BIOLOGICAL CONTROL OF WEEDS: A REVIEW OF PRINCIPLES AND TRENDS

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ABSTRACT - The biological control of weeds can be practiced in three different ways, i.e. by introduction of control agents (classical approach), conservation of existing control agents and the numerical augmentation of native control agents by inundative releases. The main principles, general consideration and the methodology of each of these approaches are shortly reviewed, as well as their potentials and limitations. Classical biological weed control the approach most frequently employed, provided an overall success rate of about 30%, has a positive cost to benefit ratio and is ecologically rewarding. It is pointed out that its great potentials are not yet fully realised because of limited financial support, but that the socio-economic benefits deriving from it could be important in the future. Special attention is also being paid to the inundative approach, especially to the development of bioherbicides, a novel method of biological weed control employing mainly native plant pathogens. It is expected that this control method will gain in importance in the future, after the presently existing limitations will be overcome. Biological control of weeds should be considered as one of the available options in all weed situations. It offers great socio-economic benefits and is environmentally safe and therefore should be the favoured weed control method in the future.

Index terms: biological control, weeds, bioherbicides.

CONTROLE BIOLÓGICO DE PLANTAS DANINHAS: UMA REVISÃO DOS PRINCÍPIOS E TENDÊNCIAS

RESUMO – O controle biológico de plantas daninhas pode ser feito de três formas diferentes: pela introdução de agentes de controle (método clássico), pela conservação de agentes que ocorrem localmente e pelo aumento numérico de agentes de controle nativos através de liberações inundativas. Os principais princípios, considerações gerais e a metodologia de cada uma destas estratégias são brevemente revistas, como também o potencial e limitações das mesmas. O controle biológico clássico, a estratégia mais freqüentemente empregada, apresenta um índice geral de sucesso de aproximadamente 30%, tem uma razão de custo/benefício positiva e é ecologicamente gratificante. Ênfase é dada ao fato de que seu potencial pleno ainda não é completamente explorado devido ao limitado suporte financeiro, mas que os benefícios sócio-econômicos resultantes poderão ser importantes no futuro. Atenção especial é dada à técnica inundativa, especialmente ao desenvolvimento de bioerbicidas, um novo método de controle de plantas daninhas através do uso principalmente de patógenos nativos. É esperado que este método cresça em importância, após as limitações atuais serem superadas. O controle biológico de plantas daninhas deve ser considerado como uma das formas disponíveis de controle de invasoras em qualquer situação. Ele oferece grandes benefícios sócio-econômicos, é seguro para o meio ambiente e deverá ser o método de controle de plantas daninhas preferido no futuro.

Termos para indexação: biocontrole, inças, herbicidas.

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INTRODUCTION

Until about the end of World War II man tried to control weeds mainly by mechanichal means, as well as by crop rotation and seed cleaning. The work input in weed control was considerable, but its success variable. The situation changed dramatically with the appearance of modern organic herbicides. For the first time man seemed to have found a tool to overcome most if not all his weed problems in a relatively easy, inexpensive and efficient way.

Under these circumstances, biological weed control, although first used as early as 1836 (Goeden 1988) and with increasing frequency since about 1960 (Julien 1987), remained altogether a control method of minor importance; in spite of several spectacular successes (Goeden 1988, Crawley 1989).

However, in recent years it has been realised that the abundant and extensive use of herbicides is not a panacea for weed control and may have negative side effects on the environment. The main problems encountered consist in a shift in the weed flora, the development of herbicide tolerance and resistance (LeBaron & Gressel 1982, Barralis & Gasquez 1987), the accumulation of persistent herbicides in groundwater, and negative effects on the flora and fauna when herbicides are applied along railway lines, roads, motorways, rivers and other uncultivated areas. In addition, the search for and development of new types of herbicides becomes increasingly more difficult and requires larger investments by private industries. Moreover, because of the increasing public awareness of the potential dangers of herbicide use, most governments considerably increased the safety demands and banned the use of certain types of herbicides. Last not least, the less developed countries find it more and more difficult to meet the increasing costs for imported herbicides and spray equipment, and there is increasing awareness of the importance to protect their flora and fauna.

For all these and other reasons, the application of alternative weed control methods, most of which have been used since long, again attracts interest. One of them is biological control which seems to be the logical choice for a number of weed problems, and is especially attractive for developing countries because it is cost effective, often persistent and without negative effects on the environment.

The methods used in biological weed control are: (a) the "classical" approach aiming at the control of naturalized weeds by the introduction of exotic control organisms from the weed's native range – this is the approach most frequently used, (b) the "conservation" approach employing environmental manipulation to enhance the effect of existing native or exotic control organisms – so far of little importance; and (c) the "augmentative" approach using periodic releases and/or redistribution of native control organisms – attracting increasing interest, particularly the use of native pathogens.

CLASSICAL BIOLOGICAL WEED CONTROL

The objective of classical biological weed control (or introduction) is the reduction and long term stabilization of weed density at a sub-economic level, i.e. below a given threshold, rather than immediate reduction or elimination of economic losses. Permanent control of weeds has been obtained in a sufficient number of cases to establish classical biological weed control as a valuable method of weed suppression. It is based on the observation that natural enemies (predominantly host specific phytophagous insects and pathogens) are of prime importance in limiting the distribution and abundance of plants. Intentionally or accidentally introduced without their consumers into areas outside their natural distribution, many plants become economically important weeds (Harris 1973); e.g. 78 of the 107 registered noxious weeds in

Canada are introductions (Frankton & Mulligan 1970). The same applies to other classical immigration areas like the United States, Australia, New Zealand, and to many areas in the subtropics and tropics; the abundance of the water weeds *Eichhornia crassipes* and *Salvinia molesta* outside their native range in South America is a good example.

Interestingly, the first insect used in biological weed control was the cochineal *Dactylopius ceylonicus* from Brazil; introduced into northern India in 1975 in the mistaken belief that it was *D. coccus*. *D. ceylonicus* readily reproduced on its natural host plant *Opuntia vulgaris*, which had escaped from cultivation and had become a widespread weed in India. Once the control potential of *D. ceylonicus* had been realised, it was introduced into southern India between 1836 to 1838, and transferred from India to Sri Lanka (then Ceylon) shortly before 1865 (Goeden 1988, Moran & Zimmermann 1984). Between 1903 and 1985, there are 727 programmes of biological weed control involving 94 weed species and 215 species of control agents in 50 countries (Julien 1987). The rate of success was variable, but about 30% of the programmes resulted in partial or good control (Julien et al. 1984, Lawton 1990b). The reasons for the relatively low success rate are not well known, because a large number of programmes is not well documented and the input into individual programmes has been quite variable. Nevertheless, recent analysis of the former programmes, based on Julien's catalogues (1982, 1987) and the database developed during the Silwood Project on Weed Biocontrol (Moran 1986), by Crawley (1989) and Lawton (1990a) have highlighted a number of important considerations which may help to improve the success rate in future weed biocontrol programmes. Perhaps the most disappointing result of the recent reviews of the successes and failures in classical biological weed control using insects is, that the rate of success was not improved during the past two decades (Lawton 1990a). Earlier programmes were undertaken in an empirical manner with relatively little attention being given to developing a scientific basis (Harris 1977). However, during the period 1960 to 1990 considerable effort has been made by weed biocontrol practitioners and theoretical ecologists to develop scientifically based guidelines (reviewed by Schroeder 1983, Schroeder & Goeden 1986). The fact that these efforts did not improve the overall success rate does not necessarily mean that present guidelines are useless or at least largerly imperfect. As Schroeder & Goeden (1986) have indicated, even in a number of more recent programmes the discrepancy between theory and practice may have been an important reason for an unimproved success rate.

In spite of these selfcritical statements, practitioners of classical biological control of weeds can be proud of what has been achieved in a number of successful programmes (e.g. Crawley 1989, Cullen 1986, Doeleman 1989, Goeden 1988, Julien 1987, Moran & Zimmermann 1984). Permanent control of invasive alien weeds has been achieved on large areas and annual losses of millions of Dollars have been prevented. Conservative estimates of the overall cost to benefit ratio in classical weed biological control are highly positive. It is therefore of interest to review shortly the basic rules and principles of classical biological weed control.

Basic considerations for the development of control programmes

All present programmes follow ideally the procedure described by Harris (1971) which is (a) determine the suitability of the weed for biological control; (b) conduct surveys for suitable natural enemies in the weed's natural range, (c) select the most effective natural enemies, (d) study the host specificity of these organisms to ascertain their safety, (e) introduce and establish selected agents and (f) evaluate the effect on the weed population.

