Biological control and sustainable food production

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The use of biological control for the management of pest insects pre-dates the modern pesticide era. The first major successes in biological control occurred with exotic pests controlled by natural enemy species collected from the country or area of origin of the pest (classical control). Augmentative control has been successfully applied against a range of open-field and greenhouse pests, and conservation biological control schemes have been developed with indigenous predators and parasitoids. The cost–benefit ratio for classical biological control is highly favourable (1 : 250) and for augmentative control is similar to that of insecticides (1 : 2–1 : 5), with much lower development costs. Over the past 120 years, more than 5000 introductions of approximately 2000 non-native control agents have been made against arthropod pests in 196 countries or islands with remarkably few environmental problems. Biological control is a key component of a 'systems approach' to integrated pest management, to counteract insecticide-resistant pests, withdrawal of chemicals and minimize the usage of pesticides. Current studies indicate that genetically modified insect-resistant Bt crops may have no adverse effects on the activity or function of predators or parasitoids used in biological control. The introduction of rational approaches for the environmental risk assessment of non-native control agents is an essential step in the wider application of biological control, but future success is strongly dependent on a greater level of investment in research and development by governments and related organizations that are committed to a reduced reliance on chemical control.

Keywords: biological control; integrated pest management; sustainability; genetically modified crops; risks; regulation

1. INTRODUCTION

Biological control can be defined as the use of an organism to reduce the population density of another organism and thus includes the control of animals, weeds and diseases. In this article, we focus on the biological control of arthropods, which DeBach (1964) defined as 'the study and uses of parasites, predators and pathogens for the regulation of host (pest) densities'. This definition establishes two of the main principles of biological control. Firstly, in nature, most organisms are consumed by other organisms, which in many cases leads to drastic reductions in the population of the prey species; in biological control, man exploits this 'natural control' to suppress the numbers of pest species. Secondly, biological control reduces rather than eradicates pests, such that the pest and natural enemy remain in the agro-ecosystem at low densities. A number of important pests can be kept at a low population density by biological control over long periods of time. In other cases, populations of pests are significantly reduced by natural enemies, but repeated releases or additional methods are needed to achieve an adequate level of control. These methods include, for example, resistant plants, cultural techniques, physical barriers, semio-chemicals and, as a last resort, the use of selective chemicals; this is the fundamental philosophy of integrated pest management (IPM; Stern *et al.* 1959).

Many biological control schemes use predatory insects and mites, insects that parasitize other insects (parasitoids) or nematodes, targeted against insect and mite pests; these are the so-called 'macrobial' agents. There are also various 'microbial' agents (bacteria, viruses and fungi) that have been developed and applied in arthropod biological control. Herbivorous insects and mites have also been used in the biological control of weeds (Bellows & Fisher 1999; van Lenteren 2003).

Biological control schemes operate throughout the world as part of the management of pests in agriculture, forestry and greenhouse horticulture. Although biological control has sometimes been introduced to combat arthropod pests that have developed resistance to insecticides and acaricides, the first biological control programmes pre-date the modern pesticide era. The intensification of agriculture through the twentieth century has been accompanied by increased international trade and the resultant transfer of pest species on plants and products across the globe. In addition, the introduction of new crops (such as soya in central Europe), and consumer demand for 'blemish-free' produce, have all contributed to an over-reliance on chemical control, with the well-described consequences of pest resistance, uneconomic production costs, bioaccumulation through food chains, environmental pollution, loss of biodiversity and risks for human health.

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At the start of the twenty-first century, the opportunities and need for effective biological control are greater than ever: pest resistance continues to be a problem, pesticides are being withdrawn on environmental grounds without suitable replacements, and in some areas of the world, including Europe, there is uncertainty over the durability and public acceptance of genetically modified (GM) pest-resistant crops. Against this background, this paper defines the terms used to describe different types of biological control and reviews landmark events in the development of this approach. The advantages and limitations of using natural enemy species in pest management are evaluated, as well as the common features of the most successful agents. The contribution of biological control to sustainable agriculture is reviewed on a global scale, together with recent information on the possible effects of GM crops on natural enemies of pests, and developments in the regulatory framework and risk assessment for the import and release of non-native species. We will explain how biological control can contribute to sustainable agriculture and increase biodiversity.

