PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Biological Control: Challenges and Opportunities [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1988 **318**, 111-128
doi: 10.1098/rstb.1988.0001

Phil. Trans. R. Soc. Lond. B **318**, 111–128 (1988)
Printed in Great Britain

Biological control: challenges and opportunities

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Biological control, the use of living organisms as pest control agents, has enjoyed varying popularity over the past century, but today is well established as an important component of integrated pest management. We examine some current challenges to the use of biological control and particularly to classical biological control, the introduction of exotic natural enemies. These include conflicts of interest (1) with the conservation of native species and (2) between agricultural lobbies. On a scientific level, we examine two debates over the ecological and genetic basis of successful control. The challenge of Murdoch *et al.* (*Am. Nat.* **125**, 344–366 (1985)) to the notion of stability in pest populations under biological control, reveals that the stabilizing mechanisms may differ between pest taxa with different patterns of spatial dynamics. With respect to the hypothesis of Hokkanen & Pimentel (*Can. Ent.* **116**, 1109 (1984)) on the better chances of 'new associations' in biological control, we present an analysis that reaches different conclusions. Finally, we discuss future prospects for the different approaches to biological control, and suggest that long-term control methods, such as introduction and inoculation, will be used increasingly in the future.

Introduction

The term biological control was first used by Smith (1919) to describe the introduction of exotic insect natural enemies for the permanent suppression of insect pests. It has since been applied, at times, to include virtually all pest control measures except the application of chemical pesticides: plant breeding for resistance to pests, autocidal controls, application of semiochemicals and cultural controls. We prefer to restrict the term to the use of living organisms (natural enemies) as pest control agents. These natural enemies include parasites, parasitoids, predators, antagonists, competitors and phytophages for weed control. The targets include weeds, plant-feeding invertebrates, plant pathogens and disease vectors.

Biological control was first applied, long before its definition, when man began keeping cats to protect stored grain from damage by rodents. All early efforts employed general predators: mongooses, owls, toads, ants and the like. During the 19th century, after microbes were discovered and insect life cycles began to be understood, some (usually unsuccessful) attempts were made by far-sighted scientists to use other kinds of organism (Ordish 1967). However, the spectacularly successful and well publicized introduction of the vedalia beetle, *Rodolia cardinalis*, into California from Australia in 1888 to control the cottony cushion scale, *Icerya purchasi*, is usually taken as the formal beginning of biological control as a recognized discipline (Doutt 1958).

The excitement that was generated stimulated interest in many parts of the world, and ladybirds and other predatory insects were soon being despatched haphazardly from continent to continent, usually to no avail (Lounsbury 1940). It was not long before an insect parasitoid was successfully introduced, in 1906, from the U.S.A. into Italy for control of the mulberry scale, *Pseudaulacaspis pentagona*, (Berlese 1915). However, the poor success rate during this period led to the realization that a more scientific approach was needed, and it stimulated study of the taxonomy, ecology and, above all, population dynamics of insect natural enemies. The lead in systematic foreign exploration was taken by the United States Department of Agriculture which set up a laboratory in France for the study of the natural enemies of the gypsy moth, *Lymantria dispar*. The report on this work (Howard & Fiske 1911) began the study of insect population dynamics, which was taken up by W. R. Thompson, F.R.S., who in 1928 became superintendent of the Farnham House Laboratory, which became the C.A.B. International Institute of Biological Control (Thompson 1930).

Biological control thrived in the absence of effective alternatives, until World War II put an end to foreign exploration in Europe, followed by the advent of powerful synthetic organic insecticides. However, the limitations of these new chemicals soon became apparent as insects developed resistance. Later, the adverse effects of persistent organochlorine chemicals on the environment were exposed (Carson 1962) and the cost of pesticides rose sharply after the oil crisis of 1973. These and other factors resulted in a return to a more rational approach to pest control, exemplified by the integrated pest management concept, and led to the resurgence of interest in biological control. The fluctuating course of interest in biological control is well reflected in the pattern of scientific publications on the subject over the past 60 years (Commonwealth Institute of Biological Control (CIBC) 1981).

Today, biological control is seen to comprise several techniques. The 'introduction' of exotic agents for long-term depression and regulation of pest populations is often now called 'classical biological control'. 'Inoculation' is a similar strategy, involving the periodic establishment of agents in conditions where they cannot persist all the year round, hence each inoculation provides control over a number of pest generations. 'Augmentation' involves the supplemental release of indigenous natural enemies to increase control of a pest, often strategically timed for a vulnerable stage of pest population growth. Finally, 'inundation' involves the release of large numbers of agents to control a single pest generation, with no anticipation of effects on subsequent generations. It is this method that has been the focus of much recent development of insect and plant pathogens as biological pesticides.

Although the popularity of classical biological control has waxed and waned over its first hundred years, its cumulative achievements have been many. Table 1 presents some estimates of the number of introductions of insect agents and an approximate measure of the successful controls achieved, i.e. where the establishment of an agent has greatly reduced or eliminated the need for other control measures. Data for weeds come from the Silwood International Project on the Biological Control of Weeds (Moran 1985) and data for insects from the CIBC database.

