Classical and inundative approaches to biological weed control compared

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Introduction

Biological control of weeds has progressed far since *Dactylopius ceylonicus* Green was first used against *Opuntia vulgaris* Miller in India during the mid 1800s (Tryon 1910; Julien *et al.* 1984). Up to 1982, 174 attempts had been made in more than 70 countries to control 101 species of weeds (Julien 1982). Recently, interest has developed in the inundative approach to biological weed control (Templeton *et al.* 1979; Scheepens and van Zon 1982). Although biological control has been reviewed often (Templeton and Smith 1979; Huffaker and Messenger 1976; Hussey 1985; Wapshere 1984, 1985) no one has comprehensively compared the two approaches to biocontrol. Accordingly, this review attempts such a comparison by contrasting the classical and inundative approaches to biological weed control.

The classical approach

The classical approach to biocontrol involves the importation of a foreign parasite or pathogen from the area of coevolution with its host for release into a new geographic area where the host exists at pestilence level and where natural enemies are absent (Emge and Templeton 1980; Tebeest 1984). Once established, the biocontrol agent requires no further manipulation but relies on natural spread and development to reduce the target population to tolerable levels. In some instances, this approach may be augmented, e.g. regular releases of the cochineal insect against tiger pear in New South Wales.

Suppression of *Chondrilla juncea* L. (skeleton weed) is a notable Australian example of classical biocontrol of weeds. Prior to 1971 more than 10^6 ha of wheat and rangeland were infested with this introduced weed (Cullen 1976) which occurs as three morphologically distinct biotypes in Australia. A virulent strain of chondrilla rust *Puccinia chondrillina* Bubak and Syd. was found in Italy which attacked the dominant narrow-leaved form of skeleton weed and was released in 1971. By 1972, *P. chondrillina* was widely distributed. In 1975 the annual savings due to control of skeleton weed were estimated at $18 million (Burdon *et al.* 1981) and by the 1978–79 season, the savings were put at about $49 million (Cullen 1984). Another strain of *P. chondrillina* has been found in Turkey which is pathogenic to one of the other biotypes of *C. juncea* and is now ready for release (Hasan 1981, 1984).

The inundative approach

The inundative approach, sometimes referred to as the inoculative or bioherbicide technique, is quite a different tactic. This approach employs the application of a biocontrol agent in high concentrations to a target weed (Templeton and Smith 1977; Templeton *et al.* 1979).

'Mycoherbicide' is the term used to indicate that the biocontrol agent being employed is fungal and that the application technique is similar to chemical herbicides. The inundative approach emphasizes manipulation of the pathogen to overcome the constraints which suppress disease development under natural conditions. Both exotic and indigenous pathogens could be used, although indigenous pathogens have received most attention to date (Templeton *et al.* 1979). However, exotic pathogens could be more useful under Australian conditions because most weeds susceptible to bioherbicidal control are themselves exotic (Wapshere 1987). Both exotic and indigenous weeds can be controlled this way. It must be emphasized that the control agent populations are not self-sustaining or only self-sustaining below the economic threshold of the weed and that the control achieved is specific and short term (Tisdell *et al.* 1984). To date, insects have not been used as biocontrol agents in this way.

There are two notable examples of inundative biocontrol in the literature. Both of these are registered mycoherbicides, 'Collego' and 'Devine', and represent the first commercial-scale production and use of microbes to control weeds.

'Collego' is a dry formulation of *Colletotrichum gleosporioides* (Penz.) Sacc. f.sp. *aeschynomene* spores which was originally marketed by the Upjohn Company to control northern jointvetch (*Aeschynomene viriginica* (L.) B.S.P.) in rice and soybeans in the U.S.A. It was released in 1982. The *forma specialis* of *C. gleosporioides* is indigenous to the U.S.A. occurring annually on its host, but producing only low levels of disease. 'Collego' is applied aerially at dusk at a concentration of 2×10^6 spores ml^{-1} (94 l ha^{-1}), usually only once a season when the weed emerges above the rice canopy. The expected weed kill is about 92% with the survivors heavily affected and producing only minimal numbers of seed. The shelf-life of the mycoherbicide extends beyond 1 year (Templeton 1985).

