The Potential for Managing Indigenous Natural Enemies of Aphids on Field Crops [and Discussion]

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The potential for managing indigenous natural enemies of aphids on field crops

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The co-evolution of aphids and their indigenous natural enemies means that, on field crops, biological control to a grower-acceptable level will occur only sporadically in the absence of manipulative interventions. Such interventions should focus on raising the natural enemy:aphid ratio. This ratio is far more important than the absolute number of natural enemies present. The main interventions for improving the ratio are habitat modifications, advancing in time the activity of natural enemies on the crop, reducing aphid multiplication through genetically based or induced partial plant resistance, and ingenious use of pesticide to build in relative selectivity of kill. The interactions between biological control and some of the other interventions offer exciting opportunities for managing natural enemies.

1. Introduction

The gardener who collects ladybirds from around his garden to place them on his roses for aphid control is exemplifying the underlying principle of managing indigenous natural enemies; he is increasing the natural enemy:aphid ratio. He is also aware that, without such intervention, he cannot rely on biological control being timely and effective.

The literature is generally not encouraging about the value of indigenous natural enemies for the control of aphids. Thus Jones & Jones (1984) state that aphid 'capacity for increase outstrips their enemies and is almost exponential', and in a major review of over 400 papers Hagen & van den Bosch (1968) found it striking 'that this great mass of literature has produced so little tangible evidence on the impact of these enemies'. At the end of the five-year International Biological Programme research effort on *Myzus persicae*, Mackauer & Way (1976) concluded 'No immediate improvement is apparent that would drastically increase the impact of natural enemies on the green peach aphid'. Shands *et al.* (1965) reported a maximum of only 0.63% parasitization of potato aphids in northeastern Maine over 12 years.

Southwood *et al.* (1974) analysed the life tables of 32 different insects, and from this Southwood (1975) proposed a synoptic model of the relation between population growth and population density along the *r*–*K* continuum. This model included the important concept of the 'natural enemy ravine', where many insects may be kept at stable populations by natural enemies (held on the 'endemic ridge') until or unless some enviromental disturbance (e.g. a change in host plant condition) allows the population to escape towards a much greater density (onto the 'epidemic' ridge). Should the population escape past the 'release point' on the far side of the natural enemy ravine, natural enemies can no longer exert a significant check on population growth. Southwood (1977) cites aphids as typical of pests near the *r*-end of the continuum which escape the ravine most frequently. Aphid workers frequently smooth out the population growth curve early in the season, yet inspection of the original data points frequently suggests a 'natural enemy ravine' may have been crossed, e.g. Dean & Luuring's (1970) graph of aphid populations on wheat. When the time-scale of population growth is slower, as with *Brevicoryne brassicae* (van Emden 1965), the ravine is very apparent and was identified as representing stabilization by predators until a change in host-plant condition in late summer. All this suggests that the natural enemy restraint is usually inadequate, but nevertheless often adequate enough for attempting magnification by intervention.

Even though it is possible to find several reports of predators controlling aphid populations (examples are Minoranskii 1967; Tamaki *et al.* 1967; Chambers *et al.* 1982; Holmes 1984), it is clear that such control is too unpredictable and sporadic for practical utilization without some additional measures to enhance the predictability. A measure of this unpredictability is found in the International Biological Programme analyses of *Myzus persicae* populations on potatoes on 35 occasions, over three years and in five countries in the northern hemisphere (37°–56° N). A summary of these analyses (Mackauer & Way 1976) showed that predation was theoretically able to contain the measured potential increase rate of the aphid population on half the occasions, and succeeded in preventing an increase of the aphid population on all but two of these. Shands *et al.* (1972) had similar results in northeastern Maine; predators were responsible for decreasing only 45% of 31 aphid populations on potatoes.

It is perhaps not surprising that the natural enemies of aphids have such an unpredictable impact. By many centuries of co-evolution, one would expect predators and parasites of such a mobile and erratically abundant food source to have evolved the capacity to harvest the interest without digging too deeply into the capital! Even classical biological control using imported natural enemies very often involves some intervention to forestall the natural enemy:prey ratio declining to its indigenous equilibrium level. The elimination of natural enemy mortality by pathogens and parasitoids during quarantine is an important intervention of this kind. With natural enemies of aphids, co-evolution would seem to have led to a delay in the arrival of predators and parasites after aphid immigration, and their functional and numerical responses are geared to follow rather than overtake the high innate capacity for increase of aphid populations (van Emden 1966; Dixon 1985). Interventions to improve biological control of aphids by indigenous natural enemies need to address themselves to one or both of these co-evolved responses. Resolving the co-evolved poor synchronization of predators and parasites involves creating an 'unnaturally' high natural enemy:aphid ratio, particularly early in the season. This will be reviewed under the headings of direct augmentation of natural enemies and habitat modification. Early enhancement of parasite activity in crops has recently been reviewed by Powell (1986). The problem of functional and numerical responses needs tackling by interventions which probably reduce numbers of both natural enemies and aphids, but which disproportionately maximize the natural enemy:aphid ratio. This will be reviewed under the headings of plant resistance and use of pesticides.

2. Direct augmentation

(*a*) *Releases*

Predator releases have had some success, though with doubtful economic viability. Massive releases of the ladybird *Hippodamia convergens* were attempted in North America as early as 1908 for the control of *Aphis gossypii* on canteloupes, but failed because the beetles dispersed rapidly within three days of release (Hagen 1962). Cooke (1963) made four releases (40000–150000 beetles per release) of *H. convergens* on lucerne in Washington State, but any reduction in aphids was uneconomic compared with the costs of release. Again, the beetles dispersed rapidly, even if previously fed on protein hydrolysate. However, Iperti (in Hodek 1973) found that starving the coccinellids inhibited dispersion. Shands *et al.* (1972) released laboratory bred chrysopid and coccinellid larvae in small (0.1 ha†) potato plots and obtained a maximum of 60 % aphid control with the release of 30200 coccinellid larvae and 85100 chrysopid larvae. In other experiments (Shands & Simpson 1972) 13500 coccinellid eggs were applied in an agar solution, but satisfactory aphid control was not obtained. Ankersmit (1983) has reported failure of attempts to increase parasitoid numbers in cereals early in the season by releasing them with aphids.

