

Integrated pest management of aphids and introduction to IPM case studies

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23 Integrated Pest Management and Introduction to IPM Case Studies

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Introduction

Modern IPM began with aphids, having evolved from the ‘Integrated Control’ (IC) concept of Stern *et al.* (1959). IC integrated the chemical and biological control of *Therioaphis trifolii maculata* (spotted alfalfa aphid) on lucerne (alfalfa), *Medicago sativa*. Following the arrival of the aphid from Europe to California in 1954, resistance to organophosphate insecticides (OPs) rapidly appeared. Since the OPs killed the indigenous natural enemies, *T. t. maculata* was destroying the lucerne crop in California by the late 1950s. To solve the OP resistant *T. t. maculata* problem, the Californian workers integrated a reduced dose of an OP insecticide with the biological control that the low dose allowed to survive. Stern *et al.*’s ‘integration’ referred to integration of control methodologies, therefore integrated control of an aphid pest was a meaningful concept. Its first successor, ‘Pest Management’ (PM), dates from a conference at Raleigh, North Carolina in 1970 (Beirne, 1970), and embraced both single and multiple control measures against a pest. Still later, ‘Integrated Pest Management’ (IPM) emerged (Apple and Smith, 1976), defined as follows: “The concept of Pest Management has now been broadened to include all classes of pests (pathogens, insects, nematodes and weeds) and in this context is commonly referred to as IPM”. Thus the ‘I’ of IPM originally included an integration of crop protection disciplines (i.e. entomology, plant pathology, nematology, weed science etc.), and Apple and Smith (1976) would have regarded IPM of aphids as a contradiction in terms. Yet, since 1976, definitions have loosened; today IPM seems indistinguishable from PM.

The drivers behind PM/IPM were pest *mismanagement* in the 1940s and 1950s, and the methods available for reversing this are reviewed elsewhere in this volume (Table 23.1). Apart from those representing the reciprocals of pest-mismanagement, using semiochemicals to modify the behaviour of aphids and their natural enemies (Chapter 8, this volume) is a more recent contribution of considerable potential for inclusion in the IPM armoury.

What is missing from Table 23.1 is the “I” for integration of at least two methods, which is surely implicit in the concept of IPM, and from which logically follow two “Golden rules for IPM” (van Emden, 2002):

- *If a single method gives adequate control on its own, then there is the danger of a tolerant pest strain increasing in gene frequency and no opportunity to use a second method in addition. The method therefore needs to be made less efficient (reduced dose of pesticide, partial host-plant resistance rather than immunity) for there to be value in introducing another control method to supplement it.*
- *Methods are increasingly worth combining to the extent that the control then achieved exceeds the additive effects of the two methods in isolation.*

Integration of Chemical and Biological Control

The prevalent expression of the impact of insecticides on biological control in the literature is that most insecticides are toxic to natural enemies of aphids. This is often misinterpreted as meaning that they inevitably damage biological control of aphids. However, assuming there are no harmful sublethal effects of the pesticide on the surviving natural enemies (as shown for imidacloprid with the hemerobiid *Micromus tasmaniae* (Walker) by Walker *et al.*, 2007), biological control is only damaged if the ratio of aphids to natural enemies increases after the pesticide application. If it decreases (i.e. even the application is only marginally selective), there is the potential for improved biological control, though some or even many of the natural enemies are killed (van Emden and Service, 2004).

Use of a selective active ingredient

The classic example is the carbamate pirimicarb, to which only the acetylcholinesterase in the nervous system of aphids and Diptera is sensitive (Silver *et al.*, 1995). In addition, pirimicarb increases coccinellid voracity by reducing the mobility of surviving aphids, making their capture easier (Cabral *et al.*, 2011).

Natural enemies of aphids are not necessarily more susceptible to insecticides than their aphid prey. Croft and Brown's (1975) literature review identified that, for 36 aphid–coccinellid combinations, the coccinellid was more tolerant to insecticide than the aphid in 31 cases, the extreme being a 43-fold difference. Acheampong and Stark (2004) found that pymetrozine was not only non-toxic to the parasitoid *Diaeretiella rapae* at 0.212 g a.i./ha, but also that the r_m of treated parasitoids increased by 11 per cent.

