

BIOLOGICAL CONTROL OF INSECTS: ALWAYS SAFE? RISKS OF INTRODUCTION AND RELEASE OF EXOTIC NATURAL ENEMIES

Joop C. van Lenteren & Antoon J.M. Loomans

Laboratory of Entomology, Wageningen University
P.O.Box 8031, 6700 EH Wageningen, The Netherlands

Keywords: accidental introductions, risks of introductions, exotic pest insects, exotic natural enemies, safety of biological control

Summary

Biological control of insects - the use of natural enemies to reduce pest numbers - is applied on a worldwide scale for more than 100 years and its use has considerably increased during the past decades as it offers a sustainable, economical and environmentally attractive alternative for chemical pest control. In biological control, locally occurring natural enemies are used or alien species are imported. Until now, introductions of hundreds of species of insect natural enemies have not led to environmental problems when a procedure of selection, importation and release was carefully applied. In contrast with these beneficial introductions, many intended and unintended introductions of plants and phytophagous animals have resulted in very negative effects on the environment.

Some problems have occurred with importation and release of other categories of natural enemies like amphibians, reptiles and fish which can be classified as large generalist predators. Further, the use of arthropods for weed biological control has resulted in a few problematic cases, but also here the vast majority of introductions has resulted in safe forms of biological control. Current policies on pest control in many countries support or stimulate biological control, and the number of natural enemy imports increased during the past three decades. At the same time development of regulation of biological control takes place, making import and release of exotic beneficial organisms very difficult. It is of great priority to find a balance between reasonable regulation of importation and release of new candidates for biological control and the possibility to develop sustainable, environmentally safe pest control.

To prevent making mistakes in the future, pre-introductory evaluation of natural enemies is advocated, including a step where the potential negative effects are studied. Examination of the literature, taxonomic research and host acceptance experiments are used in such studies to estimate such negative effects. A European case study on potential negative effects of natural enemies on non-target organisms is described, to illustrate recent developments in the field of study of risks of biological control, and a positive list of safe biological control agents is proposed.

INTRODUCTION

Exotic organisms enter new areas actively or passively. This process has always taken place, but man-related introductions have dramatically increased during the past 10.000 years. Three periods of introductions with exotics can be distinguished (Loomans, 2000):

- **Period before 1500.** Since the development of agriculture, insects have been imported frequently with movement of man, plant material and cattle, mainly with transport over land.
- **Period 1500-1970.** Transport over land continued, but migration of large groups of people, their cattle and crops by boat to other continents strongly developed. Cattle and crops, together with their insect fauna were imported into new areas. The result

was, among others, that the insect pest fauna of North and South America, South Africa, Australia and New Zealand originated for a large part in Europe.

- **Period 1970-now.** With the enormous increase of air transport both for business and tourism, insect species are frequently taken to new areas. This soaring number of imports of exotics leads to a redistribution of species worldwide. Changes in cropping procedures, worldwide developments in protected cultivation, continuous movement of plant material over the world, cropping of an increasing number of exotic vegetables and ornamentals year round, creates survival possibilities for tropical and subtropical pest organisms in temperate climates.

Establishment of exotics in new areas can result in important impacts on the ecosystem, and large changes in species composition may occur. In the USA, 8% of the established exotic species have resulted in local eradication of native species (Simberloff, 1992).

Releases during the past 100 years of arthropod biological control agents for control of arthropod pests in new areas have not resulted in negative non-target effects (Hokkanen & Lynch, 1995). Concern about potential risks (effects on non-targets including rare species and beneficial organisms, and a reduction of biodiversity) is increasing because worldwide commercial biological control activities are expanding worldwide (Howarth, 1991; Hokkanen & Lynch, 1995; Simberloff & Stiling, 1996; Haynes & Lockwood, 1997). Use of biological control has considerably increased during the past decades as it offers a sustainable, economical and environmentally attractive alternative for chemical pest control. Before long, the introduction of natural enemies has largely been an empirical activity and has depended on the knowledge and insight of the biological control practitioner. Recently, a more scientific approach of evaluation of natural enemies before introduction is advocated and applied with the aims (1) to obtain insight in what constitutes an efficient natural enemy, (2) to reduce research costs and (3) to limit risks of introductions (van Lenteren, 1995, 1997).

Biological control practitioners are currently confronted with criticism from environmentalists. The latter are fearful that the released natural enemies may attack (1) beneficial non-target organisms like pollinators or other natural enemies, (2) rare/endangered insects like butterflies, (3) other non-target organisms, and this can result in changes in agro- or natural ecosystems. Unbalanced criticism from environmentalists results in a bizarre conflict situation: on the one hand biological control offers a very powerful option to reduce the many potentially negative environmental and human health effects of chemical pest control, on the other hand - though not found until now - the natural enemies may influence ecosystems in unwanted ways. The International Institute of Biological Control (IIBC) has made a comprehensive analysis of all insect biological control projects, which indicated no negative effects (Greathead, 1995). To date, however, very few studies evaluating the effect of biological control introductions on the native fauna have been made, with the exception of some Australian, New Zealand and Californian projects (for examples, see Aeschlimann, 1995). In order to continue improving the reliability of our biological control profession, several in-depth ecosystem studies need to be performed before and after releasing new species of natural enemies. Several European groups studying biological control, therefore, have recently started a large scale study to evaluate the potential effects of mass releases of different types of natural enemies on the local fauna and aim to develop a protocol for risk analysis concerning importation and release of biocontrol agents (see below).

HOW MANY EXOTICS ENTER NEW AREAS?

Introductions of insects into new areas are documented poorly, except for economically important organisms like pest species and natural enemies. Information on introductions relates mainly to agro-ecosystems and few or no data are available for insect introductions in other ecosystems. This could either mean that natural ecosystems are not invaded frequently, or that the effect of invaders is not dramatic, or that these other ecosystems are

considered economically so unimportant that they receive no attention. The latter explanation seems more realistic. Introductions of exotic organisms, together with disruption or destruction of habitats, are nowadays mentioned as the most important threats of biodiversity (Foin et al., 1998; Wilcove et al., 1998).

Thousands of insects of some hundred different species invade the Netherlands every year. Natural invasions occur by insects which cross borders by active flight or are carried in by wind. Man-caused invasions of insects are also numerous. The important role Holland has as producer of agricultural products is related to intensive import and export of plant material. Daily about 18 million cut flowers and 2 million plants are marketed at the Aalsmeer Flower Auction, where about 45% of the Dutch flower and plant trade takes place (situation December 1999). About 25% of the cut flowers and 4% of the plants come from abroad, including countries like Israel, Kenya, Zimbabwe, Ecuador, Colombia, Zambia etc., so every day more than 4.5 millions of flowers and plants enter the Netherlands. Circa 80 % of the cut flowers and plants are exported the same day. In addition to the import and export via the Aalsmeer Flower Auction, a number of growers import plant material from various countries to start up new cultures in the Netherlands. It is impossible to inspect all these plants for illegally entering insects, and thus there is a constant risk to import exotic insects. Annually, some 20-30,000 horticultural products are inspected when entering The Netherlands and about 150 shipments are infested with new, exotic arthropod pest species. As a result, most of the invaders causing economic damage have entered Holland unintentionally on plant material.

Some invaders are purposefully introduced, like natural enemies for biological control of pests. Part of these imports concern populations to start a mass rearing in the Netherlands and these species may originate from all over the world. This material is usually thoroughly tested for purity to exclude hyperparasitoids or other unwanted organisms. Other natural enemy imports are made for direct release of material that was mass produced in various European countries (mainly UK, Belgium, France and Italy). The species of natural enemies may have come from various locations (Asia or America). This material is usually well checked before export. Finally, vast numbers of field collected natural enemies may be imported like *Hippodamia convergens* from California, USA. In this case the control for impurities and presence of unwanted other organisms (parasitoids, microbes, entomopathogenic nematodes) is minimal, and risks are higher than with other forms of intentional import of natural enemies.