(*b*) *Synomones and kairomones*

These are naturally produced chemicals influencing insect behaviour. Synomones emanate directly from the plant whereas kairomones emanate from insects or their feeding activity. The most well-known example of the use of kairomones in aphid control is the spraying of 'artificial honeydew' in California to increase numbers of *Hippodamia* spp. and *Chrysoperla carnea* in lucerne fields. These predators respond positively to the odour of a breakdown product of tryptophane, probably indole acetaldehyde (van Emden & Hagen 1976), emanating from aphid honeydew. Both types of predator remained in the treated area even if aphids were absent; the chrysopids even oviposited in the absence of prey. Enough aphid control to prevent economic damage was achieved with artificial honeydew consisting of a mixture of cheap commercial yeast hydrolysate, sucrose and water (Hagen *et al.* 1971). More recently, Hagen (1986) has concluded that *C. carnea* must receive a synonome from the crop in order to respond to the kairomone.

With parasitoids, Schlinger & Dietrick (1960) reported that enhancement early in the season by synomones associated with strip-cutting lucerne required the presence of hosts, unlike the use of yeast hydrolysate sprays for predators. Although some parasitoids of aphids are strongly responsive to aphid and honeydew odours and do not react to the odour of the host plant, it seems more usual that parasitoids respond to host-plant produced synonomes before any response to aphids or honeydew. *Aphidius nigripes* appears to be in the former category; it responds to a wide range of aphid species and their honeydew, but not to potato, the host plant of these aphids (Bouchard & Cloutier 1985). Read *et al.* (1979) first demonstrated the attraction to a synonome (mustard oil in crucifers) of a parasitoid of aphids (*Diaretiella rapae* parasitizing *Brevicoryne brassicae*). There have since been similar reports for parasitoids of cereal aphids (Schuster & Starks 1974; Powell & Zhi-Li 1983) and at Reading University, M. G. V. Wickremasinghe (unpublished results) has also detected strong host-plant odour versus aphid odour attraction in several parasitoid and aphid combinations, including some on non-crop hosts such as nettles, oak and sycamore (figure 1).

The behaviour of natural enemies of aphids in relation to plant-derived odours is still a new research area, and the practical possibilities are still to be determined. Presumably, the crop odour could be enhanced artificially or by crop cultivars that produce such volatiles to a greater degree. The need to test the synonomes of crop cultivars has been stressed by van Emden (1978), who reported the failure of biological control of *B. brassicae* by *D. rapae* on the Brussels sprout cultivar Early Half Tall related to its lower levels of mustard oils.

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† One hectare = 10^4 m^2.

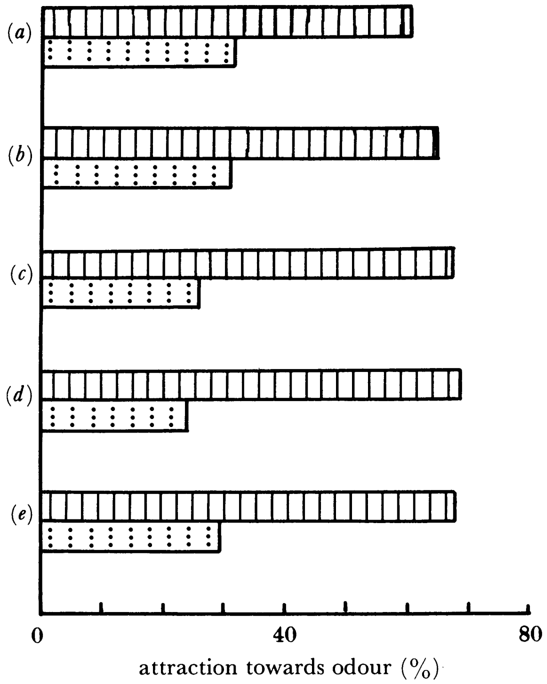

FIGURE 1. The percentage response of aphid parasitoids to plant odours (barred line) versus odours of their host aphids (dotted line). Order of listing is aphid host-plant, aphid, parasitoid (data of M. G. V. Wickremasinghe, unpublished results). (*a*) Nettle, *Microlophium carnosum*, *Aphidius ervi*; (*b*) wheat, *Rhopalosiphum padi*, *Aphidius rhopalosiphi*; (*c*) Dock, *Aphis fabae*, *Lysiphlebus fabarum*; (*d*) oak, *Tuberculoides annulatus*, *Praon* sp.; (*e*) Sycamore, *Drepanosiphum platanoides*, *Aphelinus flavus*.

3. HABITAT MODIFICATION

(*a*) *Overwintering conditions*

The provision of shelter adjacent to crop fields to promote an increase and earlier occurrence of coccinellids on crops has been demonstrated for sugar beet (Bombosch 1965), potatoes (Fenjves 1945) and recommended in Czechoslovakia to compensate for increased areas of monoculture (Hodek *et al.* 1962). Iperti (1966) found that coccinellids migrating from crops in the autumn to form aggregations in the hills around the cultivated plains of southeastern France could suffer over 60% mortality from the fungus *Beauveria* over winter. In ladybird aggregations on plants below 1000 m altitude, the fungus became a serious threat. Mortality was much reduced above 1000 m, or in aggregations in rock cracks. Iperti (1966) was able to demonstrate that coccinellids both preferred and survived better (less than 15% mortality) in artifically created rock-piles. He devised a special trap for coccinellid aggregations (Hodek 1973); this trap facilitated the transport of vast numbers of coccinellids to high altitudes and later return to the crop areas.

(*b*) *Alternative prey*

The provision of suitable non-crop plants to host alternative aphid prey for parasitoids has been extensively studied by Stary (1983, 1986) in Czechoslovakia. He regarded aphids on perennial stinging nettle (*Urtica dioica*) as a useful source of *Aphidius ervi*, which parasitizes several crop aphid pests including *Sitobion avenae* and *Acyrthosiphon pisum*. *Cirsium arvense* carries large populations of *Aphis fabae cirsiliacanthoides*. Unfortunately, the dominant parasitoid on this aphid is *Lysiphlebus cardui* and not *L. fabarum*, which is the important parasitoid for *Aphis fabae*. Eikenbary & Rogers (1974) reported that *Schizaphis graminum* on cereals was more parasitized when sunflowers infested with *Aphis helianthi* were growing nearby. The parasitoid *Lysiphlebus testaceipes* was able to maintain itself on large populations of *A. helianthi* during two critical periods of the year when *S. graminum* was scarce or absent on the cereal crop.