(a) *Types of biological control*

There are different types of biological control, but both the exact number of types, and the definition of each type vary depending on the literature consulted. The situation is further complicated when some terms are used synonymously by one author, for example 'classical biological control' and 'introductions' by Dent (2000), and the 'same' type of control (classical) is described by a different synonymous term ('inoculation') by another author (van Emden 1989), with the first author also regarding introductions and inoculation as being distinct and different.

In the context of this article, biological control will firstly be distinguished from natural control. Thus, biological control is the use of an organism *by man* to reduce the population density of another organism, whereas natural control is the reduction in numbers of the population of a species by a naturally occurring natural enemy with no human intervention.

There are three main techniques of biological control: *classical* (sometimes described as 'inoculative' biological control), *augmentative* (where a distinction can be made between 'inundation' and 'seasonal inoculation') and *conservation* control (van Lenteren 1993*a*, 2000*b*). Classical or inoculative control is used mainly against 'exotic' pests that have become established in new countries or regions of the world. Relatively, small numbers (usually less than 1000) of a certain species of natural enemy are collected from the country or region of origin of the pest, 'inoculated' into the new environment, and allowed to build up the level of control, which can be maintained over very long periods of time. This type of biological control has been most successful with perennial crops (fruit plantations and forests), where the long-term nature of the ecosystem enables the interactions between pest and natural enemy to become fully established over a period of time: for example, the successful import and release of the predatory ladybird *Rodolia cardinalis* for control of the accidentally introduced citrus pest *Icerya purchasi* in Mediterranean Europe around 1900, and release of

the parasitoid *Aphelinus mali* in the 1930s for control of the accidentally imported woolly apple aphid, *Eriosoma lanigerum*, in apple orchards throughout Europe (Greathead 1976). For a comprehensive review of examples of classical biological control, see DeBach (1964) and Bellows & Fisher (1999).

Augmentation refers to all forms of biological control in which natural enemies are periodically introduced, and usually requires the commercial production of the released agents (van Lenteren 2000*b*). Inundation involves the mass production and release of large numbers of the control agent, such as the *Trichogramma* egg parasitoids of various lepidopteran pests including the cotton bollworm *Heliothis virescens*, the sugar cane borer *Diatraea saccharalis* and the European corn borer *Ostrinia nubilalis* (Bigler 1986; Li 1994; Smith 1996; van Lenteren & Bueno 2003). The cultivation systems used for short-term annual crops destabilize the pest–natural enemy relationship, and thus often prevent the establishment of viable breeding populations of natural enemy species between the crop production cycles. The aim of inundative releases is to create a massive ratio in favour of the natural enemy, analogous to the use of a pesticide, producing a rapid reduction or local extinction of the pest. Control is achieved mainly by the individuals that have been released rather than their offspring. However, the control is usually transient, and re-releases are required, sometimes more than once a year.

Seasonal inoculative control is a form of augmentation in which natural enemies are similarly mass reared in the laboratory and periodically released into short-term crops where many pest generations can occur in each growing season (van Lenteren & Woets 1988). As with augmentative control, relatively large numbers of natural enemies are released to obtain immediate control, but in addition, a build-up of the natural enemy population occurs through successive generations during the same growing season. This method can be applied when the cropping system prevents control extending over many years as with classical (inoculative) biological control. Examples include the control of whiteflies, leafminers, thrips, aphids and mites by parasitoids and predators in greenhouses (van Lenteren 2000*a*).

