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Classical biocontrol of weeds: Its definitions, selection of effective agents, and administrative-political problems[1]

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Abstract:

Dilemmas in weed biocontrol are wide ranging. Even the term biological control is confusing as meanings may be restricted to the use of parasites and predators or extend to the use of all non-chemical means of control. Another problem is that two-thirds of the agents released do not become numerous enough to inflict major damage to the weed population, although this statistic is misleading as it includes agents costing little in prerelease studies where failure is of little consequence and those costing about two scientist years each, or currently about $400,000. Many of the suggestions for improvement are costly and time consuming. Delay is unacceptable where agent release is seen by sponsors as a mark of progress in a program likely to require 20 years and funding is difficult. Analysis of previous biocontrol attempts for attributes of "success" have been disappointing, partly because there are a number of steps involved, each with its own attributes. This paper recognizes four graded "success" steps and discusses many agent selection methods.

There are public demands for a change in emphasis from chemical to biological control; but in the absence of effective enabling legislation, the practice of biocontrol can be legally and politically hazardous; biocontrol should be carried out by a multi-disciplinary team but it is usually assigned to a single scientist; it needs to branch in new directions to remain scientifically stimulating, but this increases the risk of failure. Possible solutions for these dilemmas are discussed.

A.

[1] Invitation Paper (C.P. Alexander Fund): Classical Biocontrol of Weeds: Its Definitions, Selection of Effective Agents, and Administrative-Political Problems

Introduction

It is nearly 200 years since the first insects were introduced against prickly pear in India (Johnston and Tyron 1914) and there have been many weed biocontrol projects since, particularly in the past 20 years (Julien 1987). The result is a few spectacular successes and a fair number of qualified successes, although the number varies with the compiler. Another result is that the term "biocontrol" has acquired an excellent public image that is somewhat parallel to "motherhood." It is good but opinions differ on what is involved. On the negative side, biocontrol is not being pursued as effectively as it might. The reasons seem to be an interaction of scientific, administrative, and political constraints. Scientifically, it is often regarded as dull by ecologists and related disciplines: merely a matter of trying agents in the hope that one of them will work. The result is that although biocontrol has contributed much to ecological theory, there is less evidence that this has been reciprocated (Waage 1990). Administratively, programs that require a multidisciplinary team tend to be pursued, apparently for historical reasons, with a single scientist. Politically there is increasing public demand for more biocontrol and less chemical control. This has resulted in increased funding for research on alternatives for chemical control; but this is a mixed blessing in the absence of effective legislation as weed biocontrol can be a sensitive pursuit that may result in court challenges as has recently occurred in Australia (Cullen and Delfosse 1985); government attempts to balance budgets mean that funding tends to be dictated by the amount of favourable media attention and this causes rivalry between agencies supposedly cooperating to control the target weed.

The paper focuses on the following: (1) the definition of biocontrol; (2) the selection of effective agents, which is a weak point in weed biocontrol and approaches are discussed in five categories; (3) new directions of which three are suggested; and (4) finally, solutions are suggested for some of the administrative-political problems.

1. Definition of biocontrol

The original use of the term biological control by Smith (1919) referred to natural enemies, i.e. those that exist in nature and the paper discusses the use of entomophagous insects (predators and parasites). The term "natural" is often taken to mean all non-chemical means of pest control (see Neish 1988) and in weed control I have heard it used for displacement planting, grazing management, crop rotation, breeding for genetic resistance, and even for chemicals that are produced by organisms rather than artificially synthesized. Currently, both Agriculture Canada and the United States Department of Agriculture emphasize the importance of biocontrol, but most of their biocontrol funding goes to genetic engineering. This is clearly an exciting field of research; but as far as I am concerned only some of it is biocontrol. As pointed out by Garcia *et al*. (1988), there is a danger of biocontrol meaning whatever the speaker wants it to mean. The issue is further complicated by government legislation and regulations that define and divide biocontrol for their own purposes. I like the definition used by Harley (1985): "the study and utilization of parasites, predators, and pathogens to regulate populations of pests". This includes both natural and genetically modified organisms and implies that an agent must be alive and attack the pest.

In many countries, biocontrol as defined by Harley (1985) is regulated by two Acts. In Canada, classical weed biocontrol (the establishment of agents from other countries to give control on a continuing basis) is regulated by the Plant Protection Act (Canada 1990). This Act avoids the term biological control and classifies the biocontrol agents as pests. Inundative biocontrol (the periodic application of the agent in much the same manner as a pesticide) is regulated by the Pest Control Products Act (Canada 1985) although so far regulation has only been applied to microbial organisms. It refers to products for the control of pests and the organic functions of plants and animals. From a practical point of view, an important difference between the two approaches is that as the classical biocontrol agent finds the weed itself, the only stage at which regulation can be applied is prior to initial release. The inundative biocontrol agent can be regulated on a continuing basis as done with pesticides.

Wapshere *et al*. (1989) identified two other types of weed biocontrol: conservation and broad spectrum. Conservation of natural enemies is largely a theoretical concept in weed biocontrol. Broad-spectrum biocontrol mostly involves the use of domestic animals such as cattle. It is generally called grazing management and is unregulated by legislation.

2. Selection of effective biocontrol agents

Progress has been made in the strategy and techniques for the host range determination of prospective biocontrol agents (Harris and Zwölfer, 1968; Zwölfer and Harris, 1971; Wapshere 1974). The result is that the species authorized for release have a predictable host range. Less progress has been made in the selection of effective agents. The letters written by Koebele in 1902 (Perkins and Swezey 1924) indicate that he used intuition to select the *Lantana camara* L. insects released in Hawaii. The other extreme is to do no selection and release all “safe” species. Most classical weed biocontrol programs seem to employ a combination of these approaches and experience a high failure rate. Roughly a third of the weed biocontrol agents released in Canada have failed to become established, and a third are established at low density (Harris 1986). The international average up to 1985 (Julien 1989) of 65% established and 25% effective is similar as the level of damage inflicted by some of the abundant Canadian agents does not achieve economic weed control. Thus, approximately two-thirds of the agents released do little or no damage to the target weed. Canadian researched agents cost approximately two scientist years (currently $400,000) in pre-release studies to obtain release approval (Harris 1979), so these failures are expensive. However, biocontrol agents researched elsewhere often cost little or nothing, so it is misleading to group all failures together. Some suggestions for the improved selection of effective agents involve single step or holistic strategies whereas others select for particular aspects of effectiveness such as the ability to establish, to achieve high population densities, to inflict damage with a high impact to the weed, or to stress the weed population. Many of the suggestions need rigorous testing and it is hoped that out-lining them will stimulate this process.

2.1 Holistic strategies

The approach of Myers (1985) implies that the attributes for success in weed biocontrol are too complex for analysis, so the best that can be done is to try organisms until a successful one is found. I refuse to accept that success cannot be improved and several methods are discussed.

2.1.1 Proven success as a biocontrol agent

Normal biocontrol practice is to first try agents that have worked elsewhere. These have the advantage that much is known about them and normally large numbers can be obtained cheaply. Agents such as *Dactylopius ceylonicus* (Green), *Rhinocyllus conicus* Froel., and *Chrysolina quadrigemina* (Suffr.) have been successful in a number of countries with a wide range of climates (Julien 1987) and so obviously have necessary qualities for effectiveness. Paradoxically, success in one region also produces large numbers of failures in other regions (Crawley 1989a). However, the high failure rate should not be deplored because proven agents can be released at little or no cost and the logical strategy is to try them even if the chances of success are small. The Canadian costs of releasing 10 agents established in the United States averaged 0.04 scientist years each in pre-release costs compared with an average of 2.2 scientist years each for agents in which the pre-release studies were pioneered by Canada (Harris 1979). The cost is even lower now that there are more pre-screening consultations between the United States and Canada. Six of the 10 American agents are established in Canada, and three of them [*C. quadrigemina*, *C. hyperici* (Forst.), and *Longitarsus jacobaeae* (Wat.)] have a major impact on the target. In terms of cost-benefits, this has been an extremely effective strategy, so studies failure rates should treat “old” and “new” agents separately if they are to make a worthwhile contribution.

