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The Predictability of Insect Host Plant Utilization from Feeding Tests and Suggested Improvements for Screening Weed Biological Control agents

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The purpose of host-specificity studies on candidate weed biological control agents is to be able to predict the plant species likely to be attacked in the new region. Traditionally this has been largely determined by equating suitability for larval development in a no-choice feeding test with vulnerability. Our survey of biological control case histories show that species with similar ranges in the tests have widely different ranges in the field. Suitable laboratory hosts may not be used while sometimes those with a low suitability in the tests are consistently attacked. The situation arises because host selection is a hierarchical sequence of opportunities and constraints of which the suitability for development is a single component near the end. Those near the beginning of the sequence are likely to be more firmly held by the insect species; but each component is a filter that limits host range and the possibilities for change. Indeed, the hurdles to a host shift are more formidable if simultaneous changes are required in several determinants of preference and suitability. Thus, screening studies need to be expanded to include phylogenetic constraints, climatic constraints, physical and biotic habitat restrictions, oviposition requirements, plant acceptability for feeding as well as suitability for development to be able to improve risk assessment.

Introduction

There are several aspects to assessing the desirability of candidate weed biological control agents. The process is to determine whether risks are acceptable to most people in return for the probable gains. First, it is necessary to predict the plant species likely to be attacked in the new region. Second, the consequences of attack on non-target species need to be assessed. Third, possible negative consequences need to be weighed against the prospective benefits of controlling the weed. The availability of other agents that could achieve the benefits with fewer detriments should be considered as well.

Here we suggest ways to improve methods for predicting host use in the field. First, the current practice of screening plants for their acceptability (oviposition preference of adults) and suitability (growth, survivorship and reproduction of their offspring) in isolation is insufficient to predict host use in the field. Host selection is a chain of events and needs to be analyzed as such. Second, we need to improve estimates of the consequences of attack. It is presently often assumed that attack and damage are synonymous; however, a 75% reduction in seed production may be of little consequence to a plant that is limited by microsites for germination and establishment. We must weigh whether harm to some native plant species is compensated by benefit to others. For example, a benefit from the control of the introduced tansy ragwort, *Senecio jacobaea* L. (Asteraceae), which has been achieved at the cost of attack on the native *S. triangularis* Hook, has been an increase in bluff mallow (*Sidalcea hirtipes* Hitchc.; Malvaceae), a threatened plant in Washington and Oregon

(McEvoy, unpublished data). The best estimates are that the attack of native *Senecio* is infrequent, affects a small part of the population and is of little consequence (Diehl and McEvoy 1990). Hence, if monophagous agents were unavailable or ineffective, some attack on native *Senecio* spp. may be acceptable in return for a greater benefit. Unfortunately, the availability and effectiveness of alternatives to the candidate agent are seldom evaluated in screening reports.

Shortcomings of Feeding Tests

Cullen (1990) detailed the shortcomings of insect screening tests for weed biological control agents and the consequent decision making problems, but he concluded that it is necessary to retain the no-choice feeding test. However, in our opinion, the deficiencies of the feeding test as the main means of determining the safety of a candidate agent are too great to overlook.

1.) Feeding tests result in a continuum of acceptability that ranges from host plants (species that are utilized in the field) to acceptable non-hosts (species that are utilized in the laboratory), and to unacceptable non-hosts (de Boer and Hanson 1984). At best biological control workers are forced into the difficult argument that plant species supporting development in the tests are not at risk in the field. The alternative is not to use agents that can develop on any desirable plant. Dunn (1978) was concerned that many safe biological control candidates are eliminated for this reason.

2.) Plants on which the insect does best in the laboratory are not necessarily the plants preferred in the field (Singer 1984). So the degree of laboratory suitability is not a reliable guide to the behaviour of the agent in the field. Szentesi and Jermy (1990), in a discussion of larval feeding tests, concluded that it is difficult to experimentally determine a host plant range even when the insect is a narrow specialist.

3.) Insect species with almost identical laboratory host ranges have different field host ranges. For example, the weevil species *Ceutorhynchus litura* (Fabricius) and *Trichosirocalus horridus* (Panzer) (Coleoptera: Curculionidae) developed in laboratory feedings tests on approximately the same range of plants in the thistle subtribe Carduinae (Asteraceae) (Zwölfer and Harris 1966, Ward *et al.* 1974, Kok 1975). In North America, *C. litura* has only been reported from its European host *Cirsium arvense* (L.) Scopoli; but *T. horridus* has been recovered from *Carduus*, *Cirsium*, and *Onopordum* (Asteraceae). The difference seems to be adult host selection rather than suitability for larval development, as *T. horridus* attacks 5 species that were relatively poor hosts in the feeding tests.