Plant extracts such as neem (Khan *et al.*, 2013) and herb extracts (Ketabi *et al.*, 2014) are often much more selective than conventional insecticides, where any selectivity tends to be partial. Cypermethrin has repeatedly been reported as partially selective (e.g. Al-Antary *et al.*, 2010; Irshaid and Hasan, 2011), and today candidate insecticides are usually screened for their effects on natural enemies of aphids (e.g. Bangels *et al.*, 2011; Morita *et al.*, 2014). Selectivity found in favour of one natural enemy may not apply to others; Bacci *et al.* (2009) tested 6 aphicides on the ladybird *Cycloneda sanguinea*, a predatory anthicid beetle and the parasitoid *D. rapae*, and found considerable specificity for any selectivity.

Fungicides and herbicides also need checking for impact on aphid natural enemies. Jansen *et al.* (2008) tested 16 fungicides and 16 herbicides for toxicity to *Aphidius rhopalosiphii*, *Adalia bipunctata*, *Episyphus balteatus* and two ground-living aphid predators, the staphylinid *Aleochara bilineata* and the carabid *Bembidion lampros*. Not all the compounds were safe for the beneficials. In Belgium, 'selectivity lists', reporting on the safety to natural enemies of a wide range of plant protection products, are available for potato and vegetable crops (Jansen, 2014).

Dose reduction

This was the approach to achieve selectivity of a broad-spectrum OP insecticide mentioned at the start of this chapter (Stern *et al.*, 1959). Similarly, Khan *et al.* (2012) reduced the dose of thiacloprid on potatoes by 20%, and recorded better survival of ladybirds with no loss of tuber yield compared to the full dose treatment.

Such studies confirm Plapp's (1981) hypothesis that percent kill of carnivores will reduce faster than that of herbivores as pesticide dose reduces. This hypothesis implies a steeper slope of the regression of probit mortality on toxin concentration for carnivores than herbivores (Fig. 23.1, comparison of green solid and red dashed line). Biologically this means that a carnivore population shows less variation in tolerance to insecticides than a herbivore population. Plapp's (1981) reasoning was that herbivores require a diverse armoury of enzymes for detoxifying foreign toxins (i.e. plant defensive compounds) to an extent carnivores do not.

In relation to the widely held view that dose reduction encourages the appearance of insecticide-tolerant genotypes, it should be remembered that predators will only have available as prey the aphids that have survived the insecticide.

Selectivity in space

Even broad-spectrum aphicides will show some selectivity if they are applied as soil treatments or as systemic compounds rapidly withdrawn into the plant. Another approach is that of spot treatments, e.g. Choi *et al.* (2009) could control aphids on peppers in glasshouses with releases of *Aphidius colemani* together with spot treatments of insecticide on limited areas of high aphid density.

Selectivity in time

Early sprays may reduce aphid populations before natural enemies appear. Thus Hull and Stern (1983) found that one early application of pesticide gave control of *Dysaphis plantaginea* (rosy apple aphid) on apples without disrupting later predation by natural enemies, though the lowered aphid numbers may also have resulted in fewer natural enemies colonizing the crop. Fagan *et al.* (2010) recommended that soil drenches to lettuce of imidacloprid should be restricted to early spring and late summer to allow natural enemies to control aphids between these periods.

Morse (1989) suggested allowing *Aphis craccivora* (cowpea aphid) to attract coccinellids but, once the beetles had laid their eggs, reducing aphid numbers with an ephemeral insecticide while the coccinellid embryos/larvae were still protected by the egg shell. It has

similarly been suggested that parasitoid larvae within mummies often survive insecticide applications provided that the residues on the mummy cuticle have reduced when the adult parasitoids emerge.

Integration of Chemical Control and Host-Plant Resistance (HPR)

Aphids are usually (but not invariably) smaller on resistant plants. Since toxicity of an insecticide is a function of body weight, one would expect aphids on resistant plants to show enhanced susceptibility to toxins. The first report of this phenomenon concerned *Myzus persicae* (peach–potato aphid), *Aphis gossypii* (cotton or melon aphid) and *Aulacorthum solani* (glasshouse and potato aphid) on chrysanthemum (*Chrysanthemum morifolium*) (Selander *et al.*, 1972). The LD₅₀ (the dose adjusted for aphid weight required to kill 50% of the aphids) of malathion, dimethoate and lindane on the resistant variety ‘Princess Anne’ was between 50 and 66% lower than on the susceptible variety ‘Tuneful’. Nicol *et al.* (1993) compared the tolerance to deltamethrin of *Sitobion avenae* (English grain aphid) on two wheat varieties, of which ‘Altar’ possessed resistance to aphids based on high DIMBOA levels (Chapter 22, this volume). On ‘Altar’, deltamethrin was three times more toxic than on the susceptible wheat (‘Dollarbird’).

