

THE SELECTION OF EFFECTIVE AGENTS FOR THE BIOLOGICAL CONTROL OF WEEDS

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INTRODUCTION

The importance of selecting biological control agents that are safe (will not attack desirable plants) has pre-empted attention from the selection of those that will be effective in controlling the target weed. The consequence is that many biological control attempts fail. For example, only 5 of the 51 cactus insects imported to Australia against prickly pear were of value for its control (Wilson, 1960). The others either did not survive or were not sufficiently damaging to reduce the density of the plant. This would not be serious except that each agent represents a substantial cost in time and money: today, in Canada, it costs at least one scientist-year (\$40,000) to obtain and demonstrate that an agent is safe to release and several man-years of subsequent study if it becomes established. A simple method of recognizing effective agents, or at least of eliminating the most ineffective, before host specificity studies are started, would reduce costs and encourage the use of biological control. Seven approaches to this problem, some of which have not been tried, are discussed and a scoring system is proposed that incorporates the more promising criteria involved.

This paper is not concerned with the determination of the safety of biological control agents: the criteria for this are distinct and sometimes contrary to those for effectiveness. Thus a high 'effectiveness score' even if it is a completely accurate reflection of an agent's ability to control the target weed, does not eliminate the necessity for host specificity studies, as discussed by Zwölfer and Harris (1971).

THE VARIOUS APPROACHES USED TO SELECT EFFECTIVE AGENTS

The original method for selecting a biological control agent for a weed was the researcher's intuition. This is epitomized in the letters between Perkins and Koebele (Perkins and Swezey, 1924) during their search for insects to control *Lantana* in Hawaii around 1902. It is a credit to their knowledge, good judgement, and imagination that on a small budget they were successful in checking the spread of *Lantana* and that none of the insects they used became pests (Fullaway, 1954). However, the extent to which intuition is still used means that biological control of weeds is

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an art rather than a science. Any alternative that increases the proportion of the decision that is based on conscious analysis is to be preferred.

The easiest approach is to select agents in order of availability. Foreign exploration is always difficult so it is tempting to solicit control agents from colleagues in other countries. The species normally received are those most abundant in the collector's vicinity without regard to their possible value as control agents. Indeed, an insect found routinely on a weed regardless of plant density is presumably not inflicting serious damage, and is therefore unlikely to be the most effective agent. Many gall-forming insects are probably in this category because they have evolved a homeostasis with their host that renders them incapable of inflicting serious damage to it. This passive approach of selecting agents in order of their availability is extravagant in terms of the number of species that have to be screened and released to obtain control of the weed.

A third approach, and a rewarding one, is to exploit previous successes. For example, prickly pear was controlled in India, Celebes, Hawaii, Mauritius and six other countries, (Andres *et al.*, 1973) with relative minor effort by using agents that had proved themselves in Australia. Likewise, the beetle *Chrysolina quadrigemina* (Suffr.) was of value against *Hypericum perforatum* L. in Australia, California and British Columbia (Wilson, 1960; Holloway, 1964; Harris and Peschken, 1971) in spite of climatic differences between these regions. Moreover, for the most part insects that failed in Australia have also failed elsewhere. This approach is strictly limited by the number of known successes.

A fourth method is to select agents on the basis of their impact on the weed within its native range in an area ecologically similar to the release site. This was done prior to the introduction of agents for the biological control of *Chondrilla juncea* Bubak and Syd. in Australia (Wapshere, 1970). Some difficulties encountered were:

- a) The multiplicity of species attacking the weed within its native range makes it difficult to distinguish the effects of each.
- b) Even if the climate and ecology of the native and release areas, are matched, there is still likely to be a difference in the density of the weed. For example, the density of *C. juncea* at Fishwick, Australia ranged from 99 to 332 plants/m² compared with 2 to 10 plants/m² at Le Soler, France (Wapshere, 1970). This may be important as it does not necessarily follow that the biotic agents prevalent at the low density are the most effective at reducing a high density of the weed.
- c) The effects of parasites and disease organisms on the biotic agent have to be discounted as the agent will be introduced without them.