2.1.2 Impact in native region

An approach suggested by Wapshere *et al*. (1976) is to use the species that controls the weed in the native climatic analogue of the release area. This is similar to using a proven agent except the assessment is done at the origin of the weed. They identified the rust *Puccinia chondrillina* Bub. and Syd. as a prime agent for *Chondrilla juncea* L. because it controlled this weed on abandoned fields in southern Europe. Their choice was justified by the spectacular results achieved in Australia (Cullen 1986). A limitation to this approach is that it overlooks species that are prevented from being effective by high parasitism. For example, Lawton (1988) suggested that the failure of native bracken (*Pteridium aquilinum* L.) herbivores to respond to increase in their host density was that their populations were controlled by predators, parasitoids, and diseases. When uncoupled from these, they increased to about 10-fold their former density. Such studies are expensive and probably more costly than pre-release studies on agents that fail. In other instances, weed stands in the native habitat decline slowly or they are in stable small stands, so it is difficult to recognize the most effective agent. Indeed, control may be by a complex of factors. However, if natural or artificial weed outbreaks are controlled by an organism, it is the obvious species to try.

2.1.3. Attack of a problem weed race in native region

This is a modification of the previous strategy used if the target weed in the country of introduction is resistant to the agent strains found. Resistance is often a problem with rust disease organisms and occasionally with phytophagous insects. For example, strains of the rust *P. chondrillina* are virulent on particular strains of its host plant *C. juncea* (Burdon *et al*. 1981). Normally the taxonomy of the weed is poorly understood at the start of the project, so there are two alternatives: a virulent strain can be found by laborious trial and error testing or the agent can be allowed to do the finding by exposing the weed strain at the centre of weed origin (the region likely to have most variation in the agent population). The latter approach is unacceptable if the escape of a new strain in the test region is a possibility.

There have been difficulties finding agents for the biocontrol of the European leafy spurge (*Euphorbia* x *pseudoesula* Schur.) on the Canadian Prairies. There is considerable disagreement among botanists whether there is a single variable species or a complex of species (Crompton *et al*. 1989) but many European leafy spurge insects do not accept the North American plant. Leafy spurge is generally sparse in its native region and something must keep it this way. Thus, if politics, logistics and safety allow, it would be rewarding to expose "Canadian" leafy spurge plants in the northern Ukraine, which on historical grounds appears to be its main source of origin and to select the candidate biocontrol agents from the organisms that attack them. This would ensure that the organisms screened are virulent on Canadian leafy spurge and are adapted to a prairie climate.

2.1.4. Life table studies at the weed origin

There is pressure from academics and those working on candidate agents overseas to assemble life tables on the weed and its natural enemies in its native habitat as a means of selecting the best agent. Overseas studies are expensive and it is not clear to me that they will speed progress or reduce costs in weed biocontrol programs. Programs currently require about 20 years and are unacceptably slow to most sponsors who regard the release of an agent as the first mark of progress. I usually cannot get agreement for more than a 1-year preliminary study and survey. Often it is necessary to select an agent for screening from the literature and find others (possibly better) in the course of the study. Waage (1990) outlined similar constraints on preliminary studies in the biocontrol of insect pests. Thus, I do not regard life table studies as a practical solution.

2.1.5. Agent selection to avoid past failures

The study of the weevil *Cryptobagous slaviniae* Cald. & Sands for *Salvinia molesta* Mich. control in New Guinea turned failure into a success by supplying a trigger in the form of nitrogen (Room and Thomas 1985). The more normal benefit is to learn to avoid repeating failures.

Peschken *et al*. (1982) established the *Cirsium arvense* (L.) Scop. stem gall fly, *Urophora cardui* (L.) in Canada; but "biological success" has been low in Saskatchewan as the galls are restricted to moist shaded sites and most occur near water. In contrast, in New Brunswick there is a high density of galls in the open away from water. The ultimate factor responsible for site suitability is that the swelling of the gall and the amount of nutritive tissue developed in it for larval development are dependent on turgor pressure. Turgor pressure is a function of both the availability of moisture to the plant and its loss through transpiration (unpublished data). In Canada, *U. cardui* attacks when 80% of the vegetative growth of *C. arvensis* is complete (Forsyth 1984). It follows that a plant with many leaves has a high potential for transpiration and so a low turgor pressure in open sunny sites. In such sites the problem is aggravated as gall formation stretches the stem stomata which are unable to close. Receptacle galls such as those made by *U. affinis* are less affected as there are no stomata on the galled tissue.

In South Africa, the gall wasp *Trichilogaster acaciaelongifolia* Froggatt was more effective at controlling the weedy tree *Acacia longifoliae* (Andr.) Willd. in the relatively humid coastal region than in the dry interior even though the tree is riverain and hence has an unlimited water supply (Dennill and Gordon 1990). Also, most of the stands with high agent populations were shaded. The interior trees should have higher transpiration, lower turgor, and hence less gall growth. It is consistent that Waring (1986) found gall-formers less abundant on water-stressed plants. However, Waring and Price (1990) found that some gall-formers were most abundant in harsh dry sites, because the stressed plants had access to moisture at the time of gall formation and that the galling process by drought-adapted species may differ from that of drought-sensitive species. Also, drought-adapted plant species have mechanisms for maintaining high turgor pressure which may predispose them to galling, so the two groups should be considered separately for biocontrol purposes.

My conclusion is that inducers of galls in tissues with stomata will have most impact in non-drought-adapted plants: (1) if they attack early in the growing season when leaf number is at a minimum; (2) if the site is moist during gall expansion, shaded, or the sky tends to be overcast and the atmosphere humid; or (3) if the stem or leaf galls develop a dense mat of hair as this will reduce transpiration loss. To use stem or leaf gall-inducers on non-drought-adapted plants in other situations is inviting failure.

2.1.6. Successful agent traits

The identification of traits associated with success and failure in past attempts is clearly attractive. Waage (1990) discussed some of the difficulties in this approach; never-the-less, useful leads can be obtained. Analysis by Crawley (1989a) of the data assembled on the agents listed in Julien (1982) indicated several traits related to the ability of agents to become established but he was less successful in identifying characteristics related to effectiveness, although weevils were the most successful taxon. However, a few agents have been successful many times and others have failed repeatedly (Crawley 1989b). Thus, some species have the necessary attributes and others do not.

There are three problems with identifying successful traits from the present data base. (1) The world lists compiled by Julien (1982,1987) did not define “effectiveness” so each contributor applied it differently. (2) Weed control depends on an agent(s)-plant-site interaction, so the contributions of single factors tend to be confounded. For example, defoliation of *Ambrosia artemisifolia* L. by *Zygogramma suturalis* F. gives outstanding control (Kovalev and Vechernin 1986) whereas defoliation of *Senecio jacobaea* L. by *Tyria jacobaeae* (L.) has been disappointing (McEvoy *et al*. 1989). Both agents inflict the same damage and achieve the population density necessary to defoliate their host over large areas, but the responses of the plants differ. Thus, the desirable agent trait of high host exploitation is hidden by the rating system that classifies one as a success and the other a failure. (3) There is often a considerable time interval between agent release and success, so older releases appear to be better than newer ones (see Julien *et al*. 1984; Julien 1989). A solution to these problems is to divide progress into smaller and more closely defined steps. This is currently done in Canada using four steps to measure progress: “establishment”, “biological success”, “host impact”, and “control success”.