TABLE 1. RECORDS OF ESTABLISHMENTS OF INSECTS FOR THE BIOLOGICAL CONTROL OF INSECT AND WEED PESTS TO DATE (SEE TEXT FOR EXPLANATION)

	insects	weeds
agent species	563	126
pest species	292	70
countries	168	55
establishments	1063	367
substantial successes	421	113
(percentage)	(40)	(31)

Classical biological control using pathogens is relatively new, but can claim about four successes against insects and two against weed pests.

Dozens of species of insect predators and parasitoids are now reared worldwide for augmentation, inoculation and inundation, and in some instances these programmes have been shown to be economically competitive with alternative methods of control (Reichelderfer 1981; Hassan 1981). The most popular agents, the egg parasitoids *Trichogramma* spp., are currently used for control of moth pests over an estimated 15 million ha† of cropland worldwide (J. Voegele, personal communication). Pathogen control agents have been the most recently developed, with commercial products that incorporate nematodes, fungi, bacteria, viruses or Protozoa for the control of weeds, insects and plant diseases. Other pathogen preparations are being developed non-commercially as cottage industries in developing countries.

Increasingly, serious consideration is given to biological control in the development of new pest control programmes – a striking change from the past two decades. Despite the fact that public and private investment in research and development of chemical pesticides far exceeds that of biological methods, and is likely to continue to do so for the forseeable future (Jutsum, this symposium), biological control has won a firm place in pest management, from which it is not now likely to be dislodged.

General papers such as this often extol the virtues of biological control, detailing spectacular examples and drawing pointed (and often defensive) comparisons with chemical control methods. This is not our intention. Having established above what we feel is the strong position of biological control today, we will look at some of the current controversies that challenge it, particulary problems raised by conflicts of interest and public perception, and conflicts raised among ecologists about how biological control works and how it should be done. This is necessarily a sample of the many current developments in biological control, and it focuses on introduction or classical biological control, because of the permanent nature and scientific complexity of this method.

BIOLOGICAL CONTROL AND PUBLIC OPINION

The disastrous use of generalist vertebrate control agents in the early days of biological control has left a frustratingly persistent public view that a natural enemy, once it has eliminated the pest, will become a pest itself. This notion has recently been joined by a growing aversion to things alien to the environment, which has perhaps accompanied the progress of genetic engineering research, and together these fears pose a new challenge in the development of biological control.

A typical example is to be found in the programme for the control of cassava mealybug, *Phenacoccus manihoti*, and mites, *Mononychellus tanajoa*, *sensu lato*, in Africa (Neuenschwander & Herren, this symposium), financially the largest biological control project in operation today, and perhaps ever. Early in this project the Organization of African Unity hesitated to sanction introductions into Africa of non-African insects, despite several very successful classical biological control programmes that had been done there (Greathead 1971). This is understandable given the havoc that non-African insects were causing on cassava at that time. Such seemingly simple misunderstandings can interfere with even very major projects, and show that scientists must not naïvely underestimate the privilege they enjoy in understanding

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† 1 hectare = 10^4 m^2.

trophic associations, host specificity and other concepts that make it unlikely that invertebrate natural enemies will become pests in their own right.

The risk of control agents becoming pests is minimized in biological control by the selection and screening of host-specific agents against economically important species. This is now routine for weeds, where agents are usually tested for oviposition, feeding or development or both, against all important crop plants in the proposed region of introduction (Schroeder 1983). These tests are conservative in that they do not consider ecological or behavioural factors that may isolate an agent from a non-target plant (Dunn 1978). Experience to date shows that the methods currently in use are reliable, because there have been only two reported cases of insects consistently damaging useful plants among the 126 species successfully introduced: these involved species first introduced against *Lantana camara* in Hawaii in 1902 (Perkins & Swezey 1924), which pre-dated systematic screening tests, and indeed they were not screened at all. There is some concern that current screening methods may not be as satisfactory for pathogen agents. Some rusts, for instance, are known to exhibit host shifts in new environments (Alcorn 1976), possibly making a single screen a poor measure of potential host range.

Insect and pathogen control agents against insect pests are, by contrast, not extensively screened before introduction, because of the very few insects of direct benefit to man. No serious mistakes have been made, although introduced parasitoids have been implicated as a factor in the failure of an introduced weed control agent in Hawaii (Howarth 1983), Mauritius and South Africa (Greathead 1971).

Thus current procedures for ensuring the safety of classical biological control are directed at protecting agriculture. Recent public concern for the environment is rapidly changing this situation, causing increasing demands that agents for introduction pose no threat to the native fauna and flora of the country of introduction, and particularly to its endangered species. The risks involved are as yet poorly assessed, because it was not previously required that screening be done on native species. Shifts of weed control agents to native plants have been documented, although none has as yet involved a serious threat to a species (Turner 1985). The same is probably occurring for insect control agents (Howarth 1983).

