HOST PLANT SELECTION BY INSECTS

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Host plant selection by insects is often divided into 'host plant finding' and 'host plant acceptance.' While the two are easy to separate conceptually, in practice, they are really part of a continuum of three, rather than two, inextricably bonded links. However, the central link of host plant finding, thought previously to be governed by volatile chemicals, has, until now, proved intractable to scientific experimentation. Thus, the focus here is on host plant selection by insects associated with cruciferous plants as, since the classical work of Verschaffelt in 1910, most theoretical studies on herbaceous plants have used the interaction between insects and cruciferous plants as their test system. Such a selection is logical, as cruciferous (Cruciferae) vegetable and oilseed crops are of high economic importance and are now cultivated on large farms in most parts of the world. In addition, cruciferous plants are ideal for biological studies, as their chemistry is well understood and they support pest species from a wide range of insect orders.

Many researchers have shown that the numbers of pest insects found on cruciferous crop plants are reduced considerably when the background of the crop is allowed to become weedy, when the crop is intercropped with another plant species, or when the crop is undersown with a living mulch. Obviously, if placing non-host plants in the vicinity of host plants reduces the numbers of insects that actually find their host plants, then this could provide a clue as to how insects find their host plants. It has been suggested that when the background of crop plants growing in bare soil is made more diverse by allowing other non-host plant species to grow in the inter-row spaces, that the additional diversity "disrupts" insects from selecting otherwise acceptable host plants. Such disruption is considered to be mediated through the non-host plants providing 1) physical obstruction, 2) visual camouflage, 3) masking of host plant odors, 4) repellent chemicals, or through 5) the non-host plants altering the physiology of the host plants. Two other suggestions, named by Root (1973) as the 'Resource Concentration Hypothesis' and the 'Enemies Hypothesis,' have also been used to explain why fewer phytophagous insects are found on host plants growing in diverse backgrounds than on similar plants growing in bare soil.

A discussion of the seven hypotheses put forward to date is presented here, followed by a description of a theory based on 'appropriate/inappropriate' landings, which the authors believe is the key, or 'missing link,' to host plant selection by phytophagous insects. Finally, the new theory will be used 1) to discuss the type of information required to make intercropping, undersowing and companion planting more successful, 2) to suggest how insect biotypes could develop, and 3) to describe why wild host plants are not decimated by pest insects.

Description and discussion of the seven earlier hypotheses

Physical obstruction - This hypothesis was used to describe those situations in which the host plants were, in effect, hidden physically by using larger or taller non-host plants. For example, tall maize plants were used to protect bean plants from pest infestations. Tall plants were considered to be effective because they obstructed the movement of the pest insect within the cropping system.

It could be argued that there is an element of physical obstruction when clover disrupts host plant finding by pest insects of brassica crops as, to have maximum impact, the foliage of the clover has to surround much of the host plant. Although clover growing in such close proximity to the host plant will obviously obstruct the searching insects, no suggestions have been made as to how this mechanism might operate.

However, a mechanism relying solely on physical obstruction is not supported by recent findings in which clover plants were desiccated so that they retained the same architecture as the living plants and differed only in color, being brown rather than green. When the cabbage root fly (*Delia radicum*), the diamondback moth (*Plutella xylostella*) and the large white butterfly (*Pieris brassicae*), were presented with host plants surrounded by desiccated (brown) clover, the number of eggs laid did not differ from the numbers laid on host plants presented in bare soil. Hence, the physical presence of the clover was not sufficient on its own to reduce the numbers of eggs laid, a reduction occurred only when the surrounding clover was green.

Visual camouflage - This hypothesis was based on the two types of visual stimuli that induce low-flying insects to land on plants. The first is a directed response to the color of the plant, which, in most cases, means green, and the second is an optomotor response in which landing is provoked by plants "looming up" along the path of the flying insect. Anything that competes with such stimuli, such as other green plants, or raising the height of the overall background with weeds so that the distance over which the host plant can be separated from the background is foreshortened, helps to visually camouflage the host plants. This makes the host plants less 'apparent' among the foliage of the non-host plants.