Some of these problems can be solved by planting dense stands of the weed within the native range to determine the main factors responsible for its decline; but even so the results may not give a clear indication of the effective organisms.

A fifth approach is to select agents that attack when the weed is physiologically most vulnerable to damage. Most perennial plants will tolerate a single annual defoliation; indeed under favourable circumstances some damage may be stimulatory (Alcock, 1964; Harris, 1972). The regrowth of a plant following defoliation is associated with a sharp decline in its carbohydrate reserves and as the level of these reserves is positively correlated with hardiness (Jamieson, 1963) the plant is likely to be vulnerable to damage inflicted at a critical period before drought or low temperatures. The length of the period will depend on the rate at which the reserves are replenished following regrowth. For example, to avoid winter kill of alfalfa it is recommended that it should not be cut or grazed 6 to 7 weeks before the first killing frost (Smith, 1964). Also, one reason for the effectiveness of *C. quadrigemina* as a biological control agent in California was that its defoliation of the *H. perforatum* rosettes during fall and winter reduced the root system which resulted in their death during the dry summer season (Huffaker, 1952). Climatic differences may be the explanation why, after four years of defoliation by the cinnabar moth (*Tyria jacobaeae* L.), ragwort (*Senecio jacobaea* L.) has declined to 0.01% of its former density at Durham, Nova Scotia, while at Nanaimo, British Columbia the number of plants has remained nearly constant. In both regions the weed is defoliated while in bloom; but because of climatic differences this is 2 months before killing frost in Nova Scotia compared with 4 months in British Columbia. The results in Nova Scotia are even more striking as several other studies indicate that defoliation causes little if any decrease in the weed. For example in New Zealand even 5 artificial defoliations at monthly intervals only killed 6 out of 10 plants (Pool and Cairns, 1940). On a Dutch dune, the influence of the moth on the density of the weed was small. Meijden (1970) and Dempster (1971) found on Weeting Heath in Britain that in wet years defoliation by the moth increased ragwort numbers by regeneration from rosette root buds. Thus, apparently depending on the climate, defoliation by the cinnabar larvae can decrease, increase, or have no effect on the number of ragwort plants.

A more general strategy and the only one likely to work against weeds not subject to periods of frost or drought is a series of defoliations or other damage. For example, Simmonds (1951) found in studies for the biological control of the tropical shrub *Cordia macrostachya* (Jacq.) R. & S. that a single defoliation increased plant production whereas even partial defoliation each month reduced both its growth and reproduction. This increase in the detrimental effects with the frequency of partial defoliation has been confirmed for other plants (Jamieson, 1963). The implication for biological control is that each attack by an agent on the vegetative parts of a weed is likely to increase its vulnerability to damage from subsequent attacks by it or other species. Hence a multivoltine species is to be

preferred as an agent to a univoltine one, unless the latter has a long feeding period (possibly a result of prolonged oviposition or emergence). The alternative is to employ several univoltine agents that attack in sequence, although this will involve more work in host specificity studies. This strategy has been effective against *Lantana camara* L. in Hawaii. Originally, a tingid, *Teleonemia scrupulosa* (Stal.) was established. It attacked the shrub during the summer, causing considerable defoliation, but allowed recovery during the remainder of the year and *L. camara* remained a serious problem. Later, three species of leaf-feeding Lepidoptera, which were most active during the winter months, were established and resulted in 'partial' to 'substantial' control of the weed (Andres and Goeden, 1971).

It may also be rewarding to synchronise the attack by the biocontrol agent with the period of rapid growth by competing vegetation. This should make maximum use of the competition between plant species for light, water or minerals in suppressing the weed. A possible example of the success of this strategy is the stem weevil, *Ceuthorrhyncus litura* F. on the thistle *Cirsium arvense* (L.) Scop. in Canada. The weevil attacks the thistle in early spring when the growth of the competing grasses is at its maximum. Four years after its establishment in Canada, thistles had declined in the release site to 3% of their former density (Peschken and Beecher, 1973).