Legislation that could require assessment of the impact of exotic biological control agents on native fauna and flora exists, or is under development, in countries like U.S.A., Australia and the U.K. In the U.K., the Wildlife and Countryside Act 1981 can be applied in this respect, and the current project on the biological control of bracken (Lawton, this symposium) may prove to be its first test case. In some countries, legislation has been linked with concern over genetic engineering: hence in the U.S.A. draft legislation exists for a Biological Control and Biotechnology Act which would treat biological control agents as imported germplasm subject to the same restrictions as recombinant DNA (Klassen & Dorschner 1985).

As biological control practitioners, we are confident that these new requirements would not seriously reduce the possibility of finding safe control agents for exotic pests. Further, we are keen to provide the public with the information they need to resolve any conflict between the agricultural and conservation consequences of an introduction. The problem is primarily one of cost, complicated by the availability of rare plant species for testing. Screening of control agents is expensive, and is already a large part of limited programme budgets. An analysis of programmes for the biological control of 28 weeds in Canada, for instance, has revealed that about 52% of pre-release costs involve host specificity screening (Harris 1979). To include native flora in screening may make the cost of some programmes prohibitive to the public institutions that usually fund them. For instance, the European thistle, *Cirsium arvense*, an introduced weed of North American pastures, has about 130 native congeners there, some of which may be endangered species (Turner 1985): how many would have to be screened to satisfy concern for the native flora? Clearly, the risk is that many potentially safe and successful biological control programmes may never be done, committing farmers in many cases to the continued use of pesticides, the environmental hazards of which can often be predicted.

Risks to native flora and fauna do not pose the only conflicts of interest in the future development of biological control. More straightforward are conflicts of interest between agricultural lobbies, a striking example of which is the recent Australian court case in which private citizens succeeded in obtaining an injunction against the Australian Government's programme of introduction of insect control agents against the pasture weed *Echium plantagineum* (L.), commonly known as Patterson's curse (Cullen & Delfosse 1985). These citizens, beekeepers and graziers (who know it as Salvation Jane), felt that this plant was beneficial to their interests. The long-term consequence of this case was the Biological Control Bill 1984 which requires the government to advertise its intention to control specified target organisms biologically, and its intention to introduce specified agent organisms for this programme. Conflicts of interest can then be resolved during a public enquiry before programmes proceed too far.

An example of the potential scale and complexity of conflicts of interest in biological control is the recent development of tree legumes as sources of fodder, wood and fuel for small farmers in developing countries. Species of tree in genera such as *Leucaena*, *Albizia*, *Acacia*, *Mimosa* and *Prosopis* are being actively developed as new crops throughout the tropical world (Nitrogen Fixing Tree Association 1985). At the same time, their desirable attributes of rapid growth, high seed production and an ability to colonize and stabilize poor soils make them invasive weeds, and species in all these genera are targets for proposed biological control programmes. This conflict is complicated by the recent appearance in Asia of a neotropical legume-feeding psyllid, *Heteropsylla cubana*, which defoliates the major cultivated tree legume, *Leucaena leucocephala*, (Mitchell & Waterhouse 1986). At CIBC, we have been asked to explore the possibility of classical biological control for this insect pest by using agents from Central America. However, for those who consider *L. leucocephala* a weed, now under increasingly effective (if fortuitous) biological control by *H. cubana*, such a programme would be a disaster! A final twist to this story is that another species of *Heteropsylla* is being considered as a control agent for the neotropical *Mimosa invisa*, a weed of plantations in Asia. Introduction of control agents for the *Heteropsylla* on *L. leucocephala* might interfere with the success of the programme against *M. invisa* (Waterhouse & Norris 1986).

How we quantify, let alone resolve, complex conflicts of interest such as these is a new and exciting challenge to agricultural economists. An equivalent challenge for basic research is to understand the genetic and ecological basis of host specificity in insects and pathogens, so helping to evaluate better the limits to host range and the risk of host shifts in biological control agents.

What makes biological control work?

A practitioner of biological control might answer this question with 'money, time, luck and a little bit of scientific insight'. The logistic constraints on mounting successful biological control, particularly on an international scale, are formidable and (as discussed above) likely to become more so. But in this forum, we would like to concentrate on scientific constraints, namely those that limit our understanding of how biological control works and hence of what makes a good biological control agent.

The greatest challenge to understanding biological control must certainly be associated with programmes involving introduction and inoculation, where change in pest populations depends not only on the mortality imposed by natural enemies in a generation, but that imposed over time by the progeny of established natural enemy populations. By contrast, understanding how inundative biological control works over a single generation is relatively simple: for pathogens it can involve dose–response studies similar to those used for chemicals (Huber & Hughes 1984), whereas for mass-released nematodes, predators and parasitoids, where searching behaviour and hence host distribution must be considered, the functional response model (Holling 1959) offers a good conceptual framework. Surprisingly, this model has been little used in practical inundation studies (Knipling & McGuire 1968; Ridgway *et al.* 1979; Zhou Li-Tzu 1988) but recent improvements for field quantification (see, for example, Hopper & King 1986) hold promise for its wider use.