“Establishment” is defined as survival of an open release for 2 or more years. It is the first step toward successful biocontrol and Crawley (1989a) identified agent criteria that relate to establishment success. Also, multiple releases with a large number of individuals increase the chances of successful establishment (Crawley 1989b). It was possible to identify them because establishment was identified separately and not confounded with economic success in the data base.

"Biological success" is a measure of resource use by the agent in relation to the resource available. An agent that attacks 70% of seed-heads over half the area infested by the weed in the country of introduction receives a rating of 70 x 50%. Organisms attacking the roots, stem, and leaves are rated by the percentage of plants attacked. An agent that remains rare in relation to the available resource contributes little to control and so is a failure. Newly released agents that have promise will have a high density at the release site but infest a small portion of the weed infestation. Increases in the area infested over a period of years show the rate of spread and whether distribution is necessary. Several of the subsequently discussed agent selection methods could be tested for "biological success" if the data were collected as suggested.

"Host impact" is a measure of the decrease of reproduction or biomass of the weed at sites favourable to the agent. Differences in the impact of "biologically successful" agents doing the same type of damage reflect differences of the biological characteristics of the weed species. The effect of damage type on a plant can be determined experimentally, as is discussed later, so the strategy is to select an agent that is likely to be "biologically successful" and have a high impact on the plant. I rate the impact on a scale of 0-3 (agents scoring 2 or 3 inflict major damage even if it is not enough to achieve control by themselves; but they could give control if supplemented):

0 = Reduction of weed reproduction (seeds or ramets) or biomass < 10%.
1 = Reduction of weed reproduction or biomass 10-34%.
2 = Reduction of weed reproduction or biomass 35-64%.
3 = Reduction of weed reproduction or biomass >65%.

"Control success" relates to objectives of the project. The objectives should be determined at the start of the project and need not be in terms of weed density or increased crop production. If public concern about pesticide use continues, it is likely that objectives increasingly will be in terms of the amount of herbicide displaced, or in environmental terms such as reduction of ground water contamination by a herbicide. The objective reflects economic and human values rather that the biological characteristics of either the agent or the weed. Again, I use four categories for rating "control success":

0 = No control.
1 = Control achieved in <35% of infested area: 1a = with the agent alone; 1b = with a combination of agents.
2 = Control achieved in 35-65% of infested area: 2a = with the agent alone; 2b = with a combination of agents.
3 = Control achieved in >65% of infested area: 3a = with the agent alone; 3b = with a combination of agents.

2.2 Selection for specificity and establishment ability

The first step toward weed control is the establishment of an organism with a narrow host range. Crawley (1989a) found that endophagous insects tend to have narrower host ranges than exophagous species and that agent establishment was correlated with a high intrinsic rate of increase (potential reproduction) and small body size. These attributes are a help in the selection of an agent for pre-release studies and the data base could be analyzed for other criteria such as whether root- or leaf-feeders establish better. Ease of establishment should also be increased by importing the agent from the climatic analogue of the release area, as emphasized by Wapshere (1970).

2.3 Selection for high biological success

2.3.1. Agent distribution in native region

Zwölfer (personal communication in 1991) found that the best biocontrol agents of thistles and knapweeds in North America were those that in their native region had a uniform distribution (which implies that most weed stands are suitable) and a high frequency of occurrence (in over 80% of the samples). Examples are *Urophora affinis* Frfld., *U. quadrifasciata* (Meig), and *R. conicus* which have become abundant over most of the North American range of the target weed and have reduced seed production considerably. Species with an irregular and low occurrence have been unsuccessful. For example, *U. cardui*, which was found in less than 50% of the European samples, is locally established but has little impact and *Altica carduorum* Guer. (found in less than 5% of European samples) is not established.

Parasitism of the agent is less critical in this strategy than in 2.2.1. Overseas investigations often are started with a general survey of the weed in the climatic analogue of the release area; the species of choice can then easily be selected from their distribution in the samples.

2.3.2. Competitive inferiority

Zwölfer (1973) suggested that the most valuable agents were the common, competitively inferior species. He recommended the weevil *R. conicus* for the biocontrol of *Carduus nutans* L. as other seed-head insects normally displaced it. The implication was that it survived by producing many eggs, spread widely and uniformly. These are desirable characteristics in a biocontrol agent. Strict application of this hypothesis would have selected the gall fly *U. solstitialis* L. as it is displaced by *R. conicus* when both attack simultaneously although not if it attacks after the gall has hardened.

2.3.3. High mortality from specialized natural enemies

Harris (1973) suggested that high mortality from specialized natural enemies (parasites, predators, and disease) in its native area is beneficial in a candidate agent. The rationale, as for the competitive inferiority, is that to survive the high loss, the organism is likely to have the desirable characteristics of producing many offspring and spreading them widely. Myers *et al*. (1989a) supported the choice of heavily parasitized species, but suggested the reason for their effectiveness is that their rarity will have prevented development of host resistance (see strategy 2.3.6). On the other hand, host resistance may be the reason for rarity of lightly parasitized organisms, so rarity itself is not a good criterion for selection.

2.3.4. Early aggregated attack

Zwölfer (1985) suggested that for the seed-heads of thistles and knapweeds, the most valuable agents were species with an early aggregated attack. The gall fly *U. affinis* introduced into Canada for the biocontrol of *Centaurea diffusa* Lam. and *C. maculosa* Lam. qualifies and it has greatly reduced knapweed seed production in Canada and it has more impact than *U. quadrifasciata*, which is a gall-former that attacks more mature capitula (Harris 1980). Forsyth (1984) found that when *C. arvense* plants with stems 4 - 7 cm high were attacked by the aggregated stem-gall fly *U. cardui*, after 11 weeks the plants produced only 0.25 ramets each compared with 4.25 ramets in the controls and those attacked when the stems were up to 27 cm high. Thus, as far as gall-formers are concerned the impact is greatest when it occurs at the start of vegetative growth or of flowering.

2.3.5. Avoiding parasitism and predation

A requirement for successful biocontrol is that the target weed should become sufficiently scarce that there is inter- or intraspecific competition for it, as already discussed. Hairston *et al*. (1960) postulated that although carnivores should compete interspecifically, herbivores should not because their populations are held down by predators. This hypothesis is supported by Lawton and Strong (1981) who found that competition between folivorous insects is usually low. Similarly, the analysis by Schoener (1986) of 164 studies supported a difference in competition between terrestrial herbivores and higher trophic levels although granivores and nectarivores were comparable with carnivores. Clearly, successful biocontrol depends on low parasitism and predation.

Nothing is gained if parasitism at the origin is exchanged for parasitism at the release site. For example, the eggs of the European flea beetle *A. carduorum* were eaten in Canada by the native specialized Altica predator *Lebia viridis* Say (Peschken 1977). Also, the externally exposed eggs and larvae were vulnerable to general predators (Peschken *et al*. 1970). Goeden and Louda(1976) found the reported losses from native parasites and predators at the release sites run from the inconsequential to over 90%. One of the criteria used by Burge *et al*. (1988) for avoiding parasitism in agents imported for the biocontrol of bracken in Britain is to select species that are taxonomically and ecologically distinct from any of the native bracken-feeding species. The Cecidomyiidae gall-formers have acquired parasitoids readily: *Zeuxidiplosis giardi* Kieff (Goeden and Louda 1976), *Cystiphora sonchi* (Bremi)(D. Peschken, personal communication), and *Spurgia esulae* Gagne in North Dakota (Carlson and Mundal 1990), and *Zatropis* sp. at Regina, Sask. Thus, gall midges should be given a low priority as biocontrol agents. The thistle capitulum weevil *R. conicus* is attacked by boll weevil parasites in the United States as well as a parasite of the thistle plume moth (Surles 1974). Some of this might have been predicted and the capitulum gall fly *U. solstitialis* is a better prospect for escaping native parasites.