Reduced aphid size alone cannot usually account for their susceptibility to insecticides on resistant plants. After correction for differences in aphid weight between the varieties in the DIMBOA example above, the LD₅₀ on ‘Altar’ was still reduced by over 90%. With *M. persicae* on Brussels sprouts, Mohamad and van Emden (1989) calculated that the 45% increase in mortality from malathion on the only slightly aphid-resistant variety ‘Early Half Tall’ was still as large as 42% after correcting for the small difference in aphid weight on the two varieties. Similarly with *Metopolophium dirhodum* (rose–grain aphid) on the susceptible wheat variety ‘Maris Kinsman’ and the partially aphid-resistant ‘Emmer’ wheat (*Triticum dicoccoides*), Attah and van Emden (1993) found that the mortality increase of over 50% on the resistant variety was only reduced by about 5% after correction for weight. Some stress of HPR on the aphids, perhaps poorer nutrition and lower fat levels in the body, appear more important than body weight differences. Clayson *et al.* (2014) found that a 35% reduction in the concentration of malathion was possible on the partially resistant wheat ‘Rapier’ compared with that on the susceptible ‘Huntsman’ to achieve 50% mortality of *M. dirhodum*. Again, correction for aphid

weight still left an unexplained 20% reduction. It would appear that a reduction of 30% in aphicide concentration on a variety that is only slightly aphid-resistant should give control equal to that on a susceptible variety.

However, aphids on resistant plants may sometimes show the converse phenomenon, i.e. greater tolerance to insecticides. Ahmad and Shakoori (2001) found higher mortality from demeton-S-methyl of *Brevicoryne brassicae* (cabbage aphid) on the aphid-susceptible Ethiopian mustard (*Brassica carinata*) than on four aphid-resistant accessions of Indian mustard (*B. juncea*). With caterpillars (Lepidoptera), it has been shown that such results arise from the induction by secondary plant compounds of insecticide-detoxifying enzymes in the insect (Kennedy, 1984; Yu and Hsu, 1985).

Integration of Biological Control and Host-Plant Resistance (HPR)

Of 53 examples of the interaction of HPR with biological control in the literature, 31 show positive synergism, 8 show simple additivity and 14 show a negative interaction. Negative interactions are typical of strong HPR (e.g. Kersch-Becker and Thaler, 2015). In this chapter, however, the emphasis will be on the contribution positive synergy may make to IPM of aphids.

There are a few data sets (Fig. 23.2) where, across a time interval, measurements have been made of the effect on an aphid population of plant resistance without biological control, biological control without plant resistance (i.e. on the aphid-susceptible variety) and the combination of plant resistance and biological control. From these data, a population can be expressed as a proportion of that on the susceptible variety without biological control. The expected reduction by the combination of plant resistance and biological control, assuming no synergy between them, is the product of the proportions after their effect in isolation (van Emden, 2003). This can then be compared with the actual experimental outcome. In five of the eight data sets, there is very strong positive synergism – the population reduction is between twice and twenty times that expected with no synergism between the two restraints. In one of the data sets (Fig. 23.2G) the positive synergism is rather small, but even so resulted in an enormous (99.3%) reduction in aphid numbers over the season (McCarville and O’Neal, 2012).

The phenomena for positive synergism can be divided into numerical and functional responses of the natural enemies:

Numerical responses

- Slower reproduction of aphids on resistant varieties increases the potential of natural enemies to contain the aphid population (van Emden and Wearing, 1965).
- Aphids on resistant varieties usually show increased development times (e.g. Sotherton and Lee, 1988). This increases their chance of being predated before they reproduce.
- Parasitoids may show constancy to variety (van Emden et al., 2015) and so will continue searching on resistant varieties even though aphid numbers are reduced.
- Both coccinellids and parasitoids sometimes show shorter development time and increased fecundity on aphid-resistant varieties (Table 23.2). Such differences in reproductive rates may even be found between crop varieties with no HPR to aphids (e.g. *Aphidius matricariae* and *Aphis fabae* (black bean aphid) on sugar beet – Adabi *et al.*, 2010).