The Plant Protection Service and the Dutch Entomological Society keep track of cases of invasion and establishment, but this information is often biased and anecdotal. In their publications most attention is paid to either damaging species or a few peculiar species. For international studies on numbers of insect invasions we refer to e.g. DeBach (1974), Elton (1954), Pimentel (1986), and Yano et al. (1997). Case studies of introductions are summarized in van Lenteren (1992, 1995).

HOW MANY INTRODUCED EXOTIC SPECIES DO ESTABLISH?

Despite import inspections and phytosanitary checks at holdings, many insects enter Europe and establishment cannot always be prevented. For The Netherlands this means that on average one new pest species establishes every year, which compares favourably with Hawaii, where the average number of new pest species has been 20 per year during the past decade. In Japan about 4 insect species establish per year, in Australia about 0.6 per year (Kiritani, 1997). Eradication of newly introduced pests is almost always impossible, very expensive and results in negative environmental and health effects. A large number of invading species remains unnoticed because of their small size or lack of strong effects (negatively or positively) on ecosystems.

Di Castri (1989), in an article on the history of unintentional introductions of plants and animals in the old world, estimated that 5 out of 100 introduced species did

establish and 3 out of 100 became widely established and resulted in problems. Williamson (1996) concludes that about 10% of the imported exotics is capable to establish and that 1% of the invaders develops to pest status.

The percentage establishment is much higher when species are purposefully introduced. From the literature on biological control of insects it is known that 25 - 34 % of the introduced arthropod species were able to establish and that 9% were successful in reducing the target pest (e.g. Hall & Ehler, 1979; van Lenteren, 1995). In weed control the success of establishment of natural enemies is much higher: 65% (Crawley, 1986) of the species established after release and 32% reduced the target weeds successfully. The higher success of establishment of weed natural enemies is largely the result of a much tougher pre-introduction evaluation of control agents.

WHICH PART OF THE INSECT FAUNA IS EXOTIC?

About 750,000 species of insects had been described worldwide around 1980 (Arnett, 1985). Recent estimates of the number of insect species in existence range from 2.5 to 50 million, and are likely around 10 million (Gaston & Hudson, 1994). The number of species known as insect colonizers does not exceed a few thousand, however, so the data on which we build our generalizations about invasions are very limited indeed.

Sailer (1983) made a compilation of historical insect introductions into the USA and gives 1683 successful introductions, 66% from western Palearctic origin, and 10% of the species each originates from the northern Neotropical and Oriental region. If we make a further selection of these data we come to the following results for insect pests: forty percent of the insect species that are pests in USA agriculture were accidentally introduced (57 from 148); many (25 of 57) came from Europe (Pimentel, 1986). Sailer (1983) believes that the pattern of human activities is largely responsible for this phenomenon, because (1) most commerce and travel was and still is with Europe, (2) many of the crops in Europe are the same as those in the USA, (3) similar climatic areas can be found on both continents, and (4) the seasons are synchronized, which does not hold for e.g. South America and Africa. Even for recent years this reasoning seems to hold: 40 of the 68 new insect and mite pests introduced to the USA between 1970 and 1982 are of European origin (Sailer, 1983). About 13 new insect species establish in the USA yearly (Sailer, 1978). It is not surprising, therefore, that most of the really successful invaders are the ones that are able to cross major barriers because of their relationship with *Homo sapiens* (Ehrlich, 1986).

In continental USA, some 2500 established exotic insects had established about 10 years ago (Danks, 1988). On a total number of 100,000 insect species, colonists made up 2.5% (Table 1). There are, however, large differences among the states. The percentage exotics is much higher than average in Hawaii (33.5%) and Florida (7.9%) (Frank & McCoy, 1995). In New Zealand the percentage exotic insects is also very high: 13% of insects of the about 20,000 species are invaders; of these 97.5% was introduced accidentally, while 2.5% was introduced on purpose for biological control (W.M. Lonsdale, pers. comm., Emberson, 1998). In the Netherlands colonizers make up 0.6 % of the total number of insect species (120 colonizers out of 20,000 species; van Lenteren et al., 1987 and additions). This is much lower than in the USA and New Zealand, and it should be realized that half of the exotic species in the Netherlands are only able to survive in greenhouses. For the UK the percentage exotics is 0.82% (169 out of 20,553 spp; Williamson & Brown, 1986).

Table 1. Contribution of exotic insects to the local insect fauna

Country / state	Total number of insects	Number of exotic insects	Percentage exotic insects
The Netherlands	20,000	85	0.5
United Kingdom	20,553	169	0.8
United States	100,000	2,500	2.5
Florida			7.9
Hawaii			33.5
New Zealand	20,000	260	13.0

When the number of successful invaders is compared with the number of species per insect order occurring in the USA, it appears that some orders contain more successful colonizers than others: proportionally too many of certain phytophages (Homoptera and Thysanoptera), Coleoptera and Hymenoptera and too few Diptera and Lepidoptera (Simberloff, 1986) are found on the list. A large fraction of the systematic distribution of successful colonists can be attributed to timing of commerce, plant introduction and biological control, and to differential intensity of study for different orders. The fact that beetle introductions predominated before 1900 is the result of their capability to cross the ocean in ship ballast and stored grain. The overrepresentation of Homoptera in the middle of the 19th century is a consequence of both the faster oceanic crossing by steamships and the explosion of nursery stock imported into the USA from Europe. The burst of Hymenoptera introductions starting around 1920 reflects increasing biological control efforts (Sailer, 1978, 1983). Such information helps us to explain part of the invasion history, they do not provide, however, the material we need to formulate hypotheses leading to predictions about characteristics of successful invaders. To illustrate this point: of the 212 accidentally introduced insects that have become major pests in the USA, 65% were not known as pest insect in their native areas and would therefore initially be classified as harmless (Calkins, 1983).

WHAT ARE THE CHARACTERISTICS OF ALIEN INVADERS?

Quite a number of attempts have been made to list characteristics of successful invaders. We will present here only one list (Table 2) which originates from Ehrlich (1986, 1989) and relates to characteristics for animal invaders. For plants similar lists have been made (see e.g. Bazzaz, 1986). Such lists are based on case studies of invasions.

Characteristics such as mentioned in table 2 seem logical, but there are so many exceptions that it is not justified to use these lists as reliable indicators of a species' potential to invade. Further, additions can be made to the list for specific groups of invaders. For herbivore insects, for example, it has been found that polyphagous, external feeders (chewers and suckers) are much more successful colonizers of new plants than monophagous/oligophagous internal feeders (leaf-miners and gall-formers) (Strong et al., 1984). Crawley (1986) and Pimm (1989) support the importance of several of the factors listed by Ehrlich (Table 2). They particularly stress a high reproductive rate as important for successful invaders. Levin (1989) emphasizes good dispersal capabilities as elementary for colonization success.

One category of insect invaders deserves special attention: insect predators. Maynard Smith (1989), in discussing the causes of extinction, distinguishes a category of man-caused extinctions, with a subcategory of introduction of foreign species.

