects apple production (DE BERARDINIS et al. 1994) the threshold of economic damage, surprisingly, has not been determined (WHALON & CROFT 1984). Technical advisers use empirically derived action thresholds, which depending on the geographic area, vary from 1 to 10 aphids per 100 fruit clusters (WHALON & CROFT 1984). In Europe the action threshold is 1 aphid (BLOMMERS 1994). Thus not surprisingly, the majority of orchards are sprayed every year in early spring. This frequent use of insecticides probably accounts for the existence of resistant clones of *D. plantaginea*. This threshold hampers any change in the control of apple aphids. It indicates that *D. plantaginea* is extremely harmful and as a consequence technical advisers and farmers are reluctant to reconsider the methods used to control this aphid. The widespread and frequent use of insecticides in apple orchards is contrary to the political desire for the development of sustainable agriculture in Europe. Therefore, there is an urgent need to develop other strategies for controlling *D. plantaginea*.

The guilds of natural enemies associated with apple aphids have been extensively recorded (HODEK 1973; TOURNEUR et al. 1992; HODEK & HONĚK 1996). They generally consist of a minimum of 50 species of insects belonging to several families. Coccinellidae is one of the three most important families contributing 4 to 6 species to these guilds. This diversity of beneficial insects encourages the view that biological control is feasible. Thus the exploitation of the entire guild as a biological control agent is an attractive strategy. The objective is to keep the beneficial insects in the orchards and increase their abundance. To encourage them overwintering sites are provided and/or additional sources of food such as cover crops, strips of flowers or hedgerows are sown or planted. Alternatively the guilds can be used as a catalogue of potential biological control agents. Those selected can be reared in factories and released in the orchards. This paper considers these two approaches to the biological control of apple aphids with special emphasis on ladybird beetles.

CONSERVATION AND ENHANCEMENT OF NATURAL ENEMIES IN APPLE ORCHARDS

Since at least the beginning of the XXth Century circumstantial evidence was thought to favour the concept that simple communities on cultivated land were more prone to insect outbreaks than more natural communities (ELTON 1958). As the later harbour more species than the former, the stability of these communities was seen as a consequence of their greater biological diversity. The structure of food webs was often invoked as an explanation. In complex communities, there are not only more species of herbivore but also of carnivore. That is, there are more pathways to channel the energy from one trophic level to the next. If one or few carnivore species are temporarily absent, there are still enough consumers to exploit the herbivore productivity. As a consequence, populations show slight fluctuations in abundance around an equilibrium (KREBS 1994). This ecological concept probably inspired the use of biological control based on natural enemy conservation and enhancement by making fields more hospitable to natural enemies by cultivating hedgerows, cover crops or weed strips.

This idea is not new and was already practised in the first decade of the XXth Century in attempts at controlling aphids (DIXON 2000). Later it received some theoretical support from ROOT (1973) who proposed two hypotheses to account for the fact that herbivorous insects are less abundant in complex agroecosystems than in simple ones (Fig. 1).

a)

	Simple	**Complex**
Diversity of prey/hosts species	Low	High
Fluctuations of natural enemies	Large	Small
Availability of pollen and nectar	Low	High
Functional response of natural enemies	Low	High

b)

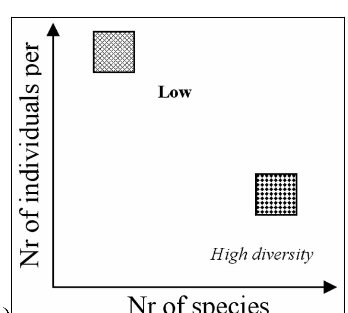

Fig. 1. Summary of Root's two hypotheses: a) the four main characteristics of the enemies hypothesis and b) the relationship between the number of species and the number of individuals per species in a community according to the resource concentration hypothesis.