2.3.6. New association strategy

Others things equal, the most effective biocontrol agents will be those to which the host lacks resistance. Pimentel (1961) suggested that stabilizing selection in favour of host resistance and presumably parasite races with no unnecessary virulence (Person *et al*. 1976) will result in a reduced parasite impact over time. Pimentel favoured new parasite-host associations to avoid this situation. Hokkanen and Pimentel (1984) claimed that weed biocontrol was 2.2-fold more successful with new agents rather than those from old associations and that for biocontrol as a whole there was a 75% greater chance of success with new associations. Goeden and Kok (1986) criticized the analysis and Waage (1990), with larger data base confined to the control of arthropods with arthropods, did not support the superiority of new associations. He obtained almost twice the percentage of establishments and consistently more control success regardless whether they were partial, substantial, or complete with agents of old associations. The limited Canadian data on weed biocontrol had just over twice the establishment success with old associations, a ratio of 1:4 of old to new associations for low host utilization and 14:1 for high utilization (Harris 1986). The analysis of the pests on introduced South African crops by Dennill and Moran (1989) showed that many of them had been recruited from the native fauna (new associations) and had a narrow host range. Clearly, there is nothing wrong with new association if they meet all the requirements. However, if a choice has to be made, the old association is a better bet than the new association.

Many North American weed biocontrol targets such as *E.* x *pseudovirgata* and *C. diffusa* have a Eurasian origin. Most European organisms that can attack them, do attack them. It might be possible to find new associates on African spurges that would attack leafy spurge but this ability is likely to predispose them to attack North American native spurges in the same subgenus. Myers *et al*. (1989a) suggested that rare organisms will have avoided stabilizing selection and should be the species of choice. This is contrary to strategy 2.3.1, which, in a few examples tried, has given poor success. For example, Zwölfer (1965), in a European survey, found *Larinus jaceae* F. but not *R. conicus* on *C. acanthoides* L. *Rhinocyllus conicus* has attacked this thistle in North America, but it has been less successful on it than against *C. nutans*, which is the European host on which it is common. The reason for the poor success on *C. acanthoides* is that oviposition only covers the early flowering period (Rowe and Kok 1984), which is a form of host resistance. My advice is to select an organism that is common on the target weed. Host resistance is less of a problem with insects than pathogens where the strategy should be to find an agent strain with the necessary virulence genes. This was done (see strategy 2.1.3) for *P. chondrillinae* on *C. juncea* in Australia and I suspect the strain found is an old associate of the weed genotype.

2.4. Prediction of vulnerable points in weed survival strategies

The response of plant species to defoliation or other types of damage varies with their survival strategy. Hence, the crucial stage to attack with a biocontrol agent also varies.

2.4.1. Plant survival strategies

Grime (1977,1985) identified three basic survival strategies, which he called "competitive" (C), "stress-tolerant" (S), and "ruderal" (R). "Competitive" plants have a high intake of water and mineral nutrients, and accumulated reserves that can be rapidly mobilized. Leafy spurge is a "competitive" dominant on the steppic grasslands of North America. Providing moisture is available, the presence of reserves in the roots permits rapid regeneration following defoliation. Thus, it is not surprising that spurge defoliators have been ineffective biocontrol agents (Harris 1984a) but the plant is starting to be controlled by root-feeding beetles in the genus *Aphthona* (Harris 1990a). The root destruction interferes with the high water requirement that is characteristic of the "competitive" strategy.

Whether root-feeders are equally effective against perennial marsh plants, such as *Lythrum salicaria* L., needs to be determined.

"Stress-tolerant" plants have a range of strategies depending on the stress involved. Drought-tolerant plants such as *Opuntia* spp. are adapted to reduce water loss. Root loss is not serious as detached cladodes will root. The most critical damage is likely to be destruction of the water conservation system. I do not know how much the sucking dactylopids increased water loss, but as a group they have made a far greater contribution than the boring moth *Cactoblastis cactorum* (Berg) (Moran and Zimmermann 1984). Plants adapted to survive other stresses will have other vulnerable points. For example, evergreen alpine and arctic plants have a low photosynthetic rate, but their long leaf life gives them an advantage over deciduous species (Grime 1979). Thus defoliators are likely to be particularly damaging. Shade-tolerant plants produce less dry matter and retain photosynthate in the shoot at the expense of the root (Grime 1979) so shoot-feeding insects should be given a high priority.

"Ruderal" plants are characterized by a short life cycle, i.e. rapid seedling growth to take advantage of a temporary disturbance followed by the diversion of resources into flowering and the production of small to very small seeds (Grime 1977). Vegetative tissues are the most available to attack. Certainly defoliation has had a major impact on *A. artemisiifolia* (Kovalev and Vechernin 1986), which is a ruderal with some competitive abilities.

Most plants employ various combinations of Grime's three strategies. For example, plants of pastures and meadows tend to have a C-R-S strategy (Grime 1974) and this may mean it is necessary to attack vegetative tissues, roots, and flowers to achieve control.

The vulnerable point of some weed species is apparent from field observation. For example, the dense, self-perpetuating stands of nodding thistle, *C. nutans*, in Saskatchewan grasslands depended on rapid germination and seedling growth with fall or spring moisture to smother the site as a means of excluding perennial grasses and forbs. Intraspecific competition reduced 500-600 thistle seedlings per square metre to about 20, 2-m-tall, flowering plants, which die in early August to allow repetition of the cycle. Seed reduction of about 50% by the weevil *R. conicus* has meant that the number of seedlings is insufficient for rapid cover of the bare ground so that perennial grasses, with which the seedlings cannot compete, return over 2 or 3 years (Harris 1984b). The ability of the surviving thistle population to find temporary disturbed sites depends on different attributes and will require different measures for control. Also, in drier habitats with less grass competition a different strategy is needed. For example, Goeden and Ricker (1985) found that the weevil destroyed an estimated 55% of the seeds of *C. pycnocephalus* L. in southern California, but the thistle control was disappointing. I suggest the main reason was that competition from other vegetation was less than it was in Saskatchewan.

2.4.2. Experimental determination of weed vulnerability

Meijden *et al*. (1988) used an index to rate the relative impact of defoliation on several biennial weeds: proportion of plants alive 6 months after defoliation *x* regrowth (ratio of foliage on the survivors after 6 months to that before treatment). *Senecio jacobaeae* a rating of 0.65 compared with 0.07 for *Verbascum thapsus* L.

The high regeneration index of *S. jacobaeae* indicates that it would be difficult to control by a defoliator, and this has proved to be the case in western North America. The cinnabar moth, *T. jacobaeae*, has not controlled its host in British Columbia in spite of its "biological success" in achieving widespread annual defoliation (Harris *et al*. 1978). On the other hand, the root-crown feeding beetle *L. jacobaeae* does control the weed (McEvoy *et al*. 1989).

Hound's-tongue, *Cynoglossum officinale* L., which is targeted for biocontrol in Canada, has a regrowth index of 0.63 (similar to *S. jacobaeae*), so root-crown feeders rather than defoliators are being screened. The choice is supported by impact studies with the root-crown weevil *Ceuthorhynchus cruciger* Herbst by Prins and Nell (1989). In contrast, a defoliator seems to be a good choice for *V. thapsus*. It may be that the plants most vulnerable to damage by defoliation are species that accumulate reserves in the leaves whereas the less vulnerable species accumulate reserves in the roots, so they have resources available for regeneration (Meijden *et al*. 1988).