A detailed review of the protocol of biological weed control is given by Schroeder (1983), and an organigramme of a classical biological weed control programme is given in Table 1a-c. The review which follows will therefore be restricted to major considerations and the results of the analysis' of programmes by Crawley (1986, 1987, 1989), Moran & Zimmermann (1984) and Lawton (1990a).

The selection of suitable target weed species

Until recently, most target weeds were selected because conventional control methods had failed to control the weed, were considered to be uneconomic or could not be applied for other reasons. Now it is generally accepted that the initiation of a programme

TABLE 1. First Phase: In area (country) of introduction.

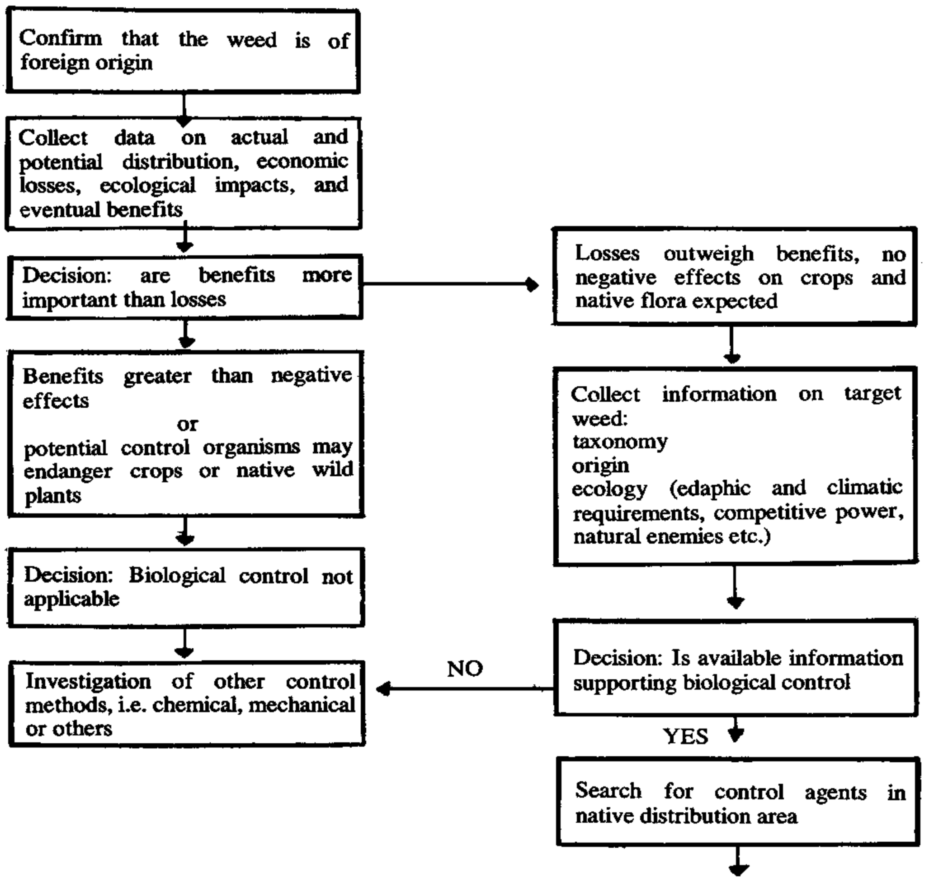


TABLE 1b. Second Phase: Work in natural distribution area.

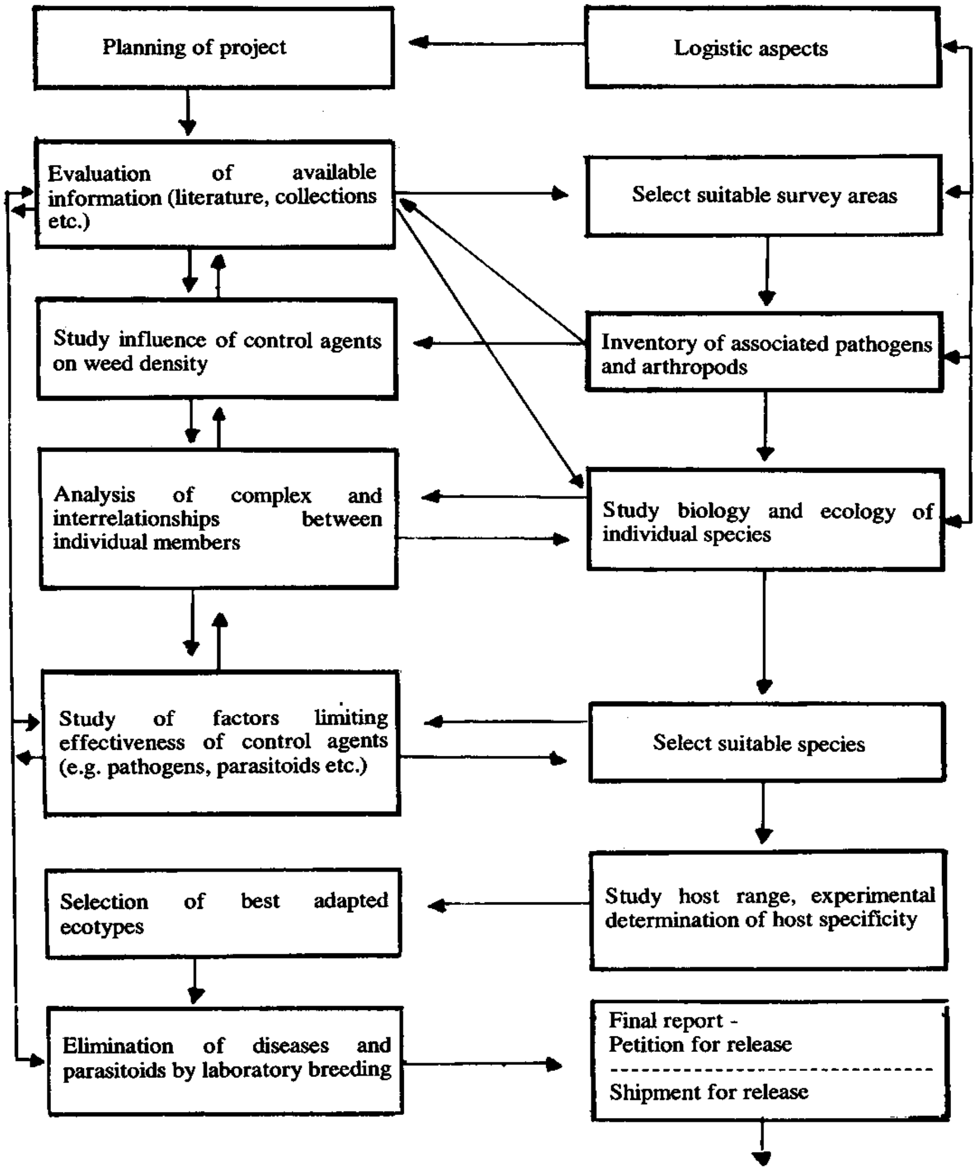
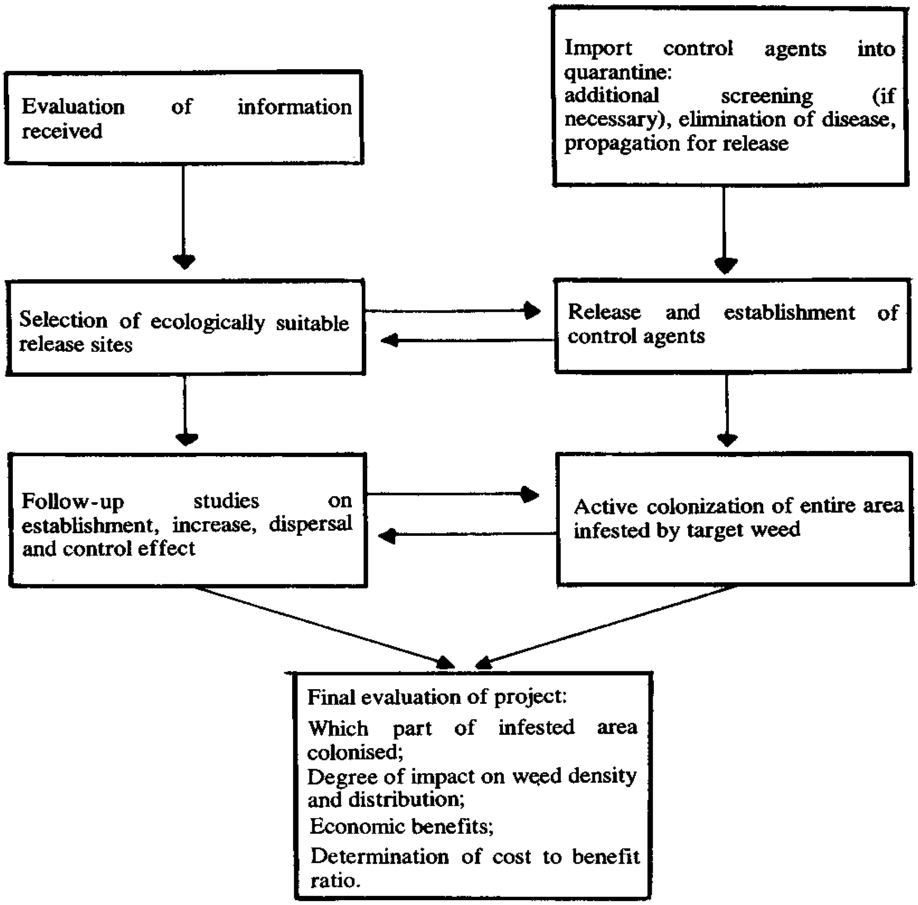