However, some doubt has been cast on the value of such reservoirs. Although in the last example the parasitoid appeared to switch aphid hosts successfully, this is not always the case. Cameron *et al.* (1984) found that *A. ervi* reared on several other aphid species parasitized few *Sitobion avenae* on wheat. That this was not just a plant synomone effect was indicated by a change in parasitoid esterase bands shown in electrophoretic analysis when the parasitoid was switched from *Acyrthosiphon pisum* to *S. avenae*. Powell (1986) found mummy production by *Aphidius rhopalosiphi* much reduced when switched to *S. avenae* after several generations on *Metopolophium dirhodum*, though the reverse switch resulted in an increase in parasitization.

An interesting recent development has been the acceptance by many cereal farmers in the U.K. of the proposal to leave an edge area of the crop unsprayed by pesticides, including herbicides. As yet, there is no evidence that this provides a reservoir of aphid predators and parasitoids, but it could lead to an increase of the natural enemy restraint on aphids in the central area of the crop.

(*c*) *Flowers*

Pollen and nectar are particularly required by the adults of adult syrphids, but also by coccinellids when aphid prey is missing (Hodek 1973). The provision of plant sources of pollen and nectar for syrphids has been recommended in the Rhône valley in France (Mackauer & Way 1976). One of few studies identifying increased predation on the crop associated with adjacent flowers is by van Emden (1965), who planted flowers along parts of two edges of a Brussels sprout crop and found significantly more syrphid eggs laid on the crop near these flowers than elsewhere. This was associated with 65–70% predation mortality of *Brevicoryne brassicae* near the edges with flowers, compared with under 50% at other edges and the centre. With the high mobility of most adult predators, it is unlikely that mortality from predation in any part of the field (0.7 ha) was totally unrelated to the presence of flowers. This is one of the problems of experimentally showing the impact of without-crop habitat modification, and it has led to many unwarranted negative conclusions in the literature. After all, Jacobson (1946) showed that damage to wheat by a pentatomid bug originating from a patch of the weed *Salsola* sp. at the edge of the field extended for at least 3 km into the crop, i.e. a square field would have to be over 1000 ha in area for the centre to be free of such edge effects!

(*d*) *Crop background*

The work of Smith (1969*a*, *b*) offers considerable opportunities for manipulating the natural enemy:aphid ratio, but has hardly been followed up. Smith compared populations of *B. brassicae* and its natural enemies in clean and weedy Brussels sprout plots. Aphid populations remained negligible on plants in the weedy plots, but reached over 100 aphids per plant on the clean plots by late September. Many fewer immigrant aphids were trapped over the weedy plots, but additionally, several predator species (particularly the syrphid *Melanostoma* spp.

ovipositing and *Anthocoris nemorum*) were more numerous on the weedy plots early in the season. Syrphids in the genus *Platycheirus*, however, laid more eggs on plants in the clean plots.

There has been a little subsequent work on the same theme. Powell *et al.* (1981) compared the numbers of polyphagous predators caught in pitfall traps in unweeded and clean plots of winter wheat (figure 2). Of the 12 significant effects among the 14 combinations of 7 beetles and 2 years, 7 indicated greater beetle numbers in the weedy plots. The other 5 showed more beetles in the clean plots. However, this is the expected result given equal numbers because the hindrance of horizontal movement by the weeds would result in a reduced chance of capturing beetles by pitfall trapping in weedy plots (Greenslade 1964).

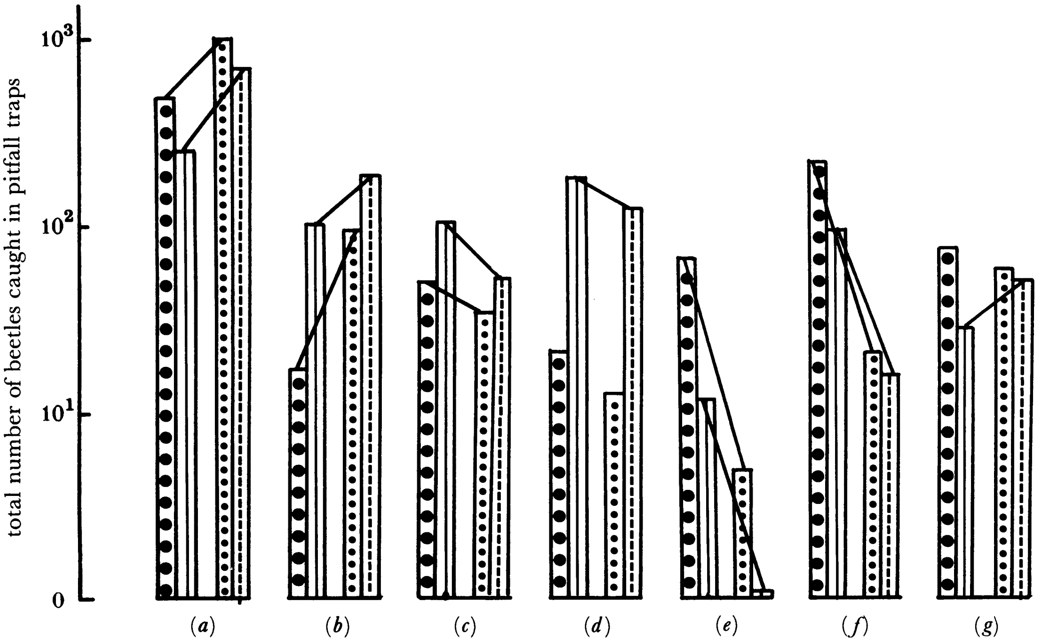

FIGURE 2. Numbers of different beetle species (*a*–*g*) caught in pitfall traps in clean (small dots or broken line) versus weedy (large dots or continuous line) cereal plots in 1980 (dots) and 1981 (lines). Bold lines join statistically significant within-year differences (data of Powell *et al.* 1981). (*a*) *Pterostichus melanarius*; (*b*) *P. madidus*; (*c*) *Loricera pilicornis*; (*d*) *Agonum dorsale*; (*e*) *Amara* spp.; (*f*) *Philonthus cognatum*; (*g*) *Tachyporus* spp.