Both species have similar life histories except that the teneral *T. horridus* emerge for about 2 wks in early summer to disperse to concentrations of thistle flowers. They then disappear until late summer when the adults emerge to feed on thistle leaves in the immediate area. *C. litura* lacks the early summer dispersal; but emerges to feed on *C. arvense* in late summer.

Oviposition in both species occurs in the early spring by walking between the plants, thus both species need dense stands. There is a concern in North America for native thistles, some of which are scarce and none of which have been encountered by the weevils previously; but the feeding tests do not indicate that the host utilization by the 2 insects is different.

Host Selection in Insects

The lack of predictability of feeding tests arises because insect host selection is the result of an hierarchical sequence of opportunities and constraints. Indeed, Courtney (1984) cites several examples of monophagy that arise because of adult restriction to a habitat although the larvae have the ability to develop on plants in other habitats. He suggested that there is a rolling threshold at each host selection step, so there is some flexibility. Nevertheless, each step is a filter that limits host range and the possibility for host change. Redundancy in the sequence improves reliability, since even if one component is defective, another is likely to compensate.

Host selection constraints can be divided into 6 groups: 1.) phylogenetic constraints that are determined by evolutionary history; 2.) climatic constraints; 3.) habitat needs; 4.) oviposition needs; 5.) host acceptability for feeding; and 6.) host suitability for development. The constraints will differ for each insect species, so while phylogenetic constraints may be important for some, they are of no consequence for others. However, according to Courtney and Kibota (1990) host selection by monophagous and stenophagous insects, favors strong discrimination early in the host-finding sequence, as this minimizes lost time spent investigating inappropriate plants. This does not mean that there cannot be change; but it does follow a pattern. Host selection theory and the analysis of the food plants of 424 species of Canadian forest Lepidoptera by Holloway and Herbert (1979) indicated that polyphagous species can be derived from monophagous ancestors with the new hosts likely to be related to the original host and secondarily to occur in the same location.

Long-term host changes arise by selection of the best adapted individuals when the optimum former food becomes scarcer than an alternative. This is reported for vertebrates such as the Galapogos finches (Grant 1991), but there are insect examples. In weed biological control a similar selection may be happening in the beetle *Chrysolina quadrigemina* (Suffrain) (Coleoptera: Chrysomelidae) on *Hypericum calycinum* L. (Hypericaceae). The mature foliage of this plant is sufficiently hard that the larvae have difficulty eating it and the small stands in Europe are rarely attacked. However, the roadside ground cover plantings in California are a large resource for a beetle which has greatly reduced the abundance of its preferred host, *H. perforatum.* Andres (1985) reported that populations from *H. calycinum* had a 2- to 3-fold better larval survival on it than those from *H. perforatum,* so the beetle has improved its performance on the locally more abundant but poorer host. Host changes may also occur on a short-term seasonal or yearly basis. For example, host selection by *Battus philenor* L. (Lepidoptera: Papilionidae) is affected by the suitability and the abundance of host species (Rausher 1980).

Screening tests must be able to predict if there is a risk of host changes in the new region. Low survival in feeding tests suggests that a plant species is safe; but if there is a selective advantage to develop on it and the appropriate genetic variation exists in the insect population, survival will improve so the plant is not safe in the long run. For such cases, feeding tests are not by themselves an adequate screening method and the full host selection sequence needs to be examined. The 6 groups of host selection constraints are discussed below.

1. Phylogenetic Constraints

These are firmly held restrictions, as a result of evolutionary history, that limit an insect taxon to a plant taxon. For example, the weevil genus *Rhinocyllus* (Coleoptera: Curculionidae) is restricted to the thistle tribe Carduinae (Asteraceae) (Zwölfer and Harris 1984) and the related genus *Bangasternus* (Coleoptera: Curculionidae) to the tribe Centaureinae (Asteraceae). The implication is that any host changes in the new region will be restricted to within the plant taxon. In terms of risk analysis this is generally a more reliable indicator of host range limits than the feeding test. Phylogenetic host range constraints are often at the subgeneric level. For example, most species in the chrysomelid beetle genus *Aphthona* (Coleoptera: Chrysomelidae) are found on *Euphorbia* spp. (Euphorbiaceae) although a few attack herbaceous plants in other families (Heikertinger 1944). Without revision of the beetle genus, it is not known whether some species are phylogenetically restricted and hence are safer than others. Ideally, the taxonomic and host-specificity studies are done in collaboration as by White and Marquardt (1989) on a seed-head fly in the genus *Chaetorellia* (Diptera: Tephritidae) for knapweed biological control in Canada. The result was to describe the new species, *C. acrolophi* White and Marq., show that it was restricted to *Centaurea* spp. in the subgenus *Acrolophus* and to occur in a species-group that, with 1 doubtful exception, was restricted to the genus *Centaurea.*

Genera that contain insects of several feeding guilds almost always need revision. For example, most species in the fly genus *Pegomya* (Diptera: Anthomyiidae) are leaf-miners; but several species, possibly a distinct taxon, mine and gall the roots of *Euphorbia* spp. (Michelsen 1988). Clearly, weed biological control screening studies in many cases would be aided by investigation and possible taxonomic revision of both the insect and the plant.

