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Conservation biological control of insect pests

Helmut F. van Emden (orcid ID 0000-0002-9968-9257)

School of Agriculture, Policy and Development, The University of Reading, Earley Gate, Reading, Berks., RG6 6EU, United Kingdom

e-mail: h.f.vanemden@reading.ac.uk

Abstract

Conservation biological control increases the control effect of locally-occurring natural enemies, and has two approaches. Ecological engineering of the agroecosystem involves improving the environment in favour of natural enemies. The second approach is to devise ways of improving the ratio of natural enemies to pests by applying an insecticide in a partially selective manner.

The tools of ecological engineering are to provide pollen and nectar sources as adult food for beneficial insects, to increase floral diversity to increase numbers of other insects which provide alternative food for beneficials, perhaps to add a single plant species to support an essential alternate host for a predator or parasitoid, or to use plant diversity to raise humidity in the crop. These tools have long been available, but have only been exploited more recently as the public and governments have required greater environmental sustainability and pests have increasingly become tolerant to the available insecticides.

Few insecticides offer intrinsic selectivity in favour of natural enemies, but selectivity of broad-spectrum compounds can be obtained by reducing the dose of the insecticide or by restricting its application in time or space.

Whatever approach is considered, its practical application is usually quite simple.

Keywords

biological control, insecticide selectivity, diversity strips, flowers, alternative host, alternate host

Review Methodology

Since this review covers the practical implementation of conservation biological control on farms and horticultural enterprises, the developments described are generally well-known in the countries where they are or have been practised, and I have learnt of them at site visits, conferences and world travel during the last 60 years of having conservation biological control as a major academic interest. The most relevant countries have been USA(California), Brazil, most of Europe, Nigeria, Tanzania, Syria, India (with Sri Lanka), Bangladesh, The Philippines, China, Australia and New Zealand. The origin of the different tools used was researched by going through every abstract in CABI's *Review of Applied Entomology (A)* and *Horticultural Abstracts* from 1930 to 1965.

Introduction

Conservation biological control (CBC) is the concept of increasing the impact on the pest of natural enemies that are already present in the agroecosystem. This contrasts with "classical biological control" which involves importing a new natural enemy from a foreign country.

The dramatic success in 1888 of the classical biological control of the cottony cushion scale (*Icerya purchasi* Maskell) moved the emphasis of biological control away from CBC and to importing new natural enemies from foreign countries. The scale had been accidentally introduced into USA citrus orchards from Australia, and had developed resistance even to hydrogen cyanide gas pumped into canvas shrouds draped over the trees. A search was made in Australia for natural enemies, and less than 500 Vedalia ladybirds (*Novius cardinalis* (Mulsant)) were released in California. Within 15 months they had brought the pest under control [1].

We distinguish two approaches to CBC. The first is ecological engineering of agroecosystems. This term has the advantage over the more frequently used "habitat manipulation" that it emphasis pest-targeted design. The approach involves improving the environment to the benefit of natural enemies. The second approach is very different and often overlooked as a technique of CBC. It involves the conservation or partial conservation of natural enemies when insecticides are used by using the latter in such a way that they have a greater impact on the pest than on its natural enemy(ies) [2].

Ecological engineering of agroecosystems

We have four main tools in this approach. How they are deployed in CBC will be described later:

1) Provision of flowers, from which the adults of many natural enemies feed on pollen and/or nectar to mature their eggs and increase their growth (if immature) and longevity [3].

2) Increasing plant biodiversity encourages insect herbivores (alternative prey) on which natural enemies can sustain themselves when the pest is scarce.

3) Establishing alternate (as opposed to alternative) prey – where natural enemies require more than one species of prey at different times of their annual life cycle.

4) A damper microclimate in the crop tends to benefit natural enemies.

All four tools have been known for many years. Already in 1938, the importance of flowers for natural enemies was shown in regard to the braconid parasitoid *Orgilus obscurator* (Nees), which provides effective biological control of the pine shoot moth (*Rhyacionia buoliana* (Denis & Schiffermüller)) in the UK [4] . Newly-emerged parasitoids are repelled by the smell of pine oil, and so leave the trees to feed and mate on flowers outside the forest. When the eggs are mature, behaviour reverses. Pine oil odour is now attractive, and so the females are pulled back into the forest to parasitise the pine shoot moth caterpillars [5].