Seeding increased the number of *Cirsium vulgare* (Savi) Ten. established by 40-fold compared with a 5-fold increase for *C. officinale* (Klinkhamer and de Jong 1988). Thus, *C. vulgare* is likely to be more susceptible to control by an insect such as *Urophora stylata* L. that reduces seed production than is *C. officinale*. The use of artificial defoliation, seed sowing, and root destruction (possibly by the agents) should be employed routinely to determine vulnerable points in the life cycle of the weed as it is much cheaper than selecting an agent for pre-release studies that inflicts damage from which the plant can readily recover.

2.4.3 Impact of gall-inducers and plant survival strategy

Harris (1989a) recognized a number of developmental stages in European Cynareae that are attacked by both gall-formers and non-gall-formers. The gall-former that attacks during receptacle development forms a "woody gall" that is a strong metabolic sink which sequesters resources from the plant as a whole. This is particularly valuable for the control of species that produce many small capitula over a long season as it eliminates the logistic problem faced by a non-gall insect of attacking a high proportion of the capitula (Harris 1980). The "woody gall"-former in diffuse and spotted knapweed is *U. affinis* and it is responsible for most of the seed reduction achieved in North America. The gall-inducer *U. quadrifasciata*, which forms a non-woody floret gall, does not increase the importation of resources to the attacked capitulum (Harris 1980) and may be of less value than the non-gall-inducer, which can forage within a capitulum.

As *U. affinis* is the single most valuable control agent of knapweed, care should be taken that other agents introduced do not harm it. In general the "woody gall"-former is consumed by the non-gall-former that attacks simultaneously; but the two coexist or the gall-former-attacked heads are avoided by non-gall-formers that attack later, when the gall is hard. In knapweed, the weevil *Bangasternus fausti* (Reitt.) attacks the immature flower bud and destroys any developing *U. affinis* galls. The other problem insect is the moth *Metzneria paucipunctella* Zell. as its ability to feed on the ripe achenes allows it to consume the *U. affinis* larvae inside the hard gall. However, Story *et al*. (1991) showed that, although it destroyed some *U. affinis*, it added to the total seed destruction without reducing the subsequent *U. affinis* population.

The "woody gall"-former loses its advantage over non-gall-formers in plants that produce a few large capitula. *Rhinocyllus conicus* rather than the "woody gall"-former *U. solstitialis* is the most abundant species in European *C. nutans* capitula and the agent of choice under strategy 2.1.2 but *U. solstitialis* would be the agent of choice under strategy 2.3.2 and 2.4.3. Both organisms have a high rating under strategy 2.3.1 (H. Zwölfer, personal communication in 1991). However, *U. solstitialis* is a clear preference for *C. acanthoides*, which produces many small capitula over a long season.

Rhinocyllus conicus has reduced seed production of *C. nutans* by over 50% and achieved good control on North American sites where grass competition is strong (Kok and Pienkowski 1985; Harris 1984b). However, *C. acanthoides* has had seed reduced by only 10% and control has been unsatisfactory. On the basis of seed destruction by *U. stylata* (Harris and Wilkinson 1984) and *U. affinis* (Harris 1980), *U. solstitialis* could be expected to reduce seed production by 60-75%. This would be a slight increase over the *R. conicus* impact on the large-headed *C. nutans* and a considerable increase over its impact on *C. acanthoides*. Clearly, *U. solstitialis* would have been the best choice for Canada as the one insect should control both thistles, and *R. conicus* was a bad choice if it has preempted *U. solstitialis* from being effective on *C. acanthoides* as they both favour the first capitula formed. The saving feature may be that many *Urophora* spp. rapidly synchronize with the appearance of capitula in the local host population as the result of limited dispersal. Varley (1947) found that dispersal of *Urophora jaceana* (Her.) from individual plants was only a few centimetres and this may also apply to *U. affinis* as it has synchronized emergence with stand flowering over small distances in British Columbia (Harris 1989b). Thus, it is possible that selection will delay *U. solstitialis* emergence to avoid the *R. conicus* attack on the first capitula.

2.5 Increasing stress on the weed population

Frequently, individual weed biocontrol agents do not do enough damage to control the weed. Myers (1985) pointed out that most successes are attributed to a single agent that displaces the previously established non-controlling species. Myers' strategy is to try new agent species until a successful one is found. However, Zwölfer (1985) found that utilization of some plant species increases with species packing. In these instances it is likely that one phytophage, even in the absence of parasites, will not achieve control. Harris (1981) suggested that the strategy should be to increase the stress on the weed population until a critical threshold is surpassed.

2.5.1. Loading exploitative competitors that attack in sequence

Competition was defined by Keddy (1989) as the negative effects that one organism has upon another by consuming or controlling access to a resource that is limited in availability. Clearly, if an agent remains so scarce that there is no competition, the weed will not be controlled. Thus, competition is essential in weed biocontrol; but not all competition is beneficial. Interference competitors [organisms directly suppressing their neighbours (Keddy 1989)] should be avoided because they reduce the exploitation of the weed, although in some instances the level of interference is too low to matter (Story *et al*. 1991). In contrast, exploitative competition is indirect and reduces the resource.

Some plants are attacked in sequence by several sympatric exploitative competitors, which increase their utilization [e.g. spotted and diffuse knapweed (Zwölfer 1985)]. The number probably depends on the richness of the resource in recent geological history (Southwood 1961). MacArthur (1972) observed that because competition often puts a premium on efficiency, this implies a division of labour among specialists. The models of Akcakaya and Ginzburg (1989) indicated that the niche overlap between sympatric competitors tends to decrease with evolution as each species specializes on what it does best. If there is little niche overlap, the consumption of the weed will increase with the number of exploitative competitors. It follows from this that the more sympatric specialists common on a weed at its origin, the more agents will be required for control. Thus, from a cost point of view, weeds with a few specialists will be cheaper to control than those with many.

The example used to illustrate the value of loading exploitative competitors that attack in sequence is the capitula of *Centaurea*. The fly *U. affinis* oviposits into knapweed capitula that are less than half grown, to form a woody gall (Berube.1980). The gall is a powerful metabolic sink, which decreases vegetative growth and subsequent flowering by *C. diffusa* (Harris 1980). *Urophora quadrifasciata* attacks capitula that are half to full grown (Berube 1980). It does not destroy *U. affinis* galls. Although the two species can coexist in the same capitula, *U. quadrifasciata* tends to avoid those with many *U. affinis*. The conclusion of Myers and Harris (1980) that both insects displace each other is an artifact of the analysis: the capitula with few or no *U. affinis* had more *U. quadrifasciata* as a result of avoidance and not by displacement of *U affinis*. The *U. quadrifasciata* also tend to increase in years when the *U. affinis* population is low (Harris 1980). Thus, the effect of *U. quadrifasciata* is to supplement the impact of *U. affinis*. The seed-head moth *M. paucipunctella* larva mines down a floret into the receptacle where it feeds. The larva leaves the receptacle to consume an average of 8.13 ripe achenes, about half in the fall and the rest in the spring (Story *et al*. 1991). Cages with the two flies alone produced 9.75 seed per capitulum compared with 4.71 with the three insects. The paper by Myers (1985) that suggested the moth was of little value, overlooked the spring feeding.