Table 2. Characteristics of animal invaders (after Ehrlich, 1986, 1989)

Successful invaders	Unsuccessful invaders
Large native range	Small native range
Abundant in original range	Rare in original range
Vagile	Sedentary
Polyphagous	Mono- or oligophagous
Short generation times	Long generation times
Much genetic variability	Little genetic variability
Gregarious	Solitary
Fertilized female able to colonize alone	Fertilized female not able to colonize alone
Larger than most relatives	Smaller than most relatives
Associated with <i>H. sapiens</i>	Not associated with <i>H. sapiens</i>
Able to function in a wide range of physical conditions	Able to function only in a narrow range of physical conditions

He concludes that of this subcategory the functional group of predators - especially if they are of an ecologically unfamiliar type - have a stronger effect on the biota (i.e. have a higher chance to eliminate species) than competitors. His conclusion is in line with that of Simberloff (1981), who provided data to show that it is mainly predators causing extinction. Competitive exclusion does occur, but this requires very close similarity in resource utilization (Maynard Smith, 1989), and the chance that a species will succeed decreases significantly with the morphological similarity between the invader and the nearest congeneric species already present (Pimm, 1989). Pimm (1989) predicts that, as a result of competition, the surviving species will be morphologically more dissimilar than one would expect by chance. He also states that the effect of an invader on the ecosystem is greater if the invader arrives at a place without having natural enemies, than at a place where natural enemies are present. This statement is abundantly supported by the biological control literature.

Examples on invasions (e.g. Crawley, 1986) emphasize how far we still are from being able to properly predict the success of anticipated invasions. But we have already indicated above that for some groups of invaders, like organisms introduced for biological control, establishment rates are much higher than for others. This higher establishment rate is the result of two developments: (1) the formulation of criteria to evaluate the effectiveness of natural enemies before they are introduced and (2) an estimation of potential negative effects of natural enemies on the local fauna. In other words: to predict the probability of establishment and the reduction effect on its target organisms, and to prevent unwanted side effects. Use of such criteria during the past century is the main reason that virtually no problems were created with introductions.

The evaluation criteria for natural enemies developed by van Lenteren (1986b, Table 3) was based on ideas earlier expressed in the biological control literature and on ecological properties which were supposed to characterize predators and parasitoids with a strong reduction effect. A procedure for selection of natural enemies with these pre-introductory evaluation criteria is given in van Lenteren (1986a). Such lists have also been made to evaluate herbivorous insects for biological control of weeds (e.g Harris, 1973). For biological control of insects these criteria have already proven their usefulness, both for evaluating natural enemies for use in the field and in protected crops (e.g. van Lenteren & Woets 1988).

Table 3. Criteria for pre-introductory evaluation of natural enemies (after van Lenteren, 1986b)

Seasonal synchronization with host
Internal synchronization with host
Climatic adaptation
No negative effects
Host specific
Great reproductive potential
Good density responsiveness

Ehrlich's list and ours show little similarity. This is mainly the result of trying to prevent negative effects with the introduction of natural enemies. Particularly polyphagy is not appreciated in biological control, which is in line with Pimm's (1989) notion that the potential negative effect of an invader is greater when it is polyphagous. Additionally, matching of the natural enemy with the climate and with its specific host increase the establishment rate.

IS INTRODUCTION AND RELEASE OF EXOTIC BIOLOGICAL CONTROL AGENTS RISKY?

Each organism that is introduced into a new region, be it for augmentative releases or for permanent biological control, may become established. Therefore, extreme care should be exerted during the evaluation phase. In inoculative biological control a low number (often < 10.000) of natural enemies is released, and these natural enemies have usually been extensively screened for potential negative effects on non-targets, as the aim of the release is long-term establishment. In seasonal inoculative and inundative control, however, massive numbers of natural enemies (100.000 – 300.000 per hectare) are released (van Lenteren, 2000). Most of these natural enemies cannot survive under Dutch environmental conditions and will die when winter sets in. During the summer period, these natural enemies may, however, be able to parasitize or feed on native host species and can influence herbivore and their native natural enemy populations.

Each year, some tens of billions of native and exotic natural enemies are mass reared and released in Europe (Ravensberg, 1998). Worldwide, for example, 2.5 - 3 billion individuals of *Encarsia formosa* parasitoids, 1 billion of *Eretmocerus eremicus* parasitoids and 1 billion *Macrolophus caliginosus* predators are released per year for control of whitefly (Loomans, 2000). Based on a recent review of use of *Trichogramma* species world wide, about 1,500 billion individuals of these parasitoids are produced and released (van Lenteren, 2000). Commercial releases in Europe are made with about equal numbers of exotic and native species of natural, but most of the species are exotic for The Netherlands as they originate from the Mediterranean or other (sub)tropic areas enemies (Table 4, for exotic or native status of natural species, see van Lenteren, 1997).

Risks of seasonal inoculative and inundative releases for agro-ecosystems have not yet been observed, although recently researchers have warned for intraguild predation (natural enemies attacking other natural enemies) which might result in lower efficiency of biocontrol agents (e.g. Rosenheim et al., 1995). The effects of inoculative, seasonal inoculative and inundative releases for natural ecosystems surrounding agro-ecosystems has hardly been studied indeed. What kind of effects of exotic natural enemies on non-target organisms can we expect? This question is not easy to answer, because rather unexpected events may occur after release, and the devil is often in the detail.

Table 4. Commercial biological control of native or exotic arthropods with native or exotic natural enemies in Europe, their respective combinations and examples (update of van Lenteren, 1997)

Use of native natural enemies for the control of native pests: example: <i>Chrysoperla carnea</i> for control of native aphid species	61
Use of native natural enemies for the control of exotic pests: example: <i>Diglyphus isaea</i> for control of exotic <i>Lyriomyza</i> species	40
Use of exotic natural enemies for the control of native pests: example: <i>Harmonia axyridis</i> for control of native aphid species	44
Use of exotic natural enemies for the control of exotic pests: example: <i>Encarsia formosa</i> for control of exotic whitefly species	47

An example: in the 1950s the myxomatosis virus was introduced in the UK to reduce the rabbit population (Crawley, 1983). After the death of the rabbits, the turf increased in height and there was a spectacular increase of the abundance of flowers, among others of orchids. But in the absence of rabbit grazing, turf was losing its density, and several plant species decreased in quantity. An increase in woody plants occurred. Brambles and gorse bushes developed. Longer-term effects of the virus were a reduction in plant-species richness, increased dominance by a small number of rank grasses and hastened succession towards woodland. Non-target effects on the fauna were also observed (certainly, many effects were not perceived): as a result of changes in ground cover, numbers of *Myrmica* ant species decreased, and this on its turn led to a strong reduction and local disappearance of myrmecophilous species of *Maculinea* butterflies.

Inoculative releases such as the one with the myxomatosis virus have received a lot of attention concerning potential negative effects as they cannot be eradicated after establishment (Howarth, 1991; Haynes & Lockwood, 1997). Seasonal inoculative and inundative releases with mono/oligophagous parasitoids that cannot survive in the area of release are expected to have few and only temporary effects on the native fauna. But massive releases with polyphagous predators could present a more serious temporary risk for the native fauna. Large scale collection of millions of the convergent ladybeetle *Hippodamia convergens* at overwintering sites in California, transport and release in the field in The Netherlands for control of aphids on trees in several Dutch towns (Loomans, 2000) is an unethical and useless affair, and might even result in negative advertisement for biological control as these ladybird beetles may contain parasitoids, entomopathogenic nematodes or microorganisms that can infect native natural enemy species.