An early report of the value of alternative prey comes from Finland [6] and concerns the gypsy moth (*Lymantria dispar* (L.)). This pest has occasional outbreakyears in which the caterpillars can potentially defoliate oak forests.
These outbreaks are naturally controlled by a complex of some six parasitoid species, provided these have been able to survive on alternative hosts during the years between gypsy moth outbreaks. In the Finnish work, 34 alternative hosts were identified in the oak canopy, but even more (45 species) were found on the vegetation on the forest floor of forests which were not managed too intensively.

An example of alternate prey, i.e. where a second species of prey is needed for a natural enemy to complete its annual life cycle, concerns the parasitoid *Diadegma fenestrale* (Holmgren), which gives good biological control on brassicas of the diamond-back moth (*Plutella xylostella* (L.)) in the UK [7]. The adult parasitoid emerges from its caterpillar host before the latter overwinters. In 1939 it was already realised [8] that the parasitoids complete an overwintering generation in some other caterpillar before new diamond-back moth caterpillars become available the next spring. This other host species, an essential link in maintaining the valuable biological control given by *Diadegma*, remained unknown until 1953 when O.W. Richards of Imperial College recognised the wasp emerging from a caterpillar of the moth *Paraswammerdamia lutarea* (Haworth) that he had collected from hawthorn. Incidentally, between 1938 and 1953, farmers in East Anglia had been busy ripping out hawthorn stock barriers to increase the size of their fields [9] in a switch to arable farming, often of brassicas .

Finally, in the 1940s, coffee farmers originating from Europe demonstrated the benefits for biological control agents of a high humidity when they decided to raise coffee yields in Africa by removing the shade trees under which coffee was traditionally grown. Unfortunately, the resulting high insolation led to the disappearance of parasitoids which had previously prevented the antestia bug (*Antestiopsis* spp.), which can taint the whole bean crop at only two individuals per coffee tree, from being a problem [10].

These examples of the four tools we use in ecological engineering were all recorded over 70 years ago, but at that time made no impact on how pests were controlled in agriculture and horticulture. There are four main explanations for this lack of interest:

1) Insecticides were highly effective and their problems had not yet become an issue.

2) The mindset was still that biological control meant importing foreign natural enemies.

3) Floral diversity on farms was equated with encouraging weeds.

4) Reaching for the spray gun was a lot simpler than trying to get one’s head around biodiversity.

In this century, however, ecological engineering of agroecosystems is being taken seriously by growers and agricultural advisers as a way of promoting biological control, largely because the public has developed an environmental conscience. Thus supermarkets are putting pressure on growers to reduce insecticide use as well as to increase so-called “organic” crop production [11], and governments are giving grants for land set-aside for floral diversity [12]. In addition, if ecological engineering works, then there is a considerable financial saving on insecticides and labour.

However, there is one further cogent motivation. Individual insecticides have been increasingly banned or withdrawn because the appearance of resistant genotypes of the pests has made them redundant, and these reductions in available compounds are happening faster than new products are coming to market [13]. Ecological engineering is one contribution to preserving the current arsenal of insecticides as it reduces the frequency of their use.

The economics of production for any crop change with time. All the examples of ecological engineering in this article are either current or have, for a substantial period in the past, in practice been found commercially advantageous.

Plant diversity can be added inside or outside the crop, and this could form a basis for listing the examples. If one did this, one would find that the majority of examples of diversity outside the crop have been proposed by entomologists, whereas most of those concerning diversity inside the crop have been designed by cropping system scientists for agronomic benefits, but also have potential benefit for biological control. However, this review will list the examples under the four tools for ecological engineering mentioned earlier.

Provision of flowers as sources of pollen and nectar

Adding pollen and nectar sources to farmland has been practised widely in both the Northern and Southern Hemispheres [14]. Buckwheat (*Fagopyrum esculentum* Moench) is frequently the flower of choice, and New Zealand is just one country where this plant is often grown as a strip at the edges of cereal fields (Fig. 1) to provide adult food for parasitoids in general as well as for hover flies, the larvae of which are voracious predators of aphids [15]. Two other flowering plants commonly used in this way are sweet alyssum (*Lobularia maritima* (L.) Desvaux) and white mustard (*Sinapis arvensis* L.). However. Even though such plantings usually increase the numbers of natural enemies, reductions of pest populations are less consistently demonstrated [16].