Conservation control refers to the use of indigenous predators and parasitoids, usually against native pests. Various measures are implemented to enhance the abundance or activity of the natural enemies, including manipulation of the crop microclimate, creation of overwintering refuges (like 'beetle banks'), increasing the availability of alternative hosts and prey, and providing essential food resources such as flowers for adult parasitoids and aphidophagous hoverflies (Gurr *et al.* 2000; Wäckers 2003; Winkler *et al.* 2005).

2. LANDMARK EVENTS IN BIOLOGICAL CONTROL

The first historical record of biological control dates back to around AD 300 when predatory ants were used to control pests in citrus orchards (van Lenteren 2005; van Lenteren & Godfray 2005). In the modern era, the control of the cottony-cushion scale *I. purchasi* on citrus crops in California in the 1880s by an imported

ladybird (the vedalia beetle *R. cardinalis*) and dipteran parasitoid (*Cryptochaetum iceryae*), is widely regarded as representing the first major success of classical biological control (DeBach 1964). The scale insect was accidentally introduced to the United States on *Acacia* plants imported from Australia. Two natural enemy species of *I. purchasi* were collected in Australia, released in small numbers in Californian citrus groves and achieved control of the scale in less than 2 years, the ladybird being the most effective agent. The success of this scheme, which has been repeated in other locations against the same pest worldwide, is attributable to a number of ecophysiological characteristics of the predator–prey relationship: both the adult and larval stages of *R. cardinalis* were active and could seek out their sedentary prey, the rate of development of the ladybird was more rapid than the scale, and the predator had no natural enemies of its own.

Another early example of classical control involved the coconut moth *Levuana iridescens* in Fiji, and established other important principles in the development of biological control. A tachinid parasitoid *Ptychomyia remota* was known to attack the moth *Artona catoxantha* in Malaysia. The parasitoid was introduced to Fiji to control a 'new' host which it had not previously encountered (*L. iridescens*), and was successful across the whole island within 2 years. The stable Fijian climate allowed year-round reproduction of *L. iridescens*, providing a continuous source of prey for *P. remota*; additionally, the island ecosystem was small and isolated (DeBach & Rosen 1991).

One of the most recent successes in biological control is a further example of classical control. Cassava (*Manihot esculenta*) is one of the staple diet crops for a number of African countries. Cassava was introduced to Africa from South America and had been grown for hundreds of years without any major pest problems, until the 1970s. The crop then became infested with an accidentally imported mealy bug from South America *Phenacoccus manihoti*, which spread rapidly over the next 15 years through many countries. A search in South America found the pest in Paraguay, together with one of its natural enemies, the parasitoid *Epidinocarsis lopezi*. The parasitoid showed good searching ability, apparently locating its host by attraction to damaged leaves, and was able to develop more quickly than the mealy bug. After its first release in Nigeria in 1981, *E. lopezi* spread rapidly through neighbouring African countries and is now regarded as one the most successful programmes in biological control with enormous economic benefits (Neuenschwander *et al.* 2003).

One of the first successes with inundative control on a field scale involved the citrophilus mealy bug, *Pseudococcus calceolariae* Fernald (equal to *gahani* Green), a pest of citrus in southern California (Luck & Forster 2003). With the discovery and spread of the mealy bug in 1913, the citrus growers were faced with a serious problem that threatened the crop's viability. In response to this problem, the citrus industry established insectaries to mass-produce the predatory beetle *Cryptolaemus montrouzieri* (Smith & Armitage 1920, 1931; Quayle 1938). Mass production techniques were developed by the early 1920s and, for the next decade, the beetle was the principal means of suppressing this pest. In 1930, at the height of the *P. calceolariae* campaign, 16 insectaries had been established and were producing 20 million beetles annually for release in infested groves (Luck & Forster 2003).