Several early biological control introductions, mostly of polyphagous, large predators (e.g. vertebrates, birds and toads) and usually not supervised by biological control experts, have led to unintended inimical effects on species in pristine habitats. For example, importation of the mongoose (*Herpestes* sp.) from India to Trinidad to control rats in sugarcane resulted in control of the rats, but after decimating the rats it turned to other organisms. This large polyphagous predatory mammal preys on soil dwelling vertebrates and contributed to the decline of native birds, and the extinction of endemic snakes and lizards on several Caribbean islands. The introduction of other large generalist predators like the giant toad (*Bufo marinus*) and predatory snails caused unfortunate side effects (Greathead, 1995) and liberation of such organisms have never been recommended by responsible biological control practitioners.

Biological control agents do not necessarily stay in the habitat where they are released. By dispersal to other habitats they may cause direct or indirect effects.

As *direct effects* of introductions and releases, extinction or reduction in numbers of native non-target species may occur. Several ecologists have stated that, because insects have more restricted diets than vertebrates and that particular categories of insects like parasitoids are extremely specific in host use, cases of introduced insects endangering

native fauna would be rare compared to those involving vertebrate introductions (e.g. Harris, 1990). Polyphagous insect predators may, however, attack non-target organisms and be harmful. Howarth (1991) presents some circumstantial evidence that natural enemy introductions may have led to reduction of nontarget species, but others (e.g. Funasaki et al., 1988) believe these charges to be unjustified. It is not an easy task to show that, in an ecosystem with a rare plant eating insect species which is attacked by many different natural enemy species, introduction of a new natural enemy further reduces the density of the herbivore, or merely replaces some other mortality factor. Extinction of pest or non-target organisms as a result of biological control is, however, extremely unlikely. Pests have never been exterminated in the more than 100 years of insect biological control. Rather, a low population level of both pest and natural enemy developed. The search behaviour of natural enemy and the ways herbivores can defend themselves to natural enemies prevent extinction.

As *indirect effects* (1) of preying or parasitizing of the introduced organism on native natural enemies, a reduction in numbers of these species may result, (2) of competition for host or prey with local organisms, non-target native natural enemies may be negatively affected and (3) the habitat may be modified. It has been suggested that in some cases releases of polyphagous predators and parasitoids has not only led to a decimation of pest caterpillars, but also to a reduction of non-target caterpillars resulting in a decline in native predaceous wasps and native bird populations (Simberloff, 1992). Myriad indirect effects are possible. Species can interact through shared prey or hosts, shared predators, parasitoids or pathogens. Natural historic information on species involved in such indirect effects can be used (or collected) for prediction of such indirect effects.

The recent literature on introductions of natural enemies for insect control has not featured the role of biological control in extinction. This is an important conclusion as thousands of intended introductions have been made worldwide, and apparently the biological control scientists have correctly identified which natural enemies can be safely exported.

HOW TO PREVENT MISTAKES WITH INTRODUCING EXOTIC NATURAL ENEMIES?

In general, attempts to make predictions of the potential invasive success of a given species have taken the form of lists of attributes - genetic, physiological and ecological - that are most often associated with successful invaders (see Table 2). Many of the ideas come from a qualitative natural history type of observations or are based on retrospection. Very little experimentation has been utilized in the study of biological invasions (Mooney & Drake, 1986, 1989). Most ecologists who published about invasions remain very sceptical about the possibility to make correct predictions on establishment and negative effects on the local fauna and flora.

Ecologists can predict with near certainty that a pest insect introduced from elsewhere will become a pest in the country of introduction, if the crop it feeds on in the country of origin is also widely grown in the country of introduction (Pimentel et al., 1989). But making predictions is much more difficult if related to non-pest species. For example, of the 212 introduced insects that have become major pests in the USA, 65% were not pests in their native ecosystems. The very serious problems created by the cottony cushion scale, the cassava mealybug and the Colorado potato beetle - to name a few - were not expected at all on basis of the knowledge of their biology in their respective native areas. Predictions based on the role these organisms played in their country of origin would have been utterly inaccurate.

Cases of good intent in purposeful introductions that ultimately have bad consequences stem from a narrow view of the potential good that can come from the introduction. Frequently the desired feature of the organism is considered in isolation

from the total impact that the organism will have on the target system as well as on those who depend on that system for a variety of purposes. The potential effects of release must be considered in a total system context (Mooney & Drake 1989). Often short-term economical considerations predominate over long-term ecological reflections. However, "Modern, carefully planned introduction for biological control have been relatively safe" (Regal, 1986). Also Levin (1989) states that if introductions were based on proper ecological studies, they usually have not created problems. But where ecological information has been lacking or faulty, deliberate introductions of other than insect natural enemies have led to major and sometimes catastrophic ecological occurrences.

Attributes likely to increase the probability of establishment are known, but we are not in a position to make accurate predictions about individual cases. One of the elements in making accurate predictions so difficult is the interaction between chance and timing of an invasion. Rare chance events that occur at just the right time may well be the cause of major, long-term structural and dynamic changes in ecological communities, of which examples can be found in Crawley (1989).

ENVIRONMENTAL RISK ASSESSMENT PROCEDURES

Risk assessment procedures for insect biocontrol agents have been used for a long time. For natural enemies used in control of weeds, detailed screening programmes have been developed (Greathead, 1995). Until recently, control agents for mites and insects were not as rigorously tested as weed control agents, as long as it was known that they did not attack economically important insects, other beneficial insects, were safe for man and were host/prey specific. Very recently, however, several organizations explicitly started to develop and use risk assessment procedures before introductions with exotic natural enemies are made.

The Food and Agriculture Organization of the UN has prepared a code of conduct for the import and release of Biological Control Agents, which aims to facilitate the safe import and release of natural enemies (FAO, 1996). The code provides a basis for the adoption of national regulations or legislation that would ensure the safe import and release of biological control agents, avoid irresponsible action, and promote the responsible use of biological pest control. This code was taken as a basis to develop guidelines for import and release of biological control agents for EPPO (European and Mediterranean Plant Protection Organization) countries, which will be published in 2000.

In the USA, the Plant Protection and Quarantine division of the Animal and Plant Health Inspection Service of the United States Department of Agriculture, demands an Environmental Assessment before a permit of introduction is released. More than 30 of these Environmental Assessments were designed from 1993-1996. For details of the procedures we refer to Royer (1995). When the release of an exotic biological control agent is expected not to result in negative effects, a Finding of No Significant Impact (FONSI) is issued based on an extensive review of the literature of the pest, pest control methods and the natural enemies, and after consultation of experts. The FONSI is supported by (a) findings about the limited host range of the organism to be introduced, (b) information on no negative effect on other natural enemies, (c) data about no negative effect on endangered or threatened species, and (d) evidence of no significant negative environmental impact.

The International Institute for Biological Control (CABI/IIBC) follows a somewhat different procedure. For new imports and releases of exotic organisms, this institute voluntarily prepares a dossier according to the FAO code of conduct. Such a dossier contains information of the pest and natural enemies, and an assessment of potential risks (a) to non-target phytophages, (b) to human and animal health, (c) to those handling the natural enemies, (d) of contaminants, and procedures for eliminating contaminants (for an example of such a dossier, see Cross & Noyes, 1995).

In present day biological control, governments which regulate the introduction of biological control agents, like Australia and New Zealand usually require that candidate agents undergo host range testing to ensure that they will not become pests or threaten desirable species. This results in a general preference for highly specific natural enemies. Today, many countries are applying rules concerning import and release of natural enemies that vary from a simple to very complicated systems (van Lenteren, 1997). Therefore, a working group of the OECD is now developing a simple, harmonized registration system for natural enemies worldwide.

Risk assessments for biological control agents usually contain the following elements:

- review of pest organism, host plants, economic importance, and benefits and disadvantages of different pest control methods,
- determination of taxonomic status of natural enemies (traditional morphological methods and molecular techniques),
- information about biology of natural enemies, and
- safety screening. Screen/evaluate a natural enemy (biotype) that it does not significantly interfere with other beneficials, endangered or other non-target organisms (expert judgement, host selection studies), has no negative effect on human and animal health, and has no significant negative environmental impact.