Functional responses

- Natural enemies can often detect the locations of aphid colonies on the plant by plant-emitted chemical cues (Storeck *et al.*, 2000), so searching time may not be increased by lower pest densities.
- Predators will eat smaller aphids (as typical on resistant varieties) in greater numbers before becoming satiated (Fig. 23.3). Hassell *et al.* (1977) showed that a positive density-dependent voracity of the ladybird *Coccinella septempunctata* extended to higher densities of prey if the latter (different instars of *B. brassicae*) were smaller (Fig. 23.3).
- Smaller aphids on resistant varieties are less able to escape natural enemies by rapid locomotion or effective kicking. Dixon (1985) showed that *Microlophium carnosum* (common nettle aphid) were able to survive encounters with larvae of *Adalia decempunctata*.
- The activity of natural enemies searching in aphid colonies disturbs aphids and causes them to fall from the plant (a so-called ‘non-consumptive’ effect); this is considerably more pronounced on resistant varieties (Gowling and van Emden, 1994; Fig. 23.4). Note in Fig. 23.4 that total percent parasitization of *M. dirhodum* on the resistant wheat ‘Rapier’ was higher than on ‘Armada’, partly because more fallen aphids were parasitized and mummified on the soil. When the data are expressed in the form of Fig. 23.2, the outcome in terms of increased impact

of biological control on 'Rapier' is almost identical to the overall comparison of the varieties (Fig. 23.2D). The greater restlessness of aphids on resistant varieties, and therefore their exposure to fungal spores, was suggested by Hatting *et al.* (2004) as explaining the improved control of *Diuraphis noxia* (Russian wheat aphid) on aphid-resistant wheat by the fungus *Beauveria bassiana*.

- Plant structure may interact with biological control. Resistant varieties may have less deformation in the form of leaf rolling. Natural enemies then find their aphid prey more easily (Reed *et al.*, 1992). Lower amounts of leaf wax give coccinellids a better grip (Eigenbrode *et al.*, 1998). Plant structures may protect natural enemies from parasitization (e.g. the eggs of predatory bugs inside leaf domatia (small pockets with hairs often induced by other organisms) (Agrawal *et al.*, 2000).
- Natural enemies may spend less time cleaning off wax particles on aphid-resistant varieties with low surface wax (Eigenbrode *et al.*, 1998). Parasitoids will also divert searching time to cleaning activity if there is copious aphid honeydew, as more characteristic of aphid-susceptible than of aphid-resistant varieties (Wickremasinghe, 1989).

Three-Way Integration of Chemical Control, Host-Plant Resistance and Biological Control

Taking together two phenomena already mentioned – that insecticide dose can often be reduced on aphid-resistant varieties and that dosage reductions are likely to increase selectivity in favour of natural enemies – a three-way interaction seems to be indicated. This is illustrated in Fig. 23.1 by the red dashed line remaining stationary while the green solid line moves left to become the green dotted line. As yet, the only experimental test to confirm this interaction in relation to aphids stems from laboratory work on cereal aphids, parasitoids and coccinellids (Tilahun and van Emden, 1997; Fig. 23.5), and here both *A. rhopalosiphi* and *C. septempunctata* actually showed greater tolerance to malathion when reared on *M. dirhodum* on the partially aphid-resistant wheat 'Rapier' than on the aphid-susceptible 'Maris Huntsman'.

Integration of Cultural Control and Biological Control

Although there is considerable interest in using cultural measures directly to promote biological control of aphids (Chapters 20 and 21, this volume), the integration of cultural measures primarily for controlling aphids and biological control seems relatively unexplored. However, such interactions almost certainly exist and therefore should not be ignored in designing IPM programmes. An attempt to investigate such interactions was made by Ul-Haq (1997), in glasshouse experiments on the effects of fertilizer applications, water stress and wheat/pea (*Pisum sativum*) 'intercrops' on aphids and the size and fecundity of parasitoids. He found that 'cultural treatments' which decreased the size of aphids also decreased the size and fecundity of the parasitoids.

One cultural control measure aimed against aphids is mixed cropping, and a potato/burseem clover cropping system in Pakistan to reduce populations of *M. persicae* on the potato increased the numbers of ladybirds, hover flies, lacewings and parasitoid mummies (Saljoqi *et al.*, 2009).

In the absence of much experimental evidence, Table 23.3 lists the principal approaches to cultural control of aphids and aphid-transmitted viruses with speculation on how biological control may be affected.

The IPM Case Studies (Chapters 24-33)

The crop scenarios

This introduction to IPM of aphids is followed by ten case studies, where scientists working on the control of aphids in particular crop scenarios were asked to report on the state of IPM in their specialized area of interest. The case studies have been chosen to represent a wide diversity, with the result that the various case studies could not be presented to a formula. At one end, cotton is a single crop with one important aphid species; at the other, the case study on temperate fruit trees and stone fruits considers over ten crops with over 25 pest aphid species.

