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BIODIVERSITY, BUSINESS AND BIOTECHNOL-OGY: SHAPING THE FUTURE OF BIOLOGICAL CONTROL

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Vijfde voordracht gehouden ter herdenking van prof.dr. J. de Wilde, hoogleraar in de entomologie aan de Landbouwuniversiteit te Wageningen (1954-1982) op vrijdag 18 november 1994

BIODIVERSITY, BUSINESS AND BIOTECHNOL-OGY: SHAPING THE FUTURE OF BIOLOGICAL CONTROL

When I arrived in 1975 in my adopted continent of Europe, as a brash young American entomologist, names like Jan de Wilde epitomised in my mind the glories of the grand European entomological tradition which I was about to experience. I had been prepared well by my American professor, V.G. Dethier, an ardent Europhile, and I felt a particularly attraction to the work of Prof. de Wilde, because I had spent the previous summer working for the Connecticut Agricultural Experiment Station, studying a parasitoid of the Colorado Beetle. It was my first experience in biological pest control and an important one, because it taught me humility. For all its fascinating behaviour, my little tachinid fly seemed to have absolutely no impact on the damaging densities of beetles in my experimental plots.

Being an alien myself, I have always had an affinity for alien pests, and when I arrived in Europe, the Colorado Beetle became something of a mental companion, a fellow wanderer. In Britain, where I studied, it had a popularity quite unbefitting an insect, which heightened its appeal. You needed only to walk into a police station in those days to see the convict-striped chrysomelid posted on the wall next to bank robbers and murderers. I had long before read the fascinating tale spun by the naturalist Willy Ley of the progress of the Colorado Beetle across Europe, greeted by World War I gas dispensers and flame throwers in France, dropped (so said the Third Reich) from British bombers across Germany in World War II, and causing an international incident between the USSR and the West in the early days of the Cold War

(Ley 1951). I was convinced that all that was needed was a better biological control agent.

I remember well my first and only meeting with Jan de Wilde. Of course I wanted to learn from him about Colorado Beetle. When he told me it was not a really serious pest, and that this was not because of effective local biological control agents, I was bewildered. When he then went on to tell me about the likely effects of climate and host plant and physiology and population genetics on the numbers and dynamics of the Colorado Beetle in Western Europe, I realised that my romantic image of the grand European entomological tradition was true, and that I had a lot to learn. And so I went and learnt it.

Like one of Henry James' more fictional New Englanders, I have never quite recovered from my Grand Tour of Europe, and from my fascination with its great entomologists. For this reason, it is truly an honour to be invited to deliver the fourth Jan de Wilde lecture.

I have chosen to speak on the subject which I have made my profession in recent years, biological control. Biological control is the use of living organisms as pest control agents. The history of biological control has been strongly entomological, and most programmes and products to date have either involved insects as control agents or been directed at insect pests, or both. It is therefore a fitting subject to review on this occasion when we honour entomology and the contributions to it of Jan de Wilde, particularly because biological control is a subject which so clearly involves the application of science to agriculture, which he so effectively advocated and achieved.

Introduction

When I am deep in the in-tray and the pressures of running a non-profit, international biological control institute. I console myself with the knowledge that there has never been a more exciting time to be in biological control. The subject today enjoys unprecedented popularity, as well as some challenging notoriety. It has emerged as the leading school of thought in the Renaissance of pest management which has followed thirty years of virtual dependence on chemical insecticides. Biological control practitioners, once a lonely if spirited community, are overwhelmed today with new students and new colleagues. They find themselves suddenly popular and in demand amongst non-specialists: businessmen, politicians, biotechnologists, environmentalists, farmers and the public at large. All of these interest groups are having an effect on what practitioners and doing and where biological control is going in a time of tremendous and rapid change. In this talk, I will survey this change and suggest how they will shape biological control in years to come.

Textbooks often identify three basic methods of biological control: introduction or classical biological control, augmentation of natural enemies (including the use of biological pesticides), and conservation of natural enemies. I have always resisted this conceptual fragmentation of my subject for the benefit of students, but it is in fact more than a teaching tool. For reasons of history, politics, finance and human nature, these three approaches have quite separate traditions. Recent events, as we shall see, are isolating them further, despite their common reliance on the action of natural enemies to suppress pests within and between generations. And therefore, I shall structure my talk under these three headings, drawing them together at the end.

While conservation is the most ubiquitous method of biological control, and I will argue later the most important to the future of biocontrol, its very local nature has made is less popular to academic scientists such as we than introduction or augmentation. These methods have a strong international research tradition, and, being interventions, a certain degree of "business" has built up around them. I will start with them.

Introduction and augmentation both have their origin in the 1880's. In 1888 the ladybird, *Rodolia cardinalis*, was introduced into California from Australia for the spectacular control of the exotic cottony cushion scale, *Icerya purchasi*, which sparked a great number of subsequent programmes against exotic insects and weeds. At about the same time, on the other side of the world, the Russian Metchnikoff carried out the first mass production and use of biopesticide, the fungus *Beauveria brongniartii*, against scarabaeid pests (Steinhaus 1956). Thus in a single decade began two great biological control traditions. Let us see where they are at today.