The main aspect of risk assessments will be to show host specificity of the natural enemy and that it cannot attack organisms in the area of release other than the pest species. Screening can never include all species at risk because that would mean testing of hundreds of non-target species. Also, the precise behaviour in the new habitat of an introduced species cannot be predicted fully from pre-introduction studies and, thus, an absolute guarantee of safety can never be provided. The degree of specificity required in a control agent should depend on circumstances. For example, an exotic natural enemy introduced for control of a greenhouse pest, which cannot survive outside the greenhouse does not have to meet as many safety criteria as an agent which does survive in the new environment.

Host and prey specificity testing will have to be performed in laboratory and field. Laboratory experiments will consist of acceptance and preference tests using a variety of potential hosts or prey which are known to occur in the ecosystems where the parasitoids or predators are released or where they may disperse after release. Host range testing for parasitoids (Hymenoptera and Diptera) can be limited as the intimate physiological relationship with their hosts prevent them from developing in unrelated host species. With general predators prey range testing is very important and procedures like those used in weed biological control can be applied.

Often, taxonomic knowledge can be used to estimate potential negative effects of new natural enemies, if they can be reliably placed in a taxonomic group of species for which biological information, among which host/prey ranges, is available.

Based on all this information, the potential benefits and risks of the introduction of a biological control agent can be judged, and an informed decision can be made about a go or no go for biological control (Greathead, 1995). In this final phase, the pros and cons of all different control methods should be evaluated, when making a choice for one specific approach.

Although the introduction of generalist natural enemies is generally not advocated because of the negative effects resulting from some introductions with generalist vertebrate predators (see above), particular species of generalists can be acceptable as biological control agents. If the predators are of very small size (smaller than 1 mm), if they cannot overwinter in the area of release and if they have to function in habitats where they mainly encounter phytophagous pest organisms like in greenhouses, their use may not result in negative effects.

Recently, at a meeting of the International Organization for Biological Control of Noxious Animals and Plants (IOBC) on Evaluating indirect ecological effects of biological control (Anonymous, 1999), a very interesting proposal was formulated by

W.M. Lonsdale (pers.comm.) concerning risk evaluations of natural enemies. Lonsdale proposed to avoid long-term and complex risk assessment studies by selecting only the most important pests or weeds for targets in biological control, and by using only monophagous natural enemies. In such a situation there will still be risk (costs), but the benefits will always be greater.

NATURAL ENEMIES KEEP THE WORLD GREEN

When discussing the potential negative effects of releases of exotic natural enemies in great detail, one might get the idea that biological control is a risky affair. In an overwhelming number of cases, however, there are only positive effects of biological control. Ecologists have long recognized the role which predators, parasitoids and pathogens play in regulating populations of plant feeding organisms (herbivores, in agro-ecosystems often pest insects), thereby "keeping the world green" (e.g. Crawley, 1992). In nature, it is the rule rather than the exception to find extremely low densities of both herbivores and their natural enemies, and these natural enemies are a substantial component of biodiversity. One single group, the parasitic wasps or parasitoids, which attack plant-feeding insects, comprise about 10% of all the species on earth (Godfray, 1994).

In agricultural production systems, biodiversity is dramatically reduced from thousands of species to only a few: the particular crop, some weeds, several pests, and a number of natural enemies. Natural enemies can prevent crop-feeding organisms and weeds from becoming abundant and devastating pests. The importance of natural enemies to agricultural production is, however, often overlooked. In fact, without their contribution, many innocuous organisms would become serious crop pests. World wide only some 2.000 important insect pest species are known, while insects of hundred-and-thousands of species do incidentally feed on our crops, but are kept at low numbers by natural enemies (van Lenteren, 1993). This becomes strikingly apparent when insecticide application accidentally eliminates key natural enemies, and new or worse pest outbreaks result. Resurgence and occurrence of secondary pests as a result of pesticide applications is now well documented. The result is that more insecticides are applied and a "pesticide tread mill" can develop. This, in turn, can lead to serious environmental pollution, human intoxication and a decline in production.

Pesticide created pests, which first emerged in the 1950's in orchards and greenhouses, have strongly encouraged the development of biological control and integrated pest management in Europe (van Lenteren et al., 1992). In these IPM programmes, risks for the environment are minimized, and value of the crop is maximized. Besides a number of national European governments and developing countries, also the United Nations Conference on Environment and Development (UNCED) in its Agenda 21, recognized IPM, in which biological control forms a cornerstone, as the preferred strategy to achieve sustainable agricultural production.

Agro-ecosystems such as orchards and forests, may have a rich fauna and flora of indigenous, local natural enemies which can protect production of food and timber. The conservation and use of these natural enemies, as for example in orchards, reduces the dependence on chemical pesticides and limits the negative effects of these biocides on the biodiversity of farmland and adjacent terrestrial and aquatic habitats (e.g. Blommers, 1994). Other agricultural production systems have a strongly reduced natural enemy complex as a result of four decades of frequent chemical treatments. When these pesticide treatments are terminated it may take a while before natural enemies reinvade, build up and perform their beneficial functions. Therefore, men sometimes assists in re-introduction of the native natural enemies. In other cases, exotic natural enemies are introduced, usually for the control of accidentally introduced exotic pests. Both activities fall under the pest control method which is called biological control (Mackauer et al., 1990).

Schizophrenically, in a period where biological control is valued high by the agriculturalists and part of the ecologists, others are voicing their concern that import or release of exotic natural enemies may have negative effects on nature and biodiversity. Therefore, as a key component of the world's biodiversity, and a key determinant of sustainable agriculture, the role of natural enemies deserves to be better understood (Lewis et al., 1997). Large-scale, long-term system ecological studies would be needed to obtain such understanding. At this moment it is of crucial priority to show relatively quick and unambiguously clear that biological control is a safe and preferred pest control method if biological control agents are carefully selected. This will lead to increased acceptance and implementation of biological control methods. It is also in line with Article 8 h of the Convention on Biological Diversity which recognizes the risk posed by alien species and requests contracting parties to: "Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species".

In recent decades, a sound ecological underpinning has been established for biological control through research into population dynamics of predators, prey and pathogens, and particularly through the development of general and specific models for parasitoid - host systems (e.g. Mackauer et al. 1990; Hawkins & Cornell, 1999). Also, our understanding of ecosystem functioning and the role of biodiversity therein has strongly increased.

A EUROPEAN CASE STUDY ON RISKS OF INTRODUCTION AND RELEASE OF EXOTIC NATURAL ENEMIES

For the control of about 50 mite and insect pests, about 130 species of natural enemies have been introduced and released in Europe (van Lenteren, 1997). Until 1970, mainly inoculative releases of biological control agents were made to control native or exotic pests by exotic natural enemies. Some 30 pest species were the target of releases of about 90 species of biological control agents. After 1970 many activities took place in greenhouses, orchards and some field crops. Commercial biological control programs for approximately 50 pest species were developed by importing more than 40 exotic species of natural enemies into Europe, and by using more than 60 native species of natural enemies (for details, see van Lenteren, 1997, 2000). In a few cases, generalist exotic predators and facultative hyperparasitoids were introduced and released. With increasing commercial biological control activities, we proposed the EU to fund a project to (1) evaluate the potential negative effect of release of exotic biological control agents, and (2) develop a protocol for risk evaluation. This four-year research project on "Evaluating Environmental Risks of Biological Control Introductions into Europe" (ERBIC), was started in 1998 and aims to develop sound methodological principles for evaluating the ecological risks from biological control introductions (Lynch et al., 2000).