Although many authors showed clearly that aphids, whiteflies and certain Lepidoptera preferred plants that stood out against a background of bare soil, no attempts were made to determine how such a mechanism might operate.

Masking of host plant odors - The release of 'odor-masking' substances into the air by non-host plant species is considered to confer some protection to the associated host plants. Although this 'associational resistance' seems a plausible hypothesis, few data have been collected during the last 25 years to support it.

The possibility that the odor of the host plant could be masked by that of the non-host plant now seems much less likely, though not impossible. For example, host plant selection by the cabbage root fly was disrupted when its host plants were surrounded by a range of different plants including the weeds fat-hen (*Chenopodium album*), fumitory (*Fumaria officinalis*) and spurrey (*Spergula arvensis*); and cultivated plants such as pea (*Pisum sativum*), onion (*Allium cepa*), carrot (*Daucus carota*), rye-grass (*Lolium perenne*), or clover (*Trifolium*). As each of these non-host plants has a different odor profile, it seems highly improbable that they would all be capable of preventing an adapted specialist insect from finding its host plants. Furthermore, observations made in wind tunnels revealed that brassica plants growing in clover were approached by cabbage root flies as readily as brassica plants growing in bare soil, indicating that the odors from the clover did not mask those of the flies' host plants. More striking, however, was that the same disruptive effect could be produced by surrounding the host plants with plant models made from green cardboard, or simply with sheets of green paper, neither of which were releasing plant chemicals. It seems that once the characteristic host plant chemicals stimulate the insects to land, the disruption is caused simply by providing the insects with a greater number of green surfaces on which to land.

Repellent chemicals - It is implicit in this hypothesis that the odors given off by the non-host plants are sufficiently strong to actually repel the searching insects. It was suggested that the diamondback moth could be repelled from cabbages by intercropping the cabbages with tomatoes (*Lycopersicon esculenta*) and that the highly odorous ragweed (*Ambrosia artemisifolia*) could be used to repel the cabbage flea beetle (*Phyllotreta cruciferae*) from crops of collard (*Brassica oleracea* var. *acephala*). Such suggestions were made to describe why pest insect numbers were different in the two situations. They were not based on scientific experimentation. Whether or not true deterrency is a mechanism still needs to be proven. Deterrency usually involves highly aromatic plants that often have to be crushed and tested in small, confined spaces in the laboratory to show that they are actually capable of repelling pest insects. As such tests are far from natural, the validity of using such data during the synthesis of new behavioral mechanisms is questionable. In reality, no experimental evidence has been produced during the last 15 years to support the hypothesis that plants produced effective levels of chemical repellents.

Plants chosen for their odorous nature, such as French marigolds (*Tagetes patula*), failed to deter the carrot fly (*Psila rosae*) when used as the intercrop in carrots. In addition, oviposition by the diamondback moth was similar on Brussels sprouts (*Brassica oleracea* var. *gemmifera*) plants intercropped with plants of sage (*Salvia officinalis* L.) and thyme (*Thymus vulgaris* L.), two plant species selected for their pungent odors. Extracts of the essential oils of sage and thyme were shown to reduce oviposition by the diamondback moth, but the effect resulted from contact stimuli and not from repellent volatile stimuli. Doubtless, many contact chemicals play a major role during host plant acceptance, but as these come into play only after an insect has landed, they are included only in the second part of this review, which is concerned with host plant acceptance.

Altering the profiles of the host plant odors - While this seems a novel mechanism, it relies upon the host plants' inability to metabolize certain chemicals they take up from the soil, so that such chemicals, in effect, change the subsequent physiology of the plant. Many claims are made that African marigolds (*Tagetes* spp.) planted between rows of crop plants reduce pest numbers. It is clear from the earlier discussions that this is unlikely to be a direct effect of the odors of the African marigolds repelling the colonizing insects. However, it is well known that species of African marigolds release large amounts of root exudates, which can be taken up by adjacent plants. It is possible, therefore, that any host plant growing in an intercrop could be affected directly by chemicals taken up through its roots rather than by having its odor masked.