For inoculation and introduction, satisfactory predictive modelling of long-term population dynamics has been possible only over short time periods in simple systems such as glasshouses. Retrospective modelling of classical biological control has been possible when data are sufficient (Hassell 1980) and current detailed studies on cassava green mites in Africa may provide the basis for the first prospective modelling of classical biological control, if satisfactory agents can be found (A. P. Gutierrez, personal communication).

Apart from these few instances, understanding of biological control has rested on ecological theory, the predictions of which are often compared with the broad patterns of success and failure of previous programmes (see, for example, DeBach 1964). Although this is a rather unsatisfactory approach, it has been much improved recently by the compilation of large data sets on past programmes, which permit quantitative analyses of factors related to success.

For programmes against insect pests a number of databases have been assembled (Clausen 1978; Luck 1982; Laing & Hamai 1976; Greathead 1986), and studies have concentrated on the relation between success and the taxonomic group to which the natural enemy and pest belong, the stability of the pest's habitat and the continuity of its populations (Ehler & Miller 1978; Hall & Ehler 1979; Hall *et al.* 1980; Noyes 1985; Hokkanen 1985; Greathead 1986). For the biological control of weeds, there now exists a database of introductions involving insect, vertebrate and disease agents (Julien 1982), which has provided information on the relation between success and the taxonomic group of both agent and pest (Julien *et al.* 1984).

The lack of precise and detailed quantitative information on most biological control programmes severely limits these analyses, as does the difficulty in establishing a consistent measure of success (Greathead 1986). To the extent that they are of value, the way forward must certainly be the elaboration of these databases with biological and ecological information on agents and pests, to explore how life history and population parameters are correlated with known outcomes. This has recently been done for weed control agents by scientists from CIBC, Imperial College and elsewhere, who have incorporated available information on the ecological niche, behaviour, population growth, release patterns and impact of each agent used into existing databases (Moran 1985). Preliminary analyses reveal intuitively satisfying results such as a positive correlation between success and intrinsic growth rate of the agent (Crawley 1986, 1987), and indicate their value in improving ecologically based scoring systems already used for selecting agents (Harris 1973; Goeden 1983; but see Schroeder & Goeden 1986). In another study using the same original database (Julien 1982), Burdon & Marshall (1981) have shown that success is greater against asexually reproducing than against sexually reproducing weeds.

Another popular approach to understanding biological control has been the exploration of theoretical models. Most of these have focused on the use of arthropod natural enemies (Hassell 1978), particularly parasitoids, which are relatively easy to model. More recently, models for the use of pathogens have been explored (Anderson 1982; May & Hassell, this symposium). The kinds of models used, and their structure, are discussed in more detail by May & Hassell (this symposium).

As a general comment, we feel that the past five years have seen a dramatic and valuable shift in the emphasis of these models, from one directed at the desirable properties of control agents, for which their general form was perhaps not best adapted, to one of exploring broad interactions between different kinds of agents and between biological control agents and other pest management practices. This includes studies of interactions between generalist and specialist natural enemies (Hassell & May 1986), natural enemies acting at different stages of the pest life cycle (Wang & Gutierrez 1980; May *et al.* 1981), parasitoids and insecticides (Barclay 1982; Waage *et al.* 1985), and pathogens and arthropod agents (Carpenter 1981), some of which are discussed by May & Hassell (this symposium). The broad, and often simple, conclusions that emerge from these studies will, we feel, be of much greater value in planning future biological controls, particularly in integrated pest management (IPM) systems, than further elaboration of models that explore the minutiae of dynamical interactions between agents and pests.

In the current profusion of database analyses and theoretical models, little has emerged to challenge the conventional ecological wisdom used in biological control, with two striking exceptions. The first deals with the role, even the existence, of population stabilizing processes in biological control (Murdoch *et al.* 1985), and the second with the role of genetic variation in successful biological control (Hokkanen & Pimentel 1984). We will now consider both challenges, which if real, might greatly alter our views of what makes biological control work.

Stability in successful biological control

According to theory, successful biological control is associated with two population processes: the depression of pest population size and the maintenance of pest populations at a new lower level: depression and stability (Waage & Hassell 1982; May & Hassell, this symposium). It has long been accepted that stability in biological control is conferred by some kind of refuge generated in space or time that protects the pest population from being driven to extinction by the control agent, which itself would otherwise die out.

In an important paper, Beddington *et al.* (1978) used analytical parasitoid–host models to compare the ability of different biological properties of parasitoids and hosts to create these refuges and thereby stabilize pest populations at the high levels of depression observed in biological control. Comparing sigmoid functional responses, relative parasitoid–host generation times, mutual interference between parasitoids and non-random distribution of attacks by parasitoids on hosts, only the last mechanism was able to regulate pest populations several orders of magnitude below the equilibrium generated by density-dependent food limitation acting on the host in the absence of the parasitoid.