The soft achene stage in diffuse and spotted knapweed (Harris 1989 a) is unattacked by insects in North America and it should be possible to supplement seed reduction by establishing the European insects from this niche; the tephritids *Terellia virens* (Loew) (Groppe and Marquardt 1989a) and *Chaetorellia acrolophi* White and Marq. (Groppe and Marquardt 1989b), and the weevils *Larinus minutus* Gyll. (Groppe 1990) and *L. obtusus* Gyll. It is probably desirable to establish several of these species because they have different ecological requirements. For example, *T. virens* is found in spotted knapweed stands in western Europe whereas *C. acrolophi* tends to attack the more scattered plants. The two weevils have a more eastern distribution in Europe and hence are likely to be of value in the drier and more continental parts of the North American knapweed range.

2.5.2. Loading agents to attack different organs

A modification of strategy 2.5.1 is to employ species that attack different parts of the plant. Many weeds compensate for mortality at one stage by increased survival at another. Myers *et al*. (1989b) found that intraspecific competition in *C. diffusa* compensated for decreased seed production as well as reduced seedling and rosettes losses. Similarly, Powell (1990) found that seedling mortality decreased with the distance from an established plant. Faced with this situation, the best approach is a multi-pronged strategy: to reduce seed production, weaken the established plants with root-feeding insects, decrease the space available for seedlings by pasture management to increase grass vigour, and increase seedling mortality with the rust *Puccinia jaceae* Otth. Myers *et al*. (1989b) suggested the need to kill the rosettes, and depreciated organisms such as *S. jugoslavica* that merely weaken them. However, the beetle does indirectly increase rosette mortality as Powell (1990) found that almost all the rosettes (about 40% of the first year plants) that died pre-flowering had been attacked by *S. jugoslavica*. He concluded that this resulted from the reduced competitive ability of the attacked plants. If so, management to increase pasture vigour will increase further the mortality of *S. jugoslavica* attacked plants.

The effect of supplementing *U. affinis* and *U. quadrifasciata* on *C. diffusa* at White Lake, B.C., with the root-feeding *S. jugoslavica* has been to decrease seed production by a further 20% (Powell and Myers 1988) and the beetle is not deleterious to biocontrol as claimed by Myers (1985). Diffuse knapweed capitulum production varies greatly with the summer precipitation but the number of developed seed per capitulum is little affected by moisture. *Sphenoptera jugoslavica* was introduced in 1976 and the two seed-head flies spread into the area by themselves somewhat later. All three insects reduce the number of seed per capitulum as well as the number of capitula per plant. Seed production per head has dropped from 12.5 in 1972 (Watson and Renney 1974) to an average of 3.6 in 1983 and 1984 (Powell and Myers 1988). Total seed production has declined from about 33,000 per square metre in 1978 to 2038 in 1987, 598 in 1988, 478 in 1989, and 1240 in 1990. Powell and Myers (1988) suggested that production in 1987 was at or slightly below the replacement level and this conclusion is supported by a decline in knapweed ground from 100% to around 40%.

Results are similar for *C. maculosa* at Chase, B.C. In 1972 there were 26.6 seeds per capitulum (Watson and Renney 1974) but in 1986 this had declined to 15.4 seeds and the seeds were smaller. The result is a drop from over 40,000 seeds per square metre in 1974 to 108 in the dry summer of 1987, 1660 in 1988, 7200 in 1989 and 3303 in 1990. This is slightly over the threshold of 1500 seeds per square metre suggested by Roze (1974) needed for population maintenance. Thus one more agent that becomes abundant should reduce seed production to below the 1500 seeds per square metre threshold. This is unlikely to be a root-feeder because the surviving plants are too small, so the best prospect is other capitulum feeders as outlined in strategy 2.5.1.

Sphenoptera jugoslavica only thrives at the dry half of the diffuse knapweed range and its numbers decline in years with a moist July and August. However, knapweed roots like the seed-heads, are attacked by a complex of exploitative competitors with slightly different needs (Muller 1989a; Muller *et al*. 1989). The moth *Agapeta zoegana* Lam. (Muller 1989b; Muller *et al*. 1988) is thriving in British Columbia on spotted knapweed at the moist end of its range. The weevil *Cyphocleonus achates* Fab. (Stinson 1987) is established on plants with large roots in regions of the province suitable for grape growing. The moth *Pelochrista medullana* Stgr. appears to be most suitable for the zone between *A. zoegana* and *S. jugoslavica*. The species of most doubtful value is *Pterolonche inspersa* Strg. as it is an interference competitor of *S. jugoslavica* (Muller 1989a). There is also a knapweed rust, *P. jacaea*, which attacks the leaves and stems of diffuse knapweed at the moist end of its range (Mortensen *et al*. 1991).

The establishment of organisms of different parts of the plant will undoubtedly increase the pressure on knapweed, but I doubt if satisfactory control will be achieved without good management to maintain pasture vigour. In Europe there is little knapweed on sites where grass competition is high, but stands of dense knapweed can be found on disturbed and overgrazed sites. I am sure that we can achieve the European situation; but we may not be able to improve on it enough to get knapweed control in overgrazed sites.

2.5.3. Increasing weed stress from other vegetation

The normal effect of a successful biocontrol agent is to reduce the competitive edge of the target weed rather than kill it. For example, Huffaker (1953) showed that the effect of clipping *Hypericum perforatum* L. foliage to stimulate damage by *C. quadrigemina* was to reduce root mass and length, which made it less competitive with other pasture species. The capitulum weevil *R. conicus* has controlled *C. nutans* in sites with good grass competition (Kok *et al*. 1986) but not in gravel pits and other sites with little competing vegetation (Zwölfer and Harris 1984). For both *C. diffusa* at White Lake, B.C. and *C. maculosa* at Chase, B.C., the establishment of a competitive grass, such as crested wheat grass, might be enough to achieve control with the agents already established.

2.6. Comparison of selection methods

For comparative purposes I have listed (Table 1) the agent of choice by each strategy for four weeds targeted for biocontrol in Canada.

Target No. 1 is *C. nutans*, a monocarpic thistle that on rangeland produces an early flush of relatively few, large seed-heads and then dies. Rosette leaves are lost during dry summer periods followed by rapid regrowth when moisture is available, which indicates that reserves are in the root and defoliation by insects would do relatively little harm. Zwölfer (1965) recorded seven monophagous and stenophagous insects (possible biocontrol agents) in the capitula and 14 on other parts of the plant. The plant has been controlled by the capitulum weevil *R. conicus* in most places and the rosette weevil, *Trichosirocalus horridus* (Panz.) has also been established on it.

Target No. 2 is *C. acanthoides*, a similar thistle that produces a succession of small capitula until freeze-up. Zwölfer (1965) recorded seven capitula (*R. conicus* was not included) of possible biocontrol interest and nine on other parts of the plant. It is attacked by *R. conicus* in North America, but at an insufficient level. However, the rosette weevil *T. horridus* has more impact than it does on the larger *C. nutans* (Cartwright and Kok 1985).

Target No. 3 is *C. maculosa*, a polycarpic knapweed (lives up to 15 years) that produces capitula in a flush in most rangeland sites in British Columbia. Most European populations of *C. maculosa* are monocarpic, so the name refers to a complex that differs biologically in this and other features. On *C. maculosa sensu lato*, Schroeder (1985) encountered 15 capitula insects and mites [including *T. virens*, which was subsequently revised into three species with narrow host ranges (White 1989)] and 13 on other parts of plant. Thus, it is attacked by a larger specialized insect complex than either of the *Carduus* spp. Hence, it should require the establishment of more biocontrol agents. The largest impact has been from the capitulum gall-former *U. affinis* but it is insufficient to achieve control. The addition of *U. quadrifasciata* has lowered seed production to slightly above the level for maintenance of the weed population (see strategy 2.5.2). The moth *M. paucipunctella* has added to the seed destruction in some sites and currently root-feeders are being established.

