Proc. 3rd Int. Symp. Biol. Control Weeds
Montpellier, France, 1973

TOWARDS A SCIENCE OF BIOLOGICAL CONTROL OF WEEDS

A. J. Wapshere*

INTRODUCTION

In the past ten years the biological control of weeds has developed so rapidly that it is timely to lay the basis for a more rational and methodical approach to such studies.

In the present discussion consideration will be given only to projects involving the introduction of phytophagous organisms from one part of the world to another where they are not present on a weed species, as this technique poses more scientific and technical problems than other methods of biological weed control.

It will be postulated that control is required in a country where a plant has become noxious without its pathogens and phytophagous organisms, that these pathogens and organisms are unknown even in the native range of the plant and that no previous attempt has been made to control the weed by biological means in other countries it has invaded.

However, the approach should be the same even if there has been a successful attempt to control the weed biologically in another country, as success there does not necessarily imply that the organisms used will be successful elsewhere. For instance, *Chrysolina quadrigemina* (Suffr.) was relatively ineffective against *Hypericum perforatum* L. in Victoria (Australia), but beetles of the same genetic stock were highly successful against the same weed in California, apparently because of more suitable climatic conditions there (Huffaker, 1967).

THE BASIC STUDIES

A programme for the biological control of a weed using phytophagous organisms and plant pathogens can be divided into two main phases:

A. Pre-introduction studies
B. Post-introduction studies

* C.S.I.R.O., 335 Avenue Abbe Paul Parguel, 34000 Montpellier, France.

The pre-introduction studies comprise five main sections :

(1) The study of the distribution and ecology of the weed in the country it has colonised and in its native range.
(2) Discovery of organisms adapted to the weed.
(3) Estimation of the effectiveness of the organisms adapted to the weed.
(4) Selection of the most damaging strain of the most effective organisms.
(5) Confirmation of the safety of the most damaging strain of the selected organisms.

The post-introduction phase comprises two main sections :

(1) The establishment of a predator-, parasite- and pathogen-free population of the safe and effective strains of the organisms.
(2) The study of the effect of the introduced organisms on the weed population.

A. *The pre-introduction studies*

(1) Distribution and ecology of the weed

The eco-climatic adaptation of a biological control organism determines whether or not it will become established in the new environment. For instance, during the study of organisms attacking *Chondrilla juncea* L. it became apparent that climate, soil type, agricultural practices and plant competition affected the biological control effectiveness of the organisms. In particular the different methods of wheat cultivation differentially reduced the effectiveness of the organisms whereas plant competitors added to their effect in reducing weed populations (Wapshere, 1971).

Furthermore, the organisms attacking the rootstock of *C. juncea* are more common in sandy soils and the infestation levels of the shoot attacking aphid, *Dactynotus chondrillae* Nev., and eriophyid, *Aceria chondrillae* Can., were considerably reduced in hot, dry climates. In more general terms there was evidence that the root moth, *Bradyrrhoa gilveolella* Tr., was ill-adapted to hot, dry, mediterranean climates similar to those within which *C. juncea* infestations occur in Australia whereas *Cystiphora schmidti* Rubs. was better adapted to such climates (Wapshere, 1973c).

It is therefore necessary to detail by appropriate surveys the eco-climatic situation of the weed in the country it has colonised and to use this knowledge to search for and discover eco-climatic homologous situations in the native range of the weed (Wapshere, 1970).

(2) Discovery of organisms adapted to the weed

Early in the development of biological control of weeds organisms for study were selected largely on literature records and published descriptions of their effect on the plant. However, literature records are notoriously biased towards certain groups of organisms such as Lepidoptera and Coleoptera, and are inadequate for many other less conspicuous groups of plant-attacking organisms.

Literature surveys are now used only as an adjunct to very widespread field surveys, the prime purpose of which is to record all the organisms attacking a particular weed species. The number of organisms that can be recorded as attacking a weed species over the full range of its occurrence is usually very large.

However, only organisms highly adapted to the weed will possess a combination of specificity and effectiveness that will make them useful as biocontrol agents. A method must therefore be adopted which will increase the possibility of discovering the greatest number of highly adapted organisms.

Goeden (1971) found that the number of specific insects attacking *Solanum elaeagnifolium* Cav. increased as one approached the apparent centre of origin of this weed in northern Mexico.