In order to make it easier to compare and contrast IPM in the case studies, each finishes with an 'executive summary' recapitulating the main points in a consistent order.

Each case study is written by a scientist working in a particular region of the world, mostly in developed agriculture. Thus the case studies are both crop-specific and to a large extent location-specific, though often reference has been made to contrasts with other regions. This specificity to location is seen clearly in the active ingredients of the insecticides mentioned; products mentioned may well be banned or have been withdrawn in other regions of the world.

Conclusions from the case studies

For certain crops (e.g. potatoes, cucurbits and some berry crops where virus is the main problem) economic thresholds are probably not relevant, though they are available in cucurbits based on monitoring water traps. Otherwise economic thresholds have been developed, although with variable uptake; increasingly abundance of natural enemies is being included in the calculation. Insecticides clearly remain the mainstay of aphid control. However, in nearly all the scenarios considerable emphasis is placed on selecting active ingredients so as to avoid damage to natural enemies as far as possible. This is very much 'stage one IPM', the 'Integrated Control' of Stern *et al.* (1959) (see earlier). Particularly in salad crops, brassicas, potato and cotton, the development of aphid resistance to insecticides is a constant challenge to this approach.

Examples of inundative biological control are very limited. Parasitoids are commercially available for release on salad crops and cucurbits in glasshouses, and are also released on some berry crops; control of *Eriosoma lanigerum* (woolly apple aphid) on apples by *Aphelinus mali* on apples has been practised for very many years.

What we can regard as 'stage two IPM', where host-plant resistance and/or cultural control are key additions, is found in the sorghum, potato and berry scenarios. Greenbug control in sorghum, phylloxera control in grapes and aphid control in raspberries has for many years relied principally on plant resistance. Rouging of virus sources such as groundkeepers is important with potatoes and strip-intercropping and early harvesting/termination of irrigation can contribute to control of aphids in cotton. Crop covers are used to reduce aphid immigration in salad crops, brassicas and cucurbits.

Supporting one control approach which is inadequate on its own with another can be said to represent 'stage 3 IPM', and clearly shows its potential against greenbug in sorghum and

aphids in wheat. In the sorghum scenario from the USA, resistant varieties and biological control by indigenous natural enemies were not only together able to control greenbug in most years without the need for insecticides, but also made the resistance less vulnerable to the selection of resistance-breaking greenbug biotypes. In wheat, agri-environmental schemes (including the provision of nectar sources) may reduce or even eliminate the need to use insecticides against aphids.

The case histories give no example of manipulating the behaviour of aphids and their natural enemies with semiochemicals, a 'stiletto' addition to the traditional IPM components of chemical, biological, varietal and cultural control. Such methods have huge potential and are currently being actively researched; perhaps their addition to future practice will constitute a 'stage 4 IPM'.

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Table 23 1. Pest Mismanagement and the techniques for reversing it, with relevant chapters in this volume in brackets.

Elements of Pest Mismanagement	The Pest Management Techniques
Overdosing with pesticides and prophylactic treatments resulting in the appearance of tolerant pest populations	Decisions on chemical control are thresholds, and selective materials (Chapters 16, 17, 18)
Loss of biological control through use of broad-spectrum pesticides and loss of habitat diversity in agroecosystems	Biological control is conserved by habitat modification, including plant management Agents may be re-colonized or new agents, especially from overseas
Introduction of genetically uniform high-yielding but pest-susceptible crop cultivars	The use of aphid-resistant crop varieties
Abandonment of labour-intensive cultural controls	Introduction or re-introduction of pests to improve conditions for natural enemies

Table 23.2. Some examples of positive effects of HPR on natural enemies of aphids.

HPR	Aphid(s)	Natural enemy(ies)	Form of effect on natural enemy	Reference
Transgenic potato expressing protease inhibitor	<i>Macrosiphum euphorbiae</i>	<i>Aphidius nigripes</i>	Increased size and fecundity	Ashouri <i>et al.</i> (2001)
High gossypol cotton	<i>Aphis gossypii</i>	<i>Propylaea japonica</i>	Reduced development time; greater adult weight	Du <i>et al.</i> (2004)
Partially resistant cabbage varieties	<i>Brevicoryne brassicae</i> and <i>Myzus persicae</i>	<i>Aphidius colemani</i>	Usually a reduced development time	Kalule and Wright (2005)
Partially resistant broad bean (glasshouse experiments)	<i>Aphis fabae</i>	<i>Coccinella septempunctata</i>	Increased weight; delayed development but increased fecundity	Shannag and Obeidat (2008)

Partially resistant wheat

Cereal aphids

Coccinellids

Increased populations

Khan *et al.* (2011)

Resistant 'Ommid' wheat

Diuraphis noxia

Hippodamia variegata

Reduced development
time; increased longevity
and voracity

Zangeneh *et al.* (2014)

Table 21.3. Cultural control of aphids and potential effects on natural enemies.