It has been a general hypothesis that the vigour of plant regrowth is related to the level of carbohydrate reserves at the time of cutting. Thus it was recommended that weeds should be cut or cultivated when their root reserves were at a seasonal minimum (Wilson, 1944). More recently the validity of this hypothesis has been questioned. Thus according to May (1960) the role of carbohydrate reserves in initiating regrowth and in determining the rate or ultimate extent of regrowth cannot be considered to be firmly established. Klingman and McCarty (1958) found for two pasture weeds that cutting two weeks after the low point in the carbohydrate cycle resulted in their greatest reduction, although the effects were only slightly greater than at other times. In general they concluded that although mowing gave an immediate improvement in appearance, it only resulted in slight to moderate weed control. Thus synchronization of the control agent with the minimum reserves in the weed does not appear to be a rewarding strategy for biological control.

A sixth approach is to select for minimum host-parasite homeostasis. In general, parasites that have had a long and close association with a host do not severely restrict its abundance as there has been a selection for resistance in the host and for non-virulence in the parasite (Pimentel, 1961). This was the basis of Pimentel's (1963) suggestion that parasites from related host species or genera often make particularly effective control agents. The extent to which non host-specific agents can be used for biological control of weeds is limited but not excluded altogether. For example, Wapshere (1973) considered the beetle *Sphenoptera foveola* Gebl. could on these grounds be a promising control agent for *C. juncea* in Australia as it

occurs on *C. ambigua* Fisch. in Kazakhstan, where *C. juncea* is uncommon. On the other hand, the aphid *Uroleucon chondrillae* Nev. which is frequent and widespread on *C. juncea* would be a poor candidate. Indeed its prevalence is an indication that it is not damaging and that there is a high degree of host-parasite homeostasis. High homeostasis can be expected with phytophages that have an intimate association with their host such as those forming histioid galls and possibly leaf miners; with those confined to a single species or a single race of plants and those that are both prevalent and widespread on the host. Low homeostasis can be expected with phytophages that are not prevalent either because they tend to eliminate their host or they have a high mortality from natural enemies; with those that are not associated with a single host species and those associated with hosts related to the pest but occurring in other regions of the world.

A seventh approach is to select the agent on the basis of attributes that have proved successful. Unfortunately it is difficult to draw conclusions from the few and diverse biological control successes against weeds. However, there are similarities between serious crop pests and successful agents: both reduce the yield of the host plant, particularly when it occurs in large, pure stands (except for pests that cause loss through 'cosmetic' defects that affect marketability). In other words a biological control agent is a weed pest and the more successful it is, the larger the loss in weed yield either caused directly or by reducing the competitive advantage of the weed.

The world crop losses compiled by Cramer (1967) show that the annual loss from insects (12.2%) is only slightly greater than that from plant diseases (11.8%). The obvious conclusion is that if host specificity restrictions can be met, about half the agents used for biological control of weeds should be pathogens. There is an interest in pathogens for this purpose (Wilson, 1969) but with few exceptions such as the use of the *C. juncea* rust (*P. chondrillina*) (Hasan, 1972; Hasan & Wapshere, 1973) in Australia and the proposed use of the dock rust (*Uromyces rumicis* (Schum.) in the United States (Inman, 1970) there has been little action. A lack of host specificity does not seem to be the problem, indeed the tendency of pathogens to form races restricted to particular genotypes of the host may limit their effectiveness against weeds (which in contrast to crops are highly polygenic). However, the main reasons for the paucity of trials with disease organisms are the pathophobia present in many people, and the practice of using entomologists rather than pathologists for biological control programs.