Although other possible stabilizing factors were not examined (e.g. temporal synchrony (Griffiths 1969)) or have since emerged (e.g. variation in susceptibility between hosts (Hassell & Anderson 1984); density-dependent parasitoid sex ratios (Hassell *et al.* 1983)), the bold conclusion of Beddington *et al.* (1978) has left non-random search the single most popular explanation of stability in successful biological control. In addition, it has engendered a veritable explosion of studies on spatial density dependence in parasitoid–host systems (see, for example, Morrison & Strong 1980, 1981; Morrison *et al.* 1980; Hassell 1980; Heads & Lawton 1983; Weis 1983; Waage 1983; Murdoch *et al.* 1984).

Initially, the concept of non-random search was associated with aggregation by natural enemies on high density 'patches' of hosts, perhaps because concurrent studies on optimal foraging by predators and parasitoids predicated that aggregation would be adaptive and widespread (Charnov 1976; Cook & Hubbard 1977). As a result, aggregative behaviour was identified as a desirable attribute for a control agent.

The discovery that parasitism between patches is frequently not positively density dependent, led Murdoch *et al.* (1984, 1985) and others to challenge the contention that non-random search is an important stabilizing mechanism in parasitoid–host interactions, and therefore that aggregative ability is an important attribute in a control agent.

However, more recent studies have reaffirmed that spatial patterns of parasitism need not be positively density dependent to be stabilizing (Hassell 1984; Chesson & Murdoch 1986): stability is conferred simply by the concentration of attacks in some patches and not others. In addition aggregation is not always adaptive (Lessells 1985; Iwasa *et al.* 1981), but depends upon parasitoid behaviour and host distribution. Thus studies of the spatial distribution of mortality cannot, unless detailed, tell us much about the ability of parasitoids to depress or stabilize host populations.

A more basic challenge to the designation of stability-conferring attributes for selecting natural enemies is the argument of Murdoch *et al.* (1985) that successful biological control agents do not stabilize host populations at all. Rather, they suggest that the persistence of pest populations after successful biological control is a consequence of stochastic processes involving the creation of host patches by colonization and their extinction after discovery by the agent. In essence, they argue that spatial refuges are products of spatio-temporal patchiness, not of the non-random search of natural enemies. It might be argued that these are two ways of looking at the same process. None the less, it has led the authors to suggest that the most efficient natural enemies are not those showing patterns of search or activity that leave some hosts safe in refuges, but those that are efficient at finding and killing pests at any density and time. This, in turn, indicates a very different set of natural enemies as desirable candidates for selection.

Murdoch and his colleagues feel that their claim is supported by the frequent local extinction of pest populations in biological control which they argue would not arise simply from non-random search. Their most firm evidence comes from scale insect populations (Murdoch *et al.* 1984; but see Huffaker *et al.* 1986). However, extinction of host patches is characteristic of other biological control systems, including whiteflies (van Lenteren 1986) and mites (Sabelis & van de Meer 1986; Nachman 1987).

What is common to Homoptera and mites is that patches constitute populations of pests reproducing over several generations, on which natural enemies can exhibit not only a functional but a numerical response. Simulation studies have demonstrated the existence of stabilizing mechanisms in patchy mite-like predator–prey systems (Hastings 1977; Sabelis & Diekmann, unpublished data) which are not associated with non-random search between patches: indeed Huffaker's (1958) classical orange and mite system may be an example. This situation contrasts with that where spatial heterogeneity has been claimed as a stabilizing factor (e.g. Hassell 1980). Here, patches represent a transient life stage, say, eggs or caterpillars on plants, which do not reproduce or persist for more than a generation and where natural enemies are limited to a functional response only.

Perhaps Murdoch *et al.* (1985) have not refuted the importance of non-random search to stability of biological control interactions, but have found a mechanism of stability characteristic of certain kinds of natural enemy – pest interactions. If true, this would force us to rethink the argument of Beddington *et al.* (1978) for a stabilizing mechanism common to all biological control systems. It is interesting that, of the six examples given by Beddington *et al.* (1978), the four associated with the greatest depression involve Homoptera, and the other two involve 'life stage patch' interactions of parasitoids with Lepidoptera and Hymenoptera.

TABLE 2. HYPOTHETICAL CONTINUUM OF PEST TYPES, THE NATURE OF THEIR PATCHY DISTRIBUTION, AND THE SPATIALLY MEDIATED STABILIZING MECHANISMS THAT MAY OPERATE IN THEIR BIOLOGICAL CONTROL

	◄────────	────────►
patch duration:	many generations (colony)	single generation (life stage)
stabilizing mechanism:	asynchronous patch dynamics	non-random search
examples:	mites, Homoptera	Lepidoptera, Hymenoptera

We believe that there may be a range of spatially mediated stabilizing mechanisms (table 2) associated with different degrees of patch permanence ranging from transient, 'life stage patches' where non-random search may be an important factor, to 'colonial patches' where other mechanisms may act, with or without non-random search. If this is true, it would suggest that desirable attributes for natural enemies may vary between pest systems, with obvious implications for selection of control agents.

