

Stan Finch and Rosemary Collier

Horticulture Research International, Wellesbourne, UK

Why do we need to apply so much insecticide to prevent crop plants being destroyed by insects, when similar plants growing in natural ecosystems are rarely damaged? The answer lies 'in the soil' and 'in biodiversity' – but not in the way that most people suspect.

We live in a green world in which the organisms that dominate our view are plants. Yet virtually everywhere there are plants, there will be insects. Since man first started to cultivate plants, he has had to battle to prevent his crops being destroyed by insects. As an example, the main picture shows the impact of just one pest insect, the cabbage root fly (Delia radicum), when alternate rows of cauliflower plants were not treated with a soil insecticide. At present, we use only about 30 of the 250 000 species of higher plants to produce 95% of our food (Schoonhoven $et\ al.,\ 1998$). We also protect such plants using routine applications of highly effective insecticides. With such potent insecticides and with such a small number of plant species to protect, how have insects remained, and possibly increased their status, as pests of crops? The answer lies in the way current horticultural practices help insects to find crop plants.

Insect-plant relationships

Although about 45 books and 6000 scientific papers have been written during the last 30 years on the relationships between insects and plants, the way in which insects find their host plants has received little attention. The main stumbling block has centred on the belief held by most, but not all (e.g. Kennedy et al., 1961) entomologists, that plant odours govern all aspects of host-plant finding by insects. It is easy to understand how such a belief has arisen, as the secondary plant compounds, which give rise to plant odours, are characteristic for each plant species. Hence,

insects should be able to find their host plants using odour alone. The question is 'Do they?' In contrast, it is not easy to envisage how visual cues, and in particular plant colour, could help insects to find their host plants amongst surrounding vegetation, as most plants are green. Workers have suggested that insects could respond to specific wavelengths of light, or to the shapes and forms of their host plants, but such hypotheses have not been confirmed. This might seem surprising, as insects are credited with incredible powers for detecting mates, food and host-plants, often from long distances. Such opinions are usually based on the premise that because insects have been around for so long (first records in Upper Carboniferous period), they have had sufficient time to become highly specialised and hence successful. We believe that insects have become successful because they have kept things simple.

Host-plant finding – the clue; and earlier hypotheses

How then do insects find their host plants? A major clue is that many specialist insects (those that feed on specific species of plants) can be prevented from finding their host plants if other plants are grown alongside. Unfortunately this clue was neglected for at least 30 years, because some authors concluded somewhat forcibly that while non-host plants can prevent many herbivorous insects from finding their host plants, this is not an effective strategy against all species (see Altieri, 1994).

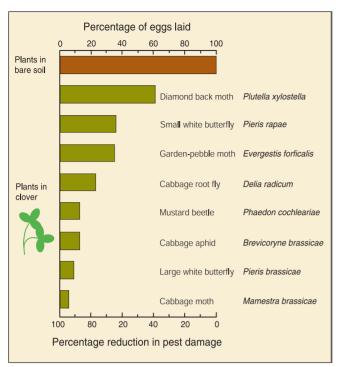


Figure 1. Numbers of eggs laid by eight insects on cabbage plants growing in clover (green columns) expressed as percentage of eggs laid on similar plants growing in bare soil (top brown column).

As a result of this constraint, earlier authors used their existing knowledge to explain why insects had greater difficulty in finding host-plants when they were growing amongst other plants. Some suggested that non-host plants camouflaged the host plants or simply obstructed the insects during their search. Others suggested that the odours given off by the non-host plants 'masked' those of the host-plant, or were sufficiently strong to deter the insects from entering such areas. Another hypothesis was that host plants took up chemicals, released into the soil by non-host plants, and that these chemicals altered the odour profile of the plant so that it was no longer 'recognized' by the searching insect. Even though these hypotheses have been reiterated many times during the last 30 years, no one has used any combination of them to produce a general theory of how insects find their host plants.