Introduction of biological control agents, or classical biological control

Classical biological control involves the introduction of alien natural enemies for the permanent establishment and suppression of pests. Since the introduction of Rodolia cardinalis, there have been about 5000 introductions of arthropod agents against insect pests (Greathead and Greathead 1992), and about 700 introductions of arthropod agents against weeds (Julien 1992). Typically, these programmes are conducted against alien pests, and therefore involve first the identification of the pest and its likely area of origin, followed by exploration there for specific and effective natural enemies, research on these, safety testing, quarantine and introduction and evaluation in the affected country. In some cases, the target pest is native, and the introduction programme is aimed at complementing its indigenous natural enemies with new species so as to increase overall mortality.

Classical biological control is a bit like putting out fires. Like that other noble profession, it does not have to succeed every time in order to continue to be popular, because even when it works only occasionally, its more than justifies its existence.

This is because the benefits of a successful programme continue indefinitely, eventually dwarfing the initial outlay of funds for the introduction programme. For agricultural systems, these benefits can be measured in both increased yields and reduced expenditure on chemical or other means of control. Over time, this must be discounted, but it still can be very substantial. For instance, in the early 1980s, a mealybug from Asia, *Rastrococcus invadens*, became a major pest of mango throughout West Africa. The introduction into Togo in 1987 of a specific parasitic wasp from India rapidly reduced populations of this mango mealybug to non-damaging levels (Agricola et al. 1989). The benefits to Togo alone have been estimated at \$US 3.9 million per year in increased production for local and overseas markets, as well as the nutritional and social benefits associated with the important place of mangoes in the local culture (Voegele et al. 1991). The necessary exploration, research, quarantine and provision of the agent by IIBC scientists cost only \$US 175,000.

Similar and even greater returns on investment are associated with successful weed biological control programmes (Doeleman 1989, Tisdell 1990).

Not all programmes, however, succeed. In fact, the likelihood that a particular agent will contribute substantially to control of the target pest is not more than 30% in programmes when the target is an insect pest (Greathead & Greathead 1992) and about 60% when it is a weed (Julien and Chan 1984). So, there is room for improvement. For many years, practitioners have known that at least some of this improvement will come from a better understanding of the population ecology of biological control, and particularly what properties of agent and target pest are associated with successful suppression.

Improving the success rate of classical biological control

Some of the earliest practitioners of classical biological control, like W.R. Thompson, the first Director of my institute, saw the potential for mathematical models to explore the dynamical outcome of releasing natural enemies with certain properties against pests with certain properties (Thompson 1939).

Subsequently, true population ecologists were attracted to classical biological control by the lure of a real life system which had the apparent simplicity of the highly artificial two species predator-prey systems which they modelled. Theoreticians had a particular interest in natural enemies as stabilisers of populations. because through such trophic stability could be seen an explanation for both the diversity and continuity of life on earth. Practitioners of biological control were more interested in natural enemies as depressors of pest populations. The two properties could be explored through the same modelling process, and the result of this was the identification of properties of successful biological control agents. Not surprisingly, given the context, these properties related to characteristics by which natural enemies depressed (e.g., searching efficiency) and stabilised (e.g., aggregation) pest populations. Later, Murdoch (et al 1985) showed us that stabilising natural enemies might not be something the practitioner wants at all.

But the concept that biological control can be predicted by the properties of natural enemies which influence their population dynamics, an approach I have called "reductionist" (Waage 1990) may not be as valuable an ecological contribution to biological control as the concept that natural enemies have their effect on pest dynamic through a complex interaction with other mortalities acting on the pest, and that the effect of a natural enemy depends crucially on the magnitude and sequencing of these mortalities. This more holistic view underpins our thinking on the value of multiple introductions, density dependence and other processes which experience tells us affect the success or failure of programmes. This approach has led to the development of age-structured predator-prey models with the potential to predict the outcome of biological control (Waage & Barlow 1993). Few have ever been used as a basis for agent selection, but the have had a value in helping us identify what factors may lead to success and failure, as a basis for focusing our research.

With classical biological control, we are usually faced with more candidate natural enemies than programme funding can introduce, and it is because of this that ecological thinking can help improve success, simply by allowing us to prioritise agents according to some sensible expectations, rather than randomly (Waage & Mills 1992). Unfortunately, few programmes have every allowed predictions to be tested, e.g. by letting us try out the promising agent in one country and the unpromising one in the other! A more comprehensive look at whether biological control is become more successful is possible, but it is difficult to attribute improvement to enhanced science alone, as all contributing factors are compounded in trends. Nonetheless it is interesting to note that an analysis of IIBC's BIOCAT database of introductions for control

of insect pests reveals that success rates have been increasing in recent decades, perhaps as a result of a greater emphasis on ecological research (Greathead & Greathead 1992)

The benefits of a more ecological approach to classical biological control may be more easy to see in weed control programmes, because these often span decades of introductions, during which changing ideas are reflected in the different agents and approaches taken. An example of this can be found in the programme to control alien European spurges and knapweeds in grasslands of North America (A. Gassmann. pers. comm.). Early in the spurge programme, introductions focused on insect herbivores which were large and did, as individuals, substantial damage to plants like the spurge hawkmoth, Hyles euphorbiae (we might say that they had a strong "functional response"). Later, as the importance of numerical responses of control agents became better appreciated, introductions shifted to include very small insect species with rapid growth rates. like flea beetles of the genus Aphthona. These beetles have proven quite successful in reducing spurge populations at some sites.

This same system illustrates another area of progress, namely the consideration of plant population ecology in selecting insect agents for introduction. Early programmes against weeds like spotted and diffuse knapweed focused on highly damaging seed feeding insects, until it was understood that seed banks were large and not limiting. As a result, research shifted towards agents that would affect the vulnerable stage of the plant, such as the overwintering rosette stage, and these have proven more effective (Mueller-Schaerer & Schroeder 1993).