To test whether the uptake of such chemicals was responsible for the differences in plant colonization, several batches of the host plants were left in their pots throughout the test periods. As the effects of the clover were still evident, and often within minutes of starting an experiment, a generic mechanism based on the non-host plants (here, clover) causing physiological changes in the host plants cannot be supported.

The resource concentration hypothesis - The last two hypotheses are the ones quoted most frequently. Both were derived from one study in which Root monitored insect distribution during three field seasons in pure stands of collard plants and in single rows of collard plants bounded on each side by diverse meadow vegetation.

The "Resource Concentration Hypothesis" states that phytophagous insects are more likely to find and remain on host plants that are growing in dense or nearly pure stands. Phytophagous insects that arrive in a clump of host plants, by whatever means, and find conditions suitable, will tend to remain in the area. This "arresting effect" of host patches will depend upon several factors such as the size and the purity of the plant stand and the type of host plant required by the phytophagous insect. In many cases, this accumulation of specialist insects on a concentrated resource (here, cultivated *Brassica* plants) will be sufficient to increase the numbers of phytophagous insects in that locality. Again, this hypothesis describes simply the effect of changes in the purity of a host plant stand on insect numbers and does not include any attempt to develop a general theory to describe how phytophagous insects select their host plants.

The enemies hypothesis - Contrary to five of the earlier hypotheses, which claim that the differences are due to the direct effects of the diverse backgrounds on the behavior of the pest insects, this hypothesis, like hypothesis 5 (altering the profiles of the host plant odors), proposes that the effects are indirect. In essence, this hypothesis proposes that lower numbers of phytophagous insects are found in complex environments because predators and parasitoids are more effective in such situations. Thus, outbreaks of phytophagous insects are checked early by the higher numbers of enemies that can be supported by the diverse resources available in complex environments. Unfortunately, Root found that the effectiveness of the "enemies" did not differ significantly between collards grown as pure stands and those grown in single rows among diverse meadow vegetation. Nevertheless, Root pursued this "enemies hypothesis" by discussing sets of data collected mainly in England. His own, more extensive data, however, indicated clearly that the diversity of both predators and parasitoids was higher in the pure stands, probably because more prey/host species were also present in that habitat. Consequently, he concluded that factors other than natural enemies were responsible for much of the differences in insect numbers recorded between simple and diverse habitats. Although Root himself discounted the "enemies hypothesis," many subsequent scientists have championed the cause of predators, often on the flimsiest of evidence, or without collecting the data necessary to support their claims.

Conclusions from recent work

Although authors have indicated that diverse backgrounds can affect host plant selection in the seven ways described above, it is hard, from the results presented in recent publications, to refute the more simplistic view that one mechanism is operating against all species. Recent work published by Finch and Collier (2000) included experiments on the cabbage moth (*Mamestra brassicae*), the diamondback moth, the garden pebble moth (*Evergestis forficalis*), the small white butterfly (*Pieris rapae*), the large white butterfly, the cabbage aphid, the cabbage root fly and the mustard beetle (*Phaedon cochleariae*). Despite these eight test species being from four insect orders, the ability of each of them to find host plants was affected adversely, though to differing degrees, when their host plants were surrounded by clover. It appeared that differences in the initial rates of colonization were the factor that regulated the numbers of phytophagous insects found on host plants growing in bare soil or clover, as differences between the two situations were often apparent within minutes of starting an experiment.

Description and discussion of the new theory

Unfortunately, no one has yet developed any of the earlier hypotheses into a robust general theory, they are still only hypotheses. Hence, we have generated our own theory from detailed studies of insect behavior.