Preliminary work on host-plant finding

In an attempt to clarify the situation, studies were done at Horticulture Research International, Wellesbourne, to show why fewer pest insects colonise cruciferous crop plants (which include cabbage, cauliflower, Brussels sprouts, swedes and turnips) growing amongst other plants (here, clover). Figure 1 shows that clover had the same disruptive effect on eight pest species from four different insect orders. An identical effect was produced when host plants were surrounded by plant models made from green card (Figure 2), which do not release plant chemicals. Therefore, insects can be prevented from finding their host plants simply by providing the insects with more green surfaces on which to land.

The new theory

The above information was used to develop the 'appropriate/inappropriate landing' theory (Finch and Collier, 2000), which is based on the fact that herbivorous insects land indiscriminately on green surfaces.



Figure 2. Different sizes of plant models

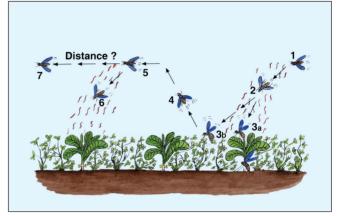


Figure 3. Diagram of how other plants, (here, clover – Trifolium spp.) influence host plant finding by the cabbage root fly. Numbers (1-7) represent insect actions (see text).

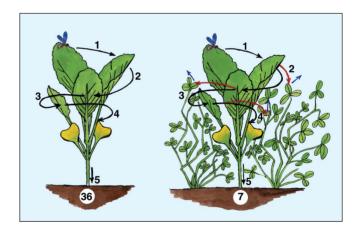


Figure 4. Diagram of how other plants influence host-plant finding by the cabbage root fly. Numbers represent the four leaf-to-leaf flights made by the fly before deciding whether the plant is a suitable one on which to lay its eggs.

The first phase of host-plant finding (Figure 3) consists of the searching insects (1) being stimulated by odours that characterise the host plant (2), simply to land. The insects land on any green surface but avoid landing on brown surfaces such as bare soil. When the insects land on the leaf of a host plant (3a), we describe the landing as 'appropriate'. When they land on any other leaf (here, clover (3b)) or green surface, we describe the landing as 'inappropriate'. Those insects that make 'inappropriate' landings (4) fly off the plant and repeat the process (5 and 6), or simply leave the area (7).

The second phase of host-plant finding (Figure 4) starts as soon as an insect lands on a host plant. Once this occurs, the

insect makes short flights (four are shown here for the cabbage root fly) from leaf to leaf to assess the overall suitability of the plant (Figure 4). The actual number of flights depends on the insect species involved and the amount of host-plant stimulus the insect receives from each leaf. To be successful, the insect must make a certain number of consecutive 'appropriate' landings to accumulate sufficient host-plant stimuli to lay eggs. However, if the insect makes an 'inappropriate landing', the process is terminated and the insect has to start again.

In effect, therefore, herbivorous insects have to find and re-find their host plants. On plants surrounded by soil, most insects land back on the same plant. On plants surrounded by other plants (e.g., clover), some insects land on the other plants and then fly off. Figure 4 shows that 36% of cabbage root flies laid eggs alongside cabbages growing in bare soil, compared to only 7% alongside cabbages growing in clover.

In essence, host plant selection consists of three main links. Chemical stimuli (plant odours) indicate when to land (Link 1), visual stimuli indicate where to land (Link 2), and stimuli (touch and taste) from the plant surface indicate whether to stay and lay, or fly away (Link 3). It is not surprising, therefore, that earlier experiments to show that Link 2 was regulated by plant odours proved intractable.

Biodiversity and bare soil

The major factors that affect host plant finding by insects are 'biodiversity' and 'bare soil'. Here, biodiversity means simply the number of other green surfaces within the insect's range of vision shortly before it lands. From a practical point of view, green surfaces are freely available as weeds, but unfortunately most growers no longer tolerate weeds within their crops. Hence, our current method of 'bare soil' cultivation is exacerbating our control problems by ensuring that crop plants are 'bound to be found' by the pest insects that pass through the cropped area. Is it any wonder, therefore, that growers who apply highly effective herbicides now believe their pest problems are getting worse? We believe that if some weeds were tolerated during critical times of crop growth, much less insecticide and fungicide would have to be applied. The information now needed by growers is how to balance leaving weeds to reduce pest infestations and removing weeds to avoid undue crop losses from plant competition.