Genetics and the 'new association' theory

Although it is usual in classical biological control to seek agents from the target pest in its area of probable origin, highly successful control has been obtained from the introduction of natural enemies that are not naturally associated with the target pest, either because they do not come from the native area of the pest, or because they come from a related pest species. Pimentel (1963) used this evidence to suggest that coevolution between pest and control agent leads to increased resistance of the pest and decreased effectiveness of the agent, making it desirable to seek control agents that do not have a close evolutionary history with the pest.

This argument has been criticized (see, for example, Huffaker *et al.* 1971), but has re-emerged recently in an analysis of a large biological control database by Hokkanen & Pimentel (1984), incorporating releases of pathogens, insects, molluscs and vertebrates for the control of insect and weed pests. They conclude that 'there is about a 75% greater chance for success if the parasite and its host are newly associated instead of an old association'. If this pattern is real, then current methods for selecting agents may need reappraisal.

Besides problems associated with the comparison of programmes as diverse as birds against insects and pathogens against plants, and the inclusion of only successful programmes in the analysis, more specific criticisms of the accuracy of both the database and analysis of Hokkanen & Pimentel (1984) have been levelled at its treatment of programmes for insect (Greathead 1986) and weed (Harris 1986; Goeden & Kok 1986) control. We feel a more refined and accurate analysis is necessary, and have therefore prepared one that uses a CIBC database and (1) considers only insect control agents for insect pests, and (2) expands the analysis to include all establishments, not just successes. (This is still conservative as it excludes failures to establish, which may be biased against new associations because of genetic or climatic incompatability, see, for example Crawley (1986) for biological weed control.) Like Hokkanen & Pimentel (1984) we identify new associations as those in which the agent came from a different geographical region to the host (and possibly from a different host), and we try to reduce the bias caused by the repetition of projects, particularly successful ones: in our case we select agent records from the first project ever mounted against a particular pest and ignore subsequent ones.

TABLE 3. SUCCESS RATINGS OF INSECT AGENTS IN FIRST PROGRAMMES AGAINST INSECT PESTS: A TEST OF THE 'NEW ASSOCIATION' THEORY (SEE TEXT FOR EXPLANATION)

associations	complete (C)	substantial (S)	partial (P)	none (N)
new	20	29	13	83
old	37	81	12	166

overall: $p < 0.09$. $C+S$ against $P+N$: $p < 0.82$. $C+S+P$ against N: $p < 0.82$.

Our results are shown in table 3. The distribution of agents attributed with complete, substantial, partial or no success does not differ significantly between new and old associations (goodness of fit test, $\chi^2 = 6.4$, p less than 0.09). It is, perhaps, more realistic to pool some of these arbitrary ratings of success to give a more robust comparison, in which case we find even less difference ($\chi^2 = 0.05$, p less than 0.82). This analysis, like its predecessor, has certain flaws: for instance, several species contributing to a completely successful programme are often given a 'complete' rating, even if the relative contribution of each species is unknown. More detailed analyses are necessary to avoid these errors. In balance, we do not feel that the evidence for the superiority of new associations justifies its being given precedence as a selection criterion for biological control agents. However, the underlying concept that natural enemies become less effective with time, needs more scrutiny, particularly as it could jeopardize the future of past biological control successes!

The notion that the effectiveness of biological control agents will generally decrease as a result of coevolution with their hosts is not supported by current theory (May & Anderson 1983). This phenomenon can arise where high virulence reduces transmission by insect vectors by killing hosts too rapidly, as has been suggested for the biological control of rabbits by myxoma virus, but seems unlikely to occur with pathogens attacking insect pests, where the hosts' life cycles are short and vectors are probably not so important. Biological control has made use of the fact that exotic strains of some widely distributed pathogens are more likely to promote epizootics than local strains (Milner *et al.* 1982; Milner & Mahon 1985). However, it is not clear that this variability indicates local evolution of reduced virulence, and direct evidence for this is limited (Briese 1986).

For insect parasitoids, long-term laboratory interactions with hosts have led to a decrease in parasitoid reproductive rate (see Boulétreau (1986) for a review), and hence have been used to support Pimentel's (1963) theory. However, this does not always lead to the increase in host population levels inferred in the 'new association' argument. Further, there is no clear evidence from the field that parasitoid effectiveness has decreased during the course of classical biological control (Boulétreau 1986). Even the textbook example of the evolution of resistance to a parasitoid – *Mesoleius tenthredinus* introduced into Canada for control of the sawfly *Pristiphora erichsonii* (Muldrew 1953; Ives & Muldrew 1984) – is likely to be the result of the introduction of a competitively superior resistant host population, and not of selection acting on the original parasitoid population (Ives & Muldrew 1984).