Instead of the seven hypotheses described previously, we believe that a mechanism that we have described as 'appropriate/inappropriate landings' is the central link in host plant selection by insects. In the overall system, the new theory of host plant selection can be divided into a chain of actions involving just three links. In the first link (Link 1, Fig. 1), volatile chemicals emanating from plants indicate to flying, receptive insects that they are passing over suitable host plants. Once the odor of the host plant in the air becomes sufficiently concentrated, it induces the insect to land. In this way, the volatile chemicals bring the insects into the close vicinity of the host plants. However, during the last few milliseconds, when the insects are only a short (often less than 1 m) distance away from the plant, instead of maintaining their directed response to volatile stimuli, phytophagous insects switch to a directed response to green objects, which, in most cases, means to plant leaves. It is logical that vision takes over at this stage, as most flying animals use vision to 'pin-point' a suitable object on which to land. Therefore, insects that fly over plants growing in bare soil will be stimulated to land on host plants, the only green objects available to them, as most phytophagous insects avoid landing on brown surfaces, such as soil. When host plants are growing in bare soil, most landings will be what we have classed as 'appropriate,' and so, the host plants will, in effect, 'concentrate' the insects. In contrast, insects flying over host plants surrounded by clover land in proportion to the relative areas occupied by leaves of the host and non-host plants, as specialist phytophagous insects do not discriminate between the two when both are green. Hence, any landings made on the non-host plant are classed as 'inappropriate.' The amount of time the insects spend on the leaves of the non-host plants before taking off again is governed by whether the insects receive acceptable or antagonistic stimuli through their tarsal receptors. Once the insects are again airborne, if they are stimulated to land after flying only a relatively short distance, they could land on a host plant. In all situations, however, the plant on which the insect first lands, even if it is a 'host plant,' may not stimulate the insect sufficiently to cause it to remain on the plant, and the overall process will be repeated. If this represented the complete system, then under 'no-choice' situations in the field, it would just be a matter of time before the numbers of eggs laid on host plants growing in diverse backgrounds were similar to those laid on host plants growing in bare soil. However, this does not occur, as there is a second phase to host plant finding.

This second phase can be illustrated (Fig. 2) most clearly by data collected from a detailed study of the cabbage root fly. Before accepting a host plant as a suitable site for oviposition, receptive female cabbage root flies make, on average, four spiral flights before laying eggs beside the plant. Hence, the insects stand a much greater chance of "losing" the host plant in a diverse background as, on average, they repeat the initial appropriate/inappropriate landing procedure an additional three times. Observations under laboratory conditions showed that for every 100 females that landed on a brassica plant surrounded by bare soil, 36 received sufficient stimulation from the plant to be induced to lay eggs. In contrast, only seven out of 100 females that landed on host plants surrounded by clover managed to lay eggs. Fewer flies managed to lay eggs in this situation, because following each short spiral flight, a proportion of the flies landed on the leaves of the surrounding clover plants. This failure to re-contact a leaf of a host plant after any spiral flight prevented the females from accumulating, within the allotted time, sufficient stimulation from the host plant to be induced to lay eggs. Hence, the barrier that this fly faces when its host plants are grown in diverse backgrounds is not chemical nor mechanical, but behavioral, simply because during the innate series of spiral flights, the fly must continue to accumulate more positive host plant stimuli each time it lands.

The amount of stimulation the female picks up on each landing is crucial, and this is where the phase of host plant finding (Link 2) becomes truly integrated with host plant acceptance (Link 3). In essence, the complete system really involves finding and refinding the host plant. Obviously, the insect can re-find the host plant quite easily in bare soil situations, but not as easily when the plant is growing in a diverse background of other plants. The schematic representation shown in the figure indicates that the female cabbage root fly may only have to visit two leaves of a highly stimulating plant [1] compared to six leaves on a poorly-stimulating plant [3] before finding it an acceptable site to oviposit. Other insects, however, may accumulate sufficient stimuli to keep them searching [4], but not sufficient stimuli to induce oviposition and so will fly away. A similar outcome results when insects visit several leaves (here shown as 3a, 3b, 3c) but do not manage to accumulate sufficient stimuli in the allotted time to be induced to stay [5]. Two other variations occur when the insects land initially on a stimulating leaf, but subsequently on a non-stimulating leaf. It does not matter whether this leaf is from a host [6] or a non-host plant [7], as anything that interrupts (Fig. 3) the rate of accumulation of positive stimuli causes the insect both to abort its attempt to lay and to move elsewhere. In addition, interspecific competition may also become important. At any stage during the host plant selection process, many of the new immigrants may not remain on otherwise acceptable plants if those plants are colonized already by certain, but not all, of the other insect species present in the pest complex.