'Devine' is a wet preparation of *Phytophthora palmivora* Butl. which must be ordered prior to each season and is applied at 6.7×10^5 chlamydospores ml^{-1}, usually with a boom spray. Up to 96% kill of stranglevine in citrus orchards is achieved after 10 weeks and control has persisted for 2 years following a single application (Woodhead 1981). The fungus is a very poor disperser but it will infect a number of other plants including ornamentals, vegetables and other trees, so care must be taken not to spray in the vicinity of these plants (Templeton 1985).

Here in Australia, the fungus *Colletotrichum orbiculare* (Berk. et Mont) v. Arx is being assessed as a mycoherbicide against the widespread weed Bathurst burr (*Xanthium spinosum* L.) (Auld *et al.* 1988; McRae and Auld 1988). This research has already resulted in a patent (No. 18454/88) owned by the New South Wales Department of Agriculture and negotiations have commenced with commercial firms to develop a product based on this indigenous fungus.

Classical and inundative approaches compared

Economic risk is probably one of the main factors governing whether a biocontrol program gains farmer/consumer acceptance. Farmers often exhibit risk aversion behaviour, i.e. behaviour designed to reduce wide variation in income from year to year (Reichelderfer 1982; Auld and Tisdell 1987). The risk factor applies more to the inundative approach than to the classical. This is because, for the most part, classical biocontrol agents are controlled, released and monitored by government departments. Bioherbicides, on the other hand, are the responsibility of the consumers who must assess the economic benefits of using the bioherbicide against the chemical alternative (if it is available). This assessment will require farmer education programs from advisory and extension workers and good marketing strategies from the manufacturing and distributing companies of the bioherbicides.

The importance of host specificity differs sharply between the classical and inundative approaches. Classical biological control insists upon specificity. The U.S. Environmental Protection Agency (and equivalent agencies in other countries such as the Australian Plant Quarantine section of the Department of Primary Industries and Energy) require very stringent, and extensive host-range tests to ensure that classical biocontrol agents do not attack non-target plants before they are considered safe for importation and release (Charudattan 1982). Even after these precautions, there is still reason for concern because the behaviour of an exotic pathogen/parasite is extremely difficult to predict with precision (Evans 1986). Such unpredictability is demonstrated by the rapid adaptation of *Puccinia xanthii* Schaw. to both *Helianthus annuus* and *Calendula officinalis* in Australia after an accidental introduction in 1975 (Alcorn 1976). There was no indication that sunflower was susceptible to this rust in screening trials in Europe and, indeed, sunflowers have been continually exposed to the fungus in America.

Host specificity, on the contrary, is not mandatory in inundative programs because the biocontrol agent can be applied selectively and it is by definition a poor disseminator. In fact, biocontrol agents possessing the ability to attack more than one target weed may be advantageous in some situations. For instance, the control of aquatic weeds in irrigation and drainage channels in Egypt (and the Netherlands) has been achieved by the use of grass carp fish (*Ctenopharyngodon idella* Val.) (van Zon 1984) which have no observed grazing preferences and it has been reported that over 200 weed species have been consumed by them. These fish are mass raised and waterways must be restocked annually. This program also has the additional benefit of providing a lucrative fishing industry because the fish are suitable for human consumption (van Zon 1984).