However, limitation of a study to a single plant species of a particular genus is unusual. It is also undesirable, as the history of the success of *Cactoblastis cactorum* (Berg) from *Opuntia aurantiaca* Lindl. against the related *O. inermis* (DC) and *O. stricta* (Haw.) (Dodd, 1940, Pimental, 1963) indicates that relatives of the weed should also be considered.

As with *S. elaeagnifolium* the evidence from the study of skeleton weed, *C. juncea*, is that the largest number of organisms highly adapted to *Chondrilla* species occur at the centre of evolution of this genus in southern Russia (Wapshere, unpublished data). Therefore where possible the evolutionary centre or centres of the genus or sub-genus containing the weed should be determined and initial exploration should be concentrated within them. Subsequent surveys, if they are necessary, should progress radially outwards from these genetic evolutionary centres as the hypothesis predicts that there is less chance of discovering organisms well adapted to the weed at significant distances from such centres.

(3) Estimation of effectiveness

On earlier biological control programmes, only particular insect groups tended to be considered for biological control purposes and estimates of their effectiveness were chiefly based on biological attributes, such as whether they were stem or root-borers or seed-feeders or whether the species caused the greatest damage per individual insect (Wilson, 1943). In recent years it has become clear that, as Huffaker (in DeBach, 1964) noted "Any organisms which curtail plant growth or reproduction may be used as biological weed control agents. Such could potentially include animals either higher or lower than insects and, as well, parasitic higher plants, fungi, bacteria and viruses". Therefore, theoretically any type of organism attacking any biologically valuable part of a weed is a candidate for consideration in the initial stages and may later be introduced with advantage as a biological control agent. The control of *Clidemia hirta* (L.) P. Pon by a defoliating thrips *Liothrips urichi* Karny (Simmonds, 1933) and the recent epidemic spread of *Puccinia chondrillina* Bubak & Syd. against *C. juncea* confirms these conclusions (Cullen et al., 1973).

However, it is not possible to study all the different organisms that attack a weed at the same time. At first the most effective organisms have to be selected for detailed study.

Three main methods of determining the most effective organisms have been suggested recently :

a) Ecological studies are carried out in regions of the weed's native range that are eco-climatically homologous to the regions infested in the country colonised by the weed to establish the part played by each organism in determining its ecological status. 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 parasitisation, predation and disease (Wapshere, 1970).

b) Physiological studies are made during the year to determine the season when the plant is under greatest environmental stress, e.g. the period of drought or the period of lowest carbo-hydrate reserves. Organisms which inflict the greatest damage at such critical periods are considered to be the most effective (Harris, 1973).

(c) An assessment is made to determine the level of resistance that the weed has developed, through natural selection, against the potential biological control agents. If natural resistance is high this suggests that the organism has in the past and now still acts as an effective agent. This is the case for the rust *P. chondrillina* on *C. juncea* (Wapshere, 1973a).

There is also the possibility that an organism maintained at low levels by heavy predation, parasitisation, competition or high disease levels would be very effective without these restraining influences since little natural resistance to it would have developed in the weed population (Wapshere, 1973a).

Furthermore organisms not occurring in the weed's native range but attacking closely related plants elsewhere may also be highly effective since it is unlikely that the weed would possess marked resistance to organisms absent from its native range (Pimental, 1963).

A possible example of this latter case is the successful biological control of *O. stricta* and *O. inermis* of southern North American origin using *C. cactorum* which had evolved in association with *O. aurantiaca* in Argentina.

A reliable method of determining effectiveness within prescribed eco-climatic limits could consist of a suitable combination of the ecological, physiological and level-of-resistance studies discussed here with the type of scoring system proposed by Harris (1974).

(4) Selection of the most effective strain of the organisms

The recent work on *C. juncea* organisms has demonstrated the importance of discovering the most effective strain against the weed form to be controlled. Five out of six *Chondrilla* organisms, namely the rust fungus *P. chondrillina* (Hasan, 1972), the two aphids, the eriophyid mite and the cecidomyid gall-midge (Caresche, 1973) all showed specific responses to various forms of *C. juncea*, and a special search had to be made for strains of the organisms which most readily attacked the Australian forms of *C. juncea*. Only the root moth, *B. gilveolella*, showed no obvious form specificity.

Insects attacking *Lantana camara* L. have also been found to damage certain varieties more than others (Harley, 1974).