To achieve the aims, and to obtain information for a proper evaluation of the consequences of inoculative or inundative releases with exotic natural enemies, four specific case studies were selected, each of which focuses on a different system and is performed by different research groups: (1) exotic host-specific parasitoids (*Encarsia*) of whiteflies (The Netherlands), (2) exotic generalist parasitoids of butterfly eggs (*Trichogramma*) (Switzerland), (3) exotic and indigenous generalist predators of aphids (coccinellids) and thrips (*Orius*) (Italy) and (4) exotic generalist microorganisms (fungi and nematodes) (Finland). Based on these studies, an ecological framework will be established for designing risk analyses for the effects of introduced biological control agents on non-target species, and to predict potential outcomes of such introductions. Population modeling (England) plays a central role in this approach. The role of natural enemies in the field is being studied with a life-table approach of potential host species; this will indicate the changing influence of the released organisms. Elements of ecosystems are analyzed in the laboratory. The range of pests and non-target organisms, which may be attacked by the natural enemies, is determined, and the effect of

competition on endemic natural enemies evaluated. This involves behavioural and population dynamical work. In the field and laboratory studies, molecular biological and genetic techniques are used to follow dispersal and population changes.

A CASE STUDY ON EXOTIC SPECIALIST PARASITIDS OF WHITEFLIES

Biological control of whitefly pests has become a key component of sustainable horticulture worldwide. Every year billions of exotic beneficial organisms are produced and released seasonally or inundatively to control the tobacco whitefly, *Bemisia tabaci* and the greenhouse whitefly *Trialeurodes vaporariorum*. These exotic, primary whitefly parasitoids interact and compete with native parasitoids that may spontaneously enter the greenhouse. On the other hand, exotic parasitoids may leave the greenhouse, attack local whiteflies in the field and compete with native parasitoid species. All *Encarsia* species are solitary endoparasitoids, exhibiting a variety of reproductive, hyperparasitic male, strategies, life history characteristics, dispersal abilities and overwintering strategies, but little is known on their ecology and host range in natural ecosystems.

Our research group has studied exotic whitefly-parasitoid systems for more than 25 years and has contributed substantially in the development of reliable and sustainable biological control method of whitefly pests (van Lenteren & Woets, 1988; van Lenteren & Martin, 1999). This system is particularly appropriate for modeling the effects of different kinds of natural enemies on competition between parasitoids, and the effects on native and alien host (whitefly) species in different climatic regions. It also allows us to test the hypothesis that exotic parasitoids originating from tropical areas cannot survive under temperate field conditions, and form, therefore, only a temporary potential risk for ecosystems they may invade. Some of the introduced parasitoids have hyperparasitic habits, which allows the exploration of how hyperparasitoids building up on primary parasitoids affect the original relationships.

The impact of these mass-releases of exotic parasitoids on the native insect fauna is currently evaluated in field studies in the Netherlands. Evaluation of ecological effects of exotic *Encarsia* species is based on: (1) surveying the whitefly and parasitoid populations in Europe, (2) reliable identification tools based on traditional and molecular methods, (3) life-table studies to analyze impacts and risks, (4) host selection and host specificity studies to determine the range of target and non-target hosts, (5) interspecific competition studies in different climatic zones (Mediterranean and temperate) and food webs, with particular emphasis on heteronomous hyperparasitoids, (6) dispersal studies to assess the capacity to migrate from the target crop and to invade natural habitats in relation to time, distance, population density and climate, (7) studies of physical requirements of exotic introduced beneficials (i.e. overwintering abilities)

Thus far, 15 species of whiteflies are known from the Netherlands, about 63 in the West Palaearctic region. Two native parasitoid species of whiteflies have been found thus far in The Netherlands (*Encarsia tricolor*, *Euderomphale chelidonii*), while over 30 species are known from Europe. Host specificity studies in the laboratory and field indicate that also non-targets (*Aleyrodes lonicerae*, *Aleyrodes proletella*) are attacked by introduced exotic (*E. formosa*) as well as native parasitoids (*E. tricolor*, *E. chelidonii*). In dispersal studies, exotics (*E. formosa*; *Eretmocerus* sp.) have been found on native hosts during summer and fall up to a distance of more than 500 meters from the release source. Overwintering studies with *E. formosa* and native species (*E. tricolor*) have been set up using both native and exotic host species, parasitized in the laboratory and exposed to natural conditions during the winter period to see if and how many of these exotics are able to survive and establish.

A "POSITIVE LIST" FOR BENEFICIAL INSECTS

As there will be an increasing demand for proper risk assessments tools for exotic natural enemies, a collection of dossiers and environmental assessments which are available for consultation at biological control organizations (e.g. CABI/IIBC, IOBC, USDA), would prevent duplication of time consuming research and data collection. Provision of a "Positive List" of biological control agents that are already safely used in certain eco-regions, may help to implement the same natural enemies in similar eco-regions. The Environmental Risk Assessments and Dossiers mentioned in a preceding section, and information about natural enemies used for many years in classical biological control programs and in commercial augmentative releases, provide an excellent basis for such a "Positive List". We suggested to prepare such a positive list and provided an overview of natural enemies that were commercially used in 1996 (van Lenteren, 1997). The idea has been taken up by EPPO, which is currently preparing a positive list for natural enemies that are used in Europe (EPPO, unpublished document 99/7348). On this provisional list, 91 species of biological control agents occur (Table 5). At first glance we may conclude that most of these natural enemies are specialists (56 out of 91), that half of the species are parasitoids of the order Hymenoptera, and that the generalists are usually small species (Nematodes, Acarina, Neuroptera, Heteroptera, Diptera and part of the Coleoptera) where risks for non-targets are limited.

Table 5. Summary of organisms on draft positive list (EPPO, unpublished document 99/7348).

Taxonomic group	Number of species
Coleoptera	14
Diptera	4
Hemiptera, Heteroptera	8
Hymenoptera	46
Neuroptera	1
Thysanoptera	1
Acarina	12
Nematoda	5
Total number of species	91

CONCLUSIONS

Many pest organisms escaped interception by the quarantine and inspection systems worldwide, and have resulted in serious food losses, economic damage and environmental problems. The number of accidental pest imports is unacceptably high. Chemical control of these unwanted introductions, on its turn, created additional environmental and health problems. Chemical control of newly invaded pest species also interfered very negatively with fine-tuned biological and integrated control programmes, which in a number of cases had to be stopped.

Biological control has been practised for more than 25 centuries, and "modern" forms of biological control, where exotic natural enemies are imported and released, for more than a century. This activity has resulted in long-term, economic and environmentally benign solutions to severe pest, disease and weed problems. In contrast with chemical control, biological control of insects and mites did not cause any significant negative environmental or health effects until now.

When biological control projects are carried out properly by experienced practitioners, risks will be very limited but can never be completely excluded. Other pest

control methods involve, however, either the same, but more often many more risks. Natural and biological control increases biodiversity, offers sustainable pest control and should, thus, always form the first line of defense employed in pest control.

The current popularity of biological control might increase the risks, as an increasing number of projects will be executed by people that are not trained in this field of pest control. Guidelines like those of FAO and EPPO, and risk assessment procedures may help in keeping the risks related to biological control very limited, also in new situations and regions where biological control is going to be applied. The various national guidelines or registration systems currently differ too much and can even be hampering implementation of safe forms of biological control. A light form of harmonized regulations now in development by an OECD working group might solve this problem.