Provision of alternative prey

When crops such as cereals are harvested and there is a gap before planting the new crop, perhaps as part of a rotation, herbivores in the edge vegetation and other adjacent uncultivated land provide prey for a reservoir of natural enemies available to move onto the new crop when this is attacked by pests arriving from the outside. Trap cropping, when farmers grow taller plants (usually of the crop) at the field edges to trap arriving pests which are then killed with insecticide or plant destruction, is not usually a form of conservation biological control. However a remarkable and relevant example comes from the control of wheat stem sawfly (*Cephus cinctus* Norton) in Canada. A 15-20 m strip of sterile brome grass (*Bromus sterilis* L.) is sown as the trap crop at the field edges. The sawflies fly near the ground and, when they encounter the brome grass, they accept is as a suitable host on which to lay their eggs. The larvae bore into the grass stems, but there is no need to destroy the trap crop or treat it with insecticide since there is not enough food in the slender grass stems to sustain the larvae to pupation [17]. The brome grass is thus a dead end for wheat stem sawflies. The icing on the cake is the biological control effect. The ichneumonid parasitoids are also mainly trapped in the brome, attacking the sawfly larvae there. The parasitoids pupate but emerge before the sawfly larvae die, and so can fly on into the wheat to attack sawflies that avoided the trap crop. So remarkably the brome grass acts as a factory converting pest into beneficial biomass.

Diversity strips

Because providing flowers and alternative prey are both so generally beneficial for biological control, combining them is an obvious step. Such “diversity strips” may indeed often not have any specific natural enemy target in mind. An early example stems from the 1980s. In the 1960s, effective herbicides made it possible to replace spring wheat with winter wheat, with the longer growing season giving a potentially higher yield. This practice brought the problem that aphid-transmitted barley yellow dwarf virus also had a longer time to develop serious symptoms, and so wheat was regularly sprayed with insecticide for the first time. These insecticides killed the insects on which grey partridge chicks depended at the crop edges, and so there was a dramatic decline in grey partridge populations. Farmers were now losing income from the sale of shooting rights, and the Game Conservancy recommended ”modified headland spraying” [18]. The outer spray boom was switched off when spraying insecticides and herbicides along the field margins (Fig.2). This allowed the partridges to flourish again and with little yield loss, as the edge of the field always has a lower yield with weed competition and often less thorough tillage.

Where crops abut environmentally sensitive areas such as watercourses and sites of special scientific interest, diversity strips are created by the compulsory shutting-off of the outside boom.

The UK government is among those who provide "agri-environment scheme" grants to farmers to grow flowering plants on parts of their land. These schemes are largely targeted to benefit pollinators, but of course provide another source of diversity strips. Increasingly councils are not cutting roadside verges as frequently as before, and are seeding the verges with wildflower mixes that provide diversity strips (Fig. 3). This is a "win-win" situation. The public applaud the biodiversity, especially in relation to pollinators, while the councils save the cost of frequent verge cutting. Another manifestation of diversity strips is the seed mixes sown between the rows in orchards, with biological control of orchard pests very much the aim [19]. Such strips have also been developed for organic vineyards, for example in New Zealand (Fig. 4), and often no insecticide is required. The latest addition to the environmentalist vocabulary, "re-wilding" involves allowing substantial areas of land (including farmland) to "revert to nature" in the interests of countering climate change and increasing general biodiversity [20]. However, I would expect that the progress of the plant succession would soon pass the point where that biodiversity would be relevant for the biological control of pioneer herbivores such as crop pests that exploit temporary vegetation early in the plant succession [21].

Intercropping is a form of plant diversity has been practiced for centuries. It involves growing two crops together on the same land area. This conserves soil moisture as well as increasing the total yield per unit area. An example, common in Africa, is maize with cowpea grown between the rows. Although not designed to provide a biological control benefit, intercropping usually will do so. Natural enemies may use insects on the two crops as alternative hosts and secondly, the higher humidity near the soil will benefit both predators and parasitoids. However, there is at least one intercropping system designed by entomologists, specifically for the control of maize stem borer (*Busseola fusca* (Fuller)) in Africa [22]. Two other plants are planted with the maize (Fig. 5). The legume *Desmodium* is planted in parallel between blocks of maize rows; it has value as a green manure as well as providing good animal fodder. A second source of animal fodder, Napier grass (*Pennisetum purpureum* Schumacher), is planted at right angles to the blocks of maize, interrupting them. Both crops produce odours which affect numbers of the moth pest by what is known as the "push-pull" technique. The "push" originates from *Desmodium*, the odour of which repels the adult moths, while the "pull" is the attraction of Napier grass odours for parasitoids.