Firstly, the enemies hypothesis postulates that predators and parasitoids are more efficient in diverse than simple communities of plants. RUSSELL (1989) reviewed the literature for evidence in favour of this hypothesis. Secondly, the resource-concentration hypothesis stipulates that specialist herbivores more easily find, stay in, and reproduce in monocultures of their host plants. Modern apple orchards typically are simplified communities: the soil below the trees is kept bare and grass between the rows of trees is mown regularly. Thus it is not surprising that attempts have been made to control aphids by increasing plant diversity in European and North American orchards (BROWN & WELKER 1992; WYSS 1995; BROWN & SCHMITT 1996; BROWN et al. 1997; KIENZLE et al. 1997; SOLOMON et al. 1999; VOGT & WEIGEL 1999). WYSS' seminal study (1995) lasted for 3 years during which *D. plantaginea* infestation and aphidophagous predators were monitored in two parts of an organic orchard. In the first year aphid infestation and predator abundance were identical in the two zones. In the second year a mixture of species of indigenous dicotyledons was sown in six one-meter wide strips located in one of the two zones. These plants flowered successively from early spring to late autumn. Some of them also host aphids when they are rare on apple. Therefore, pollen, nectar and aphids were available to the aphidophagous predators throughout the year. Later in the second and in the third year, aphidophagous predators appeared to be more abundant on the trees in the zone with the strip planting and there were fewer trees with large *D. plantaginea* colonies in this zone than in the control area (Fig. 2). Unfortunately, when VOGT & WEIGEL (1999) repeated WYSS' experiment in a much smaller orchard, they recorded more *D. plantaginea* on the trees in the zone with the strip planting than in the control zone.

These cases studies show that a greater abundance and/or diversity of natural enemies achieved by manipulating plant diversity does not automatically translate into aphid control (ANDOW 1986, 1988; VAN EMDEN 1990; VAN DRIESCHE & BELOW 1996; OBRYCKI & KRING 1998; DIXON 2000; LANDIS et al. 2000). This forces a reconsideration of the link between diversity and stability and the role of aphidophagous predators in determining aphid abundance.

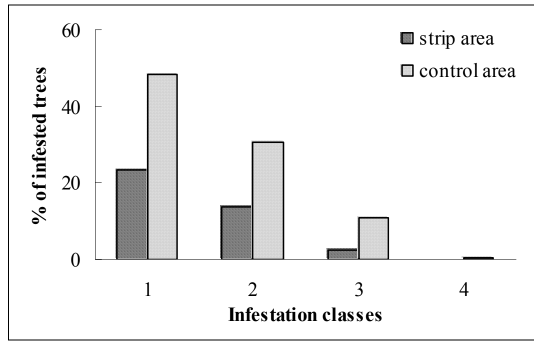

Fig. 2. Percentage of infested trees in the strip sown area and the control area in an experimental organic orchard in May 1993 (After WYSS 1995). Infestation classes: 1, 1 to 3, 2, 4 to 10, 3, 11 to 50 and 4, 51 to 200 aphid colonies.

Diversity and Stability

It is surprising that the enhancement of plant diversity in or near fields in attempts to control pests attracted such wide support, especially as it was not founded on sound scientific principles or experiments (PIMM 1984). As early as 1968, HAIRSTON et al. failed to increase the stability of experimental communities of bacteria and ciliates by increasing the number of species in his microcosms. Mathematical models of food webs showed that complex networks of consumers were not more stable than simple ones (MAY 1973). Finally, ROOT (1973) and RUSSELL (1989) based their hypotheses on circumstantial evidence. Currently, the link between diversity and stability in communities is still a highly controversial issue (KREBS 1994; DIAZ & CABIDO 2001). However, properties of communities such as resistance and/or resilience to perturbations are thought to depend on plant functional diversity rather than number of species. Plant functional types are sets of species showing similar responses to the environment and similar effects on ecosystem functioning (DIAZ & CABIDO 2001). It should be noted, however, that the impact of plant functional diversity has been studied in relatively few cases (DIAZ & CABIDO 2001). Recently, field trials in Sweden and

Switzerland yielded a positive correlation between plant functional richness and composition, and the number of aphids, and a negative one with the number of parasitoids (KORICHEVA et al. 2000). Although an interesting result the mechanism linking plant functional diversity and the abundance of these insects is unknown. Finally, in the absence of a well founded theoretical understanding it is not surprising that the results of studies on the conservation and enhancement of natural enemies in apple orchards are contradictory.