Classical biological and the environment

Classical biological control programmes set out to re-establish a natural balance between a pest and its natural enemies. In so doing, however, we must introduce an alien organisms into a new environment. Concern about alien introductions is rising amongst environmentalists, and the concept of fighting fire with fire is sometimes not easy for a non-specialist to grasp. Recent debate over the introduction of engineered organisms has no doubt contributed to concern about introductions, but the principle cause for concern is our long memory of the early history of classical biological control. As far back as the 18th century, other biological control programmes have involved the release of vertebrate predators against alien pests with generally poor and sometimes disastrous results, because predators like the mongoose, cat, mynah or toad are not specific enough to confine their attack to the pest species, and can become pests themselves.

By contrast in the 20th Century, following the successful control of cottony cushion scale, most biological control programmes have utilised specific natural enemies for introduction. This has been particularly the case for weeds, where the insects and pathogens selected have to be shown to pose no risk to crops. Those governments which regulate the introduction of biological control agents usually require that candidate biological control agents undergo (1) host range testing to ensure that they will not become pests or threaten desirable species and (2) quarantine to ensure that the introduced agent does not bring in with it as contaminants other pests or diseases, or its own natural enemies which might limit its effectiveness.

Over this century, most host range testing has been directed at ensuring that the introduced agent will not become a pest of agriculture. In a pre-environmental era, effects of agents on non-target indigenous species of conservation value were not a priority for assessment. However, a general preference for highly specific natural enemies, and the host-range testing procedures in place, has had the result that only a handful of the approximately 6000 introductions of alien biological control agents are reported to have significantly reduced populations of non-target indigenous species (Howarth 1991, Simberloff 1992). Of course, observation of such side effects has generally been poor, with the consequence that even some of these claims of environmental effects are disputed (Funasaki et al 1988) and many introductions remain unevaluated for their environmental effects.

Future biological control programmes world-wide must take care to assess the potential impact of introduced agents on non-target species and on ecosystems as a whole. Existing safety testing procedures can be modified to accommodate much of this need. In most cases, the biological host range of candidate agents is established from existing knowledge of its biology and that of related species, and where necessary through a process of centrifugal screening, where the agent is tested in choice and/or no-choice tests against relatives of the target pest, working out from congeners, to confamilials, until the taxonomic limits of host range are established. In addition, specific tests are carried out against organisms of particular importance, such as crops for weed agents, or bees for insect agents. Where there is concern for organisms of particular conservation value - an example is birdwing butterflies in Papua New Guinea, or rare indigenous North American congeners of invasive European weeds - they can be included in these testing procedures.

But safety testing procedures like this are not designed to measure the full ecological impact of the introduction of biological control agents. In particular, they do not measure the indirect effect of reducing the density of the target pest, and its effect on other species.

A case in point is the proposed biological control of bracken fern, *Pteridium aquilinum* in UK. Bracken is a native species which has invaded many highland areas as patterns of land use have changed. As it spreads at about 3% per year, it overgrows and displaces a diverse, local flora. The general environmental effect of the spread of bracken, and its control with chemical herbicides, appears to be distinctly negative (Lawton 1988). On the basis of this, a biological control programme was initiated which identified highly specific insect control agents from Africa. These were tested for host range and against wildflowers and ferns of conservation value in areas where bracken grows, and were shown to be safe. Subsequent to this, however, evidence emerged that in a few areas of bracken distribution, the fern provides useful shelter for uncommon bird species, the whinchat. The introduction programme has not proceeded, and probably will not proceed until we understand better the environmental implications of removing bracken.

It is easy to see how conflicts of interest can arise in biological control, where the perceived positive and negative aspects of an introduction differ between different groups of people or areas.

This simply means that measuring risk is not enough. After we have considered host specificity and higher level effects, there needs to be a mechanism to weigh the risks we have found against benefits, to consider the views of different interest groups and make a decision. Some countries have created such a mechanism, most have not. In Australia, a conflict over biocontrol of the weed, Echium plantagineum, arose because some farmers saw its removal as beneficial to crop production, while some beekeepers found it a useful source of nectar for their bees. Debate over this issue led Australia to create a Biological Control Act under which intended introductions must be publicised and open to public comment and debate, so that all opinions can be considered.

Taking a broad view, then, there exist a range of good approaches to assess the environmental impact of biological control agents, their host specificity, indirect effects and conflicts of interest when these arise. The challenge as I see it is to make these methods more available to governments, so that they can make safe decisions about classical biological control. There are a number of factors which make this challenge most urgent. Firstly, biological control is becoming more popular - its record of success is attracting new countries with little experience in making safe introductions of alien biological control agents. Secondly, the need for classical biological control is growing as more and more exotic pest problems appear. An increase in world commerce is responsible for this trend, and particularly the growth in North-South movements created by trade in high value export horticulture, and the recent opening to the world of the isolated agricultural economies and ecosystems of China and the former states of the Soviet Union.