Alternate hosts

A good example of a biological control agent unable to survive in an agroecosystem without the availability of an insect host/prey other than the pest requiring control is *Anagrus erythroneurae* S.Trjapitzin & Chiappini, a small parasitoid of the eggs of the grape leafhopper (*Erythroneura elegantula* Osborn). This pest overwinters as an adult, whereas *Anagrus* overwinters in leafhopper eggs. Therefore Californian wine growers have planted blackberries in the vineyards to encourage the blackberry leafhopper (*Dikrella californica* (Lawson)), which overwinters in the egg stage and so enables *Anagrus* to survive [23]. I have heard of visitors to the Napa Valley vineyards of California expressing surprise that no one bothers to control weed blackberries!

Improved microclimate

Ground beetles (Carabidae) are important predators of the eggs of a variety of root pests such as carrot fly and cabbage root fly. In cereals they feed on the many aphids which drop off the plant onto the soil, and may even climb plants to feed on aphids on the stem and leaves. In the autumn they seek drier sites to overwinter, and are found particularly in grass tussocks in front of hedges at the crop edges. To increase arable acreage, many farmers have replaced hedges between fields by post and strand fencing. Grass tussocks (known as "beetle banks") can be created under such fencing, but when beetles move out of these in the spring they do not penetrate far into the crop. For some time wheat prices made it economically viable to build long ridges sown with grass across a field [24]. These grassy mounds, known as "conservation ridges" (Fig. 6) were built to allow the passage of tractors at each end, and would last several years before the need for restoration. Some farmers turned them into diversity strips by adding flower seeds to the seed mix.

Selective insecticide use

This second approach to conservation biological control may appear to be a contradiction in terms. However, using insecticide to improve biological control is based on a very simple concept, that the ratio of natural enemies to pests is more important than their number. This is illustrated in the cartoon of 15 aphids and 5 ladybirds (Fig. 7a). If a broad-spectrum insecticide kills the same proportion of pests and natural enemies (Fig. 7b), biological control is not affected, since the ratio of aphids to ladybirds has not changed from 3:1. However, if the insecticide is just slightly selective and kills one more aphid (Fig. 7c), the ratio for biological control has improved to 2.5:1.

The tools for using insecticides proactively to improve biological control are:

1) Use of a selective or partially selective insecticide.
2) Applying the insecticide at a reduced dose.
3) Using time of application to achieve selectivity.
4) Restricting the area to which the insecticide is applied.

Selective insecticides

Selective or at least partially selective insecticides, less toxic to the natural enemies than to the pests, are sometimes discovered by the agrochemical industry. A good example is the carbamate pirimicarb. Industry does not like such insecticides because the market can be limited. For this reason, pirimicarb was not marketed when it was discovered, but it was recovered from the industrial “recycle bin” when a crisis with insecticide-resistant aphids in glasshouses created a profitable market for the chemical in combination with biological control. It was then used in other situations to maximise CBC. It is also very safe for humans, but has been “tarred with same the brush” as other carbamate compounds and has mostly been banned.

Reduced dose

The classic example is the control of organophosphate-resistant spotted alfalfa aphids (*Therioaphis trifolii maculata* (Buckton)). This aphid was accidentally introduced from Europe to California in the late 1940s and already by the mid 1950s it had developed insecticide resistance to the point that farmers were abandoning growing the crop. The seemingly bizarre recommendation to spray organophosphates on organophosphate-resistant aphids at a reduced dose solved the aphid problem in about 2 years. The work was published in a landmark paper entitled “The integrated control concept” [25]; this paper is the foundation of modern Integrated Pest Management (IPM). The authors estimated that a half-dose organophosphate would still kill about

20% of the aphids, but many natural enemies would survive to control the aphids that survived the insecticide.

Why does reducing dose give the insecticide application beneficial selectivity? In fact it is almost inevitable, because of a basic biochemical difference between herbivores and carnivores (Fig. 8). Many plants synthesise chemicals that are toxic and are a defence against herbivores, and the latter survive by evolving enzymes to detoxify foreign compounds. This detoxification mans that carnivores, by contrast, are therefore far less exposed to these chemicals, and so have a lesser armoury of detoxifying enzymes [26].