To return to pest insects, two of the characteristics of Canadian forest Lepidoptera that are applicable to biological control agents were identified by Watt (1965). He found that gregarious species had a higher mean abundance than solitary species. Also, for both gregarious and solitary species mean abundance increased and population stability decreased with polyphagy. In other words polyphagous species were able to exploit favourable circumstances, such as an increase in host abundance, more rapidly than monophagous species. Unfortunately, the hazard

of the agent to desirable plants also increases with polyphagy. Other attributes of pest insects, determined from a personal review, are as follows: they tend to achieve a high biomass rapidly when conditions are favourable because they are multivoltine, have a high fecundity, or are large in size; they tend to have a low homeostasis with the crop because they are polyphagous, normally have a high mortality from parasites, or were originally associated with another plant species; they tend to have a wide geographic distribution and hence presumably have wide ecological tolerances; and finally they tend to be sucking insects or species that damage the vascular or support systems of the plant rather than the foliage. Most of these features have already arisen in the previous discussion and except for polyphagy do not conflict with safety in a weed control agent.

A SCORING SYSTEM FOR DETERMINING EFFECTIVENESS

The more promising methods discussed for selecting agents can be combined into a scoring system (Table 1).

TABLE 1

A scoring system for determining the relative effectiveness of insects for the biological control of weeds.*

Candidate agents to receive one score, the most applicable, under each of 12 criteria.

1. <i>Host specificity</i>	
A. Restricted monophagous (specialized on a species biotype)	0
B. Monophagous (specialized on a species or species group)	1
C. Oligophagous	3
2. <i>Direct Damage Inflicted</i>	
A. Leaf mining or gall forming	0
B. Defoliating	2
C. Sucking or seedling damage	3
D. Destruction of vascular or mechanical support system	5
E. Prevention of seed production	
long lived perennials	1
short lived plants not dependent on seeds	3
annual or biennials dependent on seeds	5
3. <i>Indirect Damage Inflicted</i>	
A. None	0
B. Disease transmission or renders plant susceptible to invasion by other organisms	3

TABLE 1 - *Contd.*

4. <i>Phenology of Attack</i>	
A. Limited period of attack not increasing plant susceptibility to drought, frost or competition from other plants, or for seed-head insects, not covering the reproductive period of the weed	0
B. Limited period of activity but combining with another agent to cover the growing season or reproductive period	2
C. Limited period of activity increasing plant susceptibility to frost, drought, or competition from other vegetation	3
D. Prolonged attack covering the growing season, or the reproductive season for seed-head insects	4
5. <i>Number of Generations</i>	
A. Obligate univoltine species	0
B. Two to three generations a year climate permitting	2
C. Over four generations a year climate permitting	4
6. <i>No. Progeny per Generation</i>	
A. Under 500	0
B. 500 to 1000	1
C. Over 1000	2
7. <i>Extrinsic Mortality Factors</i>	
A. Natural control largely by non-specific enemies or ecological factors	0
B. Subject to extensive mortality from other competitors for the host combined with relatively common occurrence	3
C. Subject to extensive mortality from specialized enemies including diseases and relatively immune to non-specific enemies	4
8. <i>Feeding Behavior</i>	
A. Solitary feeders (cannibalism, avoidance or other intrinsic behavior, precluding proximate feeding of larvae)	0
B. Gregarious or colonial feeders (intrinsic behavior not precluding proximate feeding of larvae at high densities)	2
9. <i>Compatibility with other Control Agents</i>	
A. Compatibility poor or restricts possibilities of introduction of additional agents	0
B. Compatibility good	2
10. <i>Distribution</i>	
A. Local	0

TABLE 1 - *Contd.*

B.	Covers about half of the range of the target weed or the equivalent	2
C.	Covers about three-quarters of the range of the target weed or equivalent	4
D.	Covers full range of the target weed or the equivalent	6
11.	<i>Evidence of Effectiveness as a Control Agent</i>	
A.	Failure in biological control attempt(s)	0
B.	Controls host in native habitat or one region of introduction	4
C.	Successful in two or more regions of the world	6
12.	<i>Size of Agent</i>	
A.	Dry weight of full-grown insect less than 5 mg	0
B.	Dry weight 5-50 mg	2
C.	Dry weight over 50 mg.	4

* The scores may also determine the relative threat to agricultural or forest crops of pest insects not present in the country.