Finally, the development of a biological control industry, which trades in alien predators, parasitoids and pathogens is greatly increasing the number of requests every year for the introduction of new natural enemy species. Whereas most introductions of biological control agents to date have involved government institutions acting against public pests and for the public good, these new commercially-based introductions raise issues of private vs. public benefit and risk, and thereby raise the profile of the debate about the value and safety of introductions. This is a growing issue in countries like the Netherlands, which are major producers of biological control agents, but also in developing countries like Kenya, where the potential importers of commercial biological control agents has been challenged to show that their natural enemies are superior to indigenous species which could be used for the same purpose. It is possible to

introduce alien biological control agent for profit where they are not really needed, whereupon we must ask the question, is the risk, however small, worthwhile?

To address the growing need of a growing number of countries for guidance in classical biological control, the FAO has prepared a draft Code of Conduct for the Introduction of Biological Control Agents, which will be put forward for ratification in 1995. The Code aims to:

"facilitate the safe import and release of biological control agents by introducing procedures of an internationally acceptable level for all public and private entities involved, particularly where national legislation to regulate their use does not exist or is inadequate"

With respect to the safety of biological control, it recommends that governments evaluate dossier on biological agents which include accurate identification of the agent, a summary on all available information on its origin, distribution, biology, natural enemies and impact in its area of distribution, and an analysis of the host range of the biological control agent and any potential hazards posed to non-target hosts.

Over-regulating biological control introductions will certainly inhibit many programmes against alien pest species, with profound, future environmental costs. Under-regulating biological control will create the risk that one of the growing number of users of this method will make an introduction which will have a negative impact on the environment and that this, in turn, will damage both the reputation and the future useful application of this method. Both ways, agriculture and the environment, will lose out. This underlines the importance of the FAO Code and national initiatives to ensure that biological control is carried out with minimal environmental risk.

Biological control and biodiversity

While establishing globally acceptable guidelines for safety might be seen as a sufficient challenge for classical biological control in the 1990s, there is yet another challenge which is equally urgent and more far-reaching for the future of biological control. This challenge is posed by the international Convention on Biological Diversity.

So far, 156 countries have signed this Convention, which has as its objective:

"the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilisation of genetic resources"

While it is a complex document, we can pull out of it the sections particularly relevant to biological control. For instance, the Convention requests that countries take action to control alien species that threaten habitats and species, and generally to find ways of using biodiversity to support sustainability. With the environmental concern regarding the use of pesticides for pest control and eradication, and a growing number of environmental problems being caused by alien weeds and insects invading conservation areas, this recommendation opens many opportunities for biological control. But, depending on how one views introductions of alien biological control agents, it could also be interpreted to mean that we should be less inclined to introduce any alien species.

Recently, the Secretariat to the Convention has requested that IIBC prepare a document explaining biological control for the benefit of signatories to the Convention. This document is now in preparation. In it, we make the case that biological control, if practised safely, is of great value to environmental conservation. The existence of a draft FAO Code of Conduct is important to this case. I believe that this represents the first of many opportunities which biological control practitioners will have in the next few years to explain their science to those responsible for making political decisions about biodiversity. This will be a crucial and a challenging process, on which will hang the future of classical biological control.

The Code raises another important issue for biological control, the sharing of benefits from the exchange of genetic resources, such as biocontrol agents. With respect to access to genetic resources, the Convention recommends that countries:

- endeavour to create access to genetic resources for environmentally sound uses
- provide access, where granted, on mutually agreed terms and subject to prior informed consent of the country of origin
- encourage scientific research based on genetic resources in and with participation of the country of origin

 share in a fair and equitable way the results of research and the benefits arising from utilisation of genetic resources

Today, there are few mechanisms in place by which the country which provides biological control agents shares in the activity, much less the benefits, of their use in another country. I think we would all find it strange to ask one country to pay another for an exotic control agent, to give back to the country of origin a share of the economic benefits of biological control. But this is a possible interpretation of the Convention, in the context of biological control. If we have a better idea, now is the time to present it.

My view, and that which IIBC will advocate, is that classical biological control is an activity of proven benefit to all countries. All countries have exotic pest problems, and therefore all countries should make their biodiversity available to other countries for classical biological control in the knowledge that they will benefit from introductions from other countries in future.

And we can back this argument up. If we look only at the introduction of natural enemies for control of exotic insect pests, based on IIBC's global database of biocontrol introductions, we can draw the following conclusions:

The augmentation of natural enemies and the development of biological pesticides

Adding natural enemies to crops is a strategy as old as biological control itself. The first written reference to

biological control from 4th Century China involved the sale and purchase of ant colonies to put in fruit trees to augment natural control of insect pests, a method still practised there today.

Augmentation addresses particular problems which we encounter biological control in field crops which, because of their synchrony, seasonality and uniformity afford natural enemies few opportunities to build up sufficient numbers in time to check the rapid growth of colonising pest species.

The history of augmentation of predators and parasitoids has been characterised by a growing awareness of the importance of population dynamics, in much the same way as the history of classical biological control. Early efforts at augmentation, for instance with Trichogramma in the 1930s. concentrated on the killing action of released natural enemies, in ecological terms their functional response. Releases were made to suppress particular pest populations, much like a chemical pesticide. More recently, particularly through research on augmentation of arthropod natural enemies in glasshouses, it became clear that the reproductive power of natural enemies could be exploited to great effect in augmentation, and that regular releases of larger numbers of predators or parasitoids could be replaced by strategic releases of smaller numbers at the right time early in a season, which would then build up on pest populations, keeping them below damaging levels.

Hence, through greater reliance on the numerical response of natural enemies, augmentation could

achieve effective biological control at a vastly reduced investment.

But the augmentative strategy of biological control today is dominated not by arthropod natural enemies but by the manufacture of insect pathogens as biological pesticides and their widespread use as alternatives to chemical pesticides.