TABLE 1c. Third Phase: Importation of control agents, liberations, establishment, evaluation of results.



should be preceeded by a careful analysis of the weed problem to determine whether it is suited for biological control.

Main considerations in this process are: (1) The correct identification of the weed species, subspecies or strain. This is particularly important for naturalised weeds, as is illustrated by the exemples of *Chondrilla juncea* (Hasan 1972), *Lantana camara* (Harley et al. 1979), leafy spurge (*Euphorbia spp.*) (Dunn 1979), or *Salvinia molesta* (Forno & Harley 1979). (2) The collection of information on the population biology and ecology of the target weed and its interaction with the native flora, as well as on the ecological characteristics of the colonised areas. (3) The determination of the economic damage caused, and the beneficial value of the weed. The cost to benefic ratio should be estimated for biological control and other potential control methods, and in principle biocontrol should only be initiated if it gives a better return than can be achieved from alternative control methods. (4) Every effort should be made to resolve conflicts of interest which may arise between different interest groups because of economic, ecological or even aesthetic considerations (Andres 1981). A recent example of an extreme strong conflict of interest concerning *Echium plantagineum* in Australia is discussed by Delfosse & Cullen (1981). It was a catalyst for new legislation in Australia, the "Biological Control Act 1984" (Cullen & Delfosse 1986).

The analysis of former biological control programmes indicates, that asexually reproducing plants were controlled significantly more often than sexually reproducing species (Burdon & Marshall 1981). In addition, Crawley (1989) called attention to the fact that annual plants in annual crops are difficult to control with insects, and perennial weeds are difficult to control if they possess one or several of the following traits: (1) a long growing period, (2) large reserves, (3) high powers of regrowth following defoliation, (4) similar powers to replace fruits and seeds after defoliation, and (5) large seed banks and protracted dormancy. All these characteristics should be considered in surveys for and the selection of potentially suitable target weeds for biological control.

The selection of suitable biocontrol agents

It is obvious that biological control practitioners have a keen interest to rationalise the discovery and selection of potentially suitable biological control agents, i.e. agents which, following their establishment, become key-factors regulating weed density. It is impossible to review the extended literature on this topic at this occasion (for references see Schroeder 1983 and Schroeder & Goeden 1986), instead those aspects most frequently addressed will be mentioned. These are:

1. The geographic area to survey for suitable control agents. A generally accepted guideline is that the greatest number of stenophagous natural enemies occurs nearest the centre(s) of diversification of a weed genus or subgenus. Thus, surveys for potential control agents should start at or near such evolutionary centres. A second guideline, particularly strongly advocated by Wapshere (1981, 1985), is the importance of "eco-eclimatic matching" between the survey areas and future release areas. In practice the first guideline is quite often difficult to follow, because the centre of diversification may be unknown or disputed by botanists, and the present species diversity is not necessarily an indication of such centres, because of the overriding importance of human activities. The advantage of climatic matching is obvious and well documented by examples, but again, the actual distribution of species does not necessarily document their climatic preferences and tells little about the range of climatic conditions they are able to tolerate without deleterious effects.

2. Agent-related characteristics which identify potentially effective control agents. Harris (1973) was the first to propose a scoring system to determine the potential effectiveness of insects as biological control agents. He considered the degree of specificity, type of damage inflicted, period of attack, reproductive potential, feeding behaviour, extrinsic mortality factors, compatibility with other control agents, and evidence of effectiveness as control agent elsewhere. Although Harris' scoring system was modified by Goeden (1983), both are in fact not very helpful. In contrast, some possibly helpful generalizations derived from the analysis of former control

programmes by Crawley (1986, 1987, 1989). His analysis suggests that insect herbivores with high rates of intrinsic increase (r), with characteristics such as small body size, high fecundity and a short generation time, become more frequently established and also tend to lead to more effective control. Further, agents that are widespread and abundant in their native distribution area are more likely to establish than rare, local species (Crawley 1987). On the other hand, Crawley (1989) found no clear relationship with success and the mode of attack. Similarly, Lawton (1990a) reports that the effects of agent taxonomy are small. In conclusion, more data need to be collected before we can hope to select the potentially effective control agents among those associated with the target weed in its native distribution.

3. Wapshere (1974b) recommended that ecological studies should be carried out in regions ecoclimatically homologous to the release areas to identify effective control agents. He suggested that the effective organisms are those which play the major role in controlling the distribution and abundance of the plant after allowances have been made for minor ecological differences and for the part played by parasitization, predation and disease. This is in principle a valuable suggestion, but in practice a valid estimation of the impact of an organism on the abundance of its host plant is in most cases impossible. We therefore urgently need detailed experimental studies on the impact of different types of control agents, and on the relationship between types and levels of damage and plant population dynamics (Crawley 1983).

Host specificity determination of biocontrol agents

The screening of the potential host range and host specificity is the most crucial operation in any biological control programme. Because of the overriding importance of safety, the greatest care has to be taken in selecting appropriate test plants and in designing screening tests to demonstrate the safety of potential control agents beyond reasonable doubt. General considerations have been published by Harris & Zwölfer (1968), Zwölfer & Harris (1971) and Wapshere (1974a).

At present the selection of test plants is based on proposals made by Harris & Zwölfer (1968) and Wapshere (1974a). The aim is to select those plant species which are potential hosts of the organism in question, without undue expansion of the test plant list. The list must include:

(1) plants related to the target weed and other recorded hosts of the candidate agent, however dubious such records may be;
(2) host plants of species closely related to the candidate agent;
(3) unrelated plants having morphological or biochemical characteristics in common with target weed;
(4) crop plants the entomology and mycology of which is little known and those that for geographic, climatic or ecological reasons have not been exposed to attack by the candidate agent; and
(5) rare and endangered plant species in the release area related to the target weed.

In cases where little or no reliable information is available, the agent is first tested against a critical test plant (Wapshere 1974a) which is normally the crop plant most closely related to the target weed, or a closely related wild plant from the area of introduction.

Wapshere (1974a, 1975) proposes the following testing sequence which is used in most current screening programmes (Table 2).

The number of plant species which must be included depends mainly on: (1) the taxonomic position of the target weed – whether it belongs to an isolated family or a

TABLE 2. Testing sequence for host specificity determination of biocontrol agents.

Testing sequence	Plants to be tested	Host range determined if plants at that phylogenetic level remain unattacked
1st	other forms of target species	specific to clone
2nd	other species of same genus	specific to species
3rd	other members of tribe	specific to genus
4th	other members of sub-family	specific to tribe
5th	other members of family	specific to sub-family
6th	other members of order	specific to family

family with close relations; (2) the number of closely related cultivated plants, and wild plants, which should not be attacked; (3) the geographic and/or ecological isolation of the release area; and (4) whether or not the control organism belongs to a systematic group which is known to be restricted to a small group of closely related plants (genus, subtribe, tribe). In recent examples of host range determination, the number of plant species screened ranges between 40 and over one hundred. The type of tests required depends on the target weed and the type of agent organism tested. Thus, screening tests have to be carefully adapted to specific requirements (Schroeder 1983).