ACKNOWLEDGEMENTS

This study has been carried out with financial support from the Commission of the European Communities, Agriculture and Fisheries (FAIR) specific RTD program CT 3489 (ERBIC: Evaluating Environmental Risks of Biological Control Introductions into Europe). It does not necessarily reflect its views and in no way anticipates the commission's future policy in this area.

REFERENCES

- AESCHLIMANN, J.P., 1995. Lessons from post-release investigations in classical biological control: the case of *Microctonus aethiopoidea* Loan (Hym., Braconidae) introduced into Australia and New Zealand for the biological control of *Sitona discoideus* Gyllenhal (Col., Curculionidae). In: Biological Control: Benefits and Risks. H.M.T. Hokkanen & J.M. Lynch (eds.). Cambridge University Press, Cambridge: 75-83.
- ANONYMOUS, 1999. Evaluating indirect ecological effects of biological control. Proceedings International Symposium of Global IOBC, 17-20 October 1999, Montpellier, France. *Bulletin IOBC/WPRS* 22(2)1999.
- ARNETT, R.H., 1985. A Handbook of the Insects of America North of Mexico. Van Nostrand Reinhold Company, New York.
- BAZZAZ, F.A., 1986. Life history of colonizing plants: some demographic, genetic and physiological features. In: Ecology of Biological Invasions of North America and Hawaii. H.A. Mooney & J.A. Drake (eds). Springer, New York: 96-110.
- BLOMMERS, L.H.M., 1994. Integrated Pest Management in European Apple Orchards. *Annual Review of Entomology* 39: 213-242.
- CALKINS, C.O., 1983. Research on exotic insects. In: Exotic Plant Pests and North American Agriculture. C.L. Wilson & L. Graham (eds.). Academic Press, New York: 321-359.
- CRAWLEY, M.J., 1983. Herbivory: the Dynamics of Animal-Plant Interactions. Blackwell, Oxford.
- CRAWLEY, M.J., 1986. The population biology of invaders. *Philosophical Transactions Royal Society London, B* 314: 711-731.
- CRAWLEY, M.J., 1989. Chance and timing in biological invasions. In: Biological Invasions: a Global Perspective. J.A. Drake (ed.). Wiley, Chichester: 407-423.
- CRAWLEY, M.J. (ed), 1992. Natural Enemies: the Population Biology of Predators, Parasites and Diseases. Blackwell, Oxford.
- CROSS, A.E. & J.S. NOYES, 1995. Dossier on *Anagyrus kamali* Moursi, biological control agent for the pink mealybug, *Maconellicoccus hirsutus*, in Trinidad and Tobago. IIBC, 16 pp. + 1 Annex.

- DANKS, H.V., 1988. Insects of Canada: a synopsis prepared for delegates to the XVIIIth International Congress of Entomology (Vancouver, 1988). *Biological Survey of Canada Document Series No. 1, Ontario*: 18pp.
- DEBACH, P. (ed), 1964. *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London.
- DI CASTRI, F., 1989. History of biological invasions with special emphasis on the old world. In: *Biological Invasions: a Global Perspective*. J.A. Drake (ed.). Wiley, Chichester: 1-30.
- EHRlich, P.R., 1986. Which animal will invade? In: *Ecology of Biological Invasions of North America and Hawaii*. H.A. Mooney & J.A. Drake (eds). Springer, New York: 79-95.
- EHRlich, P.R., 1989. Attributes of invaders and the invading process: vertebrates. In: *Biological Invasions: a Global Perspective*. J.A. Drake (ed.). Wiley, Chichester: 315-328.
- ELTON, C.S., 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- EMBERSON, R.M., 1998. The size and shape of the New Zealand insect fauna. In: *Ecosystems, entomology and plants*. P. Lynch (ed.). *The Royal Society of New Zealand Miscellaneous Series 48*, Wellington, New Zealand: 31-37.
- FAO, 1996. *Code of Conduct on the Import and Release of Biological Control Agents*. FAO, Rome.
- FOIN, T.C., S.P.D. RILEY, A.L. PAWLEY, D.R. AYRES, T.M. CARLSEN, P.J. HODUM & P.V. SWITZER, 1998. Improving recovery planning for threatened and endangered species. Comparative analysis of recovery plans can contribute to more effective recovery planning. *BioScience* **48**: 177-184.
- FRANK, J.H. & E.D. MCCOY, 1995. Invasive adventive insects and other organisms in Florida. *Florida Entomologist* **78**: 1-15.
- FUNASAKI, G.Y., LI, P.Y., NAKAHARA, L.M., BEARDSLEY, J.W. & OTA, A.K., 1988. A review of biological control introductions in Hawaii: 1890 to 1985. *Proceedings Hawaiian Entomological Society* **28**: 293-305.
- GASTON, K.J. & E. HUDSON, 1994. Regional patterns of diversity and estimates of global insect species richness. *Biodiversity and Conservation* **3**(6): 493-500.
- GODFRAY, H.C.J., 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton.
- GREATHEAD, D.J., 1995. Benefits and risks of classical biological control. In: *Biological Control: Benefits and Risks*. H.M.T. Hokkanen & J.M. Lynch (eds.). Cambridge University Press, Cambridge: 53-63.
- HALL, R.W. & L.E. EHLER, 1979. Rate of establishment of natural enemies in classical biological control. *Bulletin Entomological Society America* **25**: 280-282.
- HARRIS, P., 1973. The selection of effective agents for the biological control of weeds. *Canadian Entomologist* **105**: 1495-1503.
- HARRIS, P., 1990. Environmental impact of introduced biological control agents. In: *Critical Issues in Biological Control*. M. Mackauer, L.E. Ehler & J. Roland (eds.). Intercept, Andover: 289-300.
- HAWKINS, B.A., & H.V. CORNELL (eds.), 1999. *Theoretical Approaches to Biological Control*. Cambridge University Press, Cambridge.
- HAYNES, R.P. & J.A. LOCKWOOD (eds.), 1997. Special Issue: Ethical issues in biological control. *Agriculture and Human Values* **14**: 203-310.
- HOKKANEN, H.M.T. & J.M. LYNCH (eds.), 1995. *Biological Control: Benefits and Risks*. Cambridge University Press, Cambridge.
- HOWARTH, F.G., 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* **36**: 485-509.
- KIRITANI, K., 1997. Formation of the exotic fauna in Japan. In: *Biological invasions of ecosystem by pests and beneficial organisms*. E. Yano, K. Matsuo, M. Shiyomi & D.A. Andov (eds.). *Proceedings International Workshop on Biological Invasions*