Inundative releases are currently used on a large scale against a range of pests. In Brazil, for example, *Cotesia* parasitoids are applied against sugar cane borer on 300 000 ha, *Anticarsia gemmatalis* multiple nucleopolyhedrovirus (AgMNPV) against soya bean caterpillar on more than 1 Mha, and egg parasitoids of soya bean bugs on 20 000 ha. Egg parasitoids of the genus *Trichogramma* are now released on more than 10 Mha worldwide (van Lenteren & Bueno 2003).

The first success of seasonal inoculative biological control in protected cultivation involved the glasshouse whitefly *Trialeurodes vaporariorum* and the parasitic wasp *Encarsia formosa*. The whitefly and other greenhouse pests (spider mite, thrips and aphids) attack a range of vegetable crops (tomato, cucumber and peppers) and ornamental flowers. These pests reduce yields, lower the market value of products that are sold on appearance, and provide a breeding medium for secondary infections such as the sooty mould (*Cladosporium sphaerospermum*). Biological control of *T. vaporariorum* was established before 1930 in the UK and ran successfully until the introduction of DDT and other organochlorine insecticides in the 1940s (van Lenteren & Woets 1988). However, the development of resistance in the whitefly, together with other concerns about the overuse of pesticides led to the re-introduction of the biological control scheme in the 1970s. For both *T. vaporariorum* and the glasshouse spider mite *Tetranychus urticae* controlled by the predatory mite *Phytoseiulus persimilis*, sophisticated management schemes have now been developed, involving the commercial production of the control agents, flexible release plans (frequency and density), introduction of the pest species to maintain natural enemy populations when required, and manipulation of the climatic environment (temperature and humidity) to optimize control. Currently, all greenhouse vegetable pests can be managed with biological control agents (van Lenteren 2000*a*).

A major success in conservation biological control was achieved with pest management in European fruit orchards. A few years after the use of blanket sprays of synthetic pesticides there were marked declines in the abundance of several species of naturally occurring predators and parasitoids. A series of related studies investigated the occurrence of pests and natural enemies in sprayed and unsprayed orchards, and the relative toxicity of different pesticides on the beneficial species. This information was used to design an IPM programme based on the re-establishment of the natural enemy fauna (predatory insects, mites and parasitoids) to control key pests such as leaf rollers, leaf miners and spider mites, and the selective and local use of chemicals against other pest species (Gruys 1982).

(a) Advantages and limitations of biological control

The advantages and limitations of biological control are often expressed by comparisons with pesticides. Thus, predators and parasitoids are naturally occurring

organisms and usually fairly specific in the range of prey that they will attack. Natural enemies actively seek out their prey and can increase the level of control over time. It is unlikely that resistance will develop to a control agent, and in many cases, the control can be self-perpetuating over long periods of time. The arguments against chemical pesticides are that they not only kill the pest organism, but also many non-target species, including natural enemy species, which in turn, may increase the pest status of species that were previously unimportant or easy to control. Furthermore, chemical control is limited to the area within which the pesticide is applied, frequent application may be required, and this selects for pest resistance.

The main limitation of biological control is that it is slower to suppress pest populations than most pesticides as parasitized organisms may take several days to die; and also, predators require a period of time to establish an economic level of pest suppression. Development costs of biological control are sometimes described as 'high', but these costs are much lower than for the equivalent synthesis, toxicological evaluation and marketing of a new pesticide, and substantial profits can be achieved from biocontrol with long term, effective natural enemies, of which *R. cardinalis*, *E. lopezi*, *E. formosa* and *P. persimilis* are good examples. The comparative advantages of pesticides are that control is rapid, and in the absence of resistance, a high and predictable level of mortality is normally guaranteed.

There are other reported limitations of biological control where pesticides seem to be the more advantageous approach, but the evidence for this conclusion is limited or absent (van Lenteren 1993*a,b*). For instance, the fact that biological control 'regulates' whereas pesticides 'eradicate' is viewed as disadvantageous, but this is a spurious argument. In biological control, pest populations are usually not eradicated, but maintained at very low densities; long-term suppression of pest species is the desirable aim. Eradication of a pest population after chemical treatment, even if this is achieved, occurs only on local scales, and the environment is then open to re-invasion, often with a much reduced natural enemy fauna.