Although there is no guarantee that an agent which is at present host-specific will continue to be so in the future, general experience tells us that host transference is a rare event (Zwölfer & Harris 1971). As stated above, classical biological control of weeds has been practised for more than 100 years and introductions of some 215 control agents have been made against 94 target weeds in 50 countries (Julien 1987). In all instances where host range tests approximating those outlined have been undertaken there have been no adverse or unpredictable results. In spite of this excellent track record of biological weed control, doubts are still being voiced about the safety of biological control introductions. It is the task of the biocontrol specialists to invalidate these doubts by presenting well written petitions for the importation and release of a weed biocontrol agent.

Introduction, liberation and establishment of control agents

The introduction of biological control agents requires the permission of the competent quarantine authority. As a rule the decision to clear an agent for introduction and (later) for release depends on the provision of a "petition" which, in the case of the United States must be accompanied by an "environmental assessment". In most recent control programmes the larger part of the pertinent investigations are being made within the native distribution area of the control agent, often followed by additional host specificity screening under quarantine in the country of introduction. Only after all safety requirements have been fulfilled, permission for field release is granted.

The source and quality of release populations are logically two important considerations. It is generally accepted that all reasonable effort should be made to release control agents free of parasitoids and diseases. Today most biocontrol practitioners also agree that release populations as far as possible should be adapted to the biotype of the target weed and ecoclimatically preadapted to the release area. In cases where this cannot be guaranteed, experience tells that agents with a broad ecological tolerance, i.e. those widespread in their native distribution area, should be favoured over those with narrow tolerances, i.e. those with local or patchy distributions (Harris 1971, Crawley 1987). Attention should also be paid to the genetic make-up of release populations. The analysis of former control programmes suggests that the optimal degree of genetic variation has to be considered in relation to the mode of propagation of the target weed (asexual or sexual) and the genetic variability of the target weed population.

The factors which favour or prevent the establishment of biocontrol agents are still a matter of debate, mainly because former biological control programmes provide apparently contradicting evidence. However, their detailed analysis (Crawley 1986, 1987, 1989, Lawton 1990a) revealed that successful establishment is significantly more likely for species with a high rate of intrinsic increase and species which are widespread or numerically abundant in their native distribution area. On the other hand, no general positive effect of climatic matching on establishment was found, and emperical evidence for the importance of a period of genetic adjustment is at best feable (Lawton 1990a). Moreover, there is no evidence that interspecific competition with native or introduced herbivore species has negatively influenced establishment of control agents. This is not surprising, because biocontrol practitioners deliberately avoid releasing potentially competing agents in the same area. Surprisingly, the data from former biocontrol programmes provide no evidence for a threshold population size for successful establishment of insect species released for weed control (Crawley 1987). Nevertheless, the probability of establishment increases both with the size of individual releases, and with the number of releases. It would seem that the number of individual releases needed for successful establishment depends both on the environmental resistance of the release area, e.g. the abundance of general predators or the rigour of climatic conditions, and the type of agent released and its mode of reproduction. Only well planned release experiments with varying agent numbers in different parts of the weed infestation will provide the information urgently needed.

Evaluation of the effect of biocontrol agents on the target weed population

The careful monitoring of the development of established control agent populations and their impact on target weed density is a general demand of biological control practitioners. Unfortunately, in most biological weed control programmes it is impossible to obtain funding for such follow-up studies, partly because of general financial constraints, partly because administrators in funding agencies do not appreciate the overriding importance of follow-up studies for testing our predictions and to elucidate the reasons of successes and failures in biocontrol programmes. The result is that even after a hundred years of practical biological control of weeds we are still totally unable to predict whether a particular introduction will be a success or fail (Crawley 1987).

The releases of biological weed control agents are unique ecological experiments which, if carefully evaluated, will not only help to improve the success rates in future control programmes, but also provide the data needed by ecologists to develop models on the population biology of plants which in turn will help to improve the predictability of biocontrol measures.

In the few cases where follow-up studies approximating those demanded by biocontrol practitioners have been made, a lot has been learned and it was demonstrated that classical biological control of weeds can reduce and permanently maintain naturalised weed populations below the economic threshold demanded. In all these cases the cost to benefit ratio was highly favourable. The overall cost to benefit ratio could certainly be improved in the future if both successes and failures were properly analysed. The problem is to obtain the funding for such investigations.

Discussion

We have seen that classical biological control is a complex control method and requires a substantial research input both in the area infested and in the native distribution area of the target weed species. It is therefore important that the targets of biocontrol programmes are carefully selected, i.e. that the present or potential future economic damage justifies the investment and that the weed species concerned is a suitable target for biological control. As documented by successful former biocontrol programmes, the cost to benefit ratio of classical biological control is highly positive, especially because it offers a permanent solution for intractable weed problems.

Although most biological weed control practitioners feel that the overall success rate of programmes needs to be increased, the 30% achieved so far is not at all bad and, as Lawton (1990a) states must be at least as good as the strikerate in the search for new pesticides. Both, biocontrol practitioners and interested ecologists have quite definitive ideas how the present success rate could be improved. They propose that in future control programmes the guidelines developed for classical biological control should be followed more strictly and that well controlled practical experiments should be underpinned by theoretical studies. To do this, it is of prime importance to convince the funding agencies that investments in these types of research are the only chance to make the outcome of biological control programmes more predictable and to increase the overall success rate and the economic benefits.

Classical biological control is rewarding as it offers permanent solutions to problems caused by invasive weeds at a positive cost to benefit ratio and without negative effects to the environment. Therefore it is of particular interest for economically less developed regions and for those dealing with invasive weeds in areas under conservation, like the International Union for the Conservation of Nature and Natural Resources (IUCN).

The conservation of biological control organisms

The conservation of locally existing biological control organisms by the reduction of pesticide sprays, the use of selective pesticides and/or changes in management, which receives increasing attention in the control of arthropod pests in orchards and vineyards, is not yet being considered in weed control. The main reason is that, especially in field crops, all non-crop plants are considered to be weeds, although their weed status, i.e. the question whether they compete with crops for important resources and cause measurable crop losses, has in most cases not been studied. The wide application of cheap broad-spectrum herbicides has accompanied and fostered the philosophy of "weed-free" crops. Therefore, the investigation of the flora and fauna associated with adventive plants in crop situations has been totally neglected and information on the herbivores and pathogens associated is therefore very scanty.

However, the great economic importance of introduced plant species in many parts of the world (Holm et al. 1977, Parsons 1973, Reed & Hughes 1977, Whistler 1983) which do not attain weed status in their native distribution indicates that their populations are under effective natural control in their areas of origin. The study of the naturally occurring consumers and their impact on host plant density and population dynamics is therefore of great interest. The fact that a number of native weeds in cultivation are also part of the floras in adjacent uncultivated land in the same area, e.g. field margins, road sides, railway lines, river banks, low productivity pastures and other uncultivated places, is important to note. It is quit probable that populations of existing phytophagous organisms could be conserved and enhanced if herbicide treatments in these plant refuges would be suspended. They could then become a source of "control agents" for adjacent areas under cultivation.

In semi-natural situations like in managed grassland or hay fields a changement in management could help to conserve and enhance the effect of locally existing antagonists of single unwanted plant species. Unfortunately, this assumption is little supported by hard facts. An example provides the investigation of the phytophagous insects associated with *Rumex spp*. (common pasture weeds in Europe which are spot-treated with the herbicid glyphosate) by Scott (pers. comm.). He found that the effect of several species of Sesiids (Lepidoptera) could certainly be enhanced considerably in a number of sites if the first mowing would be delayed by about two weeks. At present the main oviposition period and the first harvest coincide and most moth eggs are being removed before the larvae hatch and can establish in the root stocks of this perennial weed. Scott is confident that a high level of natural control of **Rumex** could be achieved by a change of management. This is just one example illustrating that the conservation of naturally occurring control agents has a control potential for certain native weed species. The potential of conservation as a means of weed management will however remain unknown until a better knowledge of the fauna of native weed will have been acquired.

It is therefore appropriate to say that biological weed control by conservation will hardly attract much attention in the near future. In contrast, biological control by augmentation and inundation has recently attracted much interest.

Biological weed control by augmentation and inundation

The effect of native antagonists on their weed hosts is often limited for a number of reasons. Spatial separation from their host plants by shifting cultivation, climatic reasons, prevention of population increase by management practices and the development of homeostasis between host plant and herbivore or pathogen through natural selection are the most important. The goal of the augmentative approach is to overcome these constraints and to increase the populations of existing local control agents to reach high population levels at the critical period of the weed's life cycle.