Control measure	Potential effects on natural enemies	Supporting evidence (if any)
Limited N fertilization	As for partial plant resistance; greater impact, but parasitoids smaller and less fecund	Ul-Haq (1997)
Avoidance of intermittent drought stress	As for partial plant resistance; greater impact, but parasitoids smaller and less fecund	Ul-Haq (1997)
Reducing late leaf area by techniques such as termination of irrigation and early harvest	Greater impact at the stage of reducing the aphid population at the end of the crop season	
High plant density	Effects of plant ground cover? Larger numbers of anthocorids, syrphids and epigeal predators	Smith (1969, 1976) Powell <i>et al.</i> (1981)
Earlier sowing	As for plant resistance (increases with plant age); greater impact, but parasitoids smaller and less fecund, and poorer temporal synchronization with natural enemies	
Delayed sowing (especially for reduction of virus problems)	Better synchronization between natural enemies and aphids	van Emden (1966)

Hand removal of terminal shoots	Probably some partial resistance, therefore greater impact, but parasitoids smaller and less fecund	
Intercropping	Effects of plant ground cover? Larger numbers of anthocorids, syrphids and epigeal predators	Saljoqi <i>et al.</i> (2009)
Trap crops	May form sink for natural enemies and delay their movement to the commercial crop	Chapter 17, this volume
Removal of weed sources of virus	Unlikely to have a major effect?	
Crop isolation	Specific predators and parasitoids may be lacking or scarce in the new areas	
Reflective mulches	May affect colonizing natural enemies less than aphids, and thus increase natural enemy:aphid ratio	
Crop covers	Likely to exclude natural enemies as well as aphids, but any reaching the crop will remain confined over it	

Legends for figures

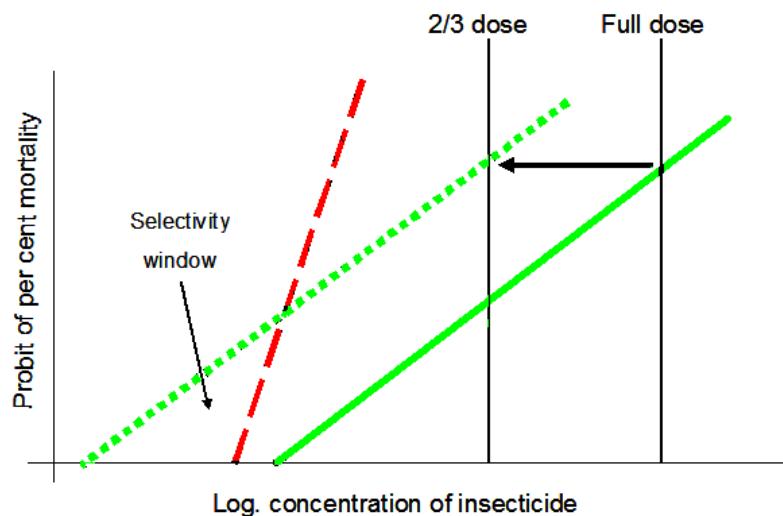


Fig. 23.1. The theoretical integration of partial host-plant resistance, biological control and insecticides. Green solid line, mortality response of aphids treated with normal dose on susceptible variety; green dotted line, mortality response of aphids treated with a dose reduction (horizontal arrow) of one-third on a resistant variety. The mortality response of a natural enemy (red dashes) is assumed to be unaffected by the plant resistance.