The physiological status of the insect, which depends partly on its age and also on how long it has been deprived of a suitable oviposition site, also has to be superimposed upon this already complex system. With time, phytophagous insects tend to become less discriminating in their choice of oviposition sites. The condition of the plant is also extremely important, as some cruciferous plant species are more highly preferred than others, and during their phase of exponential growth, many individual plants become highly stimulating to insects. However, even when the insect and the plant are both in the appropriate physiological state, it counts for nothing the moment the insect makes a wrong choice and alights on any green object other than a leaf of a host plant. This, however, is tempered by the fact that when the host plant is highly stimulating, the insect has to visit fewer leaves and so has less chance of making an inappropriate landing. In addition, the highly stimulating plants invariably induce the individual insects to lay more eggs. Detailed descriptions of the multitude of other factors involved during host plant acceptance can be found in many of the papers published in 1999 in the proceedings of the Tenth International Symposium on Insect-Plant Relationships.

Although the other seven test species mentioned earlier have not been studied in detail, records of the movements of the small white butterfly in the field showed that it always made contact with several leaves, interspersed with short flights, before laying an egg. Although the original author concluded that this butterfly needed some flight time to get the next egg ready, these short flights could also represent a behavioral repertoire similar to that of the cabbage root fly. It seems likely, therefore, that the relative differences in the effects that diverse backgrounds have on host plant selection by the test species may simply reflect the numbers of contacts/re-contacts the insect has to make to accumulate sufficient positive stimuli to lay eggs. Results from recent experiments indicated that the diamondback moth was the species affected least by diverse backgrounds. It raises the question of whether the diamondback moth has become such a major pest of cruciferous crops simply because it has a limited behavioral repertoire prior to oviposition, and so, lays eggs on more or less the first host plant leaf it encounters.

General discussion

The 'appropriate/inappropriate landing' theory can be used to explain why certain aspects of host plant finding by phytophagous insects, supposedly regulated by volatile plant chemicals, proved intractable to scientific experimentation in the past.

Compared to our simple theory of host plant finding, other theories invoke complex processes involving volatile chemicals to guide phytophagous insects to their host plants. For example, it is known that the odorous environment of a given insect is a shifting maze of overlapping active spaces. Therefore, it was suggested that it is in this shifting maze that the insect must find the active space containing those few signals that will lead it to its host plant. However, in the open air, it is turbulence rather than diffusion that determines the distribution of odorous molecules, and there is nearly always a prevailing wind to blow the odorous molecules away from the plant. Registering directional cues from odorous molecules is even more complicated for flying insects, as the movement of the air relative to the insect depends on the insect's own activity, and the wind direction has to be determined by the insect in the absence of fixed markers.

The evidence that volatile chemicals are the main regulatory stimuli in the central link of host plant finding is weak, as the maximum distance recorded for insect orientation to host plant volatiles in the field is only a few meters. In wind tunnel experiments, cabbage root flies flew upwind to a cruciferous plant odor released at 2.5g/day, a rate similar to that dispensed from field traps. This rate of release is at least 10^5 times higher than the amount of chemical released from a healthy cruciferous plant. Although the flies moved upwind in response to this odor, less than 10% of the flights lasted more than 0.5 m. While the shortness of such flights was described as unexpected, it would not have been unexpected had the chemicals involved been regarded as arrestants rather than attractants. Similarly, with insect traps releasing large amounts of chemical to provide directional cues in the field, many insects miss the trap and subsequently fail to enter, suggesting again that stimuli other than volatile chemicals take over once the insect nears the source of the odor. The current mechanism seems much more robust than one based on volatile chemicals, as the sooner an insect lands, the sooner it is freed from the plethora of problems it faces while still in the air.