It is necessary therefore to test samples of the organism from a wide geographic range against all forms of the weed from its native range to determine the most effective strain of the agent, and this strain is the one which should subsequently be tested for its safety.

(5) Demonstration of safety

Three main methods of demonstrating safety have been advocated. They are:

a) The crop testing method in which a wide range of crop plants, not necessarily related to the weed, are exposed to the agent. The difficulty with this method is that, although all crop plants tested are shown to be safe from attack, there is no certainty that other untested plants will remain unattacked (Harris and Zwolfer, 1968).

b) A series of biologically relevant investigations which attempt to elucidate the physiological, morphological, phenological, ecological, ethological and chemical bases of host selection (Harris and Zwolfer, 1968).

c) More recently the delimitation of host range by testing against a series of plants phylogenetically related to the weed has been found to be effective in demonstrating the restriction of *Longitarsus jacobaeae* Waterhouse to a group of *Senecio* species related to *S. jacobaeae* L. and its safety in regard to other plants (Frick, 1970).

The simple host range method does not, however, test plants which for geographic or climatic reasons would not have been exposed to the organism and it assumes that enough is known about the entomology or mycology, etc. of crop plants as to make their testing unnecessary. As a further precaution, Wapshere (1973b) suggested that host range method (c) should be combined with tests against cultivated plants that have never encountered the biological control agent in nature and against crop plants whose entomology, mycology, etc. are poorly known. This combination seems to be the most efficient proposed to date for demonstrating safety.

B. *The post-introduction studies*

(1) The establishment of a predator-, parasite-, and pathogen-free population of the biological control agent.

Should a strain of one or more organisms be found to have the necessary combination of safety, effectiveness and host adaptation parasites, predators and diseases should be excluded by appropriate quarantine procedures.

The importance of introducing a predator- and a parasite- free stock has been known for a considerable time. More recently the poor original establishment of *Callimorpha* (*Hypocrita*) *jacobaeae* L. against ragwort in Canada has demonstrated the importance of viral diseases of Lepidoptera (Bucher and Harris, 1961) and the necessity of obtaining a disease-free stock whenever possible.

(2) The study of the effect of the introduced biological control agents on the weed population.

This study is necessary to demonstrate the degree of success of the biological control agents and to check the estimates of effectiveness that were arrived at during the pre-introduction study. If the organisms prove to be ineffective on introduction then the studies should discover the reasons for the failure as a guide to future biological control work. Establishment of the biological control agent demonstrates that it is eco-climatically adapted to the new environment but does not demonstrate that it will be an effective agent, which depends on the population of the biological control agent building up to such levels that the weed population is reduced. Coincident with the reduction in weed population there may also be a reduction of the weed's habitat range in terms of soil, climate, and cultivation practices (Wapshere, 1971).

The post-introduction studies should therefore confirm establishment, follow the population build-up of the biological control agent and correlate this with the decline in weed population and contraction in habitat range.

During such studies it is important to take into account any other factors affecting the population of the weed. Competitive vegetation was a major additional factor aiding the Chrysomelid beetles in controlling *H. perforatum* in California (Huffaker and Kennett, 1959), and native predators, viral diseases and lack of climatic adaptation were considered to be the factors causing the failure of the ragwort moth *Callimorpha jacobaeae* in Victoria, Australia (Bornemissza, 1965).

Preliminary studies of the relationship between the biological control organism and the weed in different situations may indicate the type of population and habitat changes to be expected.

Thus it was considered that *Nupserha vexator* Pascoe, the cerambycid borer, would be ineffective against strongly growing, heavily seeding stands of noogoora burr, *Xanthium strumarium* L, but effective against poorly growing, poorly seeding stands. As *X. strumarium* is a summer seeding annual and as its populations usually consist of strongly growing plants surrounded by less vigorous plants, the effect of the cerambycid in reducing seeding rate should result in a contraction in the area of noogoora burr infestation (Wapshere, 1974).

S milarly, comparisons between infestations of *C. juncea* in Europe and Australia have indicated that the organisms are likely to reduce *C. juncea* populations considerably in pastures, to a lesser extent in poor grassland and to an even lesser extent in wheat/fallow cultivations (Wapshere, 1971).