Ever since Metchnikoff demonstrated in 1884 the potential to control scarab pests by application of spores of Beauveria brongniartii, microbial biopesticides have been a technical possibility. The delay in their emergence as an important pest control strategy is largely attributable to the rise of chemical insecticides, which were considerably more amenable to industrial production, storage and marketing to a wide range of farmers for a wide range of target pests. Real opportunities for biological pesticides have only emerged in the wake of decisions by developed countries to reduce chemical insecticide use, and the consequent need to find non-chemical, environmentally-sound alternatives. New markets, created for instance by the banning of chemicals for control of lepidopteran pests in Canadian forests, have encouraged agrochemical companies to take biopesticides off the shelf, improve their efficacy, production costs and quality and put them out into the new niche markets

Today, there are over 100 registered products on the markets, whose active ingredients include bacteria, viruses, nematodes, fungi and protozoa (Lisansky 1983). While the market for biological insecticides is still small - in 1990 it constituted 0.5-1.0% of an

global pesticide market of \$20m, it is growing rapidly. Only two products have a substantial market share, the various forms of *Bacillus thuringiensis* and entomophilic nematodes. Together, they make up over 95% of all sales.

While public sector institutions have been responsible for much of the R&D which has led to marketable biopesticide products, their future development is now clearly in the private sector. Multinational agrochemical companies, pharmaceutical and food-based companies with a fermentation capability, and young biotechnology companies have all invested heavily in biopesticides products.

Because production technology is simple relative to some chemical pesticides, there is also the potential for local, commercial production in developing countries, a possibility which IIBC is exploring through a number of projects. The potential here is considerable: developing countries presently import chemicals at considerable expense, and for local pest targets which may not be those for which the chemicals are most appropriate. Locally-produced biopesticides would help these countries to address their local pest problems with safe and effective products, to save on foreign exchange expenditure and to generate local business and employment.

Having established that the biopesticide ball is rolling, I would now like to consider where it is going, and whether its current path will maximise the potential benefits of this kind of augmentation. There is a commonly held belief that insect pathogens do not persist in crops, hence our need to repeatedly release them if we want them to have a significant, pest controlling role. Further, for such products, it is commonly held that success will be measured in their ability to compete with chemical pesticides in the same market niches, or to adequately replace a chemical in a niche left vacant by an act of political will.

These beliefs are well supported by examination of the biopesticide market to date, where *Bacillus thuringiensis* (Bt) and heterorhabditid nematodes hold sway. Neither of these organisms are particularly persistent in crops, indeed, they are less persistent than their chemical competitors. Both have a rapid killing action, competitive shelf life and good opportunities in niches where continued insecticide use is undesirable or impossible due to pest resistance.

But, as pathogens of crop feeding insects, Bt and nematodes have something else in common - they are both alien to the crop environment. Bt is naturally associated with soils (Meadows 1993), possibly tree surfaces (Smith & Couche 1991), and rarely exhibits epizootics in pest populations resident in crop vegetation, where it is usually applied. The toxin-based nature of its action means that its actual reproduction is relatively unimportant to its controlling action. A similar situation exists for nematodes. Heterorhabditid nematodes are also soil-dwelling organisms which survive poorly in crops and only rarely causes epizootics in insects (Kaya & Gaugler 1993). Like Bt, their ecology is probably alien to the crop ecosystem - indeed they seem most closely associated in nature with sandy, seaside beaches (see Waage in press).

Bt and heterorhabiditid nematodes were not selected for development because of their natural impact on pest populations, rather they were selected because of their pesticidal, killing properties. Other insect pathogens, however, do exhibit epizootics in pest populations and can be key mortalities in pest life tables. These include other bacteria, viruses, fungi and protozoa. Put in more ecological terms, the development of biological pesticides by the agrochemical industry has so far focused on the functional response of candidate agents, rather than the numerical response. Does this not seem strange, given that it is the numerical response of pathogens, their capacity to reproduce and by doing so to inflict greater or longer-lasting mortality on pest populations, that would appear to give biological pesticides an inherent advantage over chemical ones?

Some recent work at IIBC has made this point particularly strongly to me. It involves a project to develop a biological pesticide for the desert locust and other acridid pests in Africa. This biopesticide consists of African strains of the fungus, *Metarhizium flavoviride*, which are easy to produced on nutrient substrates and can be formulated like pesticides for ULV application.

A promising target for this technology is the humid zone grasshopper, *Zonocerus variegatus*, a defoliating pest of field crops, which is the regular target of national chemical spray campaigns. Field trials of the biopesticides have given quite satisfactory control of populations over a season. This effect may be a combination of the initial mortality caused by grasshoppers picking up spray droplets with fungal spores as well as subsequent mortality caused by grasshoppers coming into contact with spores from dead insects. Grasshopper cadavers release few spores when they are entire, but as they break up, they serve as point sources of subsequent infection to passing *Zonocerus*.

We have developed a population model for the interaction between the fungus and Zonocerus following a spray. Parameters for release of fungus from cadavers and transmission of infection from cadavers to grasshoppers were measured in the field. The dynamics of the fungus depends strongly on the immigration of healthy grasshoppers into the treated area, and the growth rate of the grasshopper population. Over a range of realistic values for both, the model predicted that a single fungal spray would be equivalent in its effect on populations of eight to 14 applications of a non-persistent chemical. Even more surprisingly, when the model was parameterised for the desert locust, which lives in habitats even less conducive to fungal spore survival, the biopesticide still came out several times more effective than a chemical spray.