The 'appropriate/inappropriate landing' theory works equally well for generalist feeders, where the decision of whether to stay is determined primarily by the chemicals the insect detects via its contact chemoreceptors once it has landed on a leaf. However, it should be remembered that if an insect that is considered to be a 'generalist' has been stimulated to land by volatile chemicals released from a specific plant species, the insect may continue its search for such a plant rather than choosing the first acceptable plant it encounters.

Finally, the 'appropriate/inappropriate landing' theory appears to apply equally well to nocturnal insects, as oviposition by the diamondback moth and the cabbage moth was not disrupted when their host plants were surrounded by brown clover. Although both of these moth species are considered to be nocturnal, much of their oviposition activity is concentrated at, or shortly before, dusk. The above results indicate that during this period, both species of moth appeared to be able to discriminate between green and brown objects.

From a crop protection standpoint, the more non-host plants removed from any crop area, the greater chance an insect has of finding a host plant. Hence, current cultural methods are exacerbating pest control problems, as ‘bare soil’ cultivation ensures that crop plants are exposed to the maximum pest insect attack possible in any given locality.

Future work

If the theory based on ‘appropriate/inappropriate landing’ is accepted, it raises searching questions regarding several aspects of entomological research.

In the first instance, we have expressed considerable doubts about whether host plant volatile chemicals on their own are capable of guiding phytophagous insects to their host plants. Most of the detailed experiments with host plant volatile chemicals have been done by releasing plant odors from a point source sited at one end of a wind-tunnel, introducing responsive insects and then recording whether the insects move upwind to the source of the odor. Results from this approach have been disappointing. Often, the only way to obtain data is to place a visual stimulus, normally a green object, alongside the site where the volatile chemical is being released.

If, as the ‘appropriate/inappropriate landing’ theory suggests, it is only the number of green objects surrounding a host plant that reduces colonization by pest insects, then it should not be too difficult in the future to quantify the type and number of plants needed for the diverse background to reduce pest insect numbers in any given crop. If several plant types proved appropriate for a given cultivated crop, it would then simply be a case of choosing the one that caused the least reduction in yield to the harvested product.

There is also a need to obtain a better understanding of ‘companion planting,’ a practice used frequently by organic growers. Recent data show that there is no scientific evidence proving that the odors from highly aromatic plants can actually deter pest insects. This, therefore, brings into question how these aromatic plants produce their effects. A survey of the literature should help to show whether such systems are effective only when the companion plants possess relatively large amounts of foliage when compared to the crop plants. If this idea can be substantiated, the differences recorded may simply be a reflection of appropriate/inappropriate landings, and, again, have little to do with volatile chemicals, no matter how pungent the plant odors might appear to the researcher.

Apart from its impact in practical pest control situations, the ‘appropriate/inappropriate landing’ theory helps also to explain why wild host plants growing among other plants in natural vegetation are rarely decimated by pest insects. However, some insects that are considered to be pest species do develop on wild-host plants. The question then, is do such insects prefer to remain on the wild host plants in subsequent generations, a situation that could give rise to biotypes? The answer to this question is of considerable practical importance. Future work is required to determine what proportion of any given pest population develops on wild-host plants, and whether such insects readily switch back to the cultivated crop plants. If they do not, then it should be possible to control certain pest insects by isolating new crops from earlier infestations.

Additional work is required also to determine whether appropriate/

inappropriate landings influence the overall distribution of the parasitoids of the pest species. It is well documented that such insects use both host plant chemicals and kairomones to locate their host insects. Research in the 1940s in which cabbage plants were infested with the larvae of the small white butterfly were placed in bare soil crop fields and in hedgerows, showed clearly that one specific parasitoid, (*Apanteles rubecula*), was also affected adversely when the plants on which its host insects were feeding were placed into a diverse background. Further work is needed on other parasitoids to determine whether this is a general phenomenon. If it is, then the suggestions of some researchers that diverse backgrounds have adverse effects on pest insects and no effect on their parasitoids warrant further study.