Although there is little evidence that parasitoids become less effective after prolonged exposure to hosts, there is some evidence from biological control that they get more effective (van den Bosch 1964; Messenger & van den Bosch 1971). Indeed, in classical biological control a long 'lag period' is sometimes found between the establishment of a control agent and the point at which its populations rise rapidly to control the pest (Doutt & DeBach 1964); could this indicate a period of natural selection for improved effectiveness?

Although as yet we have very little understanding of what causes spatial and temporal genetic variation in the effectiveness of control agents, the hypothesis of Hokkanen & Pimentel (1984) appears to explain some of the observed patterns.

FUTURE TRENDS IN BIOLOGICAL CONTROL

Although classical biological control continues to fascinate ecologists, practical attention has focused recently on inundative methods, and particularly the potential for commercial biopesticides. Much venture capital is being put into the development of microbials, and as this happens a veil of secrecy is rapidly falling over research in this new and exciting field. However, the small firms that develop and market such products are often short-lived, as are their products: indeed, the United Kingdom's leading microbial pesticide firm has recently closed after only two years. A number of these firms are 'bought out' by large agrochemical and biotechnological companies. Although it might be argued that this is the logical path towards the expansion of microbial methods, it should be remembered that microbial products, once in the portfolio of an agrochemical firm, must compete with pesticides with larger markets and more conventional production problems. For this and other reasons, we do not see a substantial shift in industry to microbial products in the near future; enthusiasm must be maintained, but development will be slow.

What then of classical biological control and inoculative methods? Much of the future 'market' here will be created by the continuing ability of pests to escape quarantine restrictions. To give an idea of the scale of this invasion, van Lenteren *et al.* (1988) estimate that over 70 species of exotic pest have invaded The Netherlands since 1900, whereas in the U.S.A., between 1920 and 1980, at least 837 exotic insect species became established, about 10% of them becoming serious pests (Hoy 1985). Such immigration is a continuing process: for instance, CIBC is currently investigating biological control for an Asian mealybug, *Rastrococcus invadens*, which appeared in 1982 as a pest in West Africa, a Central American psyllid, *Heteropsylla cubana*, which in 1984 began a whirlwind spread throughout the Pacific and Asia on the tree legume *Leucaena leucocephala*, and an Asian scale insect, *Aonidiella orientalis*, which appeared in 1986 as a threat to cultivated neem, *Azadirachta indica* (Meliaceae), in Central Africa.

Apart from this virtually guaranteed 'market', our increasing knowledge of how biological control works may make it profitable to re-attempt past failures (Hoy 1985), and to exploit genetic variability to find, or even produce, better or new agents for old pests. Introduction of exotic agents against native pests, still a relatively little-explored area (Carl 1982), may provide yet more opportunites as our knowledge develops. Finally, a trend is emerging away from inundative methods towards inoculative methods employing the same species. Thus recent studies in China have shown that single, carefully timed releases of the egg parasitoid *Trichogramma* early in a growing season can give as good control of moth pests on maize and sugar cane as the more conventional weekly or biweekly mass-releases later in the season (Shen Xiao-Cheng 1988; Guo Ming-Fang 1988).

To what extent will this increase in opportunities for biological control be met by an increase in demand? Biological control is generally appreciated today as an important component of IPM, and demand for it is likely to spread as IPM programmes develop worldwide. It should be remembered as well that, in economic terms, perhaps the greatest contribution of biological control to agriculture comes not through programmes of introduction, inoculation and inundation, but from the contribution of indigenous natural enemies to pest suppression in sprayed crop systems. This 'natural control' is increasingly appreciated in pest management, and has stimulated the development of selective pesticides, methods to reduce pesticide application and manipulation of cropping practices to encourage natural enemies. A paper of at least this length would be required to discuss properly this aspect of biological control; it can only be said here that the demand for improved natural control, and the need to understand how it works, are increasing rapidly (see van Emden, this symposium; Pickett, this symposium).

Thus the demand for biological control is likely to develop at least as fast as the adoption of IPM practices. In reality, we think it will develop much faster, as a result of another, less measured process, namely the rapid growth in public concern about pesticides and their effects on health and the environment. The past few years have seen many developments. In industrialized countries, these include increasing demand for organically grown produce, new laws requiring that pesticides for registration be screened for negative effects on natural enemies, and even state and federal taxes on broad spectrum compounds to fund research on non-chemical methods of control. In developing countries, where a high percentage of pesticides used are subsidized by aid organizations, a growing awareness of pesticide misuse and environmental pollution may lead to a decline in subsidies for broad-spectrum compounds, thereby leaving a gap in pest management that can be filled only by more rational management practices, and increased reliance on cultural and biological methods of control.

Whether the demand for biological control will grow at the careful pace of implementation of IPM practices, or at the rather more hurried pace of an environmental movement, the scientific skills that we need to understand and use it to implement and diversify, will be much called upon in years to come.

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Discussion

R. Brown (*ICI Plant Protection Division, Bracknell, U.K.*). What are Dr Waage's criteria for screening indigenous organisms against novel biocontrol agents and what level of confidence do you put in this process?