Table 1. Best agent choice by each strategy.

Strategy	Target 1	Target 2	Target 3	Target 4
2.1 Holistic strategies				
2.1.1	N.A.[a]	N.A.	N.A.	N.A.
2.1.2	# 8	?	# 11	# 11
2.1.3	N.A.	N.A.	N.A.	N.A.
2.1.4	Not done	Not done	Not done	Not done
2.1.5		— No stem or leaf galls or cecidomyids		
2.1.6	Not done	N.A.	N.A.	N.A.
2.2 Strategies for selecting for specificity and establishment				
2.2	# 8	# 7	#6	# 5
2.3 Strategies for selecting for "biological success"				
2.3.1	# 8 or 12	# 12	#11 or 13	# 11 or 13
2.3.2	# 8	# 12	#11	#11
2.3.3	# 8 or 12	# 12	#11 or 13	#11 or 13
2.3.4	# 12	# 12	#11	#11
2.3.5	# 12	# 12	#11	#11
2.3.6	No resistance to # 8	Resistant to rare # 8	No resistance to #11 or 13	No resistance to #11 or 13
2.4 Strategies to attack vulnerable points for weed survival				
2.4.1	Seed reducers	Seed reducers	Seed reducers	Seed reducers
	# 8 or 12	#12	# 11 + 3 - 6 - 10	# 11 - 5 + 13
	Root-feeders	Root-feeders	# 1 + 7	# 9 + 7
2.4.2	Not done	Not done	Not done	Not done
2.4.3	# 12	# 12	# 11	# 11
2.5 Strategies for increasing stress on the weed population				
2.5.1	Not needed	?	# 11 + 3- 6 + 10	# 11 + 5 + 10
2.5.2	Not needed?	# 12 + 2	# 11 + 3 - 6 – 10 - 3 - 7	# 11 - 5 + 10 + 9 + 7
2.5.3	Helpful		Probably helpful but not tried	

[a]List of agents. 1. *Agapeta zoegana* 2. *Trichosirocalus horridus* 3. *Chaetorellia acrolophi* 4. *Larinus jaceae* 5. *Larinus minutus* 6. *L. obtusus* 7. *Pelochrista medullana* 8. *Rhinocyllus conicus* 9. *Sphenoptera jugoslavica* 10. *Terellia virens* 11. *Urophora affinis* 12. *U. solstitialis* 13. *U. quadrifasciata* : N.A. not applicable.

Target No. 4 is *C. diffusa*, a largely monocarpic knapweed that produces a succession of small capitula until freeze-up. It occurs in a dry regions and, in periods of drought, rosette leaves are lost and then rapidly regenerated when moisture is available. Schroeder (1985) found 13 capitula insects and 13 on other parts of the plant. A combination of the capitula flies *U. affinis* and *U. quadrifasciata* and the root beetle *S. jugoslavica* has resulted in a slow decline in knapweed at White Lake, B.C., that should eventually lead to economic control (see strategy 2.5.1).

In conclusion, in spite of the diversity of agent selection methods many of them arrive at the same choice. One exception is strategy 2.3.6 (the selection of rare agents) that seems to have little merit in these examples. The logical approach is to determine the damage likely to have most impact on weed survival and then select the relevant agent species with a high "biological success" rating. If its damage is not enough to achieve control, additional exploitative competitors should be added.

3. New directions for biocontrol of weeds

3.1 Biocontrol of weeds in cultivated crops

Most successes with classical biocontrol of weeds have been on weeds of uncultivated land. However, the scarcity of data for weeds of cultivated land does not imply that it is a failure as there have been few attempts made and there are two spectacular successes: *C. juncea* in Australia (Cullen 1986) and *A. artemisiifolia* in the USSR (Kovalev and Vechernin 1986). Granted, many organisms cannot survive cultivations; but this is not true of all, as crop pests clearly do so. It appears that the rust *P. chondrillina* was adapted because it disperses readily and increases rapidly (Cullen *et al*. 1973) and so can rapidly colonize cultivated areas. The strategy of the ragweed beetle *Zygogramma suturalis* (F.) is to leave fields for hibernation sites in field margins before fall cultivation and then return in the following spring. If two agents are effective, there should be others that can be developed.

3.1.1. Integration with herbicides

I used to assume that classical biocontrol and chemical weed control were mutually exclusive alternatives. I now see exciting possibilities of integration that need to be explored. Story *et al*. (1988) found that 2,4-D applied to knapweed at the flowering stage was detrimental to the gall fly *U. affinis*, but not to *U. quadrifasciata*, and when applied at the rosette stage it had no effect on the survival of either fly. Thus, there is the possibility of screening biocontrol agents for compatibility with a particular herbicide or changing time of herbicide application to avoid harming the agent. There is also a possibility of using a low herbicide application to supplement the stress imposed by a biocontrol agent. Some herbicides may be stimulatory to certain insects. For example, Maxwell and Harwood (1960) reported that aphid reproduction increased on beans treated with a sublethal dose of 2,4-D. Similarly Ishii and Hirano (1963) reported that the growth of the rice stem borer was increased by treatment of the plants with 2,4-D. Phenoxy herbicides, such as 2,4-D, stimulate protein synthesis and increase both protein and amino acids (often limiting for plant-feeding insects) in the main root-stem axis (Wort 1964; Loos 1975). Campbell (1988) listed many other examples; but it needs to be determined whether it is practical to use herbicides to increase the success of biocontrol agent establishment or their impact.

3.1.2. Use of root-feeders rather than defoliators

I would like to see more thorough investigation of root-feeding insects for the control of terrestrial herbaceous perennials. I have given preference to defoliators because they are easier to screen than root-feeders. However, the root-feeding flea beetle, *L. jaco-*

baeae, is more successful than the defoliator for the control of *S. jacobaeae* (McEvoy *et al*. 1989). Similarly, the root-feeding flea beetles *Aphthona nigriscutis* Foudras, *A. flava* Guillebeau, and *A. cyparissiae* (Koch) are the only biocontrol agents that have had a major impact on leafy spurge in North America.

4. Administrative-political problems

4.1. Multidisciplinary teams

Traditionally in North America a single scientist has been assigned to the biocontrol of one or more weeds. This is a poor strategy. The results achieved in a program that requires 20 scientist years accrue so slowly that both the administration and the public lose interest before there is an impact on the weed. Also, the work often requires a multidisciplinary team. The needs vary with the project, but the disciplines normally involved are insect and plant ecology, insect and plant taxonomy, population dynamics, range agrology, and statistics. To require one scientist to do everything delays progress, lowers work quality, and increases costs.

The biocontrol of knapweed has reached the point where the input of range agrologists would be valuable. Many grasses respond to grazing by tillering which reduces the openings available for knapweed seedlings. Also, cattle graze knapweed rosettes for about 2 weeks after they start growing in the spring. Later in the summer they avoid the foliage, but eat the flowers. Knapweed acceptability to cattle may be related to toxins as the mature foliage produces hypoglycemia in rats by increasing insulin secretion, but the substance is not present in the flowers (Chucla *et al*. 1988). Spring grazing stresses the knapweed, but the summer feeding is counter productive as the gall-former *U. affinis* is consumed.

The need for multidisciplinary teams has been partially met for the pre-release studies on spurge and knapweed by the formation of consortia of Canadian federal departments, provinces, U.S. states, universities, and users. The multiplicity of participants increases both the funding sources and the flexibility for doing the work. I suggest that a consortium should be formed for all weed biocontrol projects and be extended to cover the whole project. It means relinquishing a traditional federal monopoly, but it would breathe new life into biocontrol.