When a weed population is overwhelmed by the biological control agent there is a rapid collapse of population levels, as was observed when *C. cactorum* was introduced to control prickly pear, *O. inermis*, in Queensland and Northern New South Wales (Dodd, 1940). It is then relatively easy to chart the course of the build-up of population of the biological control agent and the population decline of the plant. It is more tedious to demonstrate the effect of an agent which takes a fairly long time to reach effective levels. *N. vexator* was first introduced into Queensland nine years ago and only in the last two years has it reached levels of abundance that clearly affect the seeding of *X. strumarium*. Several years' more study are required before the effect of the cerambycid on the weed is well documented.

It is more difficult without experiment to measure the effect of agents which although established at moderate levels of abundance do not have a spectacular effect on plant populations. For instance, the long-lived arborescent shrub, *L. camara*, has had many insects established on it in Australia and only detailed comparisons between infested and insecticide-protected stands showed that the insects were having a greater effect than casual observations indicated (Harley, 1974).

DISCUSSION

The pre-introduction studies act as "filters" which eliminate from further consideration certain of the organisms attacking the colonizing form of the weed.

The surveys in eco-climatic situations similar to those of the weed infestation will eliminate organisms which would adjust poorly to the new habitat.

Search at the weed's evolutionary centre will select the organisms best adapted to the weed and tend to avoid unnecessary emphasis on ill-adapted polyphagous and stenophagous organisms.

The selection of agents on the basis of their effect on plant populations in similar eco-climatic situations, on their effect at critical physiological periods and on resistance mechanisms will eliminate all those organisms lacking the necessary combination of characteristics to be effective.

The selection of the strain of biological control agent most effective against the colonizing form of the weed will eliminate waste of effort on other less effective strains.

Finally, the screening for safety eliminates all organisms with an undesirably wide host range.

The above studies can also be considered to afford criteria indicating the likelihood of success of a biological control attempt against a weed species.

The most outstanding successes can be expected if the evolutionary centre of a group of the weed species, including the weed or species closely related to it, is in a region climatically and ecologically similar to the area of colonization, if the weed populations in the evolutionary centre are clearly under control by one or more near-specific organisms, strains of which readily attack the invasive weed form and if these organisms have the characteristics of safe and effective biological control agents.

This seems to be the case for the weed *Echium lycopsis* L. (= *E. plantagineum* L.) (Paterson's curse) which is heavily attacked by many different near-specific insect species in the evolutionary centre of the genus *Echium* in southern Spain, Portugal and Morocco which is eco-climatically very similar to the areas infested by this weed in Australia. The possibilities for the biological control of this weed in Australia are considered to be very good.

However, there will be occasions when there is neither a complete correspondence between the eco-climatic situation where control is desired and the weed's evolutionary centre nor between them and the occurrence of the most effective strain.

For instance, the evolutionary centre for the genus *Chondrilla* is in sourthern Russia (Turkmanistan-Kazakhstan) which is considerably drier, cooler and more continental in climate than the areas infested by *C. juncea* in Australia.

Under these circumstances it is necessary to compromise by finding the appropriate eco-climatic conditions situated as close as possible to the evolutionary centre, thus increasing the chances of discovering a number of organisms pre-adapted as far as possible to both the weed and to the eco-climatic situation in the colonized country. Studies of this type indicated that the rust *P. chondrillina* was the most effective agent against *C. juncea* in all eco-climatic situations with equivalents in Australia (Wapshere, 1970, 1973a). Indeed a form of this rust which was highly damaging to the Australian form of the weed (Hasan, 1972) has already spread widely in southern Australia and is beginning to reduce weed populations (Cullen, 1974).

Conversely biological control failures have occurred when the above study sequence has not been followed and the basic biological principles underlying them have been ignored. For instance, the majority of the stock of the cerambycid *Mecas saturnina* Le Conte introduced to control noogoora burr, *X. strumarium*, in the hot monsoonal climate of Queensland, Australia, were collected from *Helianthus* spp., a genus related to *Xanthium* (Stride and Straatman, 1963) growing in a cooler spring rainfall area of Texas. To date only marginal establishment is recorded (Haseler, pers. com.).

On the other hand, *N. vexator* introduced one year later and collected from *X. strumarium* growing in a hot monsoonal climate in India is now flourishing vigorously on the same weed in a similar climate in Queensland (Wapshere, unpublished results).

REFERENCES

Bornemissza G.F. 1966. An attempt to control ragwort in Australia with the Cinnabar moth, *Callimorpha jacobaeae* (L.) (Arctiidae Lepidoptera). Aust. J. Zool., **14**:201-43.

