GUEST EDITORIAL

The Role of Host Plant Resistance in Insect Pest Mis-management

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Pest management has, of course, its reciprocal - pest *mis*-management! Most textbooks on pest management indeed include a discussion which describes the components of pest mis-management as overdosing with insecticides, the destruction of biological control, the abandonment of cultural controls and the introduction over large areas of high-yielding but pest-susceptible crop varieties.

Overdosing is usually regarded as the prerogative of the insecticide applier but, as we who work on other aspects of pest control polish our halos, we would do well to reflect on whether we are totally blameless of that same sin. I propose to explore this idea in relation to the area of pest management I know best, host plant resistance to insects. I would, however, invite specialists in other areas, such as biological and cultural control, to examine their specializations from the same viewpoint.

My starting point is that if a control technique is already adequate on its own, there may be advantages in making it *less* effective if it can be used in combination with other methods. With plant resistance, for example, any yield penalty arising from the diversion by the plant of resources to the resistance mechanism is likely to be positively correlated with the degree of resistance.

'Energy or other resources which the plant diverts for defence cannot be used for growth or reproduction' (Hodkinson & Hughes, 1982). Others have argued that the cost of resistance to the plant may not be significant in relation to the overall economy of the plant or that the materials are only stored temporarily and recycled. However, it would seem remarkably easy to find apparent quantifications of the cost of resistance. For the purposes of writing this editorial I have just examined data on 31 pigeon pea varieties screened at ICRISAT (International Crops Research Institute for the Semi Arid Tropics); these data just happened to be on my desk. A regression of yield under insecticide protection against estimated resistance to insect pod damage has a strong negative slope ($P = <0.001$), with a 31% yield loss predicted for 90% resistance to insects. It therefore seems likely that partial plant resistance has the benefit over a high level of resistance of greater compatibility with yield aspirations.

A second advantage of only partial plant resistance is that the selection pressure on a pest, which could lead to an adapted biotype increasing in frequency, will be reduced compared with a high level of plant resistance, especially as the latter will often be based on a single mechanism. For example, work with which I was associated at IITA (International Institute for Tropical Agriculture) in Nigeria identified some cowpea varieties with such high levels of antibiosis to cowpea aphid that it was impossible to establish aphids on the plants. We further discovered that the resistance was based on a graft-transmissible allelochemical which has since been shown to be governed by a single gene. It is perhaps symptomatic of such resistance that we immediately found one sample of cowpea aphids from the IITA farm which was not affected by the resistance.

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This brings me to one of the main reasons for writing this article. I do have very serious reservations about the use of transgenic techniques in developing insect resistant plants. By the very nature of the technique (including the need to use an easily assayable marker), transgenic plant resistance is almost bound to involve allelochemicals governed by single genes. I understand that an armyworm (*Spodoptera*) has already, within three generations, shown tolerance to the *Bacillus thuringiensis* endotoxin transferred by biotechnology to tobacco plants.

If, then, one is going along the route of adding other control measures to exploit the advantages of the lower selection pressure on pests of a reduced control efficiency of the primary measure, it is clearly worth adding control measures where the combined effect with the primary measure is greater than simply additive. In relation to plant resistance, insecticides and biological control have been identified as having the potential for potentiation with partial resistance (van Emden, 1987).

Insecticides and plant resistance

Insects on resistant plant varieties are usually a little smaller than those on susceptible varieties. As toxicity of an insecticide to an organism is a function of the latter's body weight, the several reports in the literature that the same percentage kill of insects on susceptible and resistant plants can be obtained by reduced doses of insecticide on the latter come as no surprise. However, differences in insect weight only account for a small part (typically 10–15%) of the effect; it is clear that it is due mainly to a physiological sensitivity to the insecticide, presumably related to some stress the insect undergoes from feeding on the resistant plant. The phenomenon is shown by both sucking and chewing insects.

By contrast, other workers have shown the reverse phenomenon. These examples of increased insecticide tolerance of insects reared on resistant plants all seem to relate to an induction of heightened tolerance by allelochemicals in the resistant plants. It therefore seems that transgenic plant resistance will not carry the additional benefit of an option to use reduced insecticide doses and that it is more likely that increased doses will be necessary.

Biological control and plant resistance

Alkaloids and other allelochemicals involved in plant resistance can be toxic to parasitoids within hosts (Herzog & Funderburk, 1985) or prove toxic to predators such as ladybirds, hover fly larvae and lacewing larvae. If not lethal, allelochemicals may induce adult sterility in predators.

The smaller size of prey on resistant varieties can have knock-on effects with the emergence of smaller parasitoids having reduced fecundity. These disadvantages, however, are not apparent at low levels of plant resistance. It has also been suggested that resistant plants may induce the production of a higher proportion of male parasitoids, but the only data I have seen where sex ratios have been measured do not support this.