The scores were assigned intuitively and thus do not eliminate this aspect from biological control; but their use should increase the awareness of the factors involved and thus increase the proportion of the total decision based on conscious analysis. They can be easily modified to fit personal experience or local circumstances such as particularly high predator density. The scores establish various priorities, such as the superiority of oligophagy over restricted monophagy. It is hoped that these priorities, all of which are not yet generally accepted, will be tested either experimentally or by analysis of biological control results. However, as several of the categories achieve the same biological end, it is not likely that an effective agent will receive high scores in all of them. For example, despite a low fecundity, a large insect may maintain the same biomass and impact on a weed as a small insect with a high fecundity.

The effectiveness scores from Table 2 for agents that have been used in Canada against the thistle *Cirsium arvense* (L.) Scop. indicate that the flea beetle, *Altica carduorum* Guer. with only 9 points is a poorer prospect for biological control than the stem weevil, *C. litura* with 19 points. This appraisal is reflected by results in the field. Releases of *A. carduorum* in a range of climatic conditions have either failed to achieve establishment, or the beetle has survived at such low densities that the thistle was not reduced (Peschken *et al.*, 1970; Baker *et al.*, 1972). On the other hand, *C. litura* has not only thrived in Ontario but its establishment has been accompanied by a marked decline in the density of the thistle (Peschken and Beecher, 1973).

The scores (Table 2) of insects that have been tried in various parts of the world against *H. perforatum* indicate that the beetles *C. quadrigemina* and *C. hyperici* (Forst.) with 33 points a piece are the best prospects. In part the differential between these and the other insects used is related to their success as agents, but they retain a margin of superiority even if it is assumed that none of the insects have been previously used in biological control. What the scores do not indicate is that the species of *Chrysolina* have different ecological requirements and hence are effective in different sites (Harris, *et al.*, 1969). Thus, in spite of a high score it is still necessary to ensure that the agent is released on a site that meets its requirements.

TABLE 2

Effectiveness scores of four biological control agents

	<i>Altica</i> <i>carduorum</i>	<i>Ceuthor-</i> <i>rhynchus</i> <i>litura</i>	<i>Chrysolina</i> <i>hyperici</i>	<i>Zeuxidi-</i> <i>plosis</i> <i>giardi</i>
1. Host specificity	1	1	3	3?
2. Direct damage inflicted	2	5	2	0
3. Indirect damage inflicted	0	3?	0	0
4. Phenology of attack	2	3	4	4
5. No. of generations	0	0	0	4
6. No. progeny per generation	0	0	2	0
7. Extrinsic mortality factors	0	—	4	4
8. Feeding behavior	2	2	2	2
9. Compatibility	2	2	2	2
10. Distribution	0	4	6	2
11. Effectiveness	0	—	6	4
12. Size	0	0	2	0
Total	9	20	33	25

The other *H. perforatum* insects received scores between 24 and 26 indicating that they have a potential for biological control albeit less than *C. quadrigemina* and *C. hyperici*. There is some evidence for this from the field for two of the species. *Agrilus hyperici* Cr. showed promise in Australia (Wilson, 1960) and in California (Holloway, 1964) until overwhelmed by the competition from *C. quadrigemina*. Likewise, *Zeuxidiplosis giardi* (Kieff.) contributed to the control of *Hypericum* in Hawaii (Andres *et al.*, 1973) in the absence of a *Chrysolina* species adapted to a humid habitat. The remaining species failed to become established but for reasons that do not necessarily detract from their potential as control agents. For example, the *Anaitis* spp. released in Australia were almost certainly heavily contaminated with virus (Harris, 1967) and *Chrysolina varians* (Schall.) which has a requirement

for moist summer conditions was released in relatively dry sites (Harris *et al.* 1969). However, even though these species may have a potential for biological control, they can contribute little in competition with the more effective *C. quadrigemina* or *C. hyperici*. The determination of this fact before screening or liberating the insects would have saved a considerable amount of effort.

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