The augmentation approach

Augmentation of native biological control agents can be achieved directly or indirectly, provided their life histories and their population biologies are well known. Indirect augmentation can be achieved mainly by changes in crop management which guarantee the survival and population build-up, e.g. by better timing of spray operations, the use of selective pesticides, the provision of refugia for hibernation and estivation or, in the case of pathogens, the application of sublethal rates of herbicides to improve their weed control efficacy. In contrast, direct augmentation is aiming at the local increase in numbers of an organism by the release of larger numbers of field collected or laboratory reared individuals or, in the case of pathogens by releasing large amounts of inoculum. Lekic (1974) and Kara & Lizenko (1976) reported on the collection and later mass release of *Phytomyza orobanchia* (Diptera, Anthomyiidae) to control several species of *Orobanche*, important parasitic weeds of sunflowers, tobacco and tomatoes, in Yugoslavia and the USSR, respectively. Frick & Chandler (1978) reported on the release of laboratory reared noctuid moths *Bactra verutana* for the control of purple and yellow nutsedge, *Cyperus rotundus* and *C. esculentus* in the USA. In the same way the root nematod *Paranguinea picridis* has been used for the control of Russian knapweed, *Acroptilon repens,* in the USSR.

Most of the naturally occurring plant

pathogens are ineffective due to certain constraints such as host resistance, lack of adequate inoculum, spatial and temporal isolation between pathogen and plant, and/or the lack of virulence (Shrum 1982). These pathogens occur at "endemic" levels which are insufficient to produce acceptable levels of weed control. However, conditions for epidemic levels of disease development generally exist somewhere in a larger area or highly virulent pathogen strains suddenly appear in localized areas. Spores and/or mycelium can be collected in such places and an epidemic can be caused in other areas if massive amounts of inoculum are applied when conditions are favourable for disease onset. The augmentative approach is suited for obligate parasites such as rusts, smuts and viruses which cannot yet easily be cultured and mass-produced. Dyer et al. (1982), Phatak et al. (1983) and Massion & Lindow (1986) have demonstrated the feasibility of controlling *Cirsium arvense* with *Puccinia obtengens*, *Cyperus esculentus* with *P. canaliculata* and *Imperata cylindrica* with *Sphacelotheca holci*. Indeed, a commercial formulated product of *P. canaliculata* will shortly be on the market (J. Herren, pers. comm.).

It remains to be seen if the problems associated with the augmentative use of native natural control organisms can be solved, e.g. the collection of a sufficient number of the organism or the timing of their mass breeding, and in the case of obligate parasitic pathogens the manipulation of inoculum, namely the process of collection, storage, formulation and application. In most instances it will be difficult if not impossible to treat larger surfaces, and data need to be collected on the economics of this control approach. However, the augmentative approach may be well suited for weed control in small holdings and especially in regions where labour costs are still relatively low.

The inundative approach

The inundative use of native weed control agents has been developed by plant pathologists and has attracted great interest during the past two decades. The potential of native pathogens for the biological control of weeds was first realised during competition experiments conducted in rice interplanted with northern jointvetch, *Aeschynomena virginica* in Arkansa, USA, in 1969 when the weed was eradicated in the experimental plots by disease. The causal agent was isolated and identified as the native fungus *Colletotrichum gloeosporioides f. sp. aeschynomenae*. The fungus was found in 31 rice-growing counties of Arkansa during surveys between 1970 and 1972, but in no instance was the disease virulent enough to reduce seed production or to kill plants. Field observations indicated that the limited effect was related to low levels of inoculum at early stages of plant development in natural habitats (Smith Junior, et al. 1973).

Extensive laboratory and greenhouse experiments were conducted to determine the effect of nutrient medium and environmental factors on growth and sporulation of the fungus. TeBeest et al. (1978) note that 100% infection of *A. virginica* by *C. gloeosporioides* occurred with concentrations above 1 x 10^5 spores/ml at 28°C and 12 hours free moisture. Host specificity tests demonstrated the safety of the fungus, allowing field testing in experimental plots. Later tests in commercial rice fields demonstrated that control of *A. virginica* can be achieved with an aqueous suspension of spores at concentrations of 2-15 million spores/ml when sprayed on the weed at dusk at 94-374 l/ha. Young plants of *A. virginica* were most rapidly killed, but control reached 99% when the plants were as tall as 66 cm. The large scale industrial production of spores was started and a commercial product, Collego, was marketed in 1981 after a considerable period of field and formulation studies.

The same year, another mycoherbicide, DeVine, was registered in the USA. It consists of chlamydospores of a pathotype of *Phytophthora palmivora*, a fungus isolated in

1972 from dying milkweed vine *Morrenia odorata* in Florida. Investigations on the distribution, efficacy, host range and stability of *P. palmivora* commenced in 1974 (Ridings et al. 1977, 1978). Because of the positive results Dr. Ridings and associates began working with Abbott Laboratories in 1976 on the development of *P. palmivora* as a commercially available mycoherbicide. The unformulated product is used as a post-emergent herbicide and controls seedlings as well as mature vines. Nearly 100% control of the weed is usually obtained and control lasts for more than two years (Charudattan 1988). Indeed, this product is so successful as a residual herbicide that there is no ongoing market, ironically this makes it commercially "unsuccessful".

The innovative research in the USA has generated worldwide interest in the development of plant pathogens as bioherbicides. The number of pathogen species presently under investigation is little known because scientists working in collaboration with private companies are urged not to disclose their research in order not to compromise future patent application for commercial products. Therefore the impressive lists of fungal pathogens under consideration as inundative weed control agents published by Charudattan (1988) and Hasan (1988) are incomplete. Nevertheless, they show that an increasing number of pathologists direct their research towards the development of bioherbicides.

The development of pathogens as bioherbicides

The principles and general considerations as well as the problems associated with the bioherbicide approach have recently been reviewed by Charudattan (1988) and Watson (1988). Therefore, only the more important facts will be discussed.

As already mentioned above, the effect of native pathogens is often limited by various constraints including low levels of inoculum, weekly virulent pathogen strains, poor spore germination, as well as environmental factors such as unfavourable moisture and/or temperature conditions, and plant factors such as low susceptibility of the host and spatial isolation between host plant and pathogen (Watson 1988). The easiest human intervention to overcome these constraints is an abundant supply of virulent inoculum which is uniformly sprayed over a susceptible stage of the weed population, whereby the application is timed and/or the bioherbicide is formulated to avoid unfavourable environmental conditions. Therefore, the development of effective bioherbicides requires a comprehensive understanding of the pathogens involved, the biology and population dynamics of the target weeds and the optimum requirements for disease development in the host-pathogen development (Watson 1988).

A pathogen selected for the development of a bioherbicide has to fulfill certain demands, the most important of which are: (1) They must be easy to mass produce in vitro, because the current industrial production facilities can meet only this type of fermentation need (Churchill 1982), (2) high virulence, (3) genetic stability and restricted host range, (4) capacity to damage and quickly kill its host plant, and (5) inocuous in ecological effects. These requirements are often fulfilled by facultative parasites, and fungi have received most attention for reasons which are discussed by Templeton (1982) and Charudattan (1985).

The fungi offer a large choice of potential candidate agents, are usually aggressive parasites, are frequently host specific and fulfill the demands listed above. In addition, fungi are capable of active penetration of host tissue and infection is not dependant on insect vectors, natural openings or wounds, which are required by bacterial and viral pathogens. Thus, facultative fungal pathogens are the best candidates for spray application.

Steps in the development of bioherbicides

After isolation of an apparently suitable pathogen, its taxonomic identify must be determined. Before its safety and potential efficiency can be investigated, disease etiology, disease cycle and life cycle have to be studied. This can partly be done in the field and partly under controlled conditions in the laboratory or greenhouse. During the laboratory investigations, the most favourable conditions for infection and pathogenesis should be identified, as well as constraints reducing the effectiveness of the pathogen after field release (Trujillo & Templeton 1981).

Host specificity screening of pathogens should be conducted under optimum conditions for infection and pathogenesis, employing a standard technique for the particular class of pathogen. The selection of test plants for host specificity screening should follow the procedures described for classical biological control programmes (see above). The number of test plant species which must be screened depends mainly on the taxonomic position of the target weed – whether it belongs to an isolated family or a family with close relations, the number of closely related cultivated plants and wild plants which should not be infected, and whether or not the pathogen belongs to a systematic group closely associated with a restricted plant taxon (genus, subtribe, tribe). A pathogen is considered safe if it is unable to develop and produce disease symptoms on any of the test plants. Problems associated with host specificity screening are discussed by Watson (1986).