This result is not unique. The record of biopesticide trials reveals again and again surprisingly long periods of control from single application of fungal (e.g. Keller 1992), viral (e.g.. Moscardi 1989) and bacterial (e.g.. Jackson et al 1992) biopesticides. Rather than capitalise on this property of pathogens, the agrochemical industry has gone the other way, developing biopesticides to the specifications of the chemical products with which they are familiar. Certainly there is an economic motive - a biopesticide that need be applied only once per season will make less money than one which needs to be applied frequently. Further, frequent application gives more dependable results, even if they are not always necessary. But there are ways to capitalise on the self-perpetuating properties of biopesticides - witness the success of arthropod biological control agents in glasshouses,

Unfortunately, the trend with industrial development of biopesticides through biotechnology holds even less hope for using pathogens to their best advantage. Efforts to improve pathogens as biopesticides through genetic manipulation are presently focused on increasing host range and virulence in bacteria and viruses, by combining genomes from different strains and incorporating genes for rapid acting toxins or juvenile hormones (Waage in press). In a practical sense, these engineered micro-organisms (and, for that matter, crops engineered to express Bt toxins) are little more than variants on existing biopesticidal formulations of the same organisms. They have been designed to improve the competitiveness of these products as pesticides through making them broader spectrum, faster killing, more dependable in their delivery.

Thus there is little evidence that biotechnology, as applied to biopesticides, will enhance the persistence or numerical response of these living control agents, indeed quite the opposite. The genetic manipulation of microbes may reduce the persistence of any biopesticide relative to its natural counterpart, by increasing the cost of carriage and expression of recombinant DNA.

Further, making biopesticides more virulent and faster-acting by engineering in genes for toxin product has the effect of reducing the reproductive rate of the pathogen. Finally, companies may deliberately engineer pathogens to be less persistent - "suicide viruses" are a case in point - so as to minimise possible environmental problems with the release of transgenics.

Thus, I return again at to an earlier theme, the importance of ecology to the effective use of biological control. I suggest to you that we are not realising the true potential of biopesticides and that to do this we must take a more ecological and population dynamic approach to their study and development, to capitalise on those properties which actually make them superior to chemicals. Clearly, the discipline is presently not going in this direction. To steer it back, we need to demonstrate the value of "being alive", the numerical response and the potential for the compounding effects on pest control which it gives when we augment pathogen populations in crops.

Conservation of natural enemies, the foundation of IPM

Classical biological control and biopesticides represent the two grand traditions of intervention in biological control, the one public and the other private. While they will no doubt be used more widely in future, it is fair to say that most farmers around the world will continue to rely on a different kind of biological control, namely that provided day after day by the natural enemies already resident in their crops.

More often than not these natural enemies are poorly understood, indeed often unknown. Their importance comes dramatically to our attention when, through the misuse of insecticides, they are eliminated and the pests which they attack then resurge. This phenomenon, coupled with pesticide resistance, leads to what is commonly called the pesticide treadmill, a situation of escalating pesticide use, escalating costs to farmers, and declining yields. Made famous in recent years by the outbreaks of brown planthopper on rice, pesticide treadmills are also common today in crops such as cotton, apples, mangoes, sugar cane, cocoa and vegetables.

The restoration of the productivity of such agricultural systems by the reduction of insecticide use and the conservation of natural enemies and the reduction of insecticide use has been the foundation of the new approach to pest control which we call integrated pest management or IPM. IPM utilise a range of pest control methods so as to maximise value to the farmer, minimise negative effects on the environment and to be sustainable.

Let me illustrate several key features of IPM by means of an example from my institute.

IPM and natural enemy conservation, mangoes in Pakistan

Mangoes are grown in a number of regions of Pakistan, largely for local consumption. Insect pests are a major problem, and of these there are four kinds which have become the targets of pesticide application: mealybugs, fruit flies, scale insects and leafhoppers. Farmers apply insecticides about five times per year, but still suffer problems with these species. During the 1980s, staff of IIBC's Pakistan station worked with co-operating mango growers in the Punjab, to develop IPM methods which would give good, cost effective pest control. This required developing IPM methods for each pest, while ensuring that these were compatible with methods developed for other pests.

Mealybugs (Drosicha stebbingi) feed on the growing shoots and flowers of mangoes and thereby limit fruit production. Studies on their ecology revealed that females lay their eggs in the soil around trees and young larvae move up to the leaves in the spring. As the season progresses, a number of predators, particularly a ladybird (Sumnius renardi), reduce numbers of mealybugs dramatically. On the basis of this understanding, farmers were encouraged to hoe around the base of trees in the winter, to expose and kill eggs.

Further studies on ladybirds revealed that they spend the winter in shelters such as rough tree bark. The smooth trunks of mango did not provide this kind of refuge, and hence they have to emigrate from the crop at the end of the season. To see if this was responsible for their late appearance, artificial shelters, simple bands of rough sacking fastened around mango trunks, were put in the orchard. As anticipated, ladybirds used these shelters for overwintering and thus became active in the mango crop earlier in the season, giving better control of mealybugs. The biology of the predators was explained to farmers, and the shelter bands adopted.