Biological control has been described as 'unreliable' when compared with pesticides, but again the information for this view is equivocal. Some biological control schemes have been 'partial' rather than 'complete' successes, and in some instances, there have been periodic fluctuations in the level of control (see DeBach (1964) and Bellows & Fisher (1999) for examples). But as a counter argument, pesticides also vary in their effectiveness and over time, the development of resistance can lead to the failure of a previously successful chemical.

It is now widely acknowledged that successful biological control depends on extensive preliminary studies to gain a comprehensive understanding of the biology and ecology of the pest and natural enemy complex, and of the environments from which they originate and have subsequently colonized, or into which they will be released. This research can be time consuming, but it is essential, and analogous to the period of time (estimated to be around 10 years) between the synthesis of a new molecule as a potential

pesticide and placing a product on the market. Where all of the necessary 'efficacy studies' have been carried out, such as with *P. persimilis* and *E. formosa*, the control programmes have been consistently successful. In other situations, and under strong market pressure, control agents have sometimes been released without adequate evaluation, and control has been less successful and the pest problems have continued; for example, predatory mites released against *Frankliniella occidentalis*.

It has been suggested that the introduction of a biological control scheme against a pest, and the resultant withdrawal of broad-spectrum pesticides, can lead to new pest problems, but there is no evidence for this in several well-studied agro-ecosystems, including glasshouse systems. Research on biological control was undertaken from 1965 to 1975 to combat glasshouse pests (*P. persimilis* and *E. formosa*) that had become resistant to the then available pesticides (DDT, malathion and resmethrin), but the wide-scale introduction of natural enemies against these two species did not by itself lead to the occurrence of any new pests. The pest problems that have arisen in the European glasshouse industry since 1975 (*Spodoptera exigua*, *Liriomyza trifolii*, *Liriomyza huidobrensis*, *F. occidentalis* and *Bemisia tabaci*) have all been unintentional introductions that arrived with varying levels of resistance to most pesticides. These newly imported pests have threatened the biological control of existing pests because governments usually respond to pest invasions by initiating extermination programmes based on frequent application of pesticides, thereby killing the natural enemies of the 'old' pests. Therefore, it is crucial to identify effective natural enemies of new pests before or soon after invasion, in order to maintain stability in the commercial biological control of existing pests.

Pest control must be cost effective relative to the value of the crop. A comparison of the costs of both the development and the use of chemical and biological control indicates that, in both respects, natural enemies are more cost effective than pesticides (table 1).

Cost–benefit analyses suggest that research on biological control is more cost effective than on chemical control (30 : 1 and 5 : 1, respectively; Tisdell 1990; van Driesche & Bellows 1995). Despite this advantage, the main reason that biological control is not used on a larger scale is attributable to problems associated with the production and distribution of parasitoids and predators; particularly, the limited shelf life (days or at most weeks) of most natural enemy species and the impossibility of patenting a naturally occurring, unmodified species.

It is evident that many more chemical compounds have been tested than species of natural enemy (table 1), though there are still vast numbers of predator and parasitoid species that remain to be screened for their use in biological control. The success rate for finding a successful natural enemy is much higher than for a chemical compound, which is mainly attributable to the 'directed search' that is used for natural enemies compared with the more random approach for chemical compounds, although pesticide discovery and design has become far more rational over time. Development costs are much higher for chemical pesticides, largely as a result of the very stringent requirements for ecotoxicological

Table 1. Comparison of aspects related to the development and application of chemical and biological control. (Updated to 2004; adapted from van Lenteren (1997*a*,*b*).)