The final phase includes efficacy field trials as well as the formulation and scale-up of the pathogen. The close collaboration between the researcher and industries is required during this phase to obtain a patent or licence for a marketable product. Both Baker (1986), Scher & Castagno (1986) point out that despite intensive research and numerous apparently successful biocontrol agents, very few have reached the market-place. The main reasons are a lack of cooperation between the research scientists and industry and problems discussed below.

Important considerations in the development of bioherbicides are: they must be safe for the user, safe for the environment, easy to produce and store, inexpensive and able to provide effective (reliable) control or suppression of the target weed species (Watson 1988). The market potential of the product is also a major consideration, as well as compatibility with chemical pesticides.

Problems associated with the bioherbicide approach

Although the development of bioherbicides opens a new avenue for biological weed control in situations where its application has either not been possible or not economic, there are a number of real and potential problems in the use of bioherbicides.

Templeton et al. (1979) list those related to the biology and ecology of pathogens such as spore formation, spore dormancy and the long incubation period of fungi, host plant tolerance and resistance and the generally narrow environmental requirements for infection. They also call attention to the fact that fungi are subject to competition, predation and parasitism.

The fact that under field conditions the specific humidity and temperature requirements for spore germination and host tissue penetration often cannot be met during the period of application is a major obstacle preventing the use of bioherbicides. It is therefore of great importance to circunvent these problems by adequate formulation of bioherbicides. Watson (1988) points out that some progress has been made more recently in this respect by the use of alginate, a water soluble polysaccharid, in the formulation of bioherbicides (Connick 1988). He believes that the alginate-gel-technology will gain increasing importance in the development of effective formulations of bioherbicides in the future.

Another problem connected with pathogen

biology is that the precise conditions for optimal sporulation are still unknown for the majority of fungal pathogens. As a result, sporulation in fermentation is often not adequate. It is therefore of importance to promote investigations of the basic mechanisms regulation the growth and sporulation of fungal pathogens. Only after these mechanisms will be well known the fermentation industry will be able to produce large quantities of inoculum.

Charudattan (1988) discusses problems associated with host specificity and host plant resistance. He states that the utilization of facultative parasites as inundative biocontrol agents indeed raises some important safety questions. For example, if these pathogens which are less host specific than obligate parasites will be safe in the long run, or would such facultative parasites mutate more readily than obligate parasites? Indeed, e.g. the fungi Collego and DeVine are not absolutely host specific. Greaves et al. (1989) therefore propose to resolve this problem by genetic manipulation. Sands et al. (1989) report that they obtained by simple selection mutants of the polyphagous fungus *Sclerotina scelotiorum*, one of which is only active in the presence of cytosin, whilst the other does not produce any spores under field conditions. Such mutants of polyphagous pathogens could be used as bioherbicides without further consideration of host specificity.

Another potential problem with the application of bioherbicides is host plant resistance. However, according to Charudattan (1988) this is generally not a significant problem with mycoherbicides. He argues that native pathogens used as bioherbicides are most likely co-adapted to the genetic diversity of their host plants. Therefore it should be possible to collect pathotypes that are virulent for most weed genotypes found in a region. Experience with Collego, DeVine and several other experimentally used mycoherbicide candidates has indicated, although resistance to mycoherbicides could be a potential constraint, thus far it has not been of any concern. The important conclusion deriving from these considerations is (because of the demand for standardization of herbicides) that the pathogens selected for the development of bioherbicides can infect and kill a broad spectrum of host plant genotypes inspite of their otherwise high degree of host specificity.

Efficacy is a more serious problem, because weed control must follow a narrow time frame and must produce rapid and complete or near complete control. Some pathogens can act as quickly or nearly as quickly as chemical herbicides, others require longer periods of control. These efficacy demands must be considered in an early phase of bioherbicide development. However, experiments in several countries have demonstrated that the efficacy of potential bioherbicides can be enhanced to a sufficient degree by their application in combination with plant growth regulators or chemical herbicides. Wymore et al. (1987) report that the leaf-pathogen *Colletotrichum coccodes* can be an effective bioherbicide in combination with the growth regulator thidiazuron, which is changing the growth form of *Abutilon theophrasti*. Scheepens (1987) states that the efficacy of *Cochliobulus lunatus* against *Echinochloa crus-galli* was sufficiently increased by the application of sub-lethal doses of atrizine (up to just $2.5 g/m^2$). There are further examples for the positive synergistic effect of pathogens, growth regulators and chemical herbicides (Templeton et al. 1986, Watson 1988).

Another potential constraint is the incompatibility with chemical pesticides. In general, mycoherbicides can be expected to be sensitive to fungicides used against crop diseases, but there may be also incompatibility with certain insecticides and herbicides (Charudattan 1985). The experience with Collego and DeVine has, however, shown that such problems can be overcome by careful integration of pesticides. Wherever possible, the compatibility with commonly used pesticides should be tested in the early phase of bioherbicide development. It should also be tested if the bioherbicide can be applied in combination with one or several chemical pesticides to develop recommendations for its field application. Combined application with a broad-spectrum herbicide will be an important asset in situations where a single resistant weed occurs together with several other susceptible weed species.

Finally, another two aspects which considerably influence the development of bioherbicides need to be mentioned, economic and legal considerations. It is a justified demand of the producer of a bioherbicide that they provide similar returns on investment than those achieved with chemical pesticides. Although the cost for the development and registration of mycoherbicides is considerably less than that of a chemical herbicide (about one tenth for known examples), private industry will necessarily be preocupied by market size, return on investments and profits. Therefore, only pathogens with the capacity to solve significant weed problems, those effective against important herbicide resistant weeds or those for the control of which no chemical herbicide is available, are suitable candidates for bioherbicide development.

Another problem often mentioned as impeding the development of bioherbicides is the present uncertainty about future regulatory demands for their registration as marketable products. Although plant protection regulations have been reviewed in a number of countries and are under review in others, uniform regulations are needed at least for each continent to remove the present uncertainty. The formulation of adequate legislation requires close cooperation between research scientists, interested industries, representatives of environmental protection and nature conservation agencies, quarantine specialists and delegates of the legal bodies responsible for plant protection. The important point in the formulation of later implemented regulations is that these encompass all scientifically justified demands, but avoid unfounded "safety" requirements which prevent or considerably slow down the development of bioherbicides.

DISCUSSION

Inundative biological control of weeds, especially in form of bioherbicide application, allows the application of biological control in crop rotation systems where other biological control approaches can only rarely be employed. An analysis of the actual situation clearly demonstrates that a number of problems in the development, formulation and application of bioherbicides need to be solved to insure that competitive products reach the market in sufficient number. An important prerequisite for the acceptance of bioherbicides is that the present ecologically founded reservations are invalidated by careful tests. At the same time it has to be demonstrated that the efficacy of bioherbicides can be guaranteed. Although Waage & Greathead (1988) realistically state that they do not see a substantial shift in industry to microbial products in the near future and that their development will be slow, those involved in the development of bioherbicides are convinced that this special approach to biological weed control has a future and has a contribution to make to an economic and ecologically favourable weed control.

General discussion and outlook

Although each of the approaches to biological weed control has certain limitations, like any other method of weed control actually in use, it can be stated that biological control of weeds is a valuable and economically rewarding technique and should always be considered as one of the available options.

So far, classical biological control of naturalised alien weed species has been the approach most frequently employed (Julien 1987) and, with a few exceptions where pathogens or other types of control agents were used, herbivorous host specific insects were the agents most frequently employed. The overall success rate of classical biological weed control programmes is around 30%, but conservative estimates of the return on the investments is highly favourable. For example, the introduction of a rust into Australia in 1974 to control *Chondrilla juncea* has so far been estimated to have saved AU$ 650 million in increased crop yields and herbicide costs (S. Hasan, pers. comm.). In addition, classical biological control of weeds is ecologically highly acceptable, because it has no negative impacts on the environment if properly applied. Another advantage from a socio-economic viewpoint is that the agents once established are self-sustaining and provide long-term control without recurrent costs throughout the accesible range of their target weeds. Funding becomes therefore a critical issue, because an individual or cooperative investor cannot realise any profits beyond those attained on its own land. Public funding of classical biological control research and application is therefore the rule. However, because the political mandate to support biological control was at best feable and a well-established largely herbicide based weed control system provided generally good weed control at acceptable cost, the insentive for goverments and government controlled organisation to provide funding for biological control of weeds was low. As a result, funding for biological weed control was scanty, erratic and in most cases insufficient. In many cases funding was only made available when it was realised that a weed problem could not be resolved by conventional weed control methods and biological control was considered as the method of last resort. Even in such cases the biological control practitioner often had to accept underfunding and to do the best possible under the circumstances. Considering these facts, a success rate of 30% in classical weed biological control programmes is more than what could reasonably be expected.