Andow *et al.* (1986) found reduced populations of *B. brassicae* on cabbages grown with living mulches of grasses or clover, but did not investigate how far this was due to any enhancement of biological control. Powell (1983) released *Myzus festucae* with the parasitoid *Aphidius uzbekistanicus* onto rye grass undersown or as strips in wheat. Summer *Sitobion avenae* populations on wheat were smallest in plots that had developed the largest populations of *M. festucae* in the spring.

The effect on the biological control of aphids of increasing crop plant density has also received some attention. Increasing crop density in itself tends to reduce the number of immigrant alate aphids (see, for example, Way & Heathcote 1966), both by changing the crop background and by influencing the physiology of the crop plants and their suitability for the aphids. However, Honek (1983) showed that the ladybird *Propylaea quattordecimpunctata*, as well as syrphids, preferred dense plant stands; *Coccinella* spp. preferred less dense stands.

Table 1. The effect of strip-harvesting and normal harvesting on the average number of natural enemies of *Therioaphis trifolii* (data from Schlinger and Dietrick (1960))

natural enemies	thousands per hectare normal harvesting	strip-harvesting
coccinellid adults	114	507
coccinellid larvae	27	573
chrysopid larvae	482	509
hymenopterous parasitoids	173	709
‘big-eyed’ Heteroptera	492	991
aphidophagous spiders	259	2703
totals	1547	5992

Schlinger & Dietrick (1960) spectacularly demonstrated the disadvantages for biological control of harvesting lucerne fields completely compared with leaving refuges for natural enemies by strip-harvesting. The density of natural enemies of *Therioaphis trifolii* was nearly four times greater in strip-harvested than in totally harvested lucerne (table 1).

4. Plant resistance

(*a*) *Plant resistance and biological control*

Plant resistance decreases aphid numbers, particularly by slowing the growth of the aphid population in time. If predators and parasitoids show a less than proportional response to the reduction in the number of their prey, an improved natural enemy:aphid ratio will result and therefore the impact of biological control should be magnified. Two recent publications have discussed the interactions of plant resistance and biological control for plant pests in general. The review by Herzog & Funderburk (1985) stresses the reductions in biological control that might occur from (*a*) lower prey numbers and (*b*) anatomical and chemical barriers of the resistant varieties discouraging natural enemies directly; the review also includes some examples of a beneficial interaction. A whole book on the interaction (Boethel & Eikenbary 1986) emphasizes the potential benefits.

None of Herzog & Funderburk's examples (1985) of reduced biological control on resistant varieties concern aphids. Obrycki & Tauber (1984, 1985) studied biological control of aphids on potato cultivars with dense glandular hairs, a very strong resistance mechanism against aphids. No adverse effects of this pubescence on predators and parasitoids was found in the field, and large numbers of aphid mummies were recorded. Any less active movement by predator larvae seemed cancelled out by the preferred oviposition by predators on pubescent varieties. Karner & Manglitz (1983) investigated whether the feeding activity of *Hippodamia convergens* was reduced on a resistant lucerne cultivar (Baker) compared with a susceptible one (Vermal). They placed the same number of *Acyrthosiphon pisum* on both cultivars, and measured the proportion of aphids consumed by different instars of the ladybird at three different temperatures. With 8 of 12 instar–temperature combinations, the proportion of aphids consumed was greater on the resistant cultivar.

van Emden & Wearing (1965) used a simple model to propose that partial plant resistance should enhance biological control of a multivoltine pest such as an aphid. This was confirmed experimentally in the glasshouse by Starks *et al.* (1972) with *Schizaphis graminum* on two barley varieties ('Rogers', susceptible; 'Will', partly resistant) with the parasitoid *Lysiphlebus testaceipes* (figure 3). Without parasitoids, the number of aphids on Rogers was never more than 1.5 times the number on Will; with parasitoids, however, there was a 2.5-fold increase by the third week. With chrysanthemums, Wyatt (1970) reported that biological control of *Myzus persicae* by *Aphidius matricariae* was only effective if the variety used was partly aphid resistant.

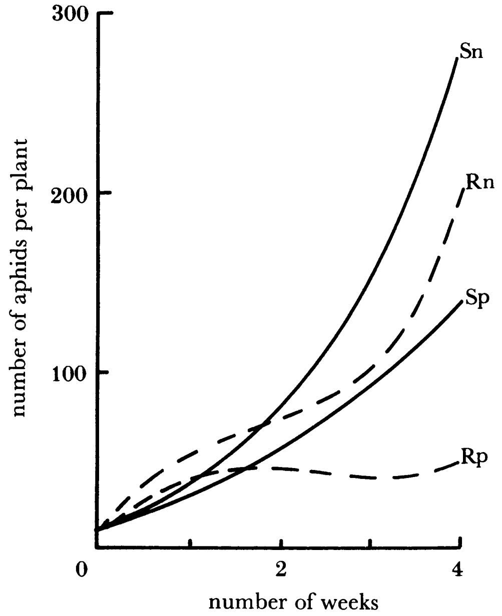

FIGURE 3. Population growth of *Schizaphis graminum* on the susceptible barley variety Rogers (S) and the partly resistant variety Will (R) in the presence (p) and absence (n) of the parasitoid *Lysiphlebus testaceipes* (Starks *et al.* 1972).