Implications of the new theory

The new theory explains why herbivorous insects do not decimate plants in natural systems and why it is difficult to find pest insects on 'wild' host plants, even though adjacent crop plants growing in bare soil may be destroyed by such species. The new theory also has implications for pest insect control involving 1) insecticides, 2) companion planting, and 3) predatory insects.

1. The insecticide conundrum

Bare soil' is rare and even in cultivated fields is colonised rapidly by plant (weed) species. The environment tries hard to counteract our ecological disturbances but as soon as new weed seedlings emerge, growers usually destroy them. As bare soil' cultivation makes crop plants so easy to find, and insecticides kill only a fixed percentage of any insect population, more insecticide may have to be applied in future to maintain our current levels of pest control. Applying more insecticide to field crops would be unacceptable to many conservationists. This conundrum could be resolved by tolerating some weeds or by growing more than one plant





Figure 5. Cabbage plants undersown with clover, shortly after transplanting and shortly before harvest. No insecticide or fungicide was applied to these plants.

species in the same field, using undersowing (Figure 5) or intercropping (Vandermeer, 1989). Figure 5 shows that undersowing acts like a broad-spectrum insecticide by reducing the numbers of all pest insect species. Other advantages are that it does not contaminate the environment nor leave undesirable residues in the produce.

Before undersowing is adopted, however, work is needed to select suitable plant combinations and to determine how best to grow the two plant types together (Vandermeer, 1989) to ensure that the yield from the main crop is acceptable. Unfortunately, like most methods of control, undersowing will be more expensive and difficult to manage than insecticides. Therefore, the question that really needs to be answered is 'Can we afford not to use insecticides?'

2. Companion planting

It was thought previously that many herbivorous insects that landed on aromatic plants, such as mint, thyme and rosemary, found chemicals on the leaf surfaces distasteful and soon flew off such plants. This is the basis of the 'companion planting' approach of organic growers in which, for example, onions and marigolds (Figure 6), chosen for their pungent odour and taste, are grown interspersed with crop plants to deter pest insects, such as the carrot fly (Figure 7). Recent results have shown, however, that onions and marigolds disrupt host plant finding by insects simply by being green. The disruption has nothing to do with their odour or taste. Of 24 plant species tested, the aromatic plants, curry, marigold, mint, onion, sage and



Figure 6. Onions and marigolds.





Figure 7. Carrot fly adult and damage done by fly larvae on unprotected plants.



Figure 8. Predatory ground beetles found commonly in cultivated soils.

thyme were no more disruptive than non-aromatic plants. From a practical point of view, therefore, growers could use any non-host plant to prevent insects from finding their crop plants.

3. Predatory insects and biodiversity

Another current belief is that increasing the diversity of plants within a field causes more predatory ground beetles (Figure 8) to aggregate around the crop plants and that these predators then eat more pest insects. This hypothesis was used by Root (1973) to explain why fewer pest insects were found on crop plants growing amongst other

plants. The question is 'Why should more predators be found around plants growing in weedy backgrounds, when most of their prey items are found on plants growing in bare soil?' Again, the difference can be explained simply because fewer pest insects colonise host plants growing amongst other plants. Care is needed to ensure that when more ground beetles are found in more diverse cropping systems, the additional beetles are those that eat pest species, and not those that feed directly on dead and decaying plant material or on other invertebrates associated with such materials.

Conclusion

'Appropriate/inappropriate landings' provides a robust description of host-plant selection by insects. Hence, to paraphrase the mock doctor from Molière's *Le Médecin Malgré Lui*, instead of accepting the current doctrine, *nous avons changé tout cela* (we have changed all that), we believe the simplicity of our theory makes it all embracing. Only time will tell whether our optimism is justified.

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Websites

None available – but further information on this subject can be obtained by mailing stan.finch@hri.ac.uk

Stan Finch is an Emeritus Fellow and Dr Rosemary Collier a Team leader at Horticulture Research International (HRI), Wellesbourne, Warwick CV35 9EF, UK.