

Acknowledgments

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SCREENING OF PHYTOPHAGOUS INSECTS FOR BIOLOGICAL CONTROL OF WEEDS

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Abstract

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It is necessary to demonstrate the host specificity of an exotic phytophagous insect before introducing it for the biological control of a weed. The widely-used "starvation test" made on economic plants is considered inadequate for this purpose and we propose that studies should be broadened to include the following: (1) study of the insect's biology, including host-plant records, with particular attention to adaptations likely to restrict the host range, (2) review of the plants attacked by related insects, (3) determination of the laboratory host range of the insect, (4) investigation of the chemical or physical basis of host-plant recognition, (5) starvation tests on economic plants to confirm the limits of the previously established host range, (6) establishment of the insects' potential effectiveness for weed control. A limited amount of feeding on economic plants in the laboratory is not reason for rejection, if other criteria show the insect has a high degree of specificity.

Introduction

The purpose of this paper is to consider how to demonstrate the host specificity of a phytophagous insect that is of interest for biological control of a weed. Most countries require that, before an exotic phytophagous insect is released, it is shown beyond reasonable doubt that the insect will not damage any desirable plant. The standard method for doing this has been the starvation

test or the negative-oviposition test, depending on the insect concerned. These tests confine the insect to a selection of important economic plants to see whether it will lay or feed on them. An insect associates itself with a particular plant by its choice of food and (or) oviposition site, so that it is logical to examine these processes to determine host specificity. However, the refusal of an insect to eat or lay on a particular plant provides no guarantee of immunity to other plants in the family, as has usually been assumed, and the alternative of screening all desirable plants is obviously impracticable. The tests are easily done and would be more than justified for the public reassurance they give (as they are often superficially convincing) if a host-specific insect could be relied on not to accept the non-host plants in the test. Unfortunately caged insects commonly lay on, eat, and survive on more plants than they attack in nature. At best this behaviour is inconsistent with proving the safety of the insect for release and it may result in the rejection of a potentially useful species (Huffaker 1962). For example, the moth *Utetheisa pulchella* (L.), which is one of the principal enemies of common heliotrope in the Mediterranean, would not pass current standards for introduction to Australia. However, the moth is already present there and causes severe damage to the weed but no recorded damage to any useful plant (Wilson 1960).

Most difficulties with present methods of assessing specificity arise from depending on just one aspect of an insect's biology studied under conditions divorced from reality. An insect restricted to a narrow range of plant species is usually specialized in many features of its biology, morphology, and physiology. The specializations both aid the survival of the insect and make its dependence on its host obligatory; but this dependence does not necessarily carry over to laboratory conditions. For example *Chrysolina quadrigemina* (Suffr.) is a beetle found on *Hypericum perforatum* L. growing in dry sites (Panin 1944). It is apparently restricted to these sites by an obligate aestival diapause which it cannot enter under continuously wet conditions (Huffaker 1967). However, in laboratory feeding tests the beetles did not show any preference between *H. perforatum* and the semiaquatic *H. boreale* (Britt.) Bickn. (Smith 1958).

We believe the answer to these difficulties is to assess the specificity of an insect on the basis of a comprehensive study embracing both experimental and empirical evidence. It is impracticable to prepare a check list of specific items that should be investigated, as what is appropriate for a gall insect is not necessarily so for a leaf-feeding caterpillar. Instead, we have proposed six investigations that we recommend be made before an insect is released for biological control of a weed in North America.

Proposed Investigations to Replace the Starvation Test

1. *An Investigation of the Insect's Biology with Attention to Any Adaptations Likely to Restrict Its Host Range*

Host plants and particularly any records of attack on economic species should be noted. Occasional records of insects on an economic plant do not necessarily indicate feeding as they often arise from misidentifications and confusion between resting sites and host-plants. They do, however, justify the inclusion of the plant in a feeding test. On the other hand substantiated records of damage to a crop of importance in the country of introduction obviously eliminate the insect from further consideration for biological control. The reliance placed on the absence of records of damage to an economic plant must vary with the

region concerned, but there can be little doubt that *Celerio euphorbiae* (L.), a common and conspicuous insect in western Europe, is not a pest. A quick survey for records of damage to crops can be obtained from the *Review of Applied Entomology* and all volumes should be checked for each insect. A field survey may also be necessary for a rare or little-known insect, both to determine its natural host range and to check for damage to economic crops.