Dodd (1973) compared two Brussels sprout varieties in field trials. Over a five day interval, predation on the cultivar Winter Harvest (susceptible) was just over 30%, but was 55% on the cultivar Earley Half Tall (very little resistance). In this example, the potential increase rate of the aphids over the same time period was 1.33 on the susceptible and 1.30 on the partly resistant cultivar. With cereals, Lykouressis (1982) found that peak populations of *Sitobion avenae* on Pamena oats in the glasshouse were only 1.25-fold greater than on a barley cultivar. Yet in the presence of the parasitoid *Aphelinus abdominalis*, aphid numbers on barley did not rise above 20 per plant, but peaked at about 70 per plant on the oats.

van Emden (1986) has run a simple population model with built-in density dependence of parasitoid impact (Hassell 1975) to simulate the interaction between partial plant resistance and biological control. Figure 4*a* shows the output of the model, as well as two additional curves for a partly resistant variety with biological control. One of these (RP) assumes that percentage mortality on the two cultivars is not affected by the differing prey densities and is identical on both, whereas the other line (RA) assumes the same numerical mortality on both cultivars (representing a large percentage mortality on the resistant cultivar). Figure 4*b* illustrates how the output of the model is reflected in the apparent difference between populations of aphids on the two varieties. The apparent resistance of the partly resistant variety increases with each generation as the growth rates of the two populations diverge, and of course is identical whether biological control is absent (R) or proportionally the same (RP)

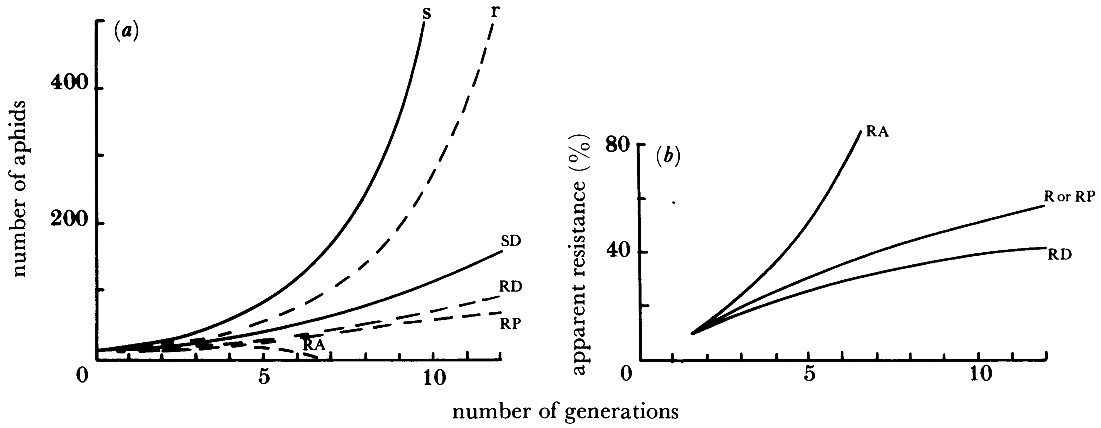

FIGURE 4. The effect of biological control on change in time of the apparent resistance (*b*) of a partly resistant variety given various aphid population growth curves (*a*). s, Susceptible variety and r, partly resistant variety, both in the absence of biological control; SD, RD, the same varieties with biological control assumed to show density dependence; RP, resistant variety with same percentage mortality from biological control between generations as on the susceptible variety; RA, resistant variety with same numerical mortality between generations as on the susceptible variety.

on both varieties. Any tendency for apparent resistance to be magnified in relation to this R or RP line, i.e. greater percentage mortality on the resistant than on the susceptible cultivar, moves the line towards RA (the same numerical mortality on both cultivars).

Figure 5 shows a response surface generated on the 'RA' assumption, i.e. higher percentage mortality on the resistant cultivar to the extent of matching the mortality on the susceptible numerically. This is, of course, across a generation with differing increase rates on the two varieties; it is therefore the apparent phenomenon and not a true quantitative estimate of mortality. The response surface shows the apparent resistance under the equal numerical mortality assumption of combinations of different percentage plant resistance with different percentage biological control occurring on the susceptible variety. A, B and C mark the data of respectively Starks *et al.* (1972), Dodd (1973) and Lykouressis (1982), the three examples quoted earlier where the level of plant resistance (in the absence of parasitoids), the degree of biological control on the susceptible variety and the final apparent resistance were all measured independently.

Figure 5 indicates that percentage biological control on the partly resistant plants in all three examples was greater than on the susceptible plants; in Dodd's (1973) work it considerably exceeded the assumption of an equal numerical impact. Possible explanations for the increase in percentage biological control on resistant plants are that host plants can be more attractive to parasitoids than aphids (see §2*b*) and also the colonial habit of aphids and the rather predictable distribution on the plant of the colonies. Rabbinge *et al.* (1984) have modelled how clustering increases the impact of parasitoids of aphids.

Nothing is yet known about the longer-term effects on predators and parasitoids when being reared on aphids on resistant varieties. Kuo (1986) has pointed out that, as resistant plants may make aphids smaller, this could affect the fecundity of natural enemies, particularly parasitoids. With parasitoids there is also the possibility that a greater proportion of males might be produced.

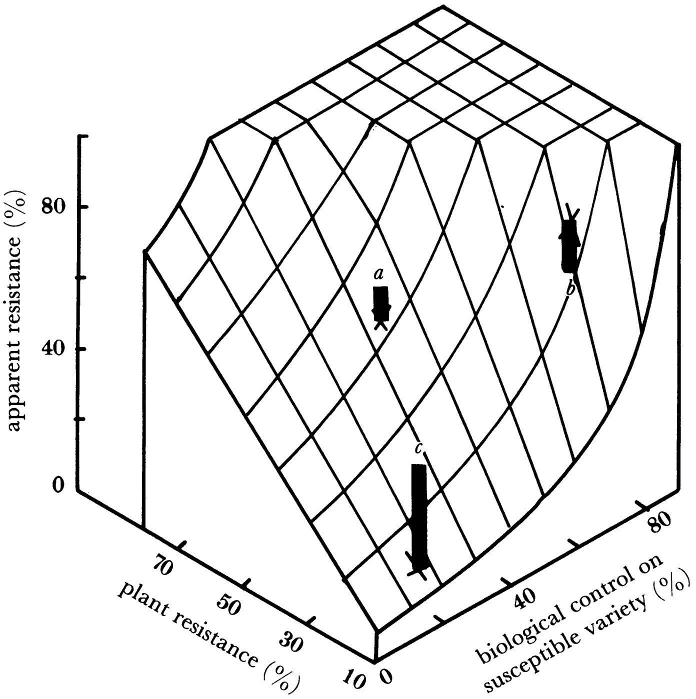

FIGURE 5. Response surface of the apparent resistance of varieties with different levels of resistance (in comparison with a susceptible variety) with varying biological control mortalities on the latter and assuming the same numerical mortality on both varieties. (*a*) Data of Starks *et al.* (1972); (*b*) data of Lykouressis (1982); (*c*) data of Dodd (1973).