Bucher G. E., and Harris P. 1961. Food plant spectrum and elimination of disease of Cinnabar moth larvae *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae). Can. Ent. **93**: 931-6.

Caresche L. 1973. The host specialisation of three insects and a mite living on *Chondrilla juncea* L. Proc. 2nd Int. Symp. Biol. Control of Weeds, Rome 1971 (in press).

Cullen J. M. 1974. Seasonal and regional variation in the success of organisms imported to combat skeleton weed, *Chondrilla juncea*, in Australia. Proc. 3rd Int. Symp. Biol. Control of Weeds, Montpellier 1973 (this meeting).

Cullen J. M., P. F. Kable and M. Catt. 1973. Epidemic spread of a rust imported for biological control. Nature **244** (5416): 462-64.

DeBach P. 1964. Biological control of insect pests and weeds. Chapman and Hall, London.
Dodd A. P. 1940. The biological campaign against prickly pear. Commonwealth Prickly Pear Board, Brisbane, Australia. 177 pp.
Frick K. E. 1970. *Longitarsus jacobaeae* (Coleoptera, Chrysomelidae) a flea beetle for the biological control of tansy ragwort. 1. Host specificity studies. Ann. Ent. Soc. America **63**, 1: 284-96.
Goeden R. D. 1971. Insect ecology of silver leaf nightshade. Weed science **19**: 1, 45-51.
Harley K. L. S. 1974. Biological control of *Lantana* in Australia. Proc. 3rd. Int. Symp. Biol. Control of Weeds, Montpellier 1973 (this meeting).
Harris P. 1973. Selection of effective agents for the biological control of weeds. Proc. 2nd Int. Symp. Biol. Control of Weeds, Rome 1971 (in press).
Harris P. 1974. The selection of effective agents for biological control of weeds. Proc. 3rd Int. Symp. Biol. Control of Weeds, Montpellier 1973 (this meeting).
Harris P. and H. Zwolfer. 1968. Screening of phytophagous insects for biological control of weeds. Can. Ent. **100**, 3: 295-303.
Hasan S. 1972. Specificity and host specialization of *Puccinia chondrillina*. Ann. Appl. Biol. **72**, 257-63.
Huffaker C. B. 1967. A comparison of the status of biological control of St. John's wort in California and Australia. Mushi **39** (Suppl.) 51-73.
Huffaker C. B. and C. E. Kennett. 1959. A ten-year study of vegetational changes associated with biological control of Klamath weed. J. Range Management, **12**: 69-82.
Pimental D. 1963. Introducing parasites and predators to control native pests. Can. Ent. **95**, 8: 785-92.
Stride G. O. and Straatman R. 1963. On the biology of *Mecas saturnina* and *Nupserha antennata*, Cerambycid beetles associated with *Xanthium* species. Aust. J. Zool. **11**: 446-69.
Wapshere A. J. 1970. The assessment of the biological control potential of the organisms attacking *Chondrilla juncea* L. Proc. First Int. Symp. Biol. Control of Weeds. Misc. Publ. No. 1, C.I.B.C., 81-89.
Wapshere A. J. 1971. The effect of human intervention on the distribution and abundance of *Chondrilla juncea* L. Proc. Adv. Study Inst. Dynamics Numbers Popul. Oosterbeek, 1970. 469-77.
Wapshere A. J. 1973a. Selection and biological control organisms of weeds. Proc. 2nd Int. Symp. Biol. Control Weeds, Rome, 1971 (in press).
Wapshere A. J. 1973b. A comparison of strategies for screening biological control organisms for weeds. Proc. 2nd Int. Symp. Biol. Control Weeds, Rome, 1971 (in press).
Wapshere A. J. 1973c. Recent work on the assessment of the biological control potential of the *Chondrilla juncea* organisms. Proc. 2nd Int. Symp. Biol. Control Weeds, Rome, 1971 (in press).
Wapshere A. J. 1974. An ecological study of an attempt at biological control of noogoora burr (*Xanthium strumarium*) Aust. Jour. Agric. Res. **25**, (in press).
Wilson F. 1943. The entomological control of St. John's wort (*Hypericum perforatum* L.) with special reference to the weed in southern France. Australian Coun. Sci. and Indus. Res. Bull. **169**, 87 pp.