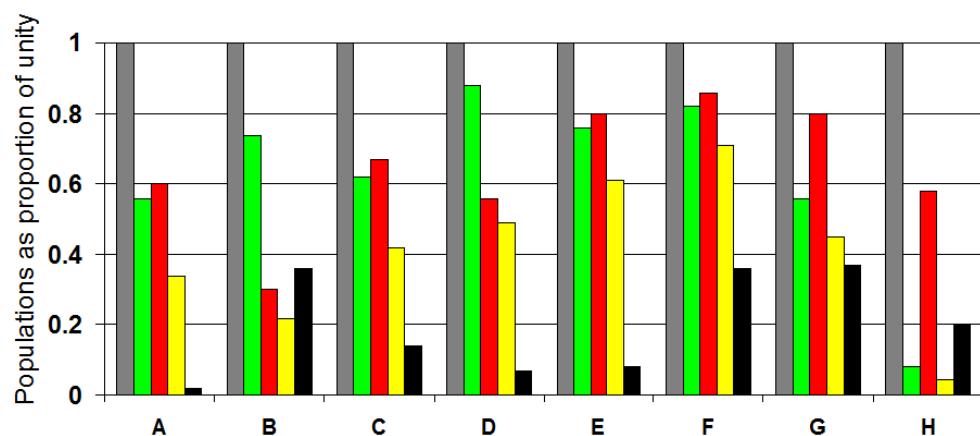


Fig. 23.2. Integration of partial host-plant resistance to aphids with biological control. Aphid populations are expressed as a proportion of that on susceptible varieties without biological control (grey). Histograms in each block from left to right: green, after reduction by plant resistance alone; red, after reduction from biological control on susceptible variety; yellow, predicted population on resistant variety with biological control (= green x red proportions); black, experimental result on resistant variety with biological control. A, *Schizaphis graminum* parasitized by *Lysiphlebus testaceipes* on barley (Starks *et al.*, 1972); B, *Sitobion avenae* parasitized by *Aphelinus abdominalis* on wheat (Lykouressis, 1982); C and D, *Metopolophium dirhodum* parasitized by *Aphidius rhopalosiphi* on wheat (Gowling, 1989); E, *Brevicoryne*

brassicae and natural predation in brassicas (Gowling, 1989); F, *Brevicoryne brassicae* and natural predation in brassicas (Dodd, 1973); G, *Aphis glycines* in soybean (McCarville and O'Neal, 2012); H, *Brevicoryne brassicae* and parasitization by *Diaeretiella rapae* on Brussels sprouts (van Emden, 1978).

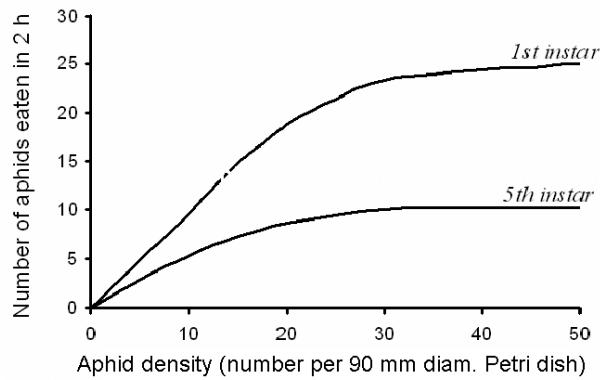


Fig. 23.3. Predation by *Coccinella septempunctata* on first and fifth instar *Brevicoryne brassicae* at different aphid densities (data from two different graphs at two different scales several pages apart in Hassell *et al.*, 1977).