The enzyme defences of individuals within a herbivore population show wide genetic variation, so that there is a wide window of insecticide concentrations (green bar in Fig. 8) between the kill of the most susceptible and the most resistant individuals. This is of course how insecticide resistant populations develop; it is only the resistant fraction after the insecticide application that survives to breed subsequent generations. Fig. 8 shows how this wide concentration range for the insecticide is expressed as a sigmoid curve for the increase in herbivore mortality with increasing insecticide concentration. With a lesser enzyme armoury, lower genetic variation in the carnivore shows as a much steeper sigmoid curve over a short insecticide concentration range (red bar in Fig. 8). So as insecticide dose is reduced, the fall in carnivore mortality is much more rapid than the decrease in mortality of the herbivore. An “equitoxic dose” may be reached where the same per cent of herbivores and carnivores is killed, below which there may even be a “selectivity window” in favour of the carnivore (Fig. 8). All this is obvious; it is certainly not rocket science, although one does wonder how the idea of reducing the dose was sold to the alfalfa growers. Sadly, many countries/states forbid farmers from deviating from the insecticide dose prescribed by the manufacturer, so in many places the virtues of reduced dose cannot be exploited.

Any mention of reduced dose invites the criticism that it encourages the development of resistance to the insecticide. Such criticism ignores include the second source of mortality acting on the survivors of lower kill provided by the biological control in CBC [27]. As pointed out above, when insecticides failed to control resistant alfalfa aphids in California in the field, it was biological control that enabled reduced dose to succeed. Also, with similar control outcomes, the combining two control methods [28] in a model delays adaptation to either method in comparison with the methods on their own. Even without a second source of mortality, modelling shows that a low kill strategy delays insecticide resistance in comparison with aiming for maximum kill [29].

Selectivity in time

Time of day for insecticide application can be used to achieve selectivity. In Nigeria it was noticed that the cowpea leafhopper (*Empoasca dolichi* Paoli), which during the heat of the day is found on the underside of the lower leaves of cowpea plants, moves to the top surface of the upper leaves at dusk to feed there at night. The natural enemies are day active, so do not follow the leafhopper. The opportunity for selectivity is obvious, and a light spray of a short-lived insecticide to the upper leaves at dusk achieves the objective [2].

There may also be possibilities of using time during the season. Two main pests of apple in the USA are the leaf-mining moth *Phyllonorycter blancardella* (F.) and the red spider mite *Panonychus ulmi* (Koch). If not damaged by insecticides, the ladybird *Stethorus punctum* (LeConte) closely follows the mite population curve and prevents the mite reaching pest proportions. Moth numbers begin increasing in the spring, and are controlled by insecticide before numbers of the mite increase. A "no-spray window" follows until potential mite problems are over, protecting the ladybird. With biological control, moth numbers do not recover to damaging levels during this window but, if necessary, spraying against the moth can resume in September [30].

Selectivity in space

Today GPS and receivers on tractors make it possible to envisage spraying almost to the level of an individual pest-infested plant, as some insects cause subtle colour changes which can be recognised by satellites. However, any commercial application of this idea is still some time away. Meanwhile less high-tech ideas for applying insecticide selectively in space have been successfully applied; indeed my third example dates from as long ago as 1963.

"Alternate swath band spraying" is also not a new idea [31] and, for example, has been used in the control of alfalfa aphids in California. The spray rig turns at the end of the field, and misses the width of its boom before making a return pass, so that only half the field is sprayed. While aphids on the sprayed swaths are killed, the passage of the sprayer flushes many of any winged natural enemies to escape onto the alternate unsprayed swaths, increasing biological control there. At any subsequent need to spray, it is the previously unsprayed swaths that are sprayed. With alfalfa, this combines very naturally with alternate swath harvesting (Fig. 9), where young alfalfa is left to retain natural enemies when the adjacent mature stems are removed at harvest [32].

Band spraying, but on a vertical plane, has been used in Australia against the Queensland fruit fly, whose larvae feed within and destroy citrus fruits. The technique exploits the preference of most adult flies to roost in the higher humidity in the lower half of the tree [33], and so restricting the spray to the lower half of the trees/bushes (Fig. 10) already considerably reduces the adult population. As in the alfalfa example, many winged biological control agents are disturbed by the spray and fly higher up the tree. Some growers went further. They added yeast hydrolysate to the spray. This is highly attractive to the fruit flies, and draws many flies from the unsprayed part of the tree to the sprayed lower half.