The adaptations likely to restrict an insect to a particular plant are of five kinds:

(1) *Physiological*.—Examples are attraction of the insect by an odour, or even the immunity to a generally toxic substance that ties the insect closely to its host. Also, the ability of gall insects to produce the host reaction necessary for its survival.

(2) *Morphological*.—Examples are restriction of oviposition on thistles to buds of a specific size by ovipositor length in trypetids and rostrum length in *Larimus* spp.

(3) *Phenological*.—The synchronization of the insect with the growth of its host hinders its transfer to other plants growing out of phase. Likewise, the lack of synchronization between oviposition and fall rains in California prevented the beetle *Chrysolina hyperici* (Forst.) from becoming abundant in California (Huffaker and Kennett 1952).

(4) *Ecological*.—The susceptibility of the insect to frost, or the susceptibility of the eggs to desiccation restrict insects to certain geographical areas. The key ecological factors involved are not necessarily obvious and may require a detailed study to determine them. On the other hand, the obligatory association of an insect with an aquatic environment will obviously prevent damage to land crops; so this aspect need not be investigated further.

(5) *Ethological*.—Behaviouristic specializations of oviposition, or egg hatching and larval feeding may restrict insects to a particular part of the plant. Hence an insect that develops inside a seed is unlikely to damage the vegetative parts of a plant.

2. *A Review of the Plants Attacked by Related Insects*

We place a high degree of reliability on host specificity, if the insect belongs to a systematic group (species, section, subgenus, or higher taxon) which is restricted to a small group of closely-related plants (genus, subtribe, or tribe). This restriction indicates that the insect taxon has speciated on the plants concerned; hence over a long time and usually wide geographical area, the insect taxon was unable to exploit successfully any other plants. The association of insect and host taxon over widely separated geographical areas is another criterion of stability of the relationship. On the other hand, an insect that shows a tendency to form host races or develop regional differences in host selections is less desirable than a monotypic species. However, many cases of host races reflect only slight differences in host pattern. These are the result of limited steps towards host transfer within the susceptible plant taxon and should not be viewed with alarm.

A knowledge of the host plants of closely-related insects provides a good basis of selecting plants to be included in laboratory feeding tests, as after the known hosts, they are the plants most likely to be attacked. For example, *C. euphorbiae* L. larvae are known to feed on *Euphorbia* but, before introducing it against this weed in Canada, the larvae should be subjected to feeding tests on

grape, a plant that other species of *Celerio* attack. However, no species in the genus *Celerio* or even in the sphingid section *Semanophorae* attack pine trees; hence pine is unlikely to be palatable and has a low priority for inclusion in the feeding tests.

3. *The Determination of the Range of Plants that the Insect Can Be Induced to Eat or Accept for Oviposition in the Laboratory*

The starvation test shows that important economic plants are immune to attack, whereas the test we advocate shows what plants are acceptable to the insects. The difference is in the plants that are used, as the tests are done in the same way. The four groups of plants that should be covered by this test are those related to the known host, the host plants of related insects, plants from which occasional host records have been obtained, and plants that have a character in common with the host that might make them acceptable, such as the presence of milky latex for a *Euphorbia* insect. Likewise *Urophora siruna-seva* (Hg.), a trypetid associated with *Centaurea* species with spiny globular buds, responded to unrelated plants with similar characteristics such as *Echinops* and even clover flowers to which spines were added (Zwölfer in press).

Ideally the results of the tests show that the plants accepted have common taxonomic, chemical, or physical features. We attach considerable reliability to the host range if this occurs; however, the ideal may not be realized as insects in captivity often accept for food and oviposition a wide assortment of plants not attacked in the field. The reason for this anomaly seems to be that, although primary host-plant recognition tokens used by a stenophagous insect are a few characteristic features of the host, it still retains the ability to respond to widely distributed substances such as sugar, water, β -sitosterol, leaf alcohol, and so on. The stenophagous insect, with a few exceptions, also retains the general nutritional requirements of the euryphagous insect (Fraenkel 1959; House 1966).