2. Climatic Constraints

Many insects have a climatically restricted distribution. For example, the beetle *Agasicles hygrophila* (Selman and Vogt) (Coleoptera: Chrysomelidae) is not effective in the more temperate parts of its host plant range (Coulson 1977). Thus, regardless of what plants it develops on in feeding tests, it is not going to become a pest in regions with cold winters. In contrast, the spurge moth *Chamaesphecia hungarica* (Tomala) (Lepidoptera: Sesiidae) is restricted in Europe to the forest-steppe interzone with a North American climatic analogue along the Canadian-USA border (Gassmann *et al.* 1991). Most of the rare and endangered native *Euphorbia* spp. occur in Florida and Hawaii, so they are not at risk from this insect in nature.

3. Habitat Selection

The most overlooked host range restriction is adult habitat selection. The habitat required by *C. hungarica* are *Euphorbia* stands in spring flood sites. The North American spurge, *E. purpurea*, that occurs in moist habitats has a more southern distribution, so the risk to it is minimal. Habitat restrictions can be extremely sharp. Chew (1977) found that *Pieris napi macdunnoughi* Rem. (Lepidoptera: Pieridae) did not oviposit on *Cardamine cordifolia* (Cruciferae) in willow seeps although numerous eggs and larvae were found on isolated plants in the adjacent sunlit area.

The habitat is often a stand of a single plant species. Courtney and Kibota (1990) cite the example of the western skunk cabbage (*Lysichitum americanus* Hulten and H. St. John; Araceae) fly, *Drosophila magnaquinaria* Wheeler (Diptera: Drosophilidae) that attacks and develops on other hosts, including mushroom, placed inside skunk cabbage patches; but not when they are outside.

The cinnabar moth (*Tyria jacobaeae* L.; Lepidoptera: Arctiidae) is a weed biological control example. Its larvae completed development on all the *Senecio* spp., including native species used in feeding tests (Bucher and Harris 1961), but in nature it prefers open sites with low vegetation such as sand dunes (probably its original habitat) and heavily grazed pastures and mowed roadsides. It is less common and intermittent in shaded sites and the pupae are unable to survive in moist sites (Dempster 1971). In the Diehl (1988) study, the percentage of the native *S. triangularis* stems attacked on Marys Peak (elevation 1,248 m) in the coast range of Oregon is given in Table 1.

Table 1. Percent of native *Senecio triangularis* stems attacked on Marys Peak, Oregon.

Habitat	1986	1987
Open roadside with much *S. jacobaea*	77	23
Forest site 1 with little *S. jacobaea*	10	0
Forest site 2 with little *S. jacobaea*	7.6	0
Open meadow dominated by *S. triangularis*	0	6

On Marys Peak, attack on *S. triangularis* was most frequent in the roadside habitat where, coincidentally, *S. jacobaea* was most prevalent. It is consistent with the low observed attack of native *Senecio* that they are only at a high risk when growing within stands of *S. jacobaea*, since few of them occur together and none of them exclusively. This should have been determined with studies in Europe before release of the moth. Indeed, we doubt that with the present concern about native species and the ability of the larvae to complete development on all *Senecio* spp., that the moth would currently be approved for release. Nevertheless, it and the other agents released against *S. jacobaea* have controlled the weed (McEvoy 1985) with little damage to the native species, so we need tests show that show they are safe in spite of a larval ability to develop on the natives.

The field studies needed in the native region are:

1.) A survey to define the habitat of the agent in terms of the abiotic conditions, resources and the agent's natural enemies that may provide insight into the mechanisms that enforce habitat restriction, and would also be valuable for selecting release sites; and

2.) Experiments to determine if field attack of other plants is restricted to within stands of the host plant. For example, the purple loosestrife (*Lythrum salicaria* L.; Lythraceae) beetles *Galerucella calmariensis* (L.) and *G. pusilla* (Duft.) (Coleoptera: Chrysomelidae) completed development in feeding tests on the native North American plants *Lythrum alatum* Pursh and *Decodon verticillatus* (L.) Elliot (Lythraceae). Potted plants of these species placed in European stands with the 2 beetles were not used by the ovipositing adults but were eaten by the teneral adults (Blossey and Schroeder 1991). To assess the risk fully it would be necessary to know: a) whether the beetles in Europe attack *L. salicaria* in dry sites as well as moist sites; b) whether they only attack the test plants within stands of *L. salicaria*; and c) the extent to which the 2 plants in North America occur in *L. salicaria* stands.