The role of aphidophagous predators

The two spot ladybird beetle *Adalia bipunctata* is one of the most abundant predators of *D. plantaginea* in European apple orchards. Its reproductive behaviour provides an explanation of why it is unable to regulate aphid abundance (HEMPTINNE et al. 1992; DOUMBIA et al. 1998). Aphids are smaller and grow much faster than two spot ladybirds (DIXON 1998, 2000). In the field, the developmental time, from egg to adult, of *A. bipunctata* is slightly shorter than the duration of an aphid colony. If a female ladybird is to maximize its fitness it has to carefully select its oviposition sites. If its larvae hatch in a very young colony, the probability of finding and catching prey is extremely low so they are likely to die of starvation. An old colony is not better because the number of prey is more likely to become scarce before the larvae can complete their development and they then have to compete for a dwindling resource and most if not all of them will die, mainly as a result of cannibalism. Between these two extremes, there is a narrow reproductive window, oviposition during which results in maximum larval survival. However, laying too many eggs in an aphid colony or in colonies where there are already ladybird larvae is likely to result in poor survival. In both cases the many predators hasten the decline in aphid abundance and increases competition for food. In addition, the youngest larvae will be the first to be eaten by older larvae (AGARWALA & DIXON 1992). Natural selection is likely to have favoured ladybird females that are able to assess the quality of aphid colonies and lay a few eggs during the reproductive window (KINDLMANN & DIXON 1993). This is more fully discussed by DIXON & HEMPTINNE (2003).

RELEASE OF APHIDOPHAGOUS PREDATORS TO CONTROL APPLE APHIDS

There have been few releases of natural enemies in apple orchards (BOUCHARD et al. 1988; HAGLEY 1989; GRASSWITZ & BURTS 1995; WYSS et al. 1999a, b).

In Europe, Wyss experimentally assessed the ability of predators to keep the numbers of *D. plantaginea* below the action threshold. As producers routinely spray against this aphid early in spring, because of the low value of the action threshold, the study was aimed at determining the effectiveness of predators to reduce the numbers of fundatrices of the aphid. According to the literature and field observations, *A. bipunctata*, *Episyrphus balteatus* (De Geer) and *Aphidoletes aphidimyza* (Rondani) are the most abundant enemies of *D. plantaginea*. In Northern Europe, climatic conditions are often harsh when aphids hatch from overwintering eggs. Therefore, preliminary trials were made in 1995 to evaluate the searching ability of these predators in the field. Apple seedlings kept in 1 m^3 cages were infested with fundatrices of *D. plantaginea*. Eggs or larvae of the three predators were then introduced in the cages. Larvae of *A. bipunctata* were the most resistant to frost and efficient at finding and killing the fundatrices (WYSS et al. 1999a). The effectiveness of this ladybird was further studied on 3-year-old apple trees and on apple branches in a commercial orchard.

On 3 year old apple trees, each infested with 5 fundatrices, were placed ladybird eggs or larvae to give four predator-prey ratios: 0:5, 1:5,1:1 and 5:1. The treatments with eggs were unsuccessful because all the batches of eggs were either destroyed by rain or frost. Larvae at the two highest predator-prey ratios prevented the increase in aphid abundance (Fig. 3; WYSS et al. 1999b). These results were confirmed using naturally infested branches of apple trees (Wyss, unpublished results).