Fruit flies (*Bactrocera dorsalis* species complex) received the majority of insecticidal sprays made in mango, because their maggots, laid in the mango fruit, can greatly reduce the market value of the crop. As an alternative to chemicals, attractant traps were made from cheap local materials and baited with an imported fruit fly attractant, methyl eugenol. These proved highly effective, reducing infestations from 35% of fruit to 3%.

Scale insects (primarily Aspidiotus destructor) caused problems in sprayed orchards, where they covered leaves and produced a honeydew which attracted mould. However, experimental studies revealed that they were a secondary pest, brought about by the use of insecticides against fruit flies and mango hoppers, which eliminated their effective natural enemies. Hence, with the use of traps for fruit fly control, the scale insect problem decreased.

Mango hoppers (Amritodus and Idioscopus spp) remained the only pest requiring insecticide applications. Ecological studies revealed that the several species involved had a range of different natural enemies, but despite these, damaging levels were still reached. This made it difficult to abandon insecticide applications, but careful study of hopper distribution on plants revealed that insecticides only had to be applied to the lower part of the trees, up to 5m to get effective control. This reduced the amount of chemical applied, and also the risk of upsetting biological control of mealybugs and scales. Farmers were encouraged to modify their spraying accordingly.

As a result of this programme of research in farmers orchards, experimentation and integration of methods for the four insect pests, annual sprays were reduced from five to one, with a 14-fold reduction in cost to the farmer, which more than compensated for the costs of IPM methods. Roughly 25% of the 13,000 ha of mango in the Punjab presently use this IPM method.

This case study identifies some typical and important properties associated with development of effective IPM systems: on-farm research and involvement of farmers; a good understanding of local practices and the local ecology of the pests; access to a range of local and externally-provided pest control methods. But, particularly, for this programme of IPM to be successful required substantial knowledge of the natural enemies of pests in mango fields in Punjab, their biology, phenology and behaviour. Indeed, most of the measures developed were designed to enhance this indigenous, biological control.

IPM - a clash of traditions and the role of biological control

IPM has a number of traditions, from the top-down, technology-driven tradition which emerged in the 1970s from the Huffaker project and other initiatives in the USA to the farmer-participatory tradition born of the FAO Intercountry Rice Insect Pest Control Project and its several substantial successes with national IPM programmes in Asia. In another paper, I have called these two perspectives the technological and ecological paradigms of IPM (Waage in press). Both take as a fundamental tenet the importance to farmers of the self-renewing and usually free biological control provided by the conservation of indigenous natural enemies in crops.

For the technological tradition, this then becomes the black box around which we build thresholds of intervention, that is, we assume that natural control will keep pests below a particular threshold most of the time, and when this is exceeded, we spray. New IPM products, like biopesticides, pheromones and engineered cotton, allow us to make our interventions, where necessary, in a way which does not disturbed the black box of biological control. The emphasis of this approach is on intervention.

For a more ecological, farmer-first approach to IPM, we open the box. It is, after all, what the farmer has to start with, and his or her understanding of it is crucial. The emphasis is on that process of local biological control. Intervention is secondary and because it is usually expensive and sometimes risky, it is used on an at-need basis. These are obviously extreme perspectives along a continuum, and the mango example I have given illustrates how they work themselves into real-world IPM, but this presentation of extremes does help us to understanding, I think, why so many people can be talking about IPM without visible signs of communication. It is a contrast which exists in many areas where science is applied to agriculture, as Robert Chambers (1991) has shown most elegantly.

The need to bring together these approaches to IPM is stated quite clearly in the document which many regard to be the environmental blueprint for the next century, Agenda 21 of the 1992 UN Conference on the Environment and Development. Under its Chapter 14, which deals with sustainable agriculture, Agenda 21 sets as a goal:

"Not later than 1999, to establish operational and interactive networks amongst farmers, researchers extension services to promote and develop IPM"

My personal affinity for the farmer-participatory approach to research on IPM and biological control is born of several experiences with farmers in Africa, Asia and Latin America, where I have been impressed and humbled by their ability to be inventive scientists and imaginative biological control specialists. My views are also affected by the failures I have seen in extension and research systems to deliver solutions to the real problems which farmers face. The capacity for scientists to invent problems to entertain their need to solve problems is endless, and has been the basis of much misdirected research in biological control and pest management. Putting farmers and scientists together creates an opportunity to get the best out of both.

This is not to say that basic research on biological control methods is not relevant, nor that emphasis on indigenous natural enemies and their conservation in IPM precludes work on interventions like biopesticides or classical biological control. In reducing dependence on conventional insecticides. IPM offers opportunities for biopesticides, which can help with the recovery of natural enemy populations. That these opportunities may be transient, in other words that biopesticides could be the "methadone of IPM", helping agroecosystems to recover from the habit of calendar insecticide application, is a distinct possibility which the agrochemical industry has yet to grasp. Where biopesticide development aimed more at the self-renewing properties of pathogens, as I have advocated earlier, biopesticides may have a greater, continuing role as a complement to natural enemy conservation in IPM.

Where pests are exotic, and even in some cases indigenous, IPM also offers opportunities for classical biological control, to improve the self-renewing contribution of natural enemies in the crop system. Recent work by IIBC and FAO in Sumatra, for instance, suggests that IPM on soybean may involve reduction of pesticide use against early season defoliators, which rarely affect yield, but that the natural enemy complex which is thereby preserved is still not always effective against a guild of late-season pod-feeding pests which do have a real effect on yield. Here, introduction of classical agents against pod sucking bugs (e.g.. Nezara viridula) and pod-boring moths (e.g.. Maruca testudinialis) may enrich the local natural enemy community and reduce the need for insecticides.

With the diamondback moth, *Plutella xylostella*, throughout the tropics, the establishment of parasitoids like *Diadegma semiclausum* and *Diadromus collaris* have been essential to IPM, as has the occasional use of Bt to enable these classical biological control agents to establish and build up numbers.

All of these biological control methods have a role, and an enhanced one I think, in a farmer-participatory approach to IPM. This is our current experience in cotton and vegetables, where we are assisting a number of Asian countries with pilot programmes for IPM implementation, involving training of trainers and farmers field schools. But in all these projects it is striking how much more we know about our interventions than about the indigenous natural enemies which they are designed to complement.

Conservation of natural enemies - whose research?

I would like to conclude, therefore, with a thought about this gap in our knowledge, one which I think is particularly appropriate to the occasion of this talk and to our presence together in this room.

The tradition of biological control, like other traditions in pest management, is a tradition of research centred at universities and government institutes. In our laboratories here in Wageningen and elsewhere, we look at fundamental processes and design solutions for perceived problems, often ones far away. It is only possible to do this if our solutions are general and location un-specific. The grand tradition of chemical pest control shows how this can be done. What satisfaction must have filled the European developers of DDT when they realised that their laboratory-born technology had a useful application in pest management in every corner of the world. It is in this tradition that today we see agrochemical companies proclaiming on billboards such messages as "World Problems, World Solutions".

In the area of biological control, interventions like classical biological control and biopesticides bring us close to this opportunity to sit in our laboratory in Europe and solve someone's pest control problem in Zambia. In our training of scientists from other countries, we impart this capacity and this dream, so that they may sit in their own countries and think of what they can discover which will help yet another part of the world.

However, when we grasp the nettle of IPM, we realise that its essential biological control component makes it very local. What was valuable in the Punjab in Pakistan for IPM on mango may not be of value in West Africa where different natural enemies and pests may prevail, or even in another part of the Punjab where mango is intercropped with trees which afford adequate overwintering sites for predators.

In undertaking research on biological control to support successful IPM, we therefore run into problems of location and scale. What can we do, sitting in our laboratories, when the useful application of our talents is sitting on someone's farm, working with them to find an appropriate means of utilising natural enemies in their two hectares? What kind of reward does such isolated, local and inherently informal science bring our scientific careers and the expectations that we will leave behind rather larger scientific footprints? How do we, as researchers, have the time to get ourselves so involved in the biological control problems of many small farming communities?

Frankly, biological control research for IPM does not lend itself easily to the research structures we have created in our first world universities and institutes or indeed in our research and extension systems in developing countries. What national programme, what army or researchers and extensionists could ever address the needs for developing IPM at the local level across their agroecosystems?

This is, perhaps, why the most important method of biological control, the conservation of local natural enemies in the crop environment, is the least studied, and why we know so much more about biocontrol interventions like biopesticides and classical biocontrol, than about the local biological control that they are intended to protect and enhance.

I think it is easy to see that there is only one "army" which can address research and development of IPM on a sufficiently large and sufficiently local scale, an army of farmers themselves, empowered to be experimenters and implementers. Our challenge is to help in preparing an effort on such a scale, and to supplying it with appropriate information and methods. It is, I think, an exciting challenge, which gives a new and refreshingly pleasant interpretation to that old academic adage "those who can, do, those who cannot, teach".

A closing word

As a biological control specialist, I came rather late in life to Rachel Carson and Silent Spring (even now, this is a difficult thing to admit in public!). In her writings on nature and its abuse, I have found a bridge between the scientific approach which I practice and the very human wonderment at the diversity of natural enemies and their role in the balance of nature which I have had the privilege to share with farmers and friends, strangers and children.

Let me finish, therefore, by presenting a few quotes from Silent Spring. Of biological control and other alternatives to conventional pesticides, she writes:

"Through all these new, imaginative, and creative approaches to the problem of sharing our earth with other creatures there runs a constant theme, the awareness that we are dealing with life - with living populations and all their pressures and counterpressures, their surges and recessions. Only by taking account of such life forces and by cautiously seeking to guide them in channels favourable to ourselves can we hope to achieve a reasonable accommodation between the insect hordes and ourselves." Of pesticide she writes,

"The chemical barrage has been hurled against the fabric of life - a fabric on the one hand delicate and destructible, on the other miraculously tough and resilient, and capable of striking back in unexpected ways. These extraordinary capacities of life have been ignored by the practitioners of chemical control who have brought to their task no high minded orientation, no humility before the vast forces with which they tamper."

While Rachel Carson was speaking here of those who developed broad-spectrum insecticides, I wonder what she would say today about the engineer of suicidal insect viruses, or indeed the irresponsible importer of alien natural enemies for the biocontrol business.

I feel that the excerpts above from Silent Spring express far more elegantly than I have here the underlying importance of understanding population ecology in making a success of biological control. Whether it is an understanding of what patterns of mortality make for the most successful classical biological control, of the ecological consequences of establishing the wrong agent, of the level of numerical response which optimises the contribution of a biological pesticide, or of the kind of crop manipulation which best enhances the spatial and temporal distribution of indigenous predators in a crop, it is the appreciation of the population level consequences of our actions in biological control that make us most effective. In tomorrow's world, we not only have to grasp this concept as scientists, but impart it in

appropriate languages to our new partners in biological control, businessmen, environmentalists, farmers and the public at large.

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