Similarly, with respect to the 'Enemies Hypothesis,' it should not be too difficult to show whether predation is higher on infested plants surrounded by non-host plants, than on similarly infested plants surrounded by bare soil.

As much of the aforementioned work has been based on detailed information on the cabbage root fly, work is needed to determine the detailed activity of each of the other pest species. It appears that diverse backgrounds may have a greater effect on the cabbage root fly than on the diamondback moth simply because, before acquiring sufficient stimulus to oviposit, the cabbage root fly repeats the sequence of host plant finding four times, but the diamondback moth only once. It would be difficult to prove that once the cabbage root fly starts one of its spiral flights it is again stimulated to land (arrested) by volatile chemicals, as the distances between taking-off and landing again are extremely short. However, olfaction is considered to be used by phytophagous caterpillars in choosing their feeding sites, so the intervention of olfactory stimuli again at this stage cannot be ruled out.

The hypothesis of 'appropriate/inappropriate landings' does appear to provide a robust description of host plant selection by insects under a wide range of different conditions. It shows how elements of all the earlier hypotheses can be incorporated into the overall system, and in particular, how the lack of detailed research on insect behavior, and in particular, on visual stimuli, has led to many of the current anomalies. Apart from the future work proposed, it will be interesting to determine whether the same theory regulates host plant selection by specialist insects found associated with plant families other than the Cruciferae. While we believe the simplicity of our theory makes it all-embracing, only time will tell whether our optimism is justified.

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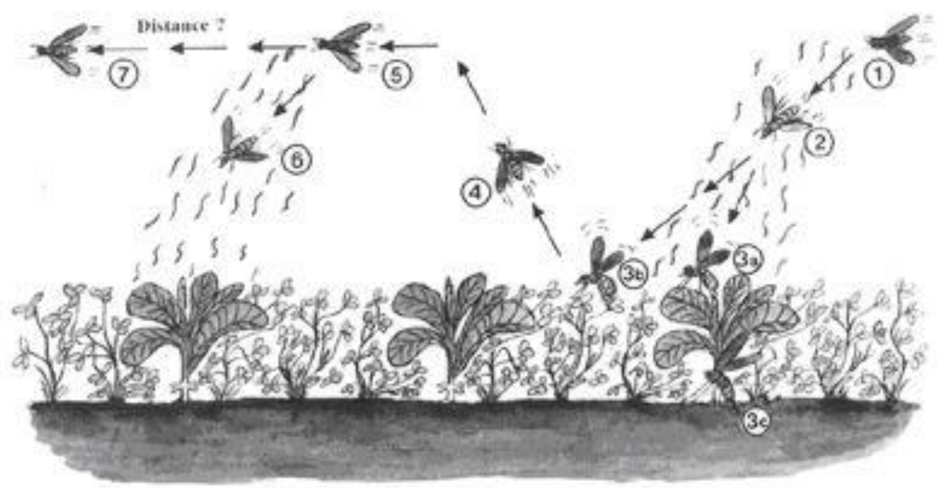

Figure 1. Schematic diagram to illustrate how diverse backgrounds, here represented by clover (*Trifolium* spp.), influence host plant finding by the cabbage root fly. Numbers represent insect actions 1-7 (see text).