	chemical control	biological control
number of 'ingredients' tested	>3.5 million	3000
success ratio	1 : 200 000	1 : 20
developmental costs	180 million US$	2 million US$
developmental time	10 years	10 years
benefit per unit of money invested	2.5–5	30
risk of resistance	large	nil/small
specificity	low	high
harmful side effects	many	nil/few

studies as part of the registration process. Interestingly, the developmental time of an effective product, be it a chemical pesticide or a natural enemy species, is the same. It is common for insect and mite pests to develop resistance against chemical pesticides, whereas as resistance against natural enemies is unknown, at least to the extent that the control agent becomes ineffective. When compared on the criterion of specificity, even the most selective chemical is likely to kill many species of arthropod, whereas natural enemy species used in biological control are usually highly specific, killing only one or a few related species of prey. When selective natural enemies are used in biological control programmes, harmful side effects do not occur, but with highly polyphagous species there may be some negative environmental effects (van Lenteren *et al.* 2006*a*).

The favourable economics of biological control relative to the use of pesticides also applies to the commercial application of the technique. In the 1980s, Ramakers (1982) estimated the cost (product and labour) of controlling glasshouse whitefly (*T. vaporariorum*) to be twice as expensive using insecticide compared with the parasitoid *E. formosa*. A similar difference in costs was found with the control of spider mites (*T. urticae*) by predatory mites compared with acaricides (van Lenteren 1990). In the control of tomato and cucumber pests in the UK, Wardlow (1992) estimates chemical control to be three- or five times more expensive than using commercially produced natural enemies, and even where different biological control agents are used in combination (as with cucumber), the costs are still not higher than when using chemicals (Ramakers 1982).

Periodic analyses of successes and failures of biological control have suggested a number of more generalized limitations that relate to the types of pests that can be more easily controlled by predators and parasitoids, features of the targeted ecosystem and suitability of climates. For classical biological control, some of the most effective schemes have been applied against relatively sedentary pests (such as scale insects and mealy bugs), living in island ecosystems and in year-round stable climates that allow continuous development and reproduction of the pest and natural enemy (DeBach 1964). This view gained support from

the control of *I. purchasi* in the citrus groves ('ecological islands') of California, *L. iridescens* in Fiji and sugar cane pests in Hawaii. However, as the scientific understanding of biological control has increased, through both theoretical and practical studies, it is apparent that these limitations are not an insurmountable obstacle to success. For example, biological control schemes have been successfully applied against mobile pests such as winter moth (*Operophtera brumata*) in Canada (by the parasitoids *Cyzenis albicans* and *Agrypon flaveolatum* from Europe), where there is a strongly seasonal climate with severe winters (DeBach & Rosen 1991). Nevertheless, it is evident that the seasonal temperate climate can be a barrier to the long-term survival of natural enemies originating from tropical or semi-tropical climates, such as the failure of the parasitoid *A. mali* to control the woolly aphid *E. lanigerum* in UK apple orchards in the 1920s and 1930s, through a lack of overwintering ability, even though the natural enemy had been successfully introduced into other countries. However, the main reason for the limited success of biological control in the field in northern Europe is not the weather, but the major changes that occurred in agricultural production systems after 1945 with the introduction of pesticide-dominated methods of pest control, and the loss of resistance to pests and diseases through plant breeding programmes that focused selectively on yield (Lewis *et al.* 1997). Where IPM schemes have been established in orchards, and thus pesticide use is highly restricted (or terminated), a number of key pests can be well-controlled by naturally occurring beneficial insects (which may have to be locally reintroduced; table 2, van Lenteren 1993*b*). There may be other pests that cannot be adequately controlled by naturally occurring natural enemies, and alternative methods will then be required (pheromones, host-plant resistance and hormonal control).