In the absence of primary recognition tokens, hunger is almost invariably redirected into a stimulus for dispersion. Consequently, though the insect may nibble on various plants (perhaps in response to water, sugar, etc.) it does not remain to feed extensively. Confined to a non-host plant in a petri dish, it still wanders on becoming hungry, although nibbles taken on repeated contacts with the plant may result in extensive damage. This damage is largely an artifact of captivity. Eventually the insect may die because it is not eating enough to satisfy its metabolic needs or it may become accommodated to eat the test plant without wandering, although normally feeding remains less than on the true host. Physiological evidence for accommodation is provided by Schoonhoven (1967), who found that acceptance of food depended on more nerve impulses being generated by the medial than the lateral styloconic sensilla on the maxillae. The response to various plants, however, was affected by what the larvae had been feeding on previously. The accommodation to a non-host plant occurs only if the plant lacks a strong feeding inhibitor. In other words, host plants are attacked because they are "nice" but in captivity the insect tends to accept any plant that is not "nasty". Most aspects of this behaviour can be imitated by an electronic analogue (Zwölfer and Harris 1966).

Two plants that are acceptable to many stenophagous insects in captivity, apparently because of the lack of feeding inhibitors, are lettuce and pea which are also bland to human taste. Jermy (1966) showed that for an individual insect, the plants lacking inhibitors were scattered through various families and

that they differed from one insect species to the next. For example, for the potato beetle the following plants lacked inhibitors: *Pisum sativum* L. (Leguminosae), *Asclepias syriaca* L. (Asclepiadaceae), *Galinsoga parviflora* Car. and *Lactuca sativa* L. (Compositae), *Allium cepa* L. (Liliaceae) as well as the Solanaceae which it attacks in nature. It is difficult to predict the actual host range of an insect from this group of plants although comparing the amount of feeding done in a given time on each plant is a help. At a feeding rate of less than 5% of that done on the normal host, most lepidopterous larvae die as rapidly as if completely starved; at a rate of around 30% life is sustained, often for considerable periods, but the larvae are unable to complete their growth; at a rate above 50% it is usually possible to rear the larvae. However, even if a plant does support development it is not a host if it lacks primary recognition tokens. For example, Gupta and Thorsteinson (1960a, b) reared *Plutella maculipennis* (Curt.) on pea although this plant is not attacked in nature because it lacks the mustard oils which seem to be the recognition token used by this insect.

It is possible to determine which plants lack feeding inhibitors with a sandwich made with the test leaf between leaves of the host plant (Jermy 1966). A complete or partial rejection of the test leaf indicates that it contains a feeding inhibitor. A bland test leaf is eaten together with the host at a greater rate than when presented alone to the insect. However, the problem of whether a particular plant contains the insect's recognition token is most satisfactorily solved by identification of the token.

4. *The Investigation of the Basis of Host Recognition*

The relation of host specificity to particular visual, tactile, or chemical features of the host plants provides a rational method of screening insects for introduction and for assessing the basis of unexpected feeding on test plants in the laboratory. Unfortunately at present the identification of the host recognition token is usually involved and difficult; however, we feel that more attention should be given to establishing that the insect is responding to a token and whether the token is physical or chemical. This assures that the insect is selecting its host on a positive basis rather than attacking all plants without deterrents, behaviour that is characteristic of euryphagous insects.

Stenophagous insects recognize their hosts by the presence of characteristic tokens, although the presence of certain nutrients such as sugar, is usually necessary for sustained feeding. The acceptance of an agar diet by many host-specific insects is probably related to the presence of nutrients in solution on the surface so that the insect is able to use them as substitutes for the missing host-plant recognition tokens. The greater reluctance to accept non-host plants (even though without inhibitors) than a diet, probably reflects the fact that most of the nutrient substances are inside the leaf and not available to stimulate feeding until the insect has taken at least one bite. Some aphids probe in order to distinguish their hosts but most lepidopterous larvae must use an external token: they rarely bite on a non-host plant even when jumbled together with their host. Thus for many Lepidoptera the primary recognition token must either be a volatile substance or be associated with the plant cuticle. Often all that is necessary to demonstrate the presence of a cuticular recognition token is to strip the waxes from the host with chloroform, and vacuum infiltrate them into lettuce or other bland plant as described by Harris and Mohyuddin (1965). The presence of an active substance in the host cuticle results in the preferential