Earlier I mentioned that there was an example of selectivity in space as early as 1963. It concerns control of the giant looper (*Ascotis selenaria* (Denis & Schiffermüller)) of coffee in Kenya [34]. First an insecticide was painted as a band around the trunk of the trees. The choice of insecticide was counterintuitive in the extreme. It was DDT, always regarded as the arch enemy of biological control. Its advantage here was its long residual life and, as it is not volatile and resists rainwash, it was really not doing harm on the tree trunks. The giant looper caterpillars fed on the leaves in the canopy and were heavily parasitised, but there were periodic outbreaks. When thus happened, the canopy was sprayed with another insecticide, again carefully chosen. It was natural pyrethrum, a very short-lived insecticide, and when applied at a low dose it merely stuns insects and they do eventually recover. So stunned caterpillars and adult parasitoids together fell out of the trees onto the ground below. It was when they recovered that the selectivity kicked in. The caterpillars could only regain the leaves by passing over the DDT band from which they picked up a lethal dose. By contrast, the reflex of the recovering winged parasitoids was to fly back to the canopy. The high selectivity of this system was based on nothing more sophisticated than that caterpillars cannot fly.

There is a final twist to this coffee story. Although the plantation owners were very content with the control system, the entomologist who devised it decided to leave the country following the receipt of death threats from the local workers who "scrumped" the large caterpillars as an important source of food. I guess one could call that a "side effect" of CBC.

Conclusions

Environmental concerns about insecticides have gained public attention, following publicity about their potential harm to pollinators [35] and the increasing emphasis placed on sustainable crop production. Biological control can contribute to improvements in both these areas, especially if it is based on predators and parasitoids already occurring naturally (CBC). Increasing floral diversity in farmland is widely accepted as one way forward, particularly as it also is likely to benefit pollinators. However success may require the addition of only one species, as for nectar/pollen provision or to harbour alternative or alternate hosts for specific natural enemies.

Manipulating insecticide application to be more selective in favour of natural enemies is not always recognised as CBC, yet is another approach to increasing the control effect of locally-occurring natural enemies. Inherently selective active ingredients are a rarity Fortunately, obtaining a CBC output with broad-spectrum compounds is not difficult and mostly involves some separation of the effect on pests and their natural enemies in time or space.

The insecticide example concerning coffee has an important message. The literature on biological control tends to focus on the interacting population dynamics of pests and natural enemies. The potential complexity has spawned much computer modelling. The only science in the coffee example is that caterpillars cannot fly. The science behind the other examples I have given of using insecticides to improve biological control is hardly much more "cutting edge", but based on familiarity with the cropping systems and the type of new intervention that farmers will accept and use.

Successful conservation biological control by both approaches can be summed up in just three words: "keep it simple".

All the examples of conservation biological control given here have been accepted by farmers as giving economic benefit in their crop production systems at the time they were proposed. Technical changes in these systems, economic factors and the release of new agrochemicals effective against resistant pest populations, may later change farmers' perception of the value to them of particular CBC programmes.

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Legends for figures

Figure 1. Buckwheat grown at the edge of a cereal field to provide pollen and nectar, particularly for adult hover flies.

Figure 2. Modified headland spraying of wheat. Above, Sprayer with outside boom switched off at field edge; below, resulting effect on headland plant diversity (photos courtesy of Dr N. W. Sotherton).

Figure 3. Flowering roadside verge in Lincolnshire, U.K.

Figure 4. Buckwheat strips sown in a vineyard in New Zealand (photo courtesy of S. D. Wratten).

Figure 5. The "push-pull" intercropping system in maize in Ethiopia, involving the legume *Desmodium* and Napier grass as the two intercrops (photo courtesy of ICIPE, The International Centre of Insect Physiology and Ecology).

Figure 6. A grassy conservation ridge in wheat in South England (photo courtesy of S. D. Wratten).

Figure 7. Cartoon illustrating the concept of "partial selectivity" of an insecticide application. a, The unsprayed population of aphids and ladybirds in a 3:1 ratio; b, insects killed (greyed out) by a non-selective spray maintaining the 3:1 ratio and c, a partially selective spray improving the ratio to 2.5:1 by killing just one more aphid.

Figure 8. The difference in slope of the sigmoid curves of increasing kill of a herbivore (green) and a carnivore (red) as insecticide concentration is increased, caused by the wider range (green bar) of concentration covering zero to 100% kill for the former compared with the carnivore (red bar) – see text.

Figure 9. Swath harvesting illustrates the principle of alternate swath treatments of alfalfa (photo courtesy of Kim L. Fritzemeier, Kim's County Line, Stafford, Kansas). With alternate swath spraying, of course, the swaths will be as wide as the span of the spray boom.

Figure 10. Citrus grower applying bait to citrus using the "continuous stream application" method for localising the part of the tree sprayed (photo courtesy of "Bugs for Bugs").