Ecology: cool science, but does it help?

Prof. dr. J.C. van Lenteren

Farewell address upon retiring as Professor of Entomology at Wageningen University on 10 June 2010

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'In the ecological vision, the salmon, and the river weeds and the water insects interact in a great, complex dance with the earth and the weather. The whole is greater than the sum of the parts. In the dance, each organism has a role: it is these multiple roles, rather than the particular beings who play them, that participate in the dance...

The irony is a terrible one. An ecological philosophy that tells us to live side by side with other creatures justifies itself by appealing to an idea, an idea of higher order than any living creature. An idea, finally – and this is the crushing twist to the irony – which, no creature except man is capable of comprehending...

We, the managers of the ecology... understand the greater dance, therefore we can decide how many trout may be fished or how many jaguar may be trapped before the stability of the dance is upset. The only organism over which we do not claim this power of life and death is man. Why? Because man is different. Man understands the dance as the other dancers do not. Man is an intellectual being.'

Elizabeth Costello, J.M. Coetzee (Viking Penguin, New York, 2003)

I would like to thank my sister Anke van Lenteren for correcting my English and my late wife Marianne Bergeman for suggesting to me what to discuss during my farewell address. Part of this lecture is influenced by discussions in and publications of the Commission on Biological Control and Access and Benefit Sharing of the International Organisation for Biological Control (IOBC-Global).

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Ecology: cool science, but does it help?

Mister Rector, ladies and gentlemen,

After finishing elementary school, I wanted to become a carpenter and my father said, 'OK, but first go to high school.' Halfway through high school, I wanted to take up electronic engineering and again my father said, 'OK, but first finish high school.' During the last year at high school I fell in love with biology and this time, my father said, 'OK, but why not go to medical school instead, because how on earth are you going to earn a living as biologist?' This time I did not follow my father's advice and listened to my heart: I was interested in the organization and functioning of life, not in healing people. Well, here I am, 47 years later, very content with the choice I made in 1963. As a result of this experience we told our own children and I also always advised my students: study what you like most, do it well and you will always find a job.

Most of the time I could work on research or policy issues which I chose myself. I never had the desire to leave university, because you are constantly surrounded by young, enthusiastic and creative people. I loved my life at university, I have enjoyed almost every minute of it. Therefore, I would like to start with thanking the most important people who have created the basis for me being so fortunate: my parents, my mentor Kees Bakker and my late wife Marianne Bergeman. My parents encouraged me to attend high school and university, even though their financial situation hardly allowed for such a luxury. My mentor Kees Bakker because he gave me much more than ecological knowledge. He made me love science, he initiated me in how to formulate and answer essential research questions, how to critically read scientific literature and how to write papers, but most importantly, he gave me self-confidence. My wife Marianne supported my work in many ways, not least by entertaining many of my colleagues, by editing and proofreading practically all my publications, by listening to draft versions of important presentations, and by guiding me what to tell you today. Numerous others have contributed to what I currently am, of course, and among these are many of you here in the audience.

Studying biology during the 1960th was certainly not a boring affair. The structure of DNA was discovered with subsequent revolutionary developments in genetics, but also environmental problems suddenly appeared high on the political agenda resulting in many practical questions for ecologists. It was in this setting that I had to find my niche. Usually, when orienting oneself for an MSc thesis – we had to write three of them in the 1960th! – one would visit a number of research groups and then make a choice. After several rather disappointing talks to researchers in fields of my first interest, a visit to Kees Bakker at the Department of Ecology resulted in a very passionate discussion about pure and applied aspects of ecological research which made me decide I wanted to work under his guidance.

In the 60th and 70th it seemed like ecology was quickly maturing. With autecological approaches, it became easy to predict where organisms could live and during which periods of the year they would be active. In population ecology several theories about determination of population size were developed and obtained enthusiastic groups of supporters. And several of the world's leading ecologists worked in the Netherlands. Wow, did we have interesting and heated discussions in the Netherlands in the 1970th! During this same period, computers became available and modelling in ecology became popular. It seemed that only a few problems remained to be solved before we knew the answers about population regulation and ecosystem functioning. We expected to be able to help environmentalists with advice for proper management of natural ecosystems and, on a more modest scale, how to select and use natural enemies in biological control. Young and naïve as we were, we started putting together a list of criteria for fast and efficient selection of biological control agents. Because we had computers available together with the models to predict population fluctuations, we thought to be able to predict numbers of natural enemies to be released in order to obtain reliable biological pest control. We were also thinking that we could tell what elements of behaviour of natural enemies needed to be changed to make them more efficient. Finally, when applying biological control, we expected to be able to test if density dependent regulation was the mechanism of pest control by natural enemies – a hypothesis which was taken for granted by many biocontrol workers at that time.

I will not summarize the pure scientific research done at Leiden University (1970 – 1983) based on which the ideas presented above were created. In 1983 I was asked to join Wageningen University to give pest control a greener face. Until then the orientation at the Laboratory of Entomology had mainly been a physiological one and was focussed on the replacement of broad spectrum pesticides by safer and more specific, biologically-based control agents like growth regulators, repellents and pheromones.

Being neither trained as an entomologist nor as a crop protection specialist, I oriented myself in both fields, but with a strong ecological input which resulted in several new research approaches. I discovered several interesting facts: (1) on the whole insects were, wrongly, considered very unpopular and this negative feeling was frequently reinforced by exaggerated stories put about by the pesticide industry; (2) pest control was almost entirely centred towards chemical control and ecological knowledge on how to prevent or reduce pests was hardly used since the emergence of chemical pesticides; (3) knowledge about the very limited number of species creating pests (worldwide some 5,000 species out of some 100,000 potential pest species) was usually not presented in lectures on pest control. Instead of studying why so many other species were not creating pests, most energy was spent on development of new pesticides; (4) the pesticide industry overstressed the role of insects in crop losses and downplayed the role of any alternatives for pest control. Well, quite some work to do for our new research team!

Today, I will address how we proceeded with one of the new research approaches – the development and application of scientifically based biological control. However, let me be clear: fundamental research at Entomology has always been the basis of our applied work, and the majority of researchers at our Laboratory work on pure science. During the past 56 years our fundamental research has been of top quality and is published extensively in leading entomological, physiological and ecological peer reviewed journals. There have been various moments in the history of our Laboratory when we were told to strongly reduce or even terminate our pure research approach. We have been stubborn in this respect and our perseverance has paid off: truly new ideas and solutions for crop protection will only be found through creative, pure scientific research.

1. Development and application of scientifically based biological control

Biological control is the use of an organism to reduce the population density of another organism. Let me illustrate this with a natural enemy – in this case a tiny wasp of only a few millimetres – which attacks an aphid host.

Intermezzo 1. Discovery of parasitoids

Allow me to tell you an anecdote related to this natural enemy. Based on literature studies, we thought that insect parasitism was discovered by Anthony van Leeuwenhoek in Delft in the year 1700. He described the attack behaviour which you have just witnessed of a related parasitoid (*Aphidius ribis*). And please realize just how good an observer he was, because the attack and injection of an egg in the aphid takes about 1/10th of a second! In 2000, we wanted to commemorate the discovery of parasitism by Van Leeuwenhoek and organized a symposium and a competition. We tempted scientists worldwide with the question: 'Did someone in your country discover insect parasitism earlier than Van Leeuwenhoek?' This attracted seven speakers and not surprisingly, the earliest record came from China where parasitism was first described by Lu in 1096 (Cai et al., 2005) and this pre-dated earlier estimates with 604 years. And even though many historical studies had been done in Europe, it still came as a surprise to discover it was not Van Leeuwenhoek, but Jan Jacob Swammerdam together with the painter Otto Marcellis who were the first to understand and describe the life cycle of an insect parasitoid in 1678 (van Lenteren & Godfray, 2005). The Dutch beat England by 7, Italy by 31, France by 58, Germany by 77 and Japan by 207 years. Could this be the reason why Holland today houses the largest commercial producer of natural enemies of the world?

When lecturing I usually ask my students or the audience how they would search for natural enemies, how many species do they expect to find and how they would evaluate their pest control efficiency. The first question is usually answered easily and correct. Finding answers to the other two questions is often problematic.

1.1. How to find natural enemies

All biological control projects are characterized by a similar overall approach. First, during the project planning phase, the literature is surveyed for knowledge about the pest and its natural enemies. Next, natural enemies are collected and their control capabilities are verified. When one or more promising candidates are found, approval for release is requested based on a dossier which, among others, contains an environmental risk analysis. Finally, post-release studies are performed to confirm their pest reduction efficiency. (For a more detailed overview of the planning and implementation of a biological control project, see Cock et al., 2010).