selection of the treated lettuce or an increase in the amount of feeding done on it. For example, the host plants of *Calophasia lunula* Hfn. appear to be determined by the presence of two chemical characteristics, one distributed throughout the tribe Antirrhineae (Scrophulariaceae) and the other restricted to a few species of *Linaria*. Thus, although in the laboratory the larvae will feed on all plants in the tribe, in nature they attack only a few species of *Linaria* (Harris 1963). An example of a response to a visual stimulus has already been mentioned for *U. siruna-seva*. Similarly, the burr seed fly, *Euaeresta aequalis* Loew, oviposited on artificial burrs made of rubber and curved pins (Currie 1932).

The nutritional requirements of most insects are remarkably similar and the best evidence to date is that food selection and specificity are determined almost entirely by non-nutritional factors (House 1966). By maxillectomizing tobacco hornworms, Walbauer (1962) was able to obtain feeding on dandelion and he found that it was as good as, or perhaps slightly better than, the host plant, tomato. The poor growth of these larvae on the other non-host plants tried was primarily related to a low intake of food. This is not to say that all plants are nutritionally equal. Auclair, Maltais, and Cartier (1957) suggested that the resistance of certain varieties of pea to *Acyrtosiphon pisum* Harr., is related to a low amino acid level which results in a reduced fecundity and growth, though the pea is still attacked. Evidence of poor nutrition on non-hosts is not a reliable indicator of host specificity as the nutritional balances required by an insect are often readily adaptive. For example Sang (1959) showed that the amino acid requirements of *Drosophila melanogaster* Meig. strains differed considerably, and Hinton (1959) found that one strain gradually changed its adenine requirement over an 8-year period. A few insects, however, are restricted to their hosts by the lack of certain metabolic systems. This is evidence of an extremely stable host association as these insects cannot change unless they acquire completely new enzyme systems. The best example is *Drosophila pachea* Pat. which required Δ^7 -stigmasterin- 3β -ol as it lacks the enzyme systems, present in most insects, to metabolize Δ^5 - 3β -sterols or C-24 methyl-substituted sterols. This restricts *D. pachea* to live in fermenting pockets in the arms of senita cactus, a situation where this sterol is in high concentration (Heed and Kircher 1965). Examples are more common where an insect depends on a symbiotic association to provide certain nutrients. The olive fly, *Dacus oleae* (Gmelin), depends on *Pseudomonas savastanoi* (Smith) Stevens to hydrolyze protein and perhaps synthesize methionine and threonine (Hagen 1966). Thus, the olive fly is restricted by the symbionts' requirements as well as its own.

5. Starvation Tests on Economic Plants Representing as Many Plant Families as Possible

We attach much less importance to starvation tests than is customary. We regard the results as confirming the previously established host range, and not as the main means of showing that economic plants are immune from attack. Also, we do not regard laboratory feeding on these plants with concern unless the plants contain the host recognition token or can support the complete development of the insect. However, there is often a need to remove the stigma attached to laboratory feeding on economic plants. This can sometimes be done by demonstrating that there is no egg development unless the insect feeds on its host, as done by Andres and Angalet (1963) for *Microlepinus* spp. In other

insects it is possible to point out that feeding on the economic plant does not prolong life compared with the starved condition.

6. *To Establish that the Insect is Potentially Effective for Weed Control*

This is not a criterion of safety, but many insects, though safe to introduce, do so little damage to the plant they attack that there is no purpose in introducing them. For example, the presence of *Mordellistena* sp. mining in the pith of *Cirsium vulgare* (Savi) Tenore are not measurably harmful to the thistle. Likewise insect attack on the leaves or stem of an annual plant after seed set is of no value, and the detrimental effects of many species of gall insects that attack the vegetative parts of a plant are questionable. Hence, any insect introduced should be capable of critically damaging the weed and this should be established by the investigator.