The simultaneous occurrence of several weed species of the same general type in a crop situation, has a negative effect on both the technical and economic feasibility of either the classical or inundative approaches. This is because most biocontrol agents exhibit host specifity. For example, rough pigweed (*Amaranthus retroflexis* L.) fat hen (*Chenopodium album* L.) and common ragweed (*Ambrosia artemisiifolia* L.) can occur simultaneously in corn (Reichelderfer 1982). These three weeds can be effectively controlled by broad-spectrum herbicides such as 2,4-D. Hence even if effective biocontrol of one of these weeds was developed, herbicides like 2,4-D would still be required to control the other two weeds. However, this situation is changing with the advent of mixtures of inundative agents capable of controlling several weed species with a single application. *Colletotrichum gleosporioides* f.sp. *aeschynomene*, which controls northern jointvetch in rice has been successfully tank-mixed with *C. gleosporioides* (Penz.) Sacc. f.sp. *jussiaeae* which controls *Jussiaea decurrens* (Walt.) DC (winged waterprimrose), also a weed in rice (Tebeest 1984). In addition, both species have been effectively tank-mixed with two chemical herbicides, acifluorfen and bentazon, to increase the weed control spectrum even further (Tebeest and Templeton 1985).

The economic benefits derived by individual farmers from biocontrol influences its acceptance and usage. Farmers are more likely to use biocontrol when they derive direct benefits. For example, if a self-sustaining and spreading agent was released in an area by only a few farmers, significant potential relative benefits would be lost by these users as the agent disperses beyond their farms. Inundative control represents a much better return proposition because these biocontrol agents do not spread or are poor disseminators, produce very high levels of control in a short time and have a short-term effectiveness. The inundative approach is also more economically feasible when the weed to be controlled affects a crop of high yield or quality. This is related to the value of the crop losses. Successful classical biocontrol agents, by their very nature, allow a steady-state level of their host weed population to survive (Reichelderfer 1982). If the damage or economic loss per individual in the steady-state population is high, then the biocontrol agent may not be sufficient to reduce the weed population below the economic threshold. Conversely, because inundative agents have a much higher percentage kill, the control level achieved is much closer to complete and therefore the weed population is more likely to be below the economic threshold.

In addition, the estimated costs of developing and implementing biocontrol vary considerably between the two approaches. Classical biocontrol is considered to cost more than inundative control during the discovery and development phase (Worsham 1982). However, this rule applies only to inundative programs employing indigenous agents. Much of this cost is attributed to the initial stages of foreign exploration — the establishment and long-term maintenance of scientists and programs in foreign lands. The costs, both in terms of money and time of this phase are less for inundative programs (Hussey 1985) mainly because research on native organisms requires fewer resources since foreign exploration is not required (Julien *et al.* 1984). However, inundative biocontrol agents do require registration similar to that required by chemical herbicides. The costs of the associated battery of environmental and animal toxicology tests are clearly an economic disadvantage of the bioherbicide approach (Bowers 1982; Charudattan 1982), although such costs are considerably below those for chemical herbicides (Mortensen 1986). The opportunity to patent novel forms of living organisms or patent the process of producing these organisms for weed control (Bowers 1982; Tisdell *et al.* 1984) may counterbalance registration costs and encourage greater public and private interest. The classical approach provides no economic incentives for private industry. Accordingly, research, development and implementation of this approach are likely to remain in the public sector. The inundative approach, on the other hand, provides incentives to private industry which can charge prices for bioherbicides similar to those of chemical herbicides. However, the economic constraints as yet do not permit adequate industry investments to identify potential biocontrol agents, conduct the required research on weed biology and finally to integrate the bioherbicide into weed management systems. Therefore, universities and other government research establishments must continue to provide the biological research requirements of this approach, while industrial scientists provide the large-scale production and distribution of the biocontrol agent.

Frequency of the weed problem is another factor determining whether a classical or inundative approach is appropriate. If the weed problem is infrequent, the economic course is wait and watch each season before taking any control action. This situation favours the use of bioherbicides. However, if the weed problem occurs consistently, e.g. a perennial weed such as skeleton weed, a self-sustaining and spreading natural enemy of the weed for long-term control is appropriate. In addition, classical biocontrol is more economic in low density, widespread weed populations because herbicide application costs are proportional to the area to be covered, whereas classical biocontrol costs are largely independent of the area to be covered (Tisdell *et al.* 1984*b*).