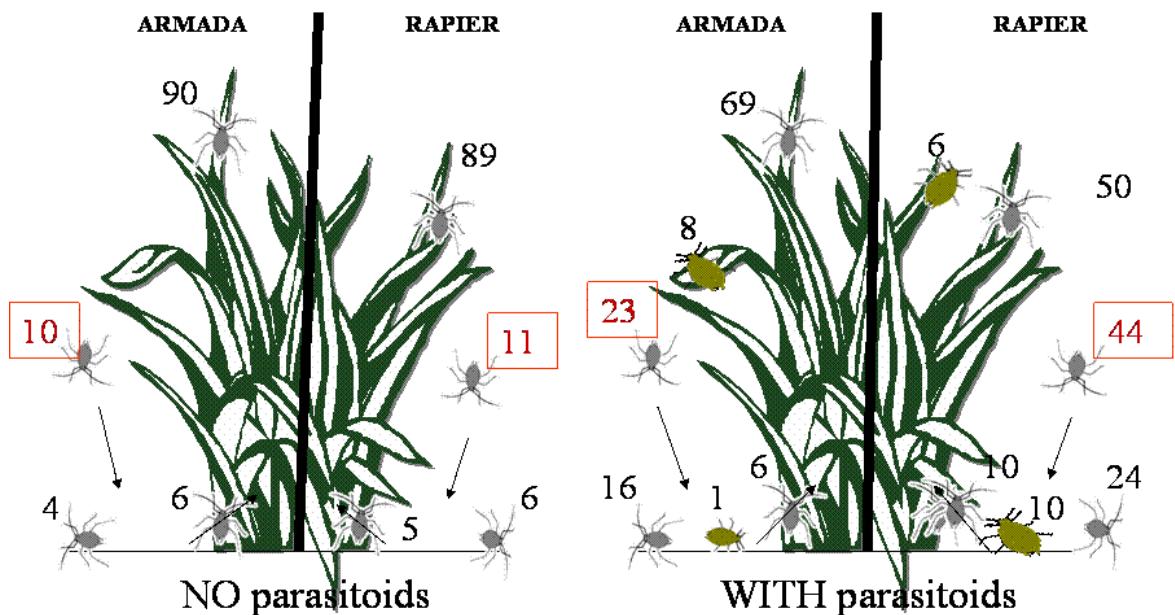


Fig. 23.4. Percentage fate of *Metopolophium dirhodum* on 'Armada' (susceptible) and 'Rapier' (partially aphid-resistant) wheat after six days with and without activity of the parasitoid *Aphidius rhopalosiphi*: The image shows live aphids (grey) on the plant, falling (percentage in red and boxed), those climbing back on the plant and those failing to do so. In dark green are aphids mummifying on the plant and on the ground (data of Gowling, 1989). The histogram to the right summarizes these data in the form of, and for comparison with, Fig. 21.2, D (which compares the same two varieties). Here unity (grey) and in green are the proportions of aphids on 'Armada' and 'Rapier' respectively in the absence of parasitoids, and in red is the proportion on 'Armada' in the presence of parasitoids. In yellow is the expected proportion of aphids on 'Rapier' in the presence of parasitoids and in black is the experimental outcome.

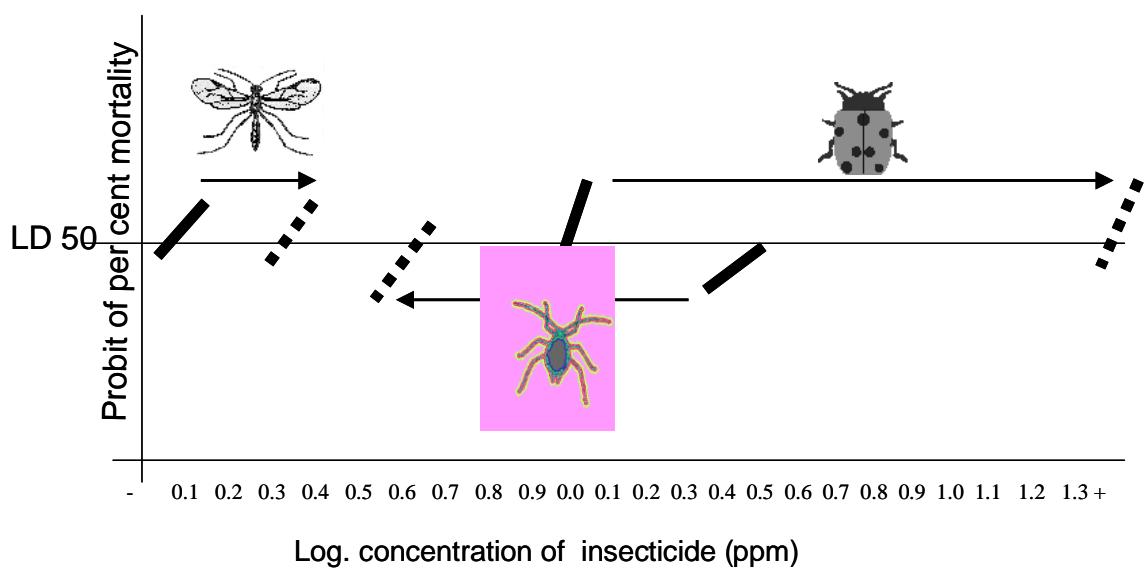


Fig. 23.5. Effect of a partial aphid-resistant wheat ('Rapier') on susceptibility to malathion of *Metopolophium dirhodum*, the parasitoid *Aphidius rhopalosiphi* and the coccinellid *Coccinella septempunctata*. Solid lines, LD₅₀ and slope of probit regression on the aphid-susceptible wheat 'Maris Huntsman'; dotted line, LD₅₀ and slope of probit regression on 'Rapier'; arrows, direction and degree of change in susceptibility to malathion (data of Tilahun and van Emden, 1977).