It should also be established that the insect to be introduced is not already present on the weed and that a habitat does in fact exist for it. This is done by a preliminary survey, made before considering the introduction of any insect, to discover what parts of the weed are attacked by insects and the species involved. Ideally such a study should include all the ecological pressures that affect the weed. This would show where the weed was most vulnerable to attack and possibly indicate that a slight change in management procedures offers a more immediate and certain control than the introduction of an insect. However, to demand that an investigator unsupported by a large staff should make an exhaustive ecological study of a weed before introducing an insect, would bring biological control to a standstill. Indeed, most of his projects are handed to him in desperation after other methods of control have been found economically or politically impracticable. Hence, although the absence of a complete study on the weed can be excused, it is inexcusable to introduce an insect already present or to try to establish a new species in a habitat effectively filled. For example, the noxious thistles *Carduus nutans* L. and *Cirsium vulgare* are not attacked by seed-destroying insects in Canada. Both these thistles are biennials: so theoretically they can be controlled if enough seeds are destroyed. *Rhinocyllus conicus* Froelich, or other seed-destroying insects, may not attack the thistles where they are most vulnerable, as seed destruction may have to reach 98% or higher to be effective. However, a sizeable destruction of seeds would reduce the aggressiveness of the weed and make it more amenable to control by an insect damaging another part of the plant or even by local eradication by chemical means. On the other hand, the seed heads of *C. arvense* are extensively attacked by a trypetid, *Orellia ruficauda* Fabr., in North America. This thistle is a perennial in which vegetative reproduction is important. The introduction of another seed-destroying insect is likely to be of little value and possibly through competition could result in a lower destruction of seeds than achieved by one insect. Hence such an introduction should not be made without keeping these points in mind.

Natural Resistance to Host Transfer in Phytophagous Insects

Plants on which an insect cannot complete its development are most unlikely ever to become hosts. However, many people are disturbed if even a slight amount of feeding occurs in the starvation test on an economic plant. They believe the feeding indicates that the insect has a potential for adaptation to these plants. Host transference has not occurred in the insect's original habitat, but

they fear it may occur with new ecological pressures in the country of introduction. We believe that the danger of this is greatly exaggerated although the potential exists for all insects, even species refusing the test plants. The host range of a stenophagous insect is presumably integrated with many features of its biology as the result of a long history of selection. A change in any major aspect of its biology will destroy the harmony of the whole and decrease fitness for survival. Hence the attempt of a stenophagous insect to breed on a non-host plant is nearly always accompanied by heavy mortality, which will maintain the *status quo* unless there is selection against the original host. Also aiding the *status quo* is the pronounced disadvantage of homozygotes under variable or severe conditions, and the fact that only genes able to coadapt harmoniously are incorporated in the gene pool (Mayr 1963). A selection against the present host will decrease the fitness of the insect for survival so that normally it will die out. Transference is most easily done to other plants containing the same or similar recognition tokens that are now avoided because of unfavourable chemical or physical features. It is much more difficult for a stenophagous insect to transfer to a plant not containing these tokens, even though that plant may be an eminently satisfactory laboratory host, as the insect has no means of recognizing this fact in the field. For example, *Plutella maculipennis* in the absence of its preferred cruciferous host is more likely to attack other plants containing mustard oils than pea, even though pea is possibly a more suitable host. In order to adopt pea as a sole host, *P. maculipennis* would probably have to revert to polyphagy and then respecialize.

There are very few examples of host changes in phytophagous insects except those that can be inferred from phylogeny. The few examples we have been able to find (Harris and Zwölfer in preparation) are the result of selection against the host resulting either from competition from a better adapted insect or from the disappearance of the host through the clearing of forests and draining of swamps for agriculture. By and large, introduced agricultural weeds in North America offer an insect a large and expanding resource with little interspecific competition. Thus there is less likelihood of these insects being forced to transfer through the extermination of their hosts, than of those associated with native vegetation. There may be a strictly temporary selection of an introduced insect to other hosts if insect numbers during the initial phases of control increase to be greatly in excess of the food supply. Many individuals will starve and there will be a survival premium on those that can do at least part of their feeding on other vegetation. However, as soon as the insect and weed have reached equilibrium, the pressure for a host change is reversed.

Both Wilson (1964) and Huffaker (1957, 1959) showed that there was little foundation for the fear that phytophagous insects will change their host ranges. For the pragmatic it should be emphasized that there have been no permanent and unexpected host transfers to desirable plants by insects introduced against weeds except for some instances when no screening tests were made before introduction (Huffaker 1959). This is in spite of many introductions of phytophagous insects in the course of weed control attempts throughout the world.

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