(*b*) *Use of pesticides in relation to biological control*

Pesticides are normally considered likely to damage biological control, yet can be a potent intervention for increasing the natural enemy:aphid ratio. The early example of integrated control of *Therioaphis trifolii* on alfalfa in California (Stern *et al.* 1959) was based on the concept that a reduced dosage of pesticide would enhance this ratio to give satisfactory control in a situation where biological control in the absence of pesticide was ineffective. Raising the natural enemy:aphid ratio is the consequence of any treatment that selectively kills aphids, even if such selectivity is only partial.

(i) *Selective pesticides*

The carbamate insecticide pirimicarb is well known for being selective against aphids and many Diptera, including Syrphidae; it is non-toxic at normal doses to coccinellids, anthocorids, chrysopids and parasitoids of aphids. Powell *et al.* (1981) compared pitfall trap catches of predators in cereal plots treated with pirimicarb and dimethoate. Pirimicarb had very little effect on Carabidae, Staphylinidae and spiders, but dimethoate immediately reduced numbers of these predators, although immigrants caused some increase after a week. The selectivity of pirimicarb has made it especially valuable because, despite limited persistance, one application may be enough for natural enemies, which have accumulated on the aphid population, to maintain control.

Less selective pesticides still have the potential of raising the natural enemy:aphid ratio, though less dramatically than pirimicarb. Appropriate screening of a range of pesticides will usually show differences in pesticide impact on aphids versus predators and parasitoids. For example, Croft & Brown (1975) reviewed the available data on the relative toxicity (as LC_{50} or LD_{50}) of pesticides to pests and natural enemies. Coccinellidae seem generally more resistant to pesticides than their prey. Of 29 pesticide–coccinellid combinations, 26 showed selectivity in favour of coccinellids. For chrysopids and nabids respectively, 2 out of 3 and 2 out of 2 combinations similarly showed greater toxicity to the aphid than to the predator. With parasitoids, however, only 1 of 4 combinations showed greater toxicity to the aphid than the parasitoid.

Bartlett (1964) catalogued the toxicity of 60 insecticides and fungicides to natural enemies. For natural enemies of aphids he identified only seven insecticides as showing low toxicity to coccinellids, three to parasitoids and three to syrphids. Zeleny (1966) found malathion far less toxic than sumithion to all stages of *Coccinella septempunctata*. Sotherton & Moreby (1984), in response to increasing evidence that foliar applied fungicides were damaging polyphagous predator populations, did laboratory bioassays of seven such fungicides at field application rates with three beetle predators common in cereal fields: *Agonum dorsale*, *Demetrias atricapillus* and *Tachyporus chrysomelinus*. The species varied in their response, but pyrazophos caused 100 % mortality of all. The other fungicides caused less mortality, especially carbendazim and tridimefon.

(ii) *Selective placement*

Systemic insecticides, particularly when applied to the soil rather than foliage, are likely to cause relatively little kill of natural enemies on the plants (see, for example, Zeleny 1966; Saharia 1985), although not necessarily of ground-dwelling polyphagous predators.

Little work appears to have been done on restricting pesticide, as far as possible, to parts of the plants where aphids are most abundant. Modern controlled droplet application makes possible accurate placement of the majority of the pesticide, so targeting toxin specifically to the sites occupied by aphids would appear practicable for raising the natural enemy:aphid ratio. For example, electrostatic sprayers offer the possibility of largely restricting insecticide deposits for the control of *Sitobion avenae* on the ears of cereals.

An interesting placement technique developed for tree fruit in the U.S.A. (Lewis & Hickey 1964) has potential for aphid control in field crops. It relies on the selectivity inherent in reduced dosages (see below). This is the 'alternative row middle' technique, translatable to field crops as 'band spraying'. The swathes (or boom spans) are so arranged that there are narrow unsprayed bands between sprayed swathes that only receive spray on a subsequent spraying occasion when different bands remain unsprayed. Reduced concentrations of pesticide can be used because the pesticide deposit is renewed over most of the field after a relatively short interval. The system has been found to increase the natural enemy:prey ratio on apples in the U.S.A. and is being used for 95 % of all applications to apples in Pennsylvania (Hull *et al.* 1983).

(iii) *Selective timing*

There are very few references to timing of pesticides to improve selectivity of kill. Bartlett (1964) discussed the general principle of avoiding pesticide treatments destructive to natural enemies as far as possible during periods of effective predator and parasitoid activity.

Early in the season before parasitoid generations overlap, it may be possible to time sprays to coincide with a high proportion of parasitoids pupated within aphid mummies (Bartlett 1964). However, emerging adult parasitoids can be killed by contact with residual insecticide on the mummies. Saharia (1985) recommended that granular systemic insecticides against *Lipaphis erysimi* should be applied to mustard crops before *Coccinella repanda* enters the crop.

(iv) *Dosage reductions*

Hull & Beers (1985) have reviewed the numerous cases where reduced doses have been used successfully in commercial control of various pests, to give double savings; first, in the amount of pesticide applied per spray and secondly, in the saving of repeat sprays where valuable natural enemy action was conserved (see §4*b* (i) for the relative toxicities of pesticides to aphids and their predators and parasitoids).

As mentioned previously (§4*b*), reduced doses of organophosphate insecticide were used successfully on lucerne in California (Stern *et al.* 1959) to raise the natural enemy:aphid ratio and give control of populations of organophosphate resistant *Therioaphis trifolii*. Reduced damage to natural enemy populations and subsequent natural enemy multiplication more than offset the initially poorer kill of the pest (Bartlett 1964).

The selectivity of reduced doses stems from the fact that dose response curves of many natural enemies are steeper than those of their prey (figure 7); Dodd (1973), for example, has shown this for coccinellids and *Diaeretiella rapae* (a parasitoid of *Brevicoryne brassicae*). The difference in slope of the response may well stem from the armoury of detoxifying enzymes needed by a herbivore to deal with plant compounds but not needed by a carnivore (Plapp 1981).