Over the past three decades biocontrol practitioners and ecologists have made a tremendous effort to make the outcome of classical biological weed control more predictable. Today it is well known which type of research would be needed to achieve this generally demanded goal, but funding is still not available.

Since classical biological control is restricted in its application to weed problems in natural or semi-natural situations, because it requires a certain environmental stability to become effective, and is difficult to use for the control of native weeds (Hokkanen & Pimentel 1984, Dennill & Moran 1989, Lawton 1990b), interest was focused to inundative biological control using naturally occurring native weed biocontrol agents. This control approach offers the chance to control weeds biologically in situations where classical control cannot be employed. But, here again a number of problems remain unresolved, mainly because of a lack in financial support.

It is hoped that with the current public awareness of, and concern about, environmental polution and the impoverishment of our flora and fauna associated with the abundant and large scale use of chemical herbicides on the one side, and the concerns of farmers about the shift in weed populations from easy to more difficult to control weed species, as well as the increasing number of herbicide tolerant or resistant weed species on the other hand, will increase the demand for biological weed control in the future.

It will be necessary that the ecological and economic potentials of biological weed control are recognised and fully realised in the future. Since decades the necessity of the development of integrated pest management systems, in which biological control could be integrated, is being discussed, but little practiced. At the same time the actual value of such an integration is put in doubt for obvious reasons. It is only fair to say that the practitioners of biological weed control so far rarely had a true chance to develop their method to full potential. As Evans (1987) rightly states, up to now the investment in basic research has been minimal compared with chemical pesticides. Nevertheless, the financial benefits of former biological weed control programmes to the farmers were considerable. The socio-economic and ecological benefits deriving from well planned and adequately funded control programmes could be much more important. The biological control of weeds has a lot to offer, especially to the less developed areas of our world. What it needs is a fair chance to develop and demonstrate its potential. This can only be brought about by a democratic public demand for the necessary changes in environmental and agricultural politics. We are optimistic that these changes will occur in the not too distant future.

ACKNOWLEDGEMENTS

I thank Harry Evans, André Gassmann, David Greathead, John Lawton and Jeff Waage for comments on the manuscript. I am very grateful to the organisers of the Second Symposium of Biological Control for their invitation to attend the Symposium, and to the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) for their generous financial support without which my participation would not have been possible.

REFERENCES

ANDRES, L.A. Conflicting interests and the biological control of weeds. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 5., 1980, Brisbane. **Proceedings...** Melbourne: CSIRO, 1981. p.11-20.

BAKER, R. Biological control: an overview **Canadian Journal of Plant Pathology**, v.8, p.218-221, 1986.

BARRALIS, G.; GASQUEZ, J. Investigation on the distribution of herbicide-resistant weeds. **Newsletter European Weed Research Society**, v.38, p.5-10, 1987.

BURDON, J.J., MARSHALL, D.R. Biological control and the reproductive mode of weeds. **Journal of Applied Ecology**, v.18, p.649-658, 1981.

CHARUDATTAN, R. Inundative control of weeds with indigenous plant pathogens. In: BURGE, M.N. (Ed.) **Fungi in biological control.** Manchester: Manchester University Press, 1988. 268p.

CHARUDATTAN, R. The use of natural and genetically altered strains of pathogens for weed control. In: HOY, M.A.; HERZOG, D.C. (Ed.) **Biological control in agricultural IPM systems.** Orlando: Academic Press, 1985. p.347-372.

CHURCHILL, B.W. Mass production of microorganisms for biological control. In: CHARUDATTAN, R.; WALKER, H.L. (Ed.) **Biological control of weeds with plant pathogens.** New York: John Wiley, 1982. p.139-156.

CONNICK JUNIOR, W.J. Formulation of living biological control agents with alginate. In: CROSS, B.; SCHER, H.B. (Ed.) **Pesticide formulations:** innovations and developments. Washington: American Chemical Society, 1988. (ACS Symposium Series, 371).

CRAWLEY, M.J. **Herbivory:** the dynamics of animal-plant interactions. Oxford: Blackwell, 1983.

CRAWLEY, M.J. Insect herbivores and plant population dynamics. **Annual Review of Entomology**, v.34, p.531-564, 1989.

CRAWLEY, M.J. The population biology of invaders. **Philosophical Transactions of the Royal Society** B, v.314, p.711-731, 1986.

CRAWLEY, J.J. What makes a community invasible? In: GRAY, A.J.; CRAWLEY, M.J.; EDWARDS, P.J. (Ed.) **Colonization, succession and stability.** Oxford: Blackwell, 1987, p.429-453.

CULLEN, J.M. Bringing the cost benefit analysis of biological control of *Chondrilla juncea* up to date. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 6. 1984, Vancouver. **Proceedings...** Ottawa: Agriculture Canada, 1986. p.145-152.

CULLEN, J.M.; DELFOSSE, E.S. *Echium plantagineum:* catalyst for conflit and change in Australia. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 6., 1984, Vancouver. **Proceedings...** Ottawa: Agriculture Canada, 1986.

DELFOSSE, E.S.; CULLEN, J.M. New activities in biological control of weeds in Australia. II.

Echium plantagineum: curse or salvation? In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 5., 1980, Brisbane **Proceedings...** 1981. p.545-561.

DENNILL, G.B.; MORAN, V.C. On insect-plant associations in agriculture and the selection of agents for weed biocontrol. **Annals of Applied Biology,** v.114, p.157-166, 1989.

DOELEMAN, J.A. **Biological control of *Salvinia molesta* in Sri Lanka:** an assessment of costs and benefits. 1989. (ACIAR Technical Reports, 12).

DUNN, P.H. The distribution of leafy spurge (*Euphorbia esula*) and other weedy *Euphorbia spp.* in the United States. **Weed Science,** v.27, p.509-516, 1979.

DYER, W.E.; TURNER, S.K., FAY, P.K.; SHARP, E.L.; SANDS, D.C. Control of Canada thistle by a rust, *Puccinia obtengens.* In: CHARUDATTAN, R.; WALKER, H.L. (ed.) **Biological control of weed with plant pathologens.** New York: Wiley, 1982. p.243-244.

EVANS, H.C. Fungal pathogens of some subtropical and tropical weeds and the possibilities for biological control. **Biocontrol News and Information,** v.8, p.7-30, 1987.

FORNO, I.W.; HARLEY, K.L.S. The occurrence of *Salvinia molesta* in Brazil. **Aquatic Botany,** v.6, p.71-83, 1979.

FRANKTON, C.; MULLIGAN, G.A. **Weeds of Canada.** Canada Department of Agriculture, 1970. (Publication, 948).

FRICK, K.E.; CHANDLER, J.M. Augmenting the moth (*Bactra verutana*) in field plots for early-season suppression of purple nutsedge (*Cyperus rotundus*). **Weed Science,** v.26, p.703-710, 1978.

GOEDEN, R.D. Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. **Protection Ecology,** v.5, p.287-301, 1983.

GOLDEN, R.D. A capsule history of biological control of weeds. **Biocontrol News and Information,** v.9, p.55-61, 1988.

GREAVES, M.P.; BAILEY, J.A.; HARGREAVES, J.A. Mycoherbicides: opportunities for genetic manipulation. **Pesticide Science,** v.26, p.93-101, 1989.

HARLEY, L.S.; KERR, J.D.; KASSULKE, R.C. Effects in S.E. Queensland during 1967-72 of insects introduced to control **Lantana camara. Entomaphaga,** v.24, p.68-72, 1979.

HARRIS, P. Biological control of weeds: from art to science. In: INTERNATIONAL CONGRESS OF ENTOMOLOGY 15., 1977, Washington. **Proceedings...** p.478-483.

HARRIS, P. **Current approaches to biological control of weeds.** Commonwealth Institute of Biological Control, 1971. p.67-76. (Technical Communication 4).

HARRIS, P. The selection of effective agents for the biological control of weeds. **Canadian Entomologist,** v.105, p.1503, 1973.

HARRIS, P.; ZWOLFER, H. Screening of phytophagous insects for biological control of weeds. **The Canadian Entomologist,** v.100, p.295-303, 1968.

HASAN, S. Biocontrol of weeds with microbes. In: MUKERJI, K.G.; GARG, K.L. (Ed.). **Biocontrol of plant disease,** Boca Raton: CRC Press, 1988, v.1. p.129-151.