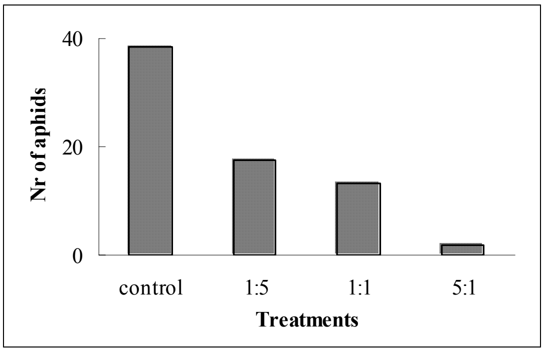

Fig. 3. The average number of aphids per tree on control trees and on trees on which larvae of *A. bipunctata* were released at one of the three predator-prey ratios: 1:5, 1:1 and 5:1 (After WYSS et al. 1999b).

INTEGRATED PEST MANAGEMENT

At a time when sustainable agriculture appears more and more frequently at the top of political agendas, it is important to convince farmers that the biological control of *D. plantaginea* is as reliable and efficient as the current methods of control. To reach this objective, research has to be developed in three directions.

Firstly, a real economic threshold of damage is needed. In conjunction with forecasts of aphid abundance, it will enable technical advisers and farmers to make more effective decisions- and is the corner stone of IPM in apple orchards.

Secondly, we have to learn more about the weak points in the *D. plantaginea* life cycle and how to use this knowledge to control the abundance of this aphid. For example, field observations (BONNEMAISON 1959) and time series analysis of the suction trap catches (HEMPTINNE et al. *in press*) indicate that mortality in autumn is important and influences the number of aphids next spring. Would it be possible to increase autumn mortality? According to two recent studies the answer to this question might be positive. WYSS et al. (1995) showed that spider webs caught many migrants. The more spider webs the more aphids caught and the fewer fundatrices next year. Release of predators seems also to be efficient in autumn. The impact of larvae of *A. bipunctata*, released before mid-October, on sexuparae and gynoparae significantly affects the number of fundatrices next spring (KEHRLI & WYSS 2001). So there is a potential for biological control in autumn, which needs to be further explored. At first sight, autumn is probably more favourable for biological control than spring: producers are less busy and the risk of bad weather interfering with natural enemies is less.

Thirdly, the protection of apple has to be thought of in terms of IPM. More attention has to be paid to planting more aphid resistant varieties of apple. They continue to bean effective mean of reducing the population growth rate of *D. plantaginea* and so maximizing the impact of natural enemies. Florina, Delorina, FloRub, Goldrush, Red Devil are resistant to *D. plantaginea* (WÜRTH et al. 1999, 2002). In addition, Ariwa, Renora, Rewena, Rubinola, Saturn are less susceptible to this aphid. All these varieties are hardly planted in Europe and the US. The major problem is to introduce them onto the market and to convince consumers to buy them. A lower productivity or a poor ability to sustain conservation might create additional problems for some of these apples. However, one should learn how to use this genetic potential in commercial orchards.

The cost of ladybird larvae is high so their use for aphid control is expensive. One way of reducing the cost is to target the fundatrices because fewer larvae are required to achieve an efficient predator-prey ratio. Time series analyses of suction trap catches show a cyclical pattern in the variation in abundance of *D. plantaginea* in France. Years with the lowest catches of aphids are separated by 6 to 4 years of higher catches (HEMPTINNE et al. *in press*; Fig. 4). If one could predict aphid outbreak years the cost of releasing natural enemies could be spread over more than one year. Currently analysis of suction trap catches has revealed that the abundance of *D. plantaginea* is regulated by density-dependence with weather acting as a disturbing factor (HEMPTINNE et al. *in press*). We do not know what regulates its abundance and cannot therefore devise a reliable forecasting system. However, the results provide working hypotheses for field and laboratory experiments, the objective of which is to identify the regulating mechanism.