That there are these problems, but also a more general beneficial potentiation between biological control and partial plant resistance, suggests there is a disadvantage in seeking a level of plant resistance greater than necessary when other restraints are added in a pest management system.

The beneficial interaction shows as a higher percentage mortality of the pest on resistant than on susceptible varieties in the presence of natural enemies, first noticed by Wyatt (1970) and since confirmed with several other examples. Some of the results in the field are quite startling, where varieties less than 20% resistant show pest populations 60% lower than those on susceptible varieties in the presence of predators on both varieties.

The interaction may arise from a variety of reasons acting singly or in combination. Some of these reasons are highly crop and predator specific, such as the switch from nectar feeding to carnivory of the ladybird *Cryptolaemus* on nectariless cotton varieties and the reduced ability of ladybirds to maintain a foothold on normal pea varieties compared with the partially aphid resistant leafless varieties with a profusion of tendrils.

However, other reasons have a more general application. The smaller insects on resistant varieties may be less able to defend themselves against attack from natural enemies; they are also more restless, and are dislodged from the plant by natural enemy activity to add to the direct mortality from predation or parasitization, since many fail to regain the plant. Additionally, predators eat more prey before satiation if the latter are smaller.

A further part of the explanation relates to the response of natural enemies to chemical cues from the plant. This has as yet only been shown for parasitoids. Several species of parasitoids of aphids have been tested, and all show similar behaviour. They orientate towards odours of the appropriate plant to a greater extent than to the odour of their host aphids or the honeydew these aphids produce. Moreover, at least one species (*Aphidius rhopalosiphi*) discriminates between wheat cultivars in favour of the cultivar on which the individual developed. This has three important implications for insect host plant resistance. Firstly, the number of parasitoids arriving to search for prey is unlikely to be reduced by plant resistance through any effect of a smaller prey population, even though there may well be such an effect on subsequent arrestment. Secondly, parasitoids which have developed on a resistant cultivar will land on that cultivar again in preference to any other, unless odour cues from the two varieties are indistinguishable. Thirdly, plant resistance based on allelochemicals may well reduce the number of parasitoids arriving. This has in fact already been documented in relation to two cabbage cultivars with different levels of mustard oil glycosides. The varieties reversed their relative resistance ranking to cabbage aphid in the presence and absence of parasitoids (van Emden, 1978).

The three-way interaction

I mentioned earlier that reductions in insecticide concentration of at least one-third are usually possible on partially resistant cultivars without a reduction in the level of control of the pest that is achieved. Although natural enemies are usually (though by no means invariably) killed at lower concentrations of toxin than their pest prey, another characteristic commonly found is that the slope of their response of increasing mortality with increasing concentration is steeper than that of their prey. This is probably because carnivores lack the highly effective enzyme systems evolved by herbivores for metabolizing plant allelochemicals. Whatever the reason, the result is a remarkable opportunity for increasing the natural enemy: pest ratio on resistant cultivars whenever insecticides are used. This is because the herbivore response curve moves 'to the left' on resistant cultivars (unless based on allelochemicals, see earlier), whereas the same shift only occurs with the carnivore to the extent of any reduction in weight through feeding on prey on resistant cultivars.

Conclusions

The interactions between host plant resistance and insecticides or biological control may be advantageous or disadvantageous in terms of their pest management effect. Yet cultivars bred for resistance to insects are rarely tested for extrinsic resistance characteristics such as mortality response of the pest to insecticide, survival and fecundity of natural enemies or attractiveness to parasitoids and predators. I hope I have been able to convince you that this can well lead to host plant resistance contributing to pest mismanagement. One can generalize that this becomes increasingly likely the stronger the resistance and the more allelochemical its nature, two characteristics I believe to be inherent in the development of plant resistance to insects by transgenic methods.

On one hand, we can produce resistant plants on which pests are easier to kill with insecticide, on which we can make insecticide applications more selective and which build up high natural enemy:pest ratios. On the other hand, we can also develop resistant plants on which pests are tolerant to pesticide and on which natural enemies are killed or reduced in fecundity.

There are, unfortunately, few commercial reasons for choosing the first alternative, however desirable. Integrating partial plant resistance with other measures, particularly biological control, has little short term attraction for the farmer or grower. It has zero appeal for commercial organisations seeking to market transgenically resistant varieties. Plant breeders are another group who will not be too enthusiastic about partial resistance, except perhaps as a bonus in varieties marketed for some other desirable character.

I suppose the history and future of pest management or pest mis-management are subject to the same laws as those that affect government research funding or indeed many other areas of life - in the end, you get what you pay for!

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