(b) Selection of successful agents

In the early stages of development, biological control of necessity followed mainly a 'trial and error' approach. But now, with a history of over 100 years, there is a large and increasing database of information that can be analysed with the aim of identifying the causes of success and failure, and hence the features that are commonly associated with the most successful agents. These analyses suggest that successful biocontrol agents show strong searching ability to locate prey and identify areas of high pest density, and ideally should have higher potential rates of increase than their prey (faster development, more generations per year, and greater fecundity or a greater predation rate than the reproduction capacity of the pest). Control agents must be able to survive at low pest density, otherwise control will fail and repeated releases will be necessary. The target pest should be the preferred prey of the natural enemy, though use of alternative prey is desirable during periods when the pest occurs at a very low density, or is not in a stage of the life cycle that is parasitized or predated by the control agent. However, it is vitally important that the released agent should not attack non-target species, and this feature is a key element in the pre-licensing environment risk assessment that is now

Table 2. Guided and integrated control programmes applied in Europe. (After van Lenteren 1993*b*.)

crop	type	elements	area under IPM in Europe/ reduction in pesticides on that area
field vegetables	guided	monitoring–sampling–warning host-plant resistance diseases/pests	5% of total area 20–80% reduction
cereals	guided	monitoring–sampling–forecasting host-plant resistance diseases	10% of total area 20–50% reduction
maize	integrated	mechanical weeding–host-plant resistance diseases–biocontrol of insects	4% of total area 30–50% reduction
vineyards	integrated	biocontrol of mites–host-plant resistance diseases–pheromone mating disruption	20% of total area 30–50% reduction
olives	integrated	cultural control–biocontrol insects host-plant resistance diseases/pests monitoring–sampling–pheromones	very limited
orchards	guided	monitoring–sampling selective pesticides	15% of total area 30% reduction
	integrated	monitoring–sampling–pheromones biocontrol–selective pesticides host-plant resistance diseases	7% of total area 50% reduction
greenhouse vegetables	integrated	monitoring–sampling–biocontrol pests and diseases–host-plant resistance diseases	30% of total area 50–99% reduction

routine in many countries (see §5). In situations where the natural enemy is strongly host specific, it is important for the life cycles of the predator and prey or parasitoid and host to be synchronous, especially in seasonal climates where diapause and the timing of post-winter emergence can influence the respective phenologies from year to year. The ability of parasitoids to detect and avoid hosts that have already been parasitized is also an advantageous feature of successful agents. The similarity in climate between collection and release sites is a further important consideration that can have a major impact on successful establishment in new environments.

It is clear that such analyses are not a guarantee of success, and there are also contradictory views among scientists that question some of the fundamental theories of biological control upon which such analyses are based. For instance, it has been argued that the most desirable biological characteristics identified in this selection process are derived from theoretical models of the interactions between prey species and predators or parasitoids without any strong evidence that such theory actually increases the frequency of success or provides an explanation for failures (Gutierrez *et al.* 1994). Likewise, it has been suggested that parasitoids and predators co-evolve with their prey such that control agents would be expected to become less effective over time (Pimentel 1963). If true, this suggests that the concept of classical biological control in which exotic pests are 'reunited' with their former natural enemies collected from the country or area of origin of both species is likely to be successful for limited periods of time; and conversely, that species collected from different locations to the native area of the pest, or from other host or prey associations, may be more successful, or maintain control for longer periods of time (Hokkanen & Pimentel 1984). Analysis of databases of successes and failures in biological control have not produced any strong evidence to support these ideas (Waage & Greathead 1988), and some of the classical control schemes based on the collection of

natural enemies associated with the pest from its country of origin (cottony-cushion scale in California and sugar cane leafhopper in Hawaii) have now been operating successfully for 50–100 years. It also has to be recognized that there are important differences in predator–prey relationships in natural environments and those occurring with pests and biological control agents in agricultural ecosystems, particularly in terms of the density and uniformity of the plant hosts; as such, observations and predictions from naturally co-evolved interactions may not be a reliable predictor of outcomes in cropping regimes.