4.2. Review of host specificity studies

The purpose of the Plant Protection Act of Canada (Canada 1990) is to prevent introducing and spreading of plant pests. It covers weed biocontrol by defining a pest as any organism injurious to a plant, even if it is a noxious weed. Thus, beneficial organisms are pests under the Act. Both the Act and the mind set of the regulators is to exclude plant-feeding organisms (see Ramsay 1973 for comments on the similar situation in the United States), but beneficial "pests" for weed biocontrol can be approved for release by authority of the minister. The Commonwealth of Australia Biocontrol Act (1984) solved a similar situation by removing biocontrol from their Quarantine Act (Kerin 1984). This Act included a positive basis, in which agents are approved for release if the benefits are likely to be greater than the detriments, but the tendency in Canada is to prohibit species that might do any damage regardless of the benefits.

Correctly, Canadian weed biocontrol agents are subject to a review before being approved for release, although this is not a requirement under the regulations of the Plant Protection Act (Canada 1990), as it should be. To my mind, the present system has several faults.

(A) Classical biocontrol is done by government in the public interest regardless of property ownership, so there may be conflicts of interest such as bee keepers wanting to retain a plant that ranchers want to eliminate. To permit public comment, the Commonwealth of Australia Biological Control Act (1984) requires that the intent to use classical biocontrol against a weed is published. After review of the comments, the project is approved, rejected, or, if the issues are extremely contentious, passed for political decision. I see several advantages in this process. (1) It puts the decision to target a weed for biocontrol on a sounder financial, moral, and probably legal basis because funding goes to projects that have wide public support and public concerns are considered. It is a safeguard that the project is in the general public interest and not just those of a small group. (2) The program can be modified to take into account special concerns, which may have been overlooked. (3) There is an opportunity to educate the public and address misunderstandings. (4) It allows for input from the provincial governments, which is not permitted at present, even though they are major funders of weed biocontrol projects. I fear that unless the provinces have a means of participating in the decisions, they will pass their own legislation so that it will be necessary to work under many Acts and regulatory bodies with different requirements. This is the situation in Canada with fish. Thus, it is not a coincidence that Canada is one of the last developed countries where the White Amur fish [*Ctenopharydon idella* (Cuv. & Val.)] is used for aquatic weed control (the province of Alberta has started research on it). Apart from the legislative difficulties, the economics of classical biocontrol decrease with the area on which it can be used. Thus, weed biocontrol is more economical on a national than a provincial basis.

(B) The review of agents for release needs to be done by a broad base of expertise that covers not only taxonomy but competition, insect behaviour, insect-plant relationships, and other aspects of plant utilization by natural enemies.

(C) There is no set process in Canada for obtaining a political ruling when there are strong lobbies for and against biocontrol. Contentious issues will always appear in the political arena; but without established procedures, they can be messy, damaging, and time consuming. The need for an appeal process leading to the political level is recognized in the Commonwealth of Australia Biological Control Act (1984). The fact that an appeal procedure exists tends to ensure that the review is thorough, and that rational and detailed reasons are given for decisions.

(D) On the basis of a need for different expertise and the amount of work involved, the proposal to target a weed for biocontrol should be reviewed by a different group from the proposals to release an agent. The former review is concerned about the public use of the target weed and the ecological consequences of reducing its abundance. The latter is concerned with the predictability and stability of the host range of the candidate biocontrol agent and the amount of damage likely to be done to non-target plants.

4.3 Politics and funding of biocontrol

The public is concerned about the environment. I frequently hear the phrase that biocontrol is environmentally compatible, so no one should worry. This is nonsense. The successful biocontrol of a weed has an ecological impact on a regional basis. The impact is perceived as good if most people like it and bad if they dislike it. Real or imaginary public concerns about the impacts must be addressed. Johnson (1985) has done this for the biocontrol of native plants and I have attempted to do it for non-target effects of biocontrol (Harris 1988, 1990b). Increasingly, the public wants to participate in the decision whether to use biocontrol, an alternative, or nothing. If researchers do not respond to this political reality, the public mood is likely to change from sympathy to antagonism.

Contrary to a widely held public myth, biocontrol of weeds is not cheap in terms of either scientific involvement or cost. At a time when governments are trying to reduce budgets, they are unlikely to spend around $4 million to control a weed biologically just because it is desirable. However, funding is available for economically sound projects on which a farm commodity group or other segment of the public puts a high priority. Delfosse (1990) estimated that there is a 50-year backlog of weed biocontrol projects in Australia and the situation is probably similar in Canada. The backlog can be reduced if there is sufficient funding. The formation of North American consortia to fund pre-release studies has helped, but other funding sources need to be explored. The consortia approach might be extended to a world basis; but this would require agreements to be signed between the cooperating government departments, which is something they are reluctant to do when their funding is dependant on an annual vote. Other possibilities that should be explored are check-offs of farm commodities and, as done by Montana, USA, a tax on chemical pesticides; these funds would be designated for finding non-chemical solutions for pest problems. Funding solutions can be found if there is sufficient public interest, but are unlikely to arise by themselves. Indeed, in my view, they should not be imposed if they do not have public support.

User groups are also helpful in many ways besides the funding aspects:

(A) To be fully effective, biocontrol needs to be integrated into the farm management system. A weed like knapweed involves managing a four-way agent-weed-grass-cattle interaction and the help of ranchers is needed to determine what works best. The more ranchers are involved, the better the chances of solving the problem.

(B) The best transfer of new technology to a select and scattered clientele is by word-of-mouth communication. Peters (1987) recommended that, for industry, 75% of marketing effort should be devoted to the word-of-mouth network. In weed biocontrol the emphasis should be still greater although obviously field days need to be used to start the process. The importance of a user group is so high in Canada that normally biocontrol of a weed is not started without their active support.

There are dilemmas associated with involving user groups as partners:

(A) They are generally not supportive of basic studies to quantify the weed problem and determine the suitability of biocontrol as a solution. They know that they have a problem and want to get on with screening agents for release; however, government funding is unlikely to be available, or at least will not be sustained for the necessary 20 years, without data to quantify the problem and to show that biocontrol offers an economically sound solution. It may be desirable to quantify the problem as a separate program for 1 or 2 years before approaching a user group.

(B) For similar reasons, user groups will not support basic studies to improve the efficiency of biocontrol if this is likely to delay or add to the cost of their program. It requires creativity to include the research component, which is essential to the well-being of biocontrol, into an applied program.

(C) User groups want to be part of the decision-making process; but they find boring discussions of technical problems and disagreement among specialists confusing. Thus, separate meetings are required to deal with the general direction of the program and the technical aspects. The user needs to be kept informed of the progress and problems, but annual reports prepared for government generally are not suitable.

(D) The researchers, federal and provincial government departments, and the user group partners on a biocontrol project have different objectives. This must be recognized and tolerated by all. The researchers want to understand the system and tell about it, government wants public recognition, and user groups want a rapid solution to the problem.

(E) It improves technology transfer and probably establishment success if the user is responsible for agent distribution. The dilemma is that governments also like doing this as it has a high and favourable public profile. However, I suggest that for the good of biocontrol, the main government involvement should be restricted to research sites and secondary distribution centres that are used for field days. Field days should meet government needs for public recognition. The knapweed program in British Columbia is getting ranchers to the field days who have not participated previously, so both government and biocontrol seem to be benefiting by letting the ranchers do the distribution.

Conclusions

Biocontrol is at an exciting stage where it can achieve major and rapid development. This requires vigorous debate and testing of hypotheses; the pooling of data for collective analysis; and the relinquishment of the traditional federal monopoly in this field to programs shared with provinces or states, universities, and users. I see a beneficial trend of such consortia to assume program management in place of a remote federal bureaucracy and to breathe new life into weed biocontrol.

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