HASAN, S. Specificity and host specialization of *Puccinia chondrillina.* **Annals of Applied Biology,** v.72, p.257-263, 1972.

HOKKANEN, H.M.T.; PIMENTEL, D. New approach for selecting biological control agents. **Canadian Entomologist,** v.116, p.1109-1121, 1984.

HOLM, L.G.; PLUCKETT, D.L.; PANCHO, J.V.; HERBERGER, J.P. **The world's worst weeds** – distribution and biology. Honolulu: The University Press of Hawaii, 1977.

JULIEN, M.H. (Ed.). **Biological control of weeds;** A world catalogue of agents and their target weeds. 2. ed. Wallingford: CAB International Institute of Biological Control, 1987. 144p.

JULIEN, M.H.; KERR, J.D.; CHAN, R.R. Biological control of weeds: an evaluation. **Protection Ecology,** v.7, p.3-25, 1984.

KARA, YU., M.; LIZENKO, S.M **Phytomyza** im Don-Gebiet. *Zashchita Rastenii,* v.7, p.21, 1976.

LAWTON, J.H. Biological control of plants: a review of generalizations rules and principles using insects as agents. In: BASSETT, C.; WHITEHOUSE, L.J.; ZABKIEWICZ, J.A. (Ed.). **Alternatives to the chemical control of weeds;** proceedings of an International conference. 1990a. p.3-17. (FRI Bulletin, 155).

LAWTON, J.H. Ecological theory and choice of biological control agents. In: DELFOSSE, E.S. (Ed.) In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 6. 1984, Vancouver. **Proceedings...** Ottawa: Agriculture Canada, 1986, p.13-26.

LAWTON, J.H. The U.K. Biological control programme for bracken. In: BASSETT, C.; WHITEHOUSE, L.J.; ZABRIEWICZ, J.A. (Ed.). Alternatives to the chemical control of weeds; proceedings of an International Conference, 1990b. p.34-39. (FRI Bulletin, 155).

LeBARON, H.M.; GRESSEL, J. (Ed.). **Herbicide resistance in plants.** New York: John Wiley, 1982.

LEKIC, M. Investigation of the dipteran *Phytomyza orobanchia* Kaltb. as a controller of parasitic phanerogames of the genus *Orobanche*. **Savremena Poljoprivreda,** v.22, p.93-99, 1974.

MASSION, C.L.; LINDOW, S.E. Effects of *Sphacelotheca holci* infection on morphology and competitiveness of johnsongrass (*Sorghum halepense*). **Weed Science,** v.34, p.883-888, 1986.

MORAN, V.C. The Silwood International Project on the biological control of weeds. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 6., 1984. Vancouver. **Proceedings...** Ottawa: Agriculture Canada, 1986. p.65-68.

MORAN, V.C.; ZIMMERMANN, H.G. The biological control of cactus weeds: achievements and prospects. **Biocontrol News and Information,** v.5, p.297-320, 1984.

PARSONS, W.I. **Noxious weeds of Victoria.** Melbourne: Intaka Press, 1973.

PHATAK, S.C.; SUMMER, D.R.; WELLS, H.D.; BELL, D.K.; GLAZE, N.C. Biological control of yellow nutsedge with the indigenous fungus *Puccinia caniculata*. **Science,** v.219, p.1446-1447, 1983.

REED, C.F.; HUGHES, R.O. **Economically important foreign weeds.** Washington: ARS-APHIS, 1977. (Agriculture Handbook, 498).

RIDINGS, W.H.; MITCHELL, D.J.; SCHOULTIES, C.L.; EL-GHOLL, N.E. Biological control of milkweed vine in Florida citrus groves with a pathotype of *Phytophthora citrophthora*. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 4., 1976, Gainesville. **Proceedings...** 1978. p.224-240.

RIDINGS, W.H. SCHOULTIES, C.L.; EL-GHOLL, A.E.; MITCHELL, D.J. The milkweed vine pathotype of *Phytophthora citrophthora* as a biological control agent of *Morrenia odorata*. **Proceedings of the International Society of Citrusculture,** v.3, p.877-881, 1977.

SANDS, D.C.; MILLER, R.V.; FORD, E.J. **Biotechnological approaches to control of weeds with pathogens.** 1989. 4p. (Report).

SCHEEPENS, P.C. Joint action of *Cochliobolus lunatus* and atrazine on *Echinochloa crus-galli* (L.) Beauv. **Weed Research,** v.27, p.43-47, 1987.

SCHER, F.M.; CASTAGNO, J.R. **Biocontrol: a view from industry. Canadian Journal of Plant Pathology,** v.8, p.222-224, 1986.

SCHROEDER, D. Biological control of weeds: In: FLETCHER, W.W. (Ed.) **Recent advances in weed research.** Farnham Royal: CAB, 1983. p.41-78.

SCHROEDER, D.; GOEDEN, R.D. The search for arthropod natural enemies of introduced weeds for biological control – in theory and practice. **Biocontrol News and Information,** v.7, p.147-155, 1986.

SHRUM, R.D. Creating epiphytotics. In: CHARUDATTAN, R.; WALKER, H.L. (Ed.) **Biological control of weeds with plant pathogens.** New York: Wiley, 1982. p.113-136.

SMITH JUNIOR, R.J.; DANIEL, J.T.; FOX, W.T.; TEMPLETON, G.E. Distribution in Arkansas of a fungus disease used for biocontrol of northern jointvetch in rice. **Plant Disease Reporter,** v.57, p. 695-697, 1973.

TeBEEST, D.O.; TEMPLETON, G.E.; SMITH JUNIOR; R.J. Temperature and moisture requirements for development of anthracnose on northern jointvetch. **Phytopathology,** v.68, p.389-393, 1978.

TEMPLETON, G.E. Biological herbicides: discovery, development, deployment. **Weed Science,** v.301, p.430-433, 1982.

TEMPLETON; G.E.; SMITH JUNIOR, R.J.; TeBEEST, D.O. Progress and potential of weed control with mycoherbicides. **Review of Weed Science,** v.2, p.1-14, 1986.

TEMPLETON, G.E.; TeBEEST, D.O.; SMITH JUNIOR, R.J. Biological weed control with mycoherbicides. **Annual Review of Phytopathology,** v.17, p.301-310, 1979.

TRUJILLO, E.E.; TEMPLETON, G.E. The use of plant pathogens in biological control of weeds. In: PIMENTEL, D. (ed.) **Agricultural Handbook Series:** integrated pest management. Boca Raton: Chemical Rubber Company Press, 1981.

WAAGE, J.K.; GREATHEAD, D.J. Biological control: challenges and opportunities. **Philosophical Transactions of the Royal Society of London,** B, v.318, p.111-128, 1988.

WAPSHERE, A.J. Effectiveness of biological control agents for weeds: present quandaries. **Agriculture, Ecosystems and Environment,** v.13, p.261-280, 1985.

WAPSHERE, A.J. A protocol for programmes for biological control of weeds. **PANS,** v.21, p. 295-303, 1975.

WAPSHERE, A.J. Recent thoughts on exploration and discovery for biological control of weeds. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 5., 1980, Brisbane. Proceedings... Melbourne: CSIRO, 1981. p.75-79.

WAPSHERE, A.J. A strategy for evaluating the safety of organisms for biological weed control. **Annals of Applied Biology,** v.77, p.201-211, 1974a.

WAPSHERE, A.J. Towards a science of biological control of weeds. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 2., 1973, Montpellier. **Proceedings...** Montpellier, 1974b. p.3-12.

WATSON, A.K. Host specificity of plant pathogens in biological control of weeds. In: INTERNATIONAL SYMPOSIUM ON BIOLOGICAL CONTROL OF WEEDS, 6., 1985, Vancouver. **Proceedings...** Ottawa: Agriculture Canada, 1986.

WATSON, A.K. Progress and prospects of bioherbicide development in Canada. In: CANADIAN PACIFIC-CAPE SYMPOSIUM ON BIOTECHNOLOGY, 1988. **Proceedings...** McGill University 1988. p.48-65.

WHISTLER, W.A. **Weed handbook of Western Polynesia.** Eschborn: 1983. (Schriftenreihe der Gtz, n.157).

WYMORE; L.A.; WATSON, A.K.; GOTLIEB, A.R. Interaction between *Colletotrichum coccodes* and thidiazoron for control of velvetleaf (*Abutilon theophrasti*). **Weed Science,** v.35, p.337-383, 1987.

ZWÖLFER, H.; HARRIS P. Host specificity determination of insects for biological control of weeds. **Annual Review of Entomology,** v.16, p.159-178, 1971.