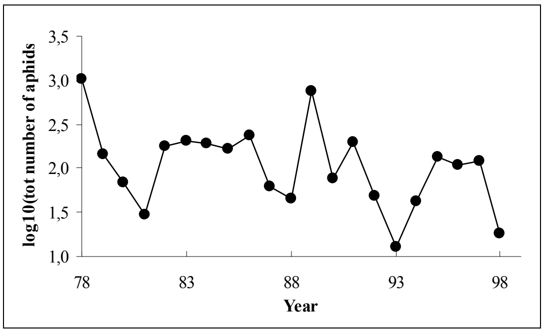

Fig. 4. The logarithm of the numbers of *Dysaphis plantaginea* caught every year from 1978 to 1999 in the suction trap at Rennes (Brittany, France).

CONCLUSION

Conservation and enhancement of natural enemies is an attractive strategy for controlling aphids, which has been tested in apple orchards. However, the results are not consistent. The problem is twofold. Firstly, it rests on the idea that diversity creates stability. Undoubtedly accumulating evidence indicate that diverse systems have interesting properties that are already visible when organic fields are compared with conventionally managed fields (MÄDER et al. 2002). Unfortunately we still do not know how these properties are generated and it is therefore difficult to engineer a system to achieve desirable properties (HINDMARCH & PIENKOWSKI 2000). Secondly, stability does not necessarily mean regulation of a population in the sense of keeping its abundance under a threshold of economic damage. The main weakness of conserving and enhancing natural enemies in order to control pests was pointed out by RUSSELL in 1989: the almost complete lack of field studies "on the behavior of individual arthropod enemies". If we do not correct this, techniques of biological control conceived from theory built on speculation will continue to yield inconsistent results.

From a purely technical point of view, it is possible to control *D. plantaginea* using natural enemies. Experiments have revealed that larvae of *A. bipunctata* can locate and kill fundatrices of this aphid early in spring even when the weather is cold and humid. They are also active and efficient in autumn when *D. plantaginea* returns to the apple. If it is decided to release predators, then it should be larvae rather than adults because they tend to stay in or in the vicinity of patches of prey where they are released. A farmer that introduces ladybird larvae in his orchard behaves like a gravid ladybird female, carefully selecting prey colonies where its larvae will later develop. However, this method of biological control is expensive because the price per predator larva is high and large numbers are required to treat an orchard.

Like Janus biological control by natural enemies has two faces. Schematically and in the evolutionary framework, natural enemies tend to aggregate where prey or hosts are abundant, that is in the more profitable patches. As their abundance gradually increases there they compete for the resource and they interfere with each other. Good patches gradually lose their value and natural enemies begin to leave and search for better patches. Two opposing forces are at work: attraction to resources and repulsion (BEGON et al. 1996). The first force is emphasized in biological control strategies, while the second is neglected. Intercrops, cover crops or hedgerows provide more resources and support more consumers. But how do consumers distribute themselves between patches of resource and what is their impact on resource abundance?

To answer such a question, one needs to focus on the ecology of the protagonists, which in this case are aphids and ladybird beetles. Aphids are particularly adapted to exploit transient and ephemeral resources, the sap flow rich in nitrogen, which only occurs in spring and in autumn (DIXON 1998). Their life history is summarized by a short motto: "going fast". Ladybird beetles evolved the ability of exploiting such prey. Their reproductive behaviour, as described for *A. bipunctata*, is an expression of their adaptation. It clearly shows the two forces mentioned above in action. Ladybird females are attracted to aphid colonies but they also avoid those colonies that are marked by the tracks left by conspecific larvae. As a result, female *A. bipunctata* tend to distribute their eggs in many colonies of prey and show a weak numerical response to aphid abundance (HEMPTINNE et al. 1992). Field work aimed at understanding how ladybird beetles behave in strip managed orchards and at assessing their impact on more diverse food sources is needed.

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