The host range of weed biological control insects are restricted by resource, physical and natural enemy parameters. If this habitat is narrow, it will also restrict host range. This is certainly true of the *Aphthona* spp. root beetles that are being used for spurge control in North America. *A. nigriscutis* Foud. will develop on several *Euphorbia* spp. in feeding tests, but in nature it is restricted to warm open sites on dry coarse soils with a steppe climate. It does not attack spurge in swales or in light shade. *A. cyparissiae* (Koch) is similar but requires slightly moister sites and so often occurs in the same region but in different microhabitats. *A. flava* Guill. thrives on coarse soils with a high water table, and *A. lacertosa* (Rosh.) in loam or clay.

4. Oviposition Site Selection

Insect oviposition errors are common if they cannot find a host. Rausher (1980) determined that oviposition was also affected by the availability host species as well as their suitability for larval development. Thus, oviposition preferences alone are not a reliable method for determining risk of attack. They may, however, be useful in conjunction with feeding tests in separating which acceptable non-hosts contain oviposition stimuli and so are likely to be used in the absence of a preferred host.

Tephritids are notorious for forming host races. For example, *Trypeta commata* Loew (Diptera: Tephritidae) has specialized on different *Cirsium* spp. in different parts of Europe (Romstöck and Arnold 1987). This ability should be taken as evidence that given time, sufficient genetic variation, and a selective advantage, the species would develop host races on native North American *Cirsium* spp. even though the plants are usually rejected for oviposition.

5. Plant Acceptability for Feeding

Plants are often acceptable to the larvae for feeding but for nutritional, physical or synchrony reasons do not support normal development. The converse also occurs. The classic example is Waldbauer's (1962) finding that maxillectomized tobacco hornworm larvae fed and developed on plants they normally reject. It is important for risk assessment that reasons for the unsuitability of critical plants are identified, as depending on circumstance, it may be possible for an insect to improve survival as has *C. quadrigemina* on *H. calycinum*. Also, in the example of the bug *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae), defoliation of the weed *Lantana camara* L. (Verbenaceae) resulted in its transfer to damage the associated sesame crop on Uganda. This damage continued until the weed was eliminated (Harris 1988).

6. Suitability for Larval Development

The unsuitability of plant species for larval development provides a cut-off beyond which plants cannot be utilized as hosts. The strategy of Harris and Zwölfer (1968) and Zwölfer and Harris (1971) to determine the host range limits was capsulized in Wapshere's (1974) phrase "centrifugal-phylogenetic testing." The critical plant species within these limits need to be field tested in the native region of the agent to help assess the risk to them. We also suggest that crop species in the same plant family should be tested as a precaution since their morphology and chemistry may have been changed sufficiently that the phylogenetic limits no longer apply.

Discussion

Host-specificity in phytophagous insects is the result of a sequence of steps which vary in importance with the insect species. The risks to non-target plants from the release of an agent can only be determined by evaluation of all the steps, since the hurdles to effecting a host shift are more formidable if several simultaneous changes in preferences and suitability are required. The difficulty is that there is resistance in North America to a decrease in the use of no-choice feeding tests for the host range prediction of candidate weed biological control agents and a tendency to equate field studies with nature study. Also, whatever their deficiencies, the no-choice test is convincing to the public that weed biological control is safe. However, it is untenable to ignore findings that host selection is the result of a hierarchy of steps, with the earlier steps likely to be more firmly held than plant suitability for larval development. There is still a place for no-choice feeding tests, but they should be restricted to the determination of the acceptable non-host plant limits and tests of economic plants in the family. Desirable plants supporting complete larval development need to be field tested in the native region of the agent to evaluate risk. The cost of screening an agent is currently about 2 scientist-yrs ($400,000) and additional studies are proposed in this paper. Nevertheless, it should be possible to do these without major increases in cost by eliminating feeding tests except for those indicated.

We suggest that guidelines for screening reports on candidate weed biological control agents should require that the 6 major steps in the host selection process should be addressed, even if only to state that they do not restrict the agent concerned. Each step is a filter that limits host range and the plants for larval development, the insect is a greater risk than if there is a sequence of constraints.

Each investigatory stage requires a different type of study. Investigation of phylogenetic constraints requires the support of taxonomists. Identification of the climatic range of the candidate agent in the new region is best done with a user-friendly computer model. Habitat constraints must be determined by field study in the native region of the candidate agent. Habitat constraints are important if the agent is restricted to only certain stands of the weed in the native region; but it is important to determine that absence is not merely the result of having a small rather immobile population. Oviposition constraints can be determined by placing test plants inside and outside stands attacked by the agent in its native region. Finally, the acceptability for feeding and suitability for development needs to be determined in laboratory tests.

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