- of Ecosystem by Pests and Beneficial Organisms, Tsukuba, Japan, 25-27 February 1997, National Institute of Agro-Environmental Studies, Tsukuba, Japan: 49-65.
- LEVIN, S.A., 1989. Analysis of risk for invasions and control programs. In: *Biological Invasions: a Global Perspective*. J.A. Drake, (ed.). Wiley, Chichester: 425-435.
- LEWIS, W.J., J.C. VAN LENTEREN, S.C. PHATAK & J.H. TUMLINSON, 1997. A total systems approach to sustainable pest management. *Proceedings of the National Academy of Sciences, USA*, **94**: 12243-12248.
- LOOMANS, A.J.M., 2000. Introduction of exotic biological control agents: evaluating environmental risks (in Dutch, with English summary). *Entomologische Berichten, Amsterdam* **60**: in press.
- LYNCH, L.D., H. M. T. HOKKANEN, D. BABENDREIER, F. BIGLER, G. BURGIO, Z.-H. GAO, S. KUSKE, A. LOOMANS, I. MENZLER-HOKKANEN, M. B. THOMAS, G. TOMMASINI, J. WAAGE, J. C. VAN LENTEREN, Q.-Q. ZENG, 2000. Indirect effects in the biological control of arthropods with arthropods. In: *Evaluating Indirect Ecological Effects of Biological Control*. E. Wajnberg, J.C. Scott & P.C. Quimby (eds.).
- MACKAUER, M. EHLE, L.E. & ROLAND, J. (eds), 1990. *Critical Issues in Biological Control*. Intercept, Andover.
- MAYNARD SMITH, J., 1989. The causes of extinction. *Philosophical Transactions of the Royal Society London B*, **325**: 241-252.
- MOONEY, H.A. & J.A. DRAKE (eds.), 1986. *Ecology of Biological Invasions of North America and Hawaii*. Springer, New York.
- PIMENTEL, D., 1986. Biological invasions of plants and animals in agriculture and forestry. In: *Ecology of Biological Invasions of North America and Hawaii*. H.A. Mooney & J.A. Drake (eds.). Springer, New York: 149-162.
- PIMENTEL, D., M.S. HUNTER, J.A. LAGRO, R.A. EFROYMSON, J.C. LANDERS, F.T. MERVIS, C.A. MCCARTHY & A.E. BOYD, 1989. Benefits and risks of genetic engineering in agriculture. *Bioscience* **39**: 606-614.
- PIMM, S.L., 1989. Theories of predicting success and impact of introduced species. In: *Biological Invasions: a Global Perspective*. J.A. Drake (ed.). Wiley, Chichester: 351-367.
- RAVENSBERG, W., 1998. De productie van natuurlijke vijanden: een continue uitdaging. In: *Biologische bestrijding en bestuiving in de glastuinbouw: een blik vooruit in de geschiedenis*. A. Vijverberg (ed.). Eburon, Delft: 39-46.
- REGAL, P.J., 1986. Models of genetically engineered organisms and their ecological impact. In: *Ecology of Biological Invasions of North America and Hawaii*. H.A. Mooney & J.A. Drake (eds.). Springer, New York: 111-129.
- ROSENHEIM, J.J., H.K. KAYA, L.E. EHLE, J.J. MAROIS & B.A. JAFFEE, 1995. Intraguild predation among biological-control agents: theory and evidence. *Biological Control*, **5**(3): 303-335.
- ROYER, M., 1995. Environmental Assessment for field releases of certain *Encarsia* species (Hymenoptera: Aphelinidae) for biological control of armored scale insects and whitefly. APHIS, USDA, 15 pp. + 9 Appendices.
- SAILER, R.I., 1978. Our immigrant insect fauna. *Bulletin of the Entomological Society of America* **24**: 3-11.
- SAILER, R.I., 1983. History of insect introductions. In: *Exotic Plant Pests and North American Agriculture*. C. Graham & C. Wilson (eds.). Academic Press, New York: 15-38.
- SIMBERLOFF, D., 1981. Community effects of introduced species. In: *Biotic Crises in Ecological and Evolutionary Time*. M.H. Nitecki (ed.). Academic Press, New York: 53-81.
- SIMBERLOFF, D., 1986. Introduced insects: a biogeographic and systematic perspective. In: *Ecology of Biological Invasions of North America and Hawaii*. H.A. Mooney & J.A. Drake (eds.). Springer, New York: 3-27.

- SIMBERLOFF, D., 1992. Conservation of pristine habitats and unintended effects of biological control. In: Selection criteria and ecological consequences of importing natural enemies. W.C. Kaufmann & R.J. Nichols (eds.). Entomological Society of America, Maryland: 103-117.
- SIMBERLOFF, D. & P. STILING, 1996. How risky is biological control? *Ecology* **77**: 1965-1974.
- STRONG, D.R., J.H. LAWTON & R. SOUTHWOOD, 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell, Oxford.
- VAN LENTEREN, J.C., 1986a. Evaluation, mass production, quality control and release of entomophagous insects. In: *Biological Plant and Health Protection*. J.M. Franz (ed.). Fischer, Stuttgart: 31-56.
- VAN LENTEREN, J.C., 1986b. Parasitoids in the greenhouse: successes with seasonal inoculative release systems. In: *Insect Parasitoids*. J.K. Waage & D.J. Greathead (eds.). Academic Press, London: 341-374.
- VAN LENTEREN, J.C., 1992. Insect invasions: origins and effects. In: *Ecological effects of genetically modified organisms*. J. Weverling & P. Schenkelaars (eds.). Proceedings of a national symposium organised by the Netherlands Ecological Society, 19 september 1991, Netherlands Ecological Society: 59-80.
- VAN LENTEREN, J.C., 1993. Parasites and predators play a paramount role in pest management. In: *Pest Management: Biologically Based Technologies*. R.D. Lumsden & J.L. Vaughn (eds.). American Chemical Society, Washington DC: 68-81.
- VAN LENTEREN, J.C., 1995. Frequency and consequences of insect invasions. In: *Biological control: benefits and risks*. H.M.T. Hokkanen & J.M. Lynch (eds.). Cambridge University Press, UK: 30-43.
- VAN LENTEREN, J.C., 1997. Benefits and risks of introducing exotic macro-biological control agents into Europe. *Bulletin OEPP/EPPO* **27**: 15-28.
- VAN LENTEREN, J.C., 2000. Measures of success in biological control of arthropods by augmentation of natural enemies. In: *Measures of Success in Biological Control*. S. Wratten & G. Gurr (eds.). Kluwer Academic Publishers, Dordrecht (in press).
- VAN LENTEREN, J.C. & N.A. MARTIN, 1999. Biological control of whitefly. In: *Integrated Pest and Disease Management in Greenhouse Crops*. R. Albajes, M.L. Gullino, J.C. van Lenteren & Y. Elad (eds.). Kluwer Publishers, Dordrecht: 202-216.
- VAN LENTEREN, J.C. & J. WOETS, 1988. Biological and integrated pest control in greenhouses. *Annual Review of Entomology* **33**: 239-269.
- VAN LENTEREN, J. C., A. K. MINKS & O.M.B. DE PONTI, O.M.B. (eds.), 1992. *Biological Control and Integrated Crop Protection: Towards Environmentally Safer Agriculture*. Pudoc, Wageningen.
- VAN LENTEREN, J.C., J. WOETS, P. GRIJPMAN, S.A. ULENBERG & O.P.J.M. MINKENBERG, 1987. Invasions of pest and beneficial insects in the Netherlands. In: *The ecology of biological invasions*. W. Joenje, K. Bakker and L. Vlijm (eds). *Proceedings of the Koninklijke Akademie van Wetenschappen. Series C: Biological and Medical Sciences*, **90**. North-Holland Publishing Company, Amsterdam: 51-58.
- WILCOVE, D.S., D. ROTHSTEIN, J. DUBOW., A. PHILLIPS, & E. LOSOS, 1998. Quantifying threats to imperiled species in the United States. Assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. *BioScience* **48**: 607-615.
- WILLIAMSON, M.H., 1996. *Biological Invasions*. Chapman & Hall, London.
- WILLIAMSON, M.H. & K.C. BROWN, 1986. The analysis and modelling of British invasions. *Philosophical Transactions of the Royal Society London B*, **314**: 505-522.
- YANO, E, K. MATSUO, M. SHIYOMI & D.A. ANDOV, 1997. Biological invasions of ecosystem by pests and beneficial organisms. Proceedings International Workshop

INTRODUCTORY LECTURE

on Biological Invasions of Ecosystem by Pests and Beneficial Organisms,
Tsukuba, Japan, 25-27 February 1997, National Institute of Agro-Environmental
Studies, Tsukuba, Japan.