The use of a partly resistant crop variety benefits biological control besides magnifying the impact of natural enemies. This additional benefit is the possibility of further raising the

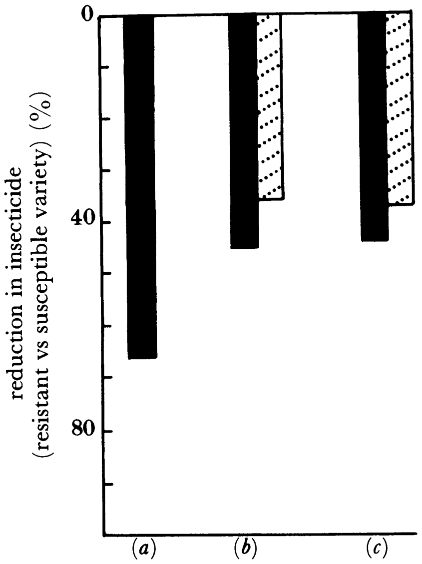

FIGURE 6. Reduction in concentration of insecticide as LC$_{50}$ (solid line) and LD$_{50}$ (dotted line) possible on partly resistant varieties in comparison with susceptible ones. (*a*) Data of Selander *et al.* (1972) on susceptibility to parathion of *Myzus persicae* on chrysanthemums; (*b*) data of Bin Muid (1977) on susceptibility to malathion of *M. persicae* on Brussels sprouts; (*c*) data of Attah (1984) on susceptibility to malathion of *Metopolophium dirhodum* on wheat.

natural enemy: aphid ratio by reducing insecticide dose. After the work of Selander *et al.* (1972) on the susceptibility to parathion of *Myzus persicae* on resistant chrysanthemum cultivars (figure 6), Bin Muid (1977) and Attah (1984) have shown enhanced susceptibility to malathion of organophosphate resistant *Myzus persicae* and of *Metopolophium dirhodum* on partly resistant varieties of Brussels sprouts and wheat respectively. The varieties studied by Bin Muid and Attah had only low levels of resistance (the Brussels sprout varieties used by Bin Muid were those used by Dodd (1973); see §4*a*), yet in each case LC$_{50}$ values were reduced by nearly one half (figure 6). Aphids on the resistant varieties were smaller, but their increased susceptibility to insecticide was mostly physiological in nature because correction for body mass did not account for the differences. The possibility of using reduced doses on partly resistant varieties has implications on selectivity far greater than are at first apparent, because it is unlikely that the dose–response curve of natural enemies is affected by the plant resistance to the aphid (figure 7). Thus a two thirds dose on a partly resistant variety gives kill of aphids equivalent to full dose on a susceptible variety, yet remains only a two thirds dose for the parasitoid or predator. The increased selectivity of kill (see figure 7) is likely to be dramatic and result in considerable amplification of the natural enemy: aphid ratio.

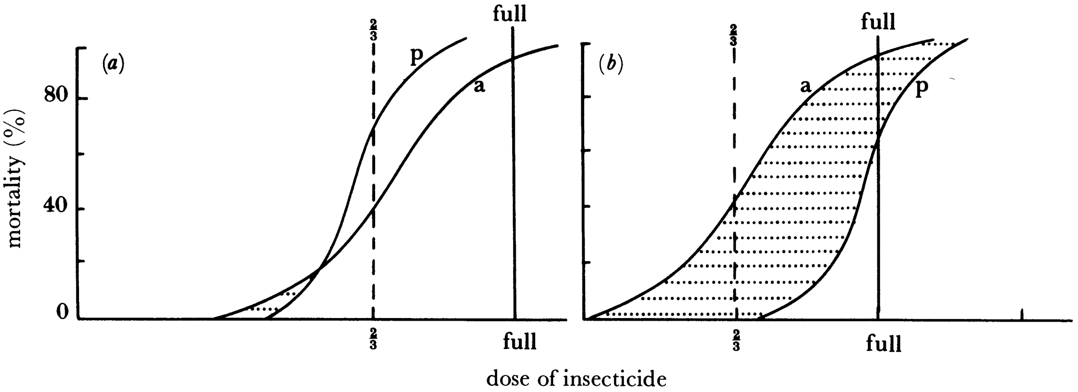

FIGURE 7. Theoretical selectivity of pesticide application on a resistant variety (*b*) compared with on a susceptible variety (*a*). a, Dose mortality curve of pest aphid; p, dose mortality curve of predator or parasitoid. Doses ($\frac{2}{3}$ or full) above graphs are relevant to the aphid, doses below graphs are relevant to predator or parasitoid. Selectivity 'window' is stippled.

The argument is often raised that advocating reduced doses carries the danger of promoting insecticide resistance in the pest by allowing the survival of individuals carrying genes for resistance in the heterozygous condition. However, if such dose reduction is advocated in pest management, then survivors of a pesticide application become the prey of the natural enemies that the dose reduction has preserved.

(*c*) *The pest management triad*

Although plant resistance and use of pesticides to improve the natural enemy: aphid ratio have been given separate headings in this account, it is clear that, with biological control, a three-way interaction exists which has been called the 'pest management triad' (van Emden 1983). The introduction of a variety partly resistant to the aphid pest enhances the ratio directly because its effect on aphid population size exceeds any similar effect on the natural enemies, and by lowering the tolerance of the pest to pesticide. This in turn allows the ratio to be built up still further by the selectivity of kill inherent in the relation described above between the response curves to pesticide of the aphids and their natural enemies. The ratio can then be further enhanced by using a selective pesticide.

5. Conclusions.

In spite of the pessimism in much of the literature about the potential of indigenous natural enemies of aphids in field crops, adequate biological control for the farmer does occur sporadically and, where it does not, there is much evidence that the aphids have suddenly or temporarily escaped the natural enemy restraint rather than that restraint is insignificant.