Conflicts of interest between different groups in society over the impact of biocontrol decisions is an important consideration in any biocontrol program. Conflicts may arise over target or non-target weeds and indigenous or introduced origin of weeds (Turner 1984). A classical approach to biocontrol attracts more conflict than an inundative approach because once the biocontrol agent is released the program is irreversible. The recent *Echium* debate in Australia illustrates this point. Patersons curse *Echium plantagineum* L. is generally considered a 'curse' in south-eastern Australia competing with improved pastures, causing grazing losses and hepatotoxicity (Dellow and Seaman 1985). However, in South Australia and some regions of other States it is considered as valuable drought fodder for sheep and has the name 'salvation Jane'. Beekeepers also value the weed as a source of pollen and nectar.

So strong was the opposition to biocontrol of *E. plantagineum* that a High Court injunction was gained in 1980 against a proposed CSIRO biocontrol program of this weed (Delfosse and Cullen 1980; Delfosse 1984). If a classic approach to control were to be used against *E. plantagineum*, such as the introduction of herbivorous insects, the outcome of the control program would be irreversible. The insects would indiscriminately attack *E. plantagineum* in New South Wales, Victoria and South Australia (assuming that the insects can adapt to the different environmental conditions). Alternatively, if an inundative biocontrol agent was available, farmers in New South Wales could spray to kill Patersons curse while farmers elsewhere could continue to rely on salvation Jane as drought fodder. To date, this conflict of interest has not been resolved, although a Supreme Court ruling is pending. The losing party in this case, however, still has the right of appeal to the High Court. In addition, this conflict of interests initiated the Biological Control Act, 1984: legislation that ensures that all views are taken into account prior to the implementation of any biocontrol program in Australia.

Inundative biocontrol is also an attractive strategy because of its flexibility. If, at any time, the status of a target plant changes from a weed to a useful plant, the control program can be terminated (or reactivated if there is a later change in status). This has become more of an issue in recent years as awareness of the economic, ecological and aesthetic loss-benefit thresholds attached to each plant has increased (Andres 1980).

One of the advantages of the classical approach to biocontrol is that the control agent can co-evolve with its host, thus alleviating development of weed resistance. Unfortunately, the maintenance of genetic stability and virulence of the biocontrol agent is a greater problem in inundative approaches (Tisdell *et al.* 1984) because the control agent is exposed to the target weed for only a short period of time and therefore has little or no opportunity to counter any shifts in weed population. To date, this is only a theoretical consideration but now that there are commercial bioherbicides on the market very careful monitoring of the target weed populations will be necessary in order to detect signs of host resistance or loss of pathogen virulence.

Summary

The classical approach to biocontrol is generally considered more suitable for the control of perennial weeds which grow in dense stands and infest large areas of land such as rangeland, along roadsides and waterways and in forests where small residual populations of the host do not cause economic losses and other weed-control practices are not economically or environmentally justified (Huffaker and Messenger 1976; Templeton *et al.* 1979). In these cases the time required to achieve control is less important than the permanency of control (Templeton and Smith 1977).

The main barrier to the classic approach of biocontrol appears to be constraints on the pathogen or insect, e.g. poor dissemination of the biocontrol agent, poor survival, inadequate host density, inadequate host specificity, low virulence, long incubation time and/or special environmental requirements or sequences (Templeton *et al.* 1979). This is not a barrier to the inundative approach because the biocontrol agent is mass produced artificially and released in high concentration at optimum infection periods which either overcomes or compensates for any innate constraints of the pathogen/insect. The major barrier to the inundative approach seems to be economic — related to investment and return expected from a bioherbicide which has a very limited market because of host specificity. This approach is better aimed at hard-to-control weeds in annual crops where specificity, immediacy and completeness of the control are essential (Templeton and Smith 1977; Templeton *et al.* 1979).

The classical approach to biocontrol will always remain. However, the main thrust of modern research is likely to concentrate on the inundative approach, particularly since the advent of genetic engineering techniques and the development of fungal toxins as bioherbicides (Duke *et al.* 1982; Woodhead *et al.* 1975; Vaughn and Duke 1982).

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