Are these criteria applied equally to both rich and poor countries, even if a poor country with an important and soluble pest problem could not afford the screening costs?

J. K. Waage. So far, routine screening is largely done for weed control agents and this is usually more concerned with crop plants than the native flora. However, especially in North America screening of endangered native species is having to be included. Screening of insect biological control agents is now being demanded by some countries, usually only against bees and species of concern to conservationists, e.g. birdwing butterflies in Papua New Guinea. We can never be absolutely sure, but we are confident that the methods used against weed and insect control agents are reliable: when they have been followed there have been no unforeseen consequences.

The same criteria are applied to potential introductions into all countries. If a country cannot afford screening then we help it find a donor to support this work.

R. R. M. Paterson (*C.A.B. International Mycological Institute, Kew, U.K.*). What are the procedures for screening weed control agents to be introduced so as to be sure that non-target plants will not be attacked?

D. J. Greathead. Nowadays, weed control agents are screened according to a centrifugal phylogenetic scheme (as Dr Hasan explains further in his paper) whereby the agent is tested first against different populations of the target weed, then species in the same genus, genera in the same tribe, and so on. Other plants are also checked, including important crops planted in the area where control is planned. Attention is also paid to any plants with similar secondary chemicals, host plants of species related to the candidate agent, and any other plants specified by the authorities who will have to decide on whether to introduce the agent. These protocols have so far avoided any unforeseen attacks on non-target plants be we can never be absolutely sure this will not happen. It is a matter of taking a calculated risk.

P. T. Haskell (*Department of Zoology, University College, Cardiff, U.K.*). Because it is impossible to give an absolute guarantee that a biocontrol agent after release will not cause any harm to non-target organisms, it is surely essential that some form of risk assessment procedure relating to release be worked out and agreed internationally? To begin with, this could be based on the 'centrifugal' procedure outlined by Dr Greathead, with extra safeguards appropriate for materials such as genetically engineered organisms. Such an international procedure could be formulated in the first place by organizations such as the CAB International Institute of Biological Control, the International Organization for Biological Control of Noxious Animals and Plants, the Food and Agricultural Organization of the United Nations and the World Health Organization.

D. J. GREATHEAD. The suggestion that there should be internationally accepted rules for screening is a good one. In fact, scientists concerned with weed control agents have taken action and the protocol I have outlined (in reply to R. R. M. Paterson) was debated and refined at successive International Symposia on Biological Control of Weeds, which take place every four years. No protocols have been worked out for insect control agents. Generally, it has been sufficient to show that they do not attack beneficial species. However, assurances that non-target native species will not be attacked are beginning to be demanded. It will, therefore, soon be necessary to adapt and apply the protocols for weed control agents to insect control agents.

It will be more difficult to obtain a consensus for an internationally accepted procedure from regulatory authorities who have differing agricultural priorities and concerns for the environment. This would require harmonizing of legislation (which has begun in Europe) and that would not be easy.

R. J. COOK (*United States Department of Agriculture Agricultural Research Service, Washington State University, Pullman, U.S.A.*). Are there any examples of a biocontrol agent, or any other potentially beneficial organism, having had a negative effect on the environment following its deliberate release into the environment? Please give examples from what you call the prescientific and postscientific areas of biological control, i.e. before and since 1888.

J. K. WAAGE. There are very few examples considering the large number of introductions that have been made, and most of these relate to the introduction of general predators, chiefly vertebrates such as mongooses, owls and the cane toad. Many of these introductions were made during the prescientific period but, unfortunately, some were made later when those concerned should have realized the dangers.

These aside, carefully selected, reasonably host specific invertebrate agents have led to few unanticipated side effects. In Hawaii and Mauritius there have been negative effects where parasitoids used to control crop pests have interfered with taxonomically similar insects introduced for weed control.

The most serious and widely publicized negative effect relates to the introduction of predatory snails (*Gonaxis* spp.) onto Pacific islands for control of the Giant African Snail (*Achatina fulica*). These non-specific predators have been blamed for the disappearance of endemic snails that were being studied by evolutionary biologists, particularly in Hawaii and Western Samoa.

K. KRISHNAIAH (*Directorate of Rice Research, Rajendranagar, Hyderabad, India*). Please indicate a few successes of biological control through conservation, and some methods practised in achieving these successes.

D. J. Greathead. Management of oil-palm estates to avoid outbreaks of defoliating caterpillars is widely practised, especially in Malaysia. Practices include growing ground cover to protect pupating parasitoids and to provide food for the adults. Measures to reduce road dust blowing into the plantations also help. Any incipient outbreaks can then usually be stopped by spraying virus that occurs naturally.

Recent work in southeast Asia by a team from the Food and Agriculture Organization of the United Nations has demonstrated that rice pests can be prevented from causing serious damage by encouraging predators, especially spiders, by such means as avoiding weeding the bunds around fields and piling up trash on them as refuges between crops.

In the U.S.A. there are several well known examples, for instance strip harvesting of alfalfa to allow natural enemy populations to move into uncut stips and maintain a high density.