There are many ways in which the natural enemy: aphid ratio can be raised by intervention to hinder the escape of the aphid population from the natural enemy restraint. These have so far largely been studied in isolation, and the degree of intervention necessary to achieve effective aphid control is usually uneconomic or unacceptable to the farmer in his management of the crop system. However, the few examples where such interventions have been integrated demonstrate a combined impact on the efficiency of biological control far higher than would have been predicted from what is known about the effect of each intervention on its own.

It appears that it is interaction between interventions, rather that the potential of those interventions in themselves, that holds the key to managing indigenous natural enemies of aphids in field crops. Adequate impact of indigenous natural enemies should often be attainable and should encourage us to seek to develop pest management packages out of the ideas already available as components.

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Discussion

M. J. Way (*Imperial College at Silwood Park*, *Ascot*, *U.K.*). Professor van Emden has dealt primarily with the role of naturally occurring biological control agents against pests on the crop. Could he please reflect on their value against pests where the latter are not on crops, especially because many pests spend most of the year in the non-crop environment?

H. F. van Emden. I certainly accept that, particularly in the case of many aphids, the most important biological control in terms of the population dynamics of the species occurs in the non-crop environment. However, I particularly titled my paper in such a way as not to get involved with the practical possibilities for farmer-acceptable control of aphids based on interventions in the non-crop environment, because as yet there is little practical guidance that can be given. I certainly believe that the possibility does exist.

T. Lewis (*Rothamsted Experimental Station*, *Harpenden*, *U.K.*). Are the slightly aphid-resistant cultivars Professor van Emden suggests also economically attractive to farmers?

H. F. van Emden. One of the advantages that partly aphid-resistant cultivars have is that they are indeed available among the cultivars grown by farmers and growers. Very few cultivars have been bred for such resistance, but nevertheless there is considerable variation among the cultivars currently available commercially. By concentrating on commercially available cultivars, the system can be used without the need for a preliminary long term breeding programme.

T. Lewis. How does Professor van Emden propose to encourage farmers to take up the approaches to control which he has described?

H. F. van Emden. The question requires a different answer for intensive agriculture and developing agriculture. In developing agriculture, reliance on pesticides for control is usually uneconomic. By maximizing indigenous biological control, it is possible to raise yields considerably with the addition of perhaps a single pesticide spray. This could still be economically feasible, although yields may still be below what might be obtained by a more blanket use of insecticide.

In intensive agriculture, the situation is different. Clearly, the combination of other restraints with pesticides, if successful in protecting yields, is going to give the farmer a saving in pesticide costs. However, I have doubts that this would present sufficient motive for farmers to take up such systems unless they became forced into it by the failure of reliance on pesticides due to insect resistance to them. The history of integrated control measures suggests that even successful integrated systems, almost invariably introduced to deal with the insecticide resistance crisis, fail to survive once an effective insecticide again becomes available.

K. D. Sunderland (*Institute of Horticultural Research*, *Littlehampton*, *U.K.*). Are the calculations Professor van Emden has made based only on the antibiosis component of resistance or do they include antixenosis? I ask because there are reasons to believe that antixenotic varieties could improve pest control by, for example, increasing the pests' movement and their exposure to contact pesticides. They could also synergize with natural enemies, which are often vertically stratified in crops; antixenosis and the resulting increased aphid movement could increase aphid–natural enemy encounter rates and thus improve control.

H. F. van Emden. The calculations are indeed based on the antibiosis component. It is much harder to model the antixenosis component, and it may well be that the surprisingly large improvement of biological control on partly resistant varieties may partly be due to the fact that antixenosis and antibiosis often occur together in a variety. The kind of relations you suggest may therefore account for the field effect of the resistance being so much greater than what one would predict from a density-dependent model.

I am also sure Dr Sunderland is right that antixenotic varieties may well improve the pests' exposure to contact pesticides, but this is of course a little outside the scope of this meeting.

J. K. Waage (*C.A.B. International Institute of Biological Control, Ascot, U.K.*). In Professor van Emden's models for the interaction of resistance and biological control, resistance is modelled as affecting the intrinsic growth rate of the pest. How does this really occur, and could it involve mortalities or changes in hosts which could actually interfere with natural enemy survival or reproduction (e.g. lower survival of parasitoids in the smaller aphids on resistant plants)?

H. F. van Emden. The main effect of resistance is probably to reduce fecundity of the pest, though it may also affect pre-adult mortality if the resistance is high and may also increase development rate. My model excludes any effects on survival, but otherwise includes both fecundity and development rate. Certainly the insects on partly resistant varieties are smaller than those on susceptible ones, and it is to be expected that this could affect the fecundity of parasitoids and even perhaps their sex ratio. This is something that needs further investigation; all I can say at the moment is that the levels of plant resistance used do not give a very dramatic decrease in pest size, and that any deleterious effects on parasitoids have not yet shown themselves within the single seasons when we have done the studies. However, it is still possible that, if such systems using biological control and plant resistance were to be used on a very wide scale and over a large area, effects of the kind on parasitoids Dr Waage suggests might well show in time.

R. J. Cook (*United States Department of Agriculture Agricultural Research Service, Washington State University, Pullman, U.S.A.*). Professor van Emden describes the benefits of what he referred to as 'plant resistance' combined with 'biological control' for management of aphid populations. Without wanting to divert our discussion to a review of terminology. I would submit that both are biological control. I believe a broad concept (i.e. the use of any living organism, plants included, for control of a pathogen or pest species has many advantages. The broad definition is certainly more futuristic. For example, the *Bt* gene for endotoxin production has now been transferred from *Bacillus thuringiensis* to the root bacterium *Pseudomonas fluorescens* and also to tobacco. The expression of this gene in tobacco is a form of host-plant resistance (antibiosis, to use entomological terminology). Our concept of biological control should not be so narrow that expression of a gene in an insect pathogen qualifies as 'biological control', but the same gene expressed in a plant as a defence against insects does not qualify as biological control.

H. F. van Emden. I certainly take the point that many methods of pest control other than the use of predators, parasitoids and insect pathogens can be regarded as biological control and I would accept your definition as justifiable. However, rightly or wrongly, the word biological control has (certainly in the entomological world) been associated with a narrower definition and it is hard to think of an appropriate alternative for its meaning in that more restricted sense. I hope it doesn't matter terribly, provided that confusion does not result.