(c) *Increasing the success of biological control*

Some biological control schemes have the potential to be successful but require additional inputs from man, either prior to release or during natural colonization of the crop environment or to encourage post-release establishment, and this is particularly true of conservation biological control. As examples, adult parasitoids and hoverflies require sources of nectar and pollen to mature their eggs (Wäckers 2003), and growers have been encouraged to plant selected nectar-producing flowers around field boundaries to increase the attractiveness of the crop environment to such natural enemies, with some experimental evidence that an increase in crop diversity with flowers can increase the natural control of pests (Landis *et al.* 2000; Winkler *et al.* 2005).

An increase in plant diversity can also attract insect herbivores that act as alternative hosts or prey for the released agents. The parasitoid *Anagrus epos* parasitizes the eggs of grape leafhoppers (*Erythromeura* species) in California. The grape leafhopper overwinters in the adult stage, leading to a loss of synchrony in the host–parasitoid relationship. A different leafhopper (*Edwardsiana prunicola*) associated with prune trees provides an alternative host for *A. epos*, ensuring effective control of the grape leafhoppers at the start of each growing season (Pickett *et al.* 1990). The importance of alternative prey has also been identified

in the control of western flower thrips (*F. occidentalis*) by the anthocorid bug *Orius majusculus* (Brodsgaard & Enkegaard 1997) and with the egg parasitoids of rice plant hoppers (Yu *et al*. 1996).

Sometimes, alternative prey, together with natural enemies, can be offered on non-crop plants adjacent to the crop, to enhance natural enemy populations by the so-called 'banker plant system'. As an example, one of the most effective methods of suppressing aphid populations in protective cultivation is to introduce the natural enemy species into the greenhouse even before any aphids have been discovered on the crop plants. This can be achieved by using open rearing units ('banker plants') consisting of wheat plants with wheat aphids (which cannot develop on the greenhouse crops) together with predators or parasitoids (van Steenis 1995). In other situations, slow-release systems are used to obtain a regular re-infestation of the crop with natural enemies as with the 'sachet-system' used for the control of thrips by predatory mites. Each sachet contains the predator with an alternative prey source; the mites consume the provided prey and emerge from the sachet progressively over several weeks and then predate the target pest (K. Bolckmans 2006, personal communication).

Assistance from man may extend to more specialized release systems such as spray equipment and machinery that 'shoots' small containers loaded with natural enemies into the crop (*Trichogramma* in maize), release by model airplane (whitefly parasitoids in infested patches of cotton), and full field release by helicopter, ultralight or small airplane (release of *Trichogramma* in maize and other crops). One of the most important actions man can take is to aid the synchronous occurrence of pest and natural enemy by well-timed releases of the control agent. A full review of this area is given by van Lenteren (1987) and Gurr *et al*. (2000).

3. CURRENT USE OF BIOLOGICAL CONTROL

Biological control can be defined as the use of an organism to reduce the population density of another organism. Natural biological control ensures that the Earth is 'green' and that plants can produce sufficient biomass to sustain other forms of life. Without biological control, the production of energy by plants would be a small fraction of current levels.

Natural biological control of pest organisms has occurred since the evolution of the first ecosystem some 500 Myr ago, and continues to the present day across 55.5 billion hectares of the world's terrestrial ecosystems and without human intervention. Its role in marine or freshwater ecosystems has not been quantified, but is certainly equally important as in terrestrial environments. In forest and agro-ecosystems, most of the potential arthropod pests (95% of the total or approximately 100 000 species; DeBach & Rosen 1991; J. C. van Lenteren 2000, unpublished data) are under natural biological control. All other modern methods of control are targeted at the remaining 5000 arthropod pest species. What is often unknown or easily ignored is that the maintenance of ecosystem functions achieved by natural biological control is estimated to have a minimum value of 400 billion US$ per year (Costanza *et al*. 1997), which is an enormous

sum of money compared with the annual expenditure on insecticides of only 8.5 billion US$.

Classical biological control is estimated to be applied on 350 Mha worldwide