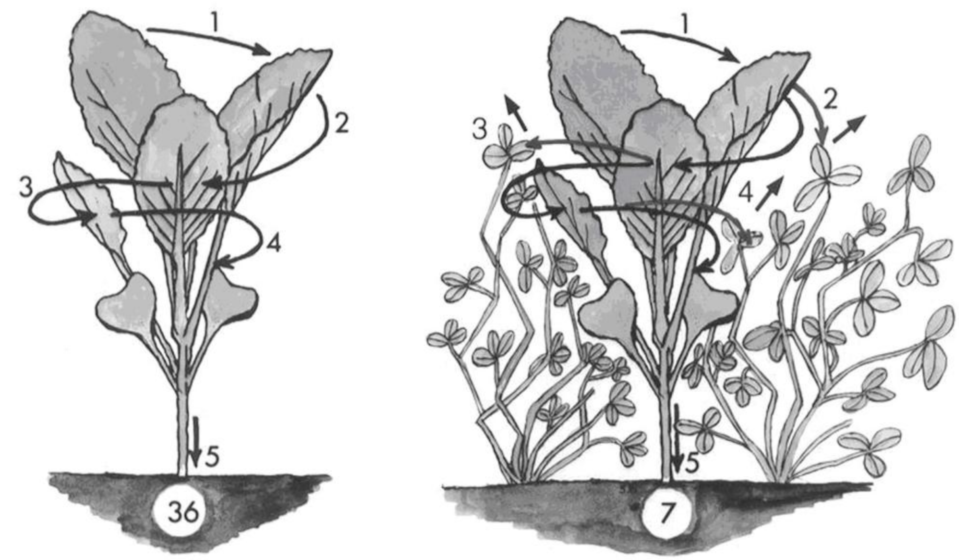

Figure 2. Schematic diagram to illustrate how diverse backgrounds, here represented by clover (*Trifolium* spp.), influence host plant acceptance by the cabbage root fly. Numbers represent the four (mean no.) leaf-to-leaf flights made by the fly to ascertain whether the plant is a suitable site to lay its eggs.

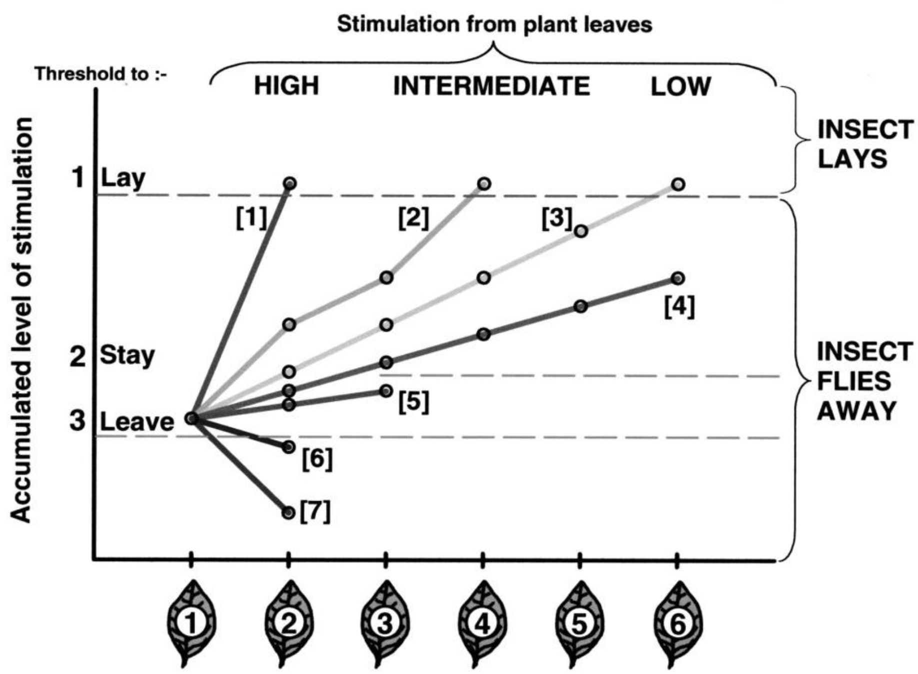

Figure 3. The number of leaf landings a cabbage root fly may have to make before accepting a plant as a suitable site for oviposition or deciding to fly elsewhere. The numbers in [ ] represent seven possible variations in the pattern of insect behavior.