1.1.1. Preparation and planning

This involves a literature survey to find out what is known about the pest and its natural enemies throughout the world. The area of origin of the pest is identified, as well as the best place to look for natural enemies, which – due to political and administrative problems – are not necessarily the same. Sometimes, very little is known about the pest and its natural range, making sampling for natural enemies very difficult. The pest, closely related species and their natural enemies are collected, and usually exported for identification, which occasionally leads to discovery of new species. Taxonomy is relevant at all steps in the project, but particularly during this phase. Accurate identification is crucial to prevent research on useless species, and this needs to be done by internationally recognized taxonomists. There is no single country that has taxonomic competence for all groups of organisms, so international cooperation is essential. Descriptions of new species and new records of previously described species improve the understanding of biodiversity. Voucher specimens in national and international museum collections ensure that the biodiversity of the source country is included in major taxonomic reviews that identify the species but also show the relationship (uniqueness) of the fauna to that in other regions.

1.1.2. Detailed studies

These evaluate the potential of natural enemies and focus on identification, biology, rearing methods, host specificity, impact, potential negative effects etc., and will later be discussed in greater detail. Some studies can be carried out in the source country, e.g. surveying related species to assess host specificity. However, living cultures of natural enemies would normally need to be established outside the source country for some of the detailed studies. The detailed studies should establish which, if any, natural enemies are suitable for use as control agent.

1.1.3. Permission for release

A dossier based on detailed studies is presented to the receiving country's regulatory authorities to evaluate the risks and benefits of making an introduction. On the basis of this dossier, permission for introduction may be given. Although the objective of the whole programme has been towards this end throughout, it is only at this stage that it becomes clear whether a release of a natural enemy from a particular country will go ahead. I am proud to say that the International Organisation for Biological Control (IOBC) has taken the initiative for and collaborated with FAO in drafting a protocol for proper procedures in biological control (IPPC, 2005). Until very recently, the research up until this point assumed that the source country will not object to the release of a natural enemy exported from their country. However, under an Access and Benefit Sharing regime in the Convention of Biological Diversity, this may become a very complicated issue (see below).

1.2. How many natural enemy species attack a certain pest organism?

When I ask this question, most people mention very low numbers, anything between 5 and 10. Fortunately for biological control researchers, it is not an exception to find hundreds of predator species, tens of parasitoid species and tens of species of diseases. But this large number of potential candidates is also a complicating factor, because it is impossible to study all species in detail. This makes the question of how to find a good natural enemy an urgent one, as it is impossible to keep a collection of some 50-100 natural enemy species in the laboratory for several years.

1.3. How to find out if a natural enemy might be a promising candidate for biological control?

When asked, people suggest several logical evaluation criteria, but usually not the most essential ones. Instead, they propose to do very time-consuming research which is not very realistic when one has found many natural enemy species. It is not really surprising that the strongest and at the same time quickest evaluation criteria do not easily surface. Due to difficulties in identifying critical criteria, early generations of biocontrol workers (period 1880 – 1980) seldom used scientific criteria. It was kind of shocking for me to find out that biocontrol workers in the 1970s hardly ever used ecological knowledge to evaluate natural enemies. While discussing this issue with Paul DeBach (one of the greatest names in biological control) during my post doc in California in 1976-1977, he reiterated one of his statements: 'no amount of planning and preliminary research can replace actual and empirical research for natural enemies in the field and their trial by release in the new environment' (DeBach & Huffaker, 1971). Although DeBach would frequently say: 'Don't bother about theory: collect, take home, release and see if it works,' I am convinced that he himself, being a very good ecologist, implicitly used criteria in selecting natural enemies as pest specificity, high pest kill rate, climate matching and safety of release. The influence of the viewpoint of the USA biocontrol community concerning the issue of selection criteria in the 1970s was clearly expressed in a report of a special study team coordinated by the USA office of environmental quality activities (Anonymous, 1978): 'There are no reliable criteria for determining, *a priori*, which of several alternatives is 'best'.' I was very disappointed by the report and felt we could do better. For this reason, I tried to draw up a list of evaluation criteria based on my ecological knowledge and a few years of experience in biological control. I concluded that an efficient natural enemy:

1. is seasonally synchronised with pest,
2. is developmentally synchronised with pest,
3. is adapted to the local climate,
4. discriminates between good and bad host/prey, and between healthy and parasitized host,
5. is pest specific,
6. has a pest kill rate which is higher than the population growth rate of pest,
7. is capable to quickly locate new pest populations,
8. is capable to react in a density dependent way to pest population fluctuations,
9. shows no negative effects, and
10. is easy to mass produce.

The various forms of biological control are explained below. Not all of the criteria listed above are relevant for each type of biological control. Several of the criteria mentioned in the list can be applied in a straightforward way and hardly need explanation. But a few need to be illustrated in more detail because of conflicting theoretical information and experience from practical applications.

1.3.1. Seasonal synchronisation with pest.

Intermezzo 2. Types of biological control

Natural biological control

Natural biological control is the reduction of pest organisms by their natural enemies and has taken place since the evolution of the first ecosystems some 500 million years ago. Natural control continues to the present day in all of the world's ecosystems and without any human intervention. Waage and Greathead (1988) stated that, in economic terms, the greatest contribution of biological control to agriculture comes not through man-made but from natural control.

During the past 100 years, natural control has been negatively influenced by the result of human activities such as pesticide sprays, many other types of pollution and environmental degradation due to industrialization and agriculture. It is, therefore, surprising that natural control continues to play such an important role: it is estimated that the majority of potential pest species is kept under natural control (DeBach & Rosen, 1981). Often, the role of natural control becomes obvious only after pesticide application: the target pest may be killed, but at the same time natural enemies of – until then unknown – pests may be unintentionally killed as well, resulting in the development of new pests. This phenomenon is known as causation of secondary pests and hundreds of cases of causation of pests by pesticide spraying have been documented.

A good example of natural control is the reduction of leafminer pests in greenhouses in The Netherlands. Parasitoids which develop in leafminers on wild plants fly into the greenhouse in spring and effectively reduce the leafminer populations free of charge!

Conservation biological control

Conservation biological control consists of actions that protect and stimulate the performance of naturally occurring natural enemies. It covers a wide field of activities (Gurr & Wratten, 2000). One of the most interesting examples of conservation biological control originates from The Netherlands. A study spanning several decades (1967-1995) in Dutch apple orchards (Gruys, 1982; Blommers, 1994) clearly showed that over half of the 24 species of arthropod pests in apple orchards can be controlled fully or substantially by conservation biological control. Natural control – which historically played an important role in fruit orchards – was disrupted in most of the orchards by routine chemical spraying after the 1940s. Reintroduction of natural enemies from unsprayed orchards, replacement of broad spectrum pesticides by more selective pesticides and better timing of sprays resulted in partial restoration of the apple orchard ecosystem so that conservation biological control could function again; the number of pesticide applications went down by 60-90%.

Inoculative (=classical) biological control

In inoculative biological control, natural enemies are collected in an exploration area (usually the area of origin of the pest) and introduced in new areas where the pest occurs. Generally, only a limited number of natural enemies – often less than 1000 – are released. The aim is that the offspring of the released natural enemies build up populations which are large enough for suppression of pest populations during many subsequent years. This type of biological control has been used most frequently against introduced pests, which are presumed to have arrived in a new area without their natural enemies. As it was the first type of biological control practised widely, it is also called "classical" biological control. The control of cottony cushion scale (*Icerya purchasi*) achieved in California (USA) more than 120 years ago with the Australian predatory beetle *Rodolia cardinalis* is the oldest example of this approach and literally saved the citrus industry. The offspring of approximately 120 Australian beetles released in 1889 in California are still controlling the scale pest not only there, but also in 50 other countries (Cock et al., 2010). A Dutch example of this approach is the import and release of North American parasitoids (*Aphelinus mali*) for the control of the woolly apple aphid (*Eriosoma lanigerum*) which entered Europe with shipments from North America in the 1920s.

Inundative biological control

Inundative biological control is the simplest type of biological control. Natural enemies are mass-reared in biofactories and periodically released in large numbers to obtain an immediate control effect of pests, either just for one or a few generations. One could say they are used as biotic insecticide with no anticipation of effects on subsequent generations. A Dutch example of this approach is the application the fungus *Verticillium lecanii* for control of aphids and whiteflies in greenhouses.

Seasonal inoculative biological control

In seasonal inoculative biological control, natural enemies are mass-reared and released in annual crops to control the pest for several generations. A large number of natural enemies is released to obtain both an immediate control effect and also a build-up of the natural enemy population for control later during the season. This method is essentially different from inundative control, because of the aim to obtain a control effect over several generations – the method therefore resembles inoculative control. An illustration of this type of biological control is the management of whitefly (*Trialeurodes vaporariorum*) pests with a parasitic wasp (*Encarsia formosa*) in greenhouses in the Netherlands and many other countries.

The natural enemy should be active during the period that the pest is around. This criterion is important for natural, conservation and inoculative types of biological control. It is a simple but vital rule: when there is a mismatch in synchronisation, the pest will not be controlled. This criterion is not important for inundative and seasonal inoculative control, because here the farmer can arrange seasonal synchronisation by timing the release of natural enemies.

1.3.2. Developmental synchronisation with pest.

The natural enemy should have generation developmental times which are similar to the pest, so that it will be around when the right pest stage is available for attack. This criterion is important for most forms of biological control, except for inundative releases where one aims at the immediate kill of the pest generation when the natural enemies are released. Also, this criterion is less important when there are many and overlapping generations of the pest.

1.3.3. Climate adaptation.

Natural enemies should be able to disperse, develop, reproduce and attack the pest under the weather conditions in which they are to be used. This is a simple and easy to understand criterion. For example, it does not make sense to collect natural enemies in the tropics and release them in a field in Scandinavia. This criterion applies to all forms of biological control.

1.3.4. Discrimination between good and bad hosts or prey.

We initially used this criterion based on our experience with basic research and literature data indicating that many predators and parasitoids were not very efficient in discriminating between good and bad hosts. However, after our basic studies related to host/prey selection and discrimination we had to conclude that most natural enemies are actually very capable to quickly select the best available host/prey (van Lenteren, 1976), and that the statements in earlier articles about their lack of ability for discrimination were based on poor experimentation or incorrect interpretation of data (van Lenteren, 1981). As a result, we no longer use this criterion. It was the first (and alas not the last!) time that a seemingly very attractive body of pure scientific information offered no possibilities for use in applied science.

1.3.5. Pest specific.

Intermezzo 3. Host discrimination

Although we no longer use the discrimination criterion, I would like to illustrate why we were so excited when studying it. In the 1960s it was largely unknown how insect parasitoids select their hosts, and in particular, if they could distinguish between parasitized and unparasitized hosts. If they are unable to discriminate, they would lay eggs in already parasitized hosts, resulting in mortality of all but one immature parasitoid. Also, we hypothesized that without the ability to discriminate, a parasitoid would not be able to determine when to leave a host patch in case of depletion of unparasitized hosts. Before we started the experiments, we first evaluated the literature.

During the first part of the 20th century two schools of thought developed about the issue of host discrimination. One group, consisting of theoretical ecologists and biocontrol workers, was convinced after analysis of many parasitoid egg distributions over hosts that parasitoids did not have the capability to discriminate (e.g. Fiske, 1910; Thompson, 1924). The other group, consisting of physiologists, ethologists and theoretical ecologists, presented data indicating that parasitoids could distinguish between parasitized and unparasitized hosts (e.g. Salt, 1934; Walker, 1937). Elegant laboratory work by Salt (1937) shed light on the issue of discrimination. He observed that parasitoids marked the host after laying an egg, that such marks are picked up by the next parasitoid visiting this host which then rejects the host and does not lay an egg. Another important observation by Salt was that parasitoids started to accept already parasitized hosts for egg laying if they had not been in contact with unparasitized hosts for a long time and were prevented from leaving an area with parasitized hosts. Salt (1934) further made an essential statement, which was apparently not picked up by many of his contemporaries and is even today sometimes neglected. He said that the avoidance of laying eggs in already parasitized hosts involved two distinct faculties: (1) the ability to discriminate between unparasitized and parasitized hosts, and (2) the ability to refrain from oviposition when suitable hosts are not available. It is similar to what happens to me when I visit the USA: each time I see cheese, I am able to distinguish between my taste for strong Dutch cheese and the less tasty American variety and initially I will not eat tasteless cheese. After a few weeks, I am still able to distinguish between the two, but I can no longer refrain from eating tasteless cheese.

At the end of the 1960s, it was clear that the two visions (parasitoids can or cannot distinguish) were still expressed in literature, but the majority of us tended to support Salt's opinion. And for most of the (many) cases where non-discrimination was concluded, I could prove that the authors either used wrong data (we could show this after a time-consuming re-analysis of many datasets), wrong terminology, wrong definitions or wrong arguments (van Lenteren, 1976, 1981). At that time, I started studying the host discrimination capacity of a parasitoid of *Drosophila* larvae, *Leptopilina heterotoma*. It had just been discovered that this species could discriminate (Bakker et al., 1967), but occasionally, surprisingly high degrees of hosts with more than one egg (i.e. superparasitism) were found. It was my task to find out why these mistakes occurred. It would be tempting to spend the remainder of this lecture about my PhD research, about the sheer frustration of losing almost an entire year due to applying the wrong methodology, the excitement of developing new methods with engineers employed at the subfaculty of biology, the first use of computer simulation, the thrill of finding something totally new and see it published in Nature, and ending up with a list of factors that may cause superparasitism. I will restrain myself and only present this list.

Factors that may cause superparasitism:
1. The female lays more than one egg per oviposition
2. The female does not recognize hosts parasitized by other females
3. The female lays a second egg within the period needed for building up a factor that causes avoidance of superparasitism
4. Two or more females lay eggs simultaneously in one host
5. The female can no longer restrain from superparasitism when she encounters only parasitized hosts for a long period
6. The female has not yet learned to discriminate

All, except the last cause could be found in the pre-1970 literature on host discrimination. Based on my own work, I could agree with many other researchers that factors 1-4 do not play an important role in the causation of superparasitism. The fifth factor –failure of restraint – is often mentioned in the literature, and my own work on various species of parasitoids also showed that superarasitism may become frequent when the parasitoid only encounters parasitized hosts and cannot leave the site. Before she starts to superparasitize, one can observe that she rejects many, many parasitized hosts, moves away from the host patch, stands still for considerable time, returns to the host patch, rejects hosts and so on. As soon as she has the opportunity to move away, she will start searching for new host patches.

It took some time before we realized that learning played a role in host discrimination. Actually, we discovered it by making a mistake. When studying factor 5, I was offering long series of parasitized hosts to a parasitoid to see when and how easily she would superparasitize. After an hour and many rejections, she started to superparasitize. Then, I made an error: I offered her an unparasitized host which she accepted and immediately afterwards started to reject already parasitized hosts. We repeated this 'mistake' and consistently found that females started to reject parasitized hosts soon after being offered one unparasitized host. Next, we offered parasitized hosts to a freshly emerged, i.e inexperienced, parasitoid that never had laid eggs. She accepted these until we offered her a single unparasitized host. This was followed by a series of other experiments which showed that an inexperienced wasp will only accept the host with the lowest number of parasitoid eggs. She will continuously change her threshold of acceptance, based on newly gained experience. She is actually learning! She is showing adaptive changes in individual behaviour as a result of experience (Thorpe, 1956). With this knowledge, we could now also interpret seemingly strange observations made by several other researchers as 'learning'. The fact that parasitoids may need to learn to discriminate casts a heavy shadow over many datasets from earlier research, because often the condition of the parasitoids (i.e. whether they are experienced or not) was not known or specified in pre-1970 literature. Not surprisingly, one will now usually find in the methodology section of a paper whether the insects used are experienced or not. Initially, we had a hard time convincing (behavioural) ecologists that an insect measuring a few millimetres was able to learn and can count, but nowadays we know – among others from work done within our own group – that insect parasitoids can learn (and forget) many things (Vet & Smid, 2006; Smid et al., 2007). After publication of my list it was demonstrated that under particular circumstances it may be profitable to superparasitize (van Alphen & Visser, 1990).

Today we know that hundreds of species spread over most parasitoid families can discriminate and that phytophagous have similar capabilities (Nufio & Papaj, 2001). I really wonder whether there are truly non-discriminating species. Also, it has been shown that parasitoids leave a patch when the majority of the hosts have been parasitized. Thus, the ability to discriminate has at least two very useful functions: it prevents parasitoids from wasting offspring and time!

During these behavioural ecological studies in 1971, I made two notes in my lab log: how does *Leptopilina* catch a host and which sensilla does she use to discriminate? These questions had to wait until a sabbatical in 1997, followed by annual visits to the section of Entomology at the University of Perugia. With a combination of Perugini anatomical expertise and Wageningen expertise on behaviour and sensory physiology, we were able to show that *Leptopilina* attacks a host, catches it with a special structure (van Lenteren et al., 1998), anaesthetizes the host and has a special sensillum at the tip of the ovipositor which she uses to determine the quality of the host (van Lenteren et al., 2007), and all this in just a few seconds! The successful Perugia/Ancona/ Wageningen collaboration made us the first to succeed in making recordings of a chemoreceptor on the tiny ovipositor of a parasitoid. We have not yet completed this work and this – I am happy to say – is a very good reason to visit Italy on a regular basis.

It is often stated in the literature that a good natural enemy should be very pest specific because only then is it able to react to specific (chemical) cues produced by the pest or by the plant on which the pest lives. Many scientific data support this statement, particularly when we consider natural, conservation and inoculative types of biological control. Another positive aspect of pest specific biological control agents is that they are less likely to attack nontarget species and cause direct or indirect negative effects. Also, it has been shown that in those cases where biological control went wrong, it concerned almost without exception large polyphagous predators, such as the notorious introduction in 1830 of the giant toad (*Bufo marinus*) into Australia for control of white grubs (*Scarabaeidae*) in sugar cane, and of the Indian mongoose (*Herpestes auropunctatus*) into Caribbean and Indian Ocean islands for rat control. These generalist predators were of some initial benefit, but soon became pests themselves and were implicated of the extinction of endemic animal species. To prevent these kinds of mistakes, biological control researchers have been studying potential negative effects of an introduction since the 1870^{th} and currently several countries demand a dossier with an environmental risk analysis of the species under consideration for release (van Lenteren et al., 2006).

Still, there are heated discussion about the importance of pest specificity, and the positive role polyphagous natural enemies may play in biological control is explained by various authors (e.g. Albajes & Alomar, 1999). However, today most biological control researchers will initially search for pest specific natural enemies for the practical reason that writing the environmental risk analysis will be more simple and it will be easier to obtain a permit for use. But there are exceptions. It seems that polyphagous predators of small size (< 1mm) can occasionally be used for pest control without negative side effects. This is illustrated by the enormous success obtained with the predatory mite *Amblyseius swirskii* in the control of thrips and other pests in Spain. During a period of only three years, chemical control of thrips was almost completely replaced by biological control. In 2006, after a scandal came to light about the extensive use of illegal pesticides and excessive residue levels, and as a result of an enormous effort of the biological control industry, the use of biological control quickly increased to 95% of the 7000 hectares with sweet pepper in Almeria (Spain) and actually saved the greenhouse industry. The positive spin-off from this scandal was a drastic change in attitude about the potentials of biological control and the use of biological control for the control of other pests.

The aspect of predator size related to safe use of polyphagous species needs further study. It is clear that exotic polyphagous mammals, birds, reptiles, amphibians and fish will generally not be proposed for release in new areas because of their environmental risks. But it is less clear when we enter the domain of arthropod species. Recently, it appeared that polyphagous exotic ladybird beetles (*Harmonia axyridis*) of only a few millimetres in size may create serious side effects by strongly reducing the populations of indigenous ladybird species. I feel guilty about not having been more alert when the issue of import and release of this ladybird beetle was considered in Europe, because a critical evaluation of the literature before the species was introduced should have provided enough information to disagree with importation and release of this species (van Lenteren et al., 2008). There may be situations where the aspect of size is less important. It appeared to be safe to use polyphagous tropical vertebrate species in greenhouses on the premise that they cannot survive and reproduce in the field in temperate climates.

The criterion of pest specificity is considered to be important for most forms of biological control.

1.3.6. High pest kill rate.

It is frequently stated in the literature that an efficient parasitoid should have a potential maximum rate of population increase (r_m) equal to or larger than that of its host. In other words, per unit of time and averaged over its life span, an individual parasitoid should be able to parasitize and kill more pest insects than the number of offspring produced by the pest insect in absence of the parasitoid. We cannot simply use the same approach for predators. In parasitoids, only adults kill the host and in doing so, they produce a new parasitoid. For predators, reproduction and killing are not so strictly linked and, in addition, predators usually kill prey during immature stages and as adults. Each of these stages has a different duration and predation efficiency. How to compare the control efficiency among predators and between predators and parasitoids? We needed to develop a

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parameter which takes the earlier mentioned problems into account. To do this, we used ecological theory of life table studies (Southwood, 1980) and we called this parameter the predator's kill rate (k_m) (Tommasini et al., 2004). In a situation where we have found both parasitoids and predators of a pest, they can now be ranked according to quickest reduction capacity of the pest population.

So, can we at this stage make a well-informed choice concerning the best natural enemy out of a set of tested species? We could, but only if the pest occurs locally and does not disperse. Thirty-five years ago I would have felt confident to make a choice for use of natural enemies in small greenhouses (and I will explain later why). However, in larger greenhouses and in the field, pest organisms disperse from the initial sites of infection, or new pest organisms migrate into the field from other locations. In such dynamic systems, knowledge about the host or prey kill rate of a natural enemy is not by itself sufficient for natural enemy efficiency, because the potential kill rate will not be realized at low pest densities and another characteristic – the capability to locate newly established pest populations – becomes relevant.

A high pest kill rate is important for natural enemies used in inoculative and seasonal inoculative releases. It is less important in inundative control, because we can compensate for too low a pest kill rate simply by releasing more natural enemies.

1.3.7. Quick detection of pest populations.

Natural enemies are released in the field or greenhouse by various means: from airplanes, by tractor, with blowers, on cards and in containers. They can be released close to the pest or metres away from it. So a good searching capacity is important and many years ago this raised the question how natural enemies actually detect pest organisms. Our laboratory has been very active in this research area, and earlier this afternoon Louise Vet and Marcel Dicke have illustrated how much knowledge and understanding we have gained over the past few decades. We now know that most insects mainly, but not exclusively, use chemical information to find their pest. They may react to pheromones emitted by the pest, to chemicals added to the substrate when the pest organism lays eggs, to substances produced by the developing immature stages of the pest, and to chemicals released by the plant as a result of attack by the pest, to mention but a few ways. Some of the reactions to chemical cues are innate responses (they 'know' to what to react), but spectacular discoveries showed that natural enemies can learn to associate the presence of a pest with the odour, shape of leaf and colour patterns of certain plants (Dicke, 2009; Vet & Smid 2006). Still, not all natural enemies react to pest-related chemical cues, and we also learned that natural enemies do not always react to chemical cues of the pest. For example, when parasitoids are hungry they only react to cues that will direct them to food (Vet et al., 2003: Waeckers, 2003). All this work resulted in a revolution in research on parasitoid-host and predator-prey relationships. In the period before 1960, usually only the bitrophic relationship parasitoid-host was studied. In the 1970s and 1980s studies on tri-trophic systems started: the host plant was included because of its importance on the parasitoid – host relationship. Since the 1990s we have been studying multitrophic systems, as it appeared that other organisms also influenced the relationship between parasitoid and host: root feeding organisms which have an effect on the development of the plant, its herbivores and parasitoids/predators living in above ground parts of the plant; hyper parasitoids; predators of parasitoids; competing organisms; neighbouring plants hampering host finding etc., etc..

Knowledge on host/prey finding helped us to improve mass-rearing and release techniques. It also assisted in selecting promising species, which I will illustrate with one of the first projects where we tried to find and evaluate new natural enemies.

Intermezzo 4. The best natural enemy showed quick detection of pest populations

In 1976, the Integrated Pest Management (IPM) programme for insect control in tomato crops often had to be interrupted with pesticides for control of dipterous leafminers. Frequent sprays could not be combined with biological control of mites and whiteflies. There was an urgent need to find an efficient natural enemy to save the IPM programme which had taken many years to develop, and to prevent the biocontrol industry from going bankrupt. My colleague Jaap Woets had a stroke of genius: why not put leafminer infested tomato plants in the field for some time, collect them and see if natural enemies have attacked the leafminers. Several species of parasitoids emerged from the leafminers and after a 6 month study we could calculate the pest kill rate and predicted that species A (*Dacnusa sibirica*) was better than B (*Opius pallipes*), because it

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developed faster and killed many more leafminers. We tested our prediction by doing an experiment in greenhouses: greenhouse A with leafminers and parasitoid A, greenhouse B with leafminers and parasitoid B, and greenhouse C with leafminers only. To our surprise, parasitoid B with the lowest pest kill rate was the first to control its assigned pest, followed by the leafminers in greenhouse A (but only partly by parasitoid A, because parasitoid B had been able to enter this greenhouse and killed 80% of the leafminers). Finally, the leafminers greenhouse C too were controlled by parasitoid B. During a follow-up experiment it became clear that parasitoid B reacted strongly to the odours produced by the leafminers and could locate infested leaves when flying, while parasitoid A could not do so. This was the first time we realized that not only is the kill rate important, but so is a quick detection of pest populations. Today, we test for the capability of pest detection in olfactometers, windtunnels, greenhouses and the field.

The criterion of quick detection of pest populations is important for natural enemies used in all types of biological control.

1.3.8. Density dependent reaction to pest population fluctuations.

I expected that the methodology for this criterion would be the most fascinating, but also the most demanding to develop. As a student, I studied various theories about population regulation, and density dependent regulation was one of the main explanations in obtaining stable populations: with an increasing pest population, the natural enemy should kill disproportionally more pest organisms in order to bring the pest back to low densities and vice versa. In inoculative and seasonal inoculative biological control, one aims first to achieve a low pest population density by introducing a natural enemy and then to keep it low over a long period. When I discussed population regulation theories and the working mechanism of biological control with Paul DeBach and other Californian experts in 1976, they were surprised I doubted whether density dependence was the backbone of biocontrol. They had experienced many cases where, after the introduction of a natural enemy, the pest population went down and permanently remained low. I will present one example: in 2000, a gall wasp (*Dryocosmus kuriphilus*) accidentally entered Italy on imported chestnut (*Castanea* spp.) from China. Not only did this gall wasp spread very quickly all over Italy, it can now also be found in France, Slovenia and Switzerland, and is expected to invade all European chestnut areas in the coming years. The wasp attacks the buds of chestnut, prevents buds from forming nuts, and chestnut production goes down by 80-90 percent. Chemical control of this gall wasp is impossible and the only solution seems inoculative biocontrol. Luckily, our Japanese colleagues had already found the solution: the same gall wasp was accidentally imported into Japan from China around 1940. Japanese researchers went to China, collected natural enemies and imported a parasitoid (later called *Torymus sinensis*) into Japan and released it. Within a few years, the pest was brought under biological control and the parasitoid is still doing its useful work year after year (Moriya et al., 2003). Within the Plant Health Panel of the European Food Safety Authority, we are currently discussing whether we will propose to follow the same strategy for Europe, but we will also propose to execute an environmental risk analysis for the exotic parasitoid (see below). Back in the 1970s, my old Californian colleagues would have said: release the parasitoid immediately to obtain long-term control based on density dependent regulation.

Theoretically, for a natural enemy to be able to react in a density dependent way, it should meet certain conditions. One of these is that an individual parasitoid should show an disproportional increase in the number of hosts attacked with increasing host density. In other words, it should switch from attacking a few hosts at very low host densities to attacking many more hosts when host density increases. For vertebrate predators like mice and birds, such a response was indeed found, and could be explained by the development of a search image for a certain prey when its numbers increased: they learn to hunt for a certain prey. For parasitoids, development of a search image had not yet been found. In a series of experiments, we were able to show that parasitoids do not develop a search image, but are able to regulate their host in a different density dependent way. When they arrive at a patch with hosts, they will search only for a certain amount of time. When they do not find a host within this time, they will leave the patch and search for a new one. However, when they find one host, they increase the search time on that patch, and as an effect of the increased search time, they may find another host, again increase the search time, etc.. This results in a strong disproportional increase of the attack rate over a relatively small range of host densities, and thus in the possibility to bring the pest density back to low numbers. We also found out why this phenomenon was not discovered earlier. Most researchers put parasitoids in a box with hosts and counted the number of hosts attacked after a certain amount of time.

We followed what we called the 'Leiden approach' developed by Tinbergen and observed the behaviour of the parasitoid continuously. We discovered that parasitoids attempt to leave a patch with very low host densities but return often and may find more hosts. Such situations lead to an overestimation of parasitism at low densities. We then decided to finish an observation when the parasitoid left the patch, and we found the density dependent effect (van Lenteren & Bakker, 1976, 1978).

After discovering the possibility of density dependent regulation, we were euphoric and thought that the combination of information on the pest kill rate, the capacity to detect a pest population and density dependent reactions to pest density fluctuations would ultimately lead to a method for natural enemy selection. But we were too optimistic: it seemed very difficult to make reliable predictions about density dependence and field efficacy of a natural enemy based solely on laboratory experiments. Experiments in greenhouses and the field were needed to obtain information about density dependence. But how to follow a parasitoid of 1 or 2 millimetres in its search for a victim in a greenhouse of 10,000 square meters or a field of several hectares? We tried another approach, we started computer modelling. We decided not to use simple analytical models as extensive work by others who used such models had yielded interesting but not always relevant information about host searching and density dependence; this work actually delayed identification of critical characteristics of efficient natural enemies (e.g. Hassell, 1986). Instead, we used individual based modelling and started to study the dynamics of whitefly (*Trialeurodes vaporariorum*), the tomato plants on which they live and a natural enemy of whitefly (*Encarsia formosa*) (van Lenteren & van Roermund, 1999). Models were made for plant growth, and for whitefly and natural enemy population dynamics and dispersal under realistic greenhouse microclimate conditions. This was an enormous task to which many MSc and PhD students, plus colleagues from several WU departments and other universities contributed. Model validation and verification showed that in greenhouses, successful biological control of whitefly by parasitoids is not obtained by creation of a stable pest-enemy equilibrium at low densities and not based on parasitoid characteristics identified with analytical modelling. In this tritrophic system, high levels of pest control are reached by randomly searching parasitoids which show one important feature: they will search longer on a site where they have discovered a whitefly nymph. The whiteflies and parasitoids seem to play hide-and-seek. Parasitoids discover a patch with whiteflies and start to attack them, but some whiteflies have already flown away in order to build up a new population, which is later discovered by parasitoids etc.. It was rather disappointing not to discover density dependent regulation in this system, but the importance of a higher probability to find large pest populations and attack more pest insects in such a population than in a small population was illustrated. However, the model helped us in many ways: in optimizing the greenhouse climate for obtaining the best biocontrol results, in determining the effect of crop species and cultivars on biological control, in fine-tuning natural enemy release schemes and numbers of natural enemies to be released, etc..

The initially proposed criterion of density dependent regulation seems no longer practical to maintain, as it takes long-term research under difficult conditions before it can be demonstrated to exist for a certain natural enemy – pest relationship. Therefore, we modified it into density responsiveness: a natural enemy should preferably be able to find and attack large pest populations better than small ones. This criterion is important for all types of biological control, with the exception of inundative biocontrol where natural enemies are released in high numbers and evenly over the field for immediate, one generation control.

1.3.9. No negative effects after release.

Use of this criterion seems obvious and applies to all types of biological control. Natural enemies should, for example, not attack and eradicate other beneficial organisms (intraguild predation) or non-pest organisms in the area where they are released. But study of indirect effects on the ecosystem as a result of direct effects on nontarget organisms can be very complicated. Although biocontrol workers have always considered direct negative effects, indirect effects have only recently been seriously taken into account.

Earlier today, Jacques Brodeur discussed the potential adverse effects of intraguild predation on biological control. I will confine myself to concluding that we have to reformulate our initial idea that intraguild predation would generally be

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detrimental to biological control. After two decades of interesting ecological research, it seems that intraguild predation does not have a negative effect on biological control (Brodeur & Boivin, 2006).

During the past ten years, methods for environmental risk analysis have been developed and are now applied by about 30 countries, which use some form of regulation concerning release of exotic natural enemies. Other countries have no regulations at all, so any species can be imported and released, although this practice is certainly not in line with the UN Convention on Biological Diversity. Within European Commission (EC) funded and OECD/IOBC supported projects, a group of mainly European researchers have studied the risk of the release of various natural enemy species and came up with designs and methods for risk analyses (Bigler et al., 2006). Eventually, this work resulted in a relatively simple, tiered evaluation system (van Lenteren et al., 2006). It would have been easier to come up with many different evaluation schemes for all types of biological control, but we thought it essential to try to compose only one evaluation scheme.

At the first step in the evaluation, a distinction is made between exotic and native natural enemies. For native natural enemies only one more step (step 6: direct and indirect effects) in the procedure needs to be followed. For exotic natural enemies, we move to step 2, in which natural enemies that are used in inundative and seasonal inoculative control (in the scheme addressed as augmentative biological control = ABC), are separated from natural enemies destined for inoculative biological control (in the scheme addressed as classical biological = CBC), where establishment is the aim. For ABC, it then needs to be demonstrated that natural enemies cannot establish themselves (step 3), and only one more step of the procedure (step 6) needs to be followed. However, if there is a possibility of them establishing themselves, they should not be released. The applicant who applies for permission to use the natural enemy can provide data from studies on the host range (step 4) to enable a reconsideration of the decision not to release the species. For CBC we move from step 2 to step 4.

At step 4, the host range issue is addressed. If the ABC or CBC agent is very host/prey specific it can be considered for release. On the other hand, if the agent attacks many nontarget species, the agent should not be considered for release. However, data can be provided from studies on dispersal (step 5) and direct/indirect nontarget effects (step 6) to allow reconsideration of the decision not to release the species. At step 5, questions about dispersal of ABC and CBC agents are addressed. If dispersal is local and mainly in the area of release and numbers that disperse out of the target area are very low, the assessment should move to step 6. But if dispersal outside the target area is extensive, the agent should not be released. At step 6, issues related to direct and indirect nontarget effects are considered. If direct and indirect effects not expected, or are transient and limited, the agent can be released. If, on the contrary, direct and indirect effects are expected which will be permanent, the agent should not be released. For each step in the procedure, specific environmental risk indices can be calculated which will show if risk thresholds are crossed and release of the natural enemy should not be considered (Bigler et al., 2006).

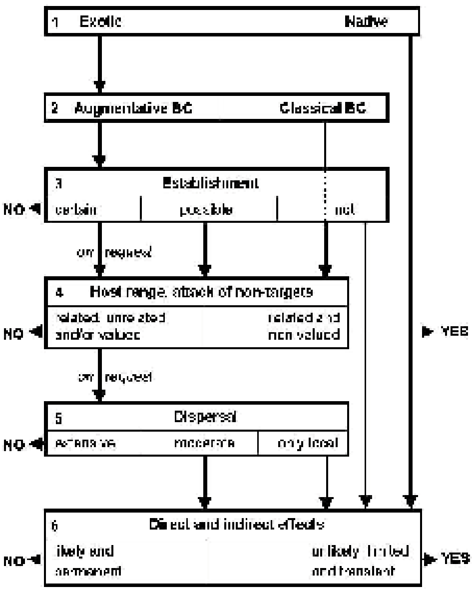

Figure 1. Environmental risk assessment scheme for arthropod biological control agents. NO: release is not recommended, YES: release is recommended.

We have applied this risk assessment scheme to all 150 species of natural enemies that are currently commercially available in North-West Europe and concluded that about 5% of these species (all of them exotic) should be considered too risky for release in this region. The scheme identifies potentially risky species at an early stage of the evaluation process, which is very important for commercial producers as well as for non-commercial groups searching for new biocontrol agents in preventing unnecessary further studies.

Most of the evaluation criteria in the scheme – establishment, host range, dispersal and environmental effects – are based on pure ecological studies and, perhaps not surprisingly, come from the emerging field of invasion biology.

1.3.10. Easy mass production.

Once a biologically effective natural enemy has been found, it can only be marketed if mass-rearing is economically viable. Good rearing methods for natural enemies are the basis for successful inundative and seasonal inoculative biological control programmes. Rearing methods largely determine the ultimate costs of the natural enemy and therewith the efficiency of application. During the past 50 years many mass production methods have been developed, as well as ways to package, store, ship and release natural enemies. An essential aspect during this period was the design and application of quality control methods. Initially, it was not easy to convince commercial producers to collaborate on development of quality control methods, but EC and IOBC funded projects carried out during the 1990^{th} yielded many important results, including a growing respect for this sector. Many elements of quality control are based on knowledge in the fields of physiology, genetics, evolution and ecology (van Lenteren, 2003). Although I am not mentioning many details about mass production and quality control, developing these methods represents a very productive period in my professional life and it was satisfying to see that – as a side effect of the work on quality control – the biocontrol companies started to work together on other issues as well.

Easy and cheap mass production is an essential criterion for seasonal and inundative releases, but not for inoculative releases where only a limited number of natural enemies is released.

1.4. Value of evaluation criteria and importance of pure ecological knowledge

Criteria for evaluation of natural enemies

Criterion	Type of Release Programme Inoculative	 Seasonal Inoculative	 Inundative
1. Seasonal synchronisation with pest	+	-	-
2. Developmental synchronisation with host	+	+	-
3. Climatic adaptation	+	+	+
4. Pest specific	+	+	+
5. High pest kill rate	+	+	-
6. Quick pest location	+	+	+
7. Density responsiveness	+	+	-
8. No negative effects	+	+	+
9. Easy mass production	-	+	+

+ = important ; - = not important

Having described the list of currently used criteria, is it easier to choose a new natural enemy than it was 40 years ago? We quickly realized after starting to work with the criteria, and after making some mistakes in rankings of the best natural enemies, it would be difficult to identify the 'very best' natural enemy, and we have been criticized for this. However, we realized an unexpected and much more important benefit of this evaluation method than just finding the best agent: with the criteria, we can easily identify useless or risky natural enemies. Useless, for example, because their kill rate would be too low. Risky because they attack many nontarget species and might cause problems when released. With the current criteria we are now able to 'throw away' the majority of natural enemy species (> 90%) found for a certain pest in an early stage of the evaluation process and, thereby, save money and time which can be spent on further study of the more promising species. By no means has the work on the criteria been in vain, and we are frequently contacted for advice on how best to apply them.

The question of importance of ecological knowledge for understanding biological control and the efficiency of selecting natural enemies can be answered with yes, but .... Yes, basic ecological knowledge was crucial for developing methods to test most criteria, to design quality control and environmental risk analysis, and

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multitrophic studies helped us to understand the functioning of natural enemies in complicated systems. But ... we still do not fully understand how biological control actually works; we still lack good methods to test searching efficiency and density responsiveness, and we are still unable to predict what the effect of behavioural changes is on the population dynamics of a species (Vet & Godfray, 2007). With the advancement of ecological science, these problems will be solved. An issue of more concern is that ecologists have frequently proposed to study elements of the biology of natural enemies or to use simulation and modelling techniques which later turned out to be utterly irrelevant. Such advice may well have been caused by the inexperience or arrogance of the ecologists concerned, but it certainly has led to obstacles with regard to the progress of biological control. I challenge ecologists to really help researchers in biological control by immersing themselves in this field of applied ecology and only come up with advice after having thoroughly discussed the usefulness of it. Both parties will benefit from this collaboration.

2. Biological control: the current state of play

Biological control is the most environmentally safe and economically profitable pest management method. To illustrate this, I compiled a table comparing chemical and biological control in the early 1980th after I gave a talk during an important meeting of the chemical industry where I realized they knew very little about the efficacy and economics of biological control. Here is the current state of affairs:

	Chemical* control	Biological control
Number of ingredients tested	> 1 million	3,500
Success ratio	1 : 200,000	1 : 10
Developmental costs	400 million $	2 million $
Developmental time	10 years	10 years
Benefit / cost ratio	2 : 1	20 : 1
Risks of resistance	large	small
Specificity	very small	very large
Harmful side-effects	many	nil/few

* = data from chemical industry

In biological control, we still have hundreds of thousands of species of natural enemies waiting to be discovered, and finding a new biocontrol agent is characterized by a very high success ratio compared to the chemical control ratio. The developmental costs for biocontrol are a fraction of those for chemical control. The time to develop a product is the same for both control methods. The benefit cost ratio for inoculative biological control is much higher than for chemical control; for commercial biological control it is similar, but higher if we take indirect costs for chemical control into account which are related to environmental pollution and human health problems. The risks of resistance are low or non-existent in biological control, while they are high in chemical control. High specificity and the lack of harmful side effects are characteristic for biological control agents, whereas the use of chemical pesticides kills many species of nontarget organisms within and outside the agro-ecosystem, and may result in various side-effects, including unexpected, indirect and long-term effects on the health of farmers and consumers.

All countries worldwide benefit from biological control. Natural control occurs on 89.5 billion ha of the world's ecosystems (land with vegetation), of which 44.4 billion ha is used for some form of agricultural activity (including forestry and grassland). Biological control contributes to managing indigenous and alien pest problems in natural and managed ecosystems, and also in controlling vectors of human and veterinary diseases. It has been practised over the last 120 years during which at least 165 pest and weed species have been brought under permanent control. During this period, more than 7,000 introductions of biological control agents involving almost 2,700 species have been made. Thirty percent of all releases have resulted in establishment and 10% achieved control of the target pest. In addition 170 species are produced and sold globally for periodical release to control more than 100 pest species with an annual monetary value of 280 million US$. The most widely used natural enemies in inoculative control (e.g. *Rodolia*, see above under inoculative biological control) have been introduced in more than 50 countries/regions worldwide and resulted in permanent control of the pest (Cock et al., 2009; 2010). Inoculative biocontrol is used on 350 million ha (10% of land under cultivation) and inundative + seasonal inoculative control on 16 million ha (0.4% of cultivated land with crops on which this type of control could be used). The 'ecosystem service' provided by natural biological control has an estimated value of at least 400 billion US$ per year (Costanzo et al.,

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1997), which is enormous, even when compared with the annual amount of money spent on all types of pesticides (30 billion US$). The impact of biocontrol is creating and sustaining public goods, such as food security, food quality, reduced pesticide use, human health (especially for farmers and farm workers), invasive alien species control, protection of biodiversity and maintenance of ecosystem services.

3. With so many benefits, will biological control soon be used on a much larger scale?

With already very large areas under natural and inoculative biological control, this question mainly applies to commercial – inundative and seasonal inoculative – biological control. There are various explanations for the currently limited use of commercial biocontrol.

3.1. Reasons for the limited use of commercial biological control

3.1.1. Attitude of the pesticide industry.

First of all, the pesticide industry is not interested in biocontrol, because natural enemies cannot be patented, cannot be stored for long periods, act very specifically, can often not be combined with chemical control and need extra training of sales personnel and farmers. The pesticide industry is not particularly concerned either with sustainable, long-term solutions for pest control as patent periods on pesticides are limited. Their concern is to develop and market new insecticides. This will be a continuous threat to biological control, although work of IOBC has resulted in an EC demand of testing side-effects on natural enemies for new pesticides, so we know at least where biocontrol agents will be killed when using certain pesticides. The attitude of the chemical industry has somewhat improved and some companies are even producing natural enemies. However, the main reason is not that the chemical industry is convinced biological control is an important solution, but with chemical control we can no longer control all pests so they actually need biological control. Another problem is that pesticides are too cheap: society ends up paying for the so-called indirect costs created by pesticide use such as death of nontarget organisms, human health problems, environmental pollution and interference with ecosystem functions (Costanzo et al., 1997). Taking these costs into account, pesticides should be two or three times more expensive, Realistic pricing of pesticides would more often lead to a choice for biocontrol.

3.1.2. Attitude of governmental institutions.

Next, there is seldom a national or international policy to stimulate or enforce the use of sustainable solutions for pest control. Farmers are incorrectly informed that registered pesticides are safe for the environment and for man, so there is no incentive for them to change. The industry, understandably, is not interested in complicated pest control systems with low profit margins. Therefore, it seems that only governments can effect change by enforcing use of non-chemical pest control (but see my remark below about the role of supermarkets). European governments were provided as early as 1992 with excellent background information in the form of the report Ground for Choices issued by the Netherlands Scientific Council for Government Policy and coordinated by our WU colleague Rudy Rabbinge (Netherlands Scientific Council for Government Policy, 1992). This report showed that with good farming practices an overall reduction in pesticide volume used of more than 90% could be reached. In this same period, IOBC had developed and tested IPM programmes for a number of crops in which use of pesticides was even lower. Although governments often react positively when asked how they think about biological and integrated control, such reactions can almost exclusively been put into the category 'paying lip service' because financial, long-term support for research and implementation is not provided. To be fair, there was a period in the Netherlands (1990 – 2000) when all publicly funded research had to be oriented towards biological and integrated control. The result was that the use of pesticides decreased by 50% and a new crop protection plan 'Integrated Management, the way ahead' was written for the period 2000-2010 where farmers were enforced to use non-chemical control as a first line of defence. However, lobbying resulted in a covenant, and the scheme collapsed. (I am tempted to congratulate the pesticide industry and conventional farming organizations for their high quality lobbying, something the biological control community has yet to learn). Personally, I am sad to see that the Ministries of Agriculture and Environment, which were internationally seen as very progressive and creative, are no longer an inspiration for new agricultural approaches in Europe. There is an overwhelming amount of information showing that agriculture is a major source of pollution and that pesticides have serious negative effects on biodiversity and biological control. In a recent publication, our WU colleague Frank Berendse and co-authors (Geiger et al., 2010) conclude: '... that despite decades of European policy to ban harmful pesticides, the negative effects of pesticides on wild plant and animal species persist, at the same time reducing the opportunities for biological pest control. If biodiversity is to be restored in Europe and opportunities are to be created for crop production utilizing biodiversity-based ecosystem services such as biological pest control, there must be a Europe-wide shift towards farming with minimal use of pesticides over large areas.' How much more needs to be done before policy makers and politicians use and implement this kind of information? Our rector, Martin Kropff, said during his speech at the 92th anniversary of our university that: .. 'scientists must stick to the real scientific evidence.... Conclusions must be made by policy makers. As scientists we have to learn how to effectively inform society and policy makers without becoming issue advocates.' I largely agree with this statement, but we are not only scientists, we are also citizens and should try to inform and influence representatives in local, national and international governments, as long as we make clear we do this as individuals and not as representatives of our university.

3.1.3. Influence of guidelines and regulations.

Another factor frustrating application of biological control is the increasing amount of guidelines and regulations. Some of these regulations like the 'Guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms' (IPPC, 2005), the guidelines for Environmental Risk Assessment (see above) and national regulations for import and release of biological control agents may delay implementation of biological control. Most of these guidelines could and should be drastically simplified and harmonized, which will result in application of more biological control. But the future of biological control might be really threatened by the plans concerning benefit sharing under the Convention of Biological Diversity (CBD). Under this convention countries have sovereign rights over their biodiversity. Agreements governing the access to these resources and the sharing of the benefits arising from their use need to be established between involved parties (i.e. Access and Benefit Sharing (ABS)). This also applies to species collected for potential use in biological control. Recent applications of CBD principles have already made it difficult or impossible to collect and export natural enemies for biological control research in several countries. The CBD is required to agree a comprehensive Access and Benefit Sharing process in 2010. In preparation for this, an IOBC Commission has prepared a position paper

(Cock et al., 2010) in which we describe the practice of biological control in relation to the principles of ABS, illustrated extensively by case studies and successes obtained with biological control. Next, we emphasize that in most biological control projects, no monetary benefits are generated for those involved in research. Subsequently, we inform the biological control community of good ABS practice and challenges, and we hope to make clear to the community involved in ABS under the CBD, the special situation with regard to biological control. Finally, we make recommendations which would facilitate the practice of collection and exchange of biological control agents, propose a workable framework to assist policy makers and biological control practitioners, and urge biological control leaders in each country to get involved in the discussions with their national ABS contact point to take their needs into consideration. In October 2010, when the final regulations will be negotiated, we will find out if our work has had any positive results.

3.1.4. Attitude of biological control community.

What about the biocontrol research community itself? As I already mentioned, we are not particularly good at lobbying, we do not blow our own trumpet, we have not learned to defend our work aggressively, we often forget to illustrate the fantastic and permanent results obtained with inoculative biological control, thereby limiting discussions to the as yet restricted application of commercial biological control. We are our own worst natural enemy!

Intermezzo 5. How not to evaluate biological control

It is sad and disappointing that so many entomologists and biological control researchers have the peculiar habit of destroying their own work. An example of this attitude was recently published by Collier and Van Steenwyk ('A critical evaluation of augmentative biological control', Biological Control, 2004). Due to several serious mistakes in the article, I wrote a rebuttal which was published in the same journal (van Lenteren, 2006). First of all, the title was wrong, because the article does not present an evaluation of augmentative biological control. Instead, the authors evaluated some research articles on augmentative biological control from the USA. Secondly, the title is also wrong in that the article is not a critical evaluation of augmentative biological control in general, but is mainly limited to experimental situations in the USA. There are, however, plenty examples of successful practical augmentative programs both within and outside the USA (see e.g. Gurr and Wratten, 2000). Moreover, because the authors

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try to answer their questions with unsuitable data, their answers are in clear disagreement with the current state of affairs in the field of commercial biological control. Inundative and seasonal inoculative biological control is in many – though not all – cases (1) as effective or more effective than chemical pesticide applications, (2) able to achieve target densities often even lower than chemical pesticides can, and (3) has costs lower than or similar to chemical pesticides. In a number of crops, biological control has either completely or largely replaced broad-spectrum pesticides (van Lenteren, 2000).

Biological control researchers have no problem with being on the receiving end of constructive criticism. It is, however, extremely frustrating and unjustified when a paper like this can be published without apparently being seriously reviewed, corrected, and the title changed into a proper indication about the contents of the paper. An unforeseen aspect of a paper like this is that policymakers, politicians and the pesticide industry may use this information to show how poorly commercial biological control performs.

3.1.5. Factors stimulating the use of biological control.

Today, there are a number of positive developments which will stimulate the use of biological control and I would like to illustrate a few.

First of all, the EC is putting non-chemical forms of pest control high on the research and implementation agenda. Again, due to EC policy, it is anticipated that 750 of 1000 active ingredients used in chemical control will be phased out in the coming years. Furthermore, a substitution principle will be applied to new pesticides, by which the economically sound and environmentally safest agents will get priority for registration. Ongoing development of resistance to pesticides, increasing demands concerning the environmental and health effects of pesticides will make their development more difficult and costly. We can already see a stabilization and decrease of pesticide use in the developed world. At the same time we see an increase of biological control agents on the market. We can even see dramatic shifts from complete chemical control to mainly biological control (in greenhouse vegetable production in North-West Europe, Spain and China, to name but a few) as a result of the impossibility to control pests with chemicals. After 60 years of chemical control, we are entering the ecology-based pest management era.

Next, there is an even more interesting development. European food retailers and supermarket chains are increasingly demanding pesticide poor or pesticide free food and prescribe pest management protocols to farmers. Supermarket chains, farmers and crop protection specialists collaborate in GLOBALGAP, a private sector body that sets standards for the certification of agricultural products around the globe. One of the GLOBALGAP guidelines concerns integrated pest management, and biological control together with other types of non-chemical control form an essential part of this guideline (www.globalgap.com).

It has also been shown that consumers themselves prefer biological control above other methods. In Canada, a professionally designed survey was conducted – a worldwide premiere – to determine the perception to the use of biocontrol as a means of pest management. The respondents clearly believed that foods produced using biocontrol were safer than those using synthetic insecticides. The majority of respondents felt that there would be less risk associated with consuming food when biological control agents, rather than synthetic chemical means, were used to control pests (Jean-Louis Swartz, personal communication, 2009; publication of the survey is expected in BioControl in 2010).

I was also happy to discover recently that biological control is recognized as an important ecosystem service by a national institute (The Netherlands Environmental Assessment Agency (PBL)) working on a strategic policy analysis in the field of environment, nature and spatial planning. Their report 'What nature offers man: ecosystem services in The Netherlands' (March 2010) presents biological control as one of the examples and discusses how policy measures can encourage the use of this ecosystem service.

As a result of these developments and in combination with the realization that ecosystem services can play such an important role, I predict that in 2030 pest management will be based for one third on biological control, for another third on host plant resistance, and the last third will be comprised of other means of intelligent management: crop rotation, pheromones, kairomones, mechanical, genetic and physical control etc., and less than 5% conventional chemical control.

4. And now for something completely different ....there are more important sustainability issues than pest management alone!

4.1. It's human numbers that count, not food.

Agriculture evolved 10,000 years ago. This may sound like a long time, but it comprises only 400 human generations. Through agriculture, the human population could grow from about 6 million to 800 million in 1800. The subsequent industrial revolution and developments in science, resulted in an enormous increase in the human population to the current level of 9 billion in just 10 generations (Goudsbloem, 2008). During the past 50 years we have experienced many negative effects of this population explosion. To my surprise, I seldom hear the WU research community (and to be fair: the research community worldwide) speak about ways to manage this population explosion. Our rector, during the same anniversary speech I earlier mentioned, said that because of the ever increasing human population: '... we need to produce more healthy and safe food in a sustainable way. A major set of scientific challenges is to develop systems that produce more food, with less land, water, energy, nutrients (especially phosphorus) and chemicals.' On many occasions, WU has shown to possess the expertise to estimate the amount of food which can be produced worldwide and to assist in realizing increased food production. But isn't it time to address the real question of how to stabilize and reduce the human population? If we do not start thinking about this issue, we ourselves might become victims of biological control. I mean this quite literally and without any cynicism. We should no longer avoid trying to answer two essential questions: how can we stabilize and reduce the human population, and how can we reduce human consumption of food, water, energy and material goods? An increasing human population, combined with the projected dramatic increase of consumption per capita will definitely lead to a higher rate of pollution, climate change and extermination of species. My only positive feeling about this black scenario is that insects will undoubtedly outlive mankind.

4.2. Finding new toys.

I am convinced that most – if not all – problems created by mankind are the result of egotism and greed, and this relates to the second question I mentioned above: how to reduce human consumption, particularly in developed countries. Egotism was an essential survival characteristic for man when food and other resources were limited; a situation which was normal for most human beings since their evolution a few million years ago. Let us not forget it is a mere 150 years ago that humans died at an average age of 35 years and the daily struggle for food was their first priority. Now that the limitation of food and other resources no longer exists in the developed world, egotism and greed are resulting in the significant negative effects mentioned above. Why are humans behaving in a irrational, unethical and selfish way while pretending they are rationally acting organisms and much better than other animals (see quote from Coetzee next to title page of this farewell address)? Mankind being so materialistically obsessed leads to forms of cheating in order to make more money. It may start with adding water to milk (the Netherlands) or wine (France), or indeed stating that olive oil originates 100% from a certain nation (Italy). It becomes more serious when one denies that illegal pesticides are used on a large scale (e.g. the Netherlands, Spain), or when representatives of the chemical industry try to downplay the importance of biological control by presenting incorrect information (which happens often) and by subtly but fundamentally changing the topic of discussion (e.g. the interview of Kouwen in Bionieuws with the industry, 27 June 2009). Very serious forms of cheating are those where poisonous materials are added to wine (Austria) or olive oil (Spain) resulting in illness and death. Not only individuals but also governments give economic priority over human health as exemplified by three recent cases from the Netherlands. One concerns the neglect of serious human Q-fever illness as a result of goat farming, the other relates to the effect of fungicides and resistance to medicines in humans, and the third involves resistance of human diseases to antibiotics due to the legal and illegal use of these antibiotics during mass production of poultry and cattle.

These are just a few examples illustrating how far we are prepared to go in order to make a quick buck. Why are we unable to obtain solutions for this dilemma and why can't we find ways to guide egotism in such a way that it does not lead to the problems just summarized? My reading of books on human behaviour, sociology and psychology have not yet resulted in more than a note in the margin: find an alternative for the behaviour which leads to over consumption.

Mr. rector, ladies and gentlemen,

It was a great honour being asked in 1983 to succeed Prof. Jan de Wilde who handed over a top quality research group. It was satisfying to see how the group further developed and how it now flourishes under the leadership of one of my best MSc and PhD students, Marcel Dicke. In this respect I feel very grateful. I will continue my policy work in the International Organization for Biological Control and the European Food Safety Authority, and I also hope to carry on with several interesting research projects in Wageningen, Perugia (Italy) and Lavras (Brazil).

Ecology is a cool science: always intriguing and often helping to solve problems!

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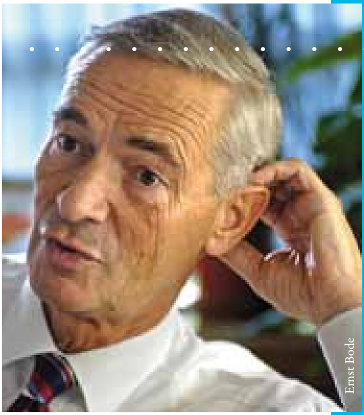

Ecologists believed they had excellent solutions in helping biological control evolve from art to science during the past 50 years. Regularly, these solutions failed to have a positive impact on biological control and in a number of cases even hampered progress. Are pure scientists arrogant, naïve or both? Are they unable or even unwilling to involve themselves in applied science? Are biological control practitioners equally naïve and and why is commercial biological control not used on a much larger scale?

Photo front page:
Hans Smid (parasitoid *Cotesia glomerata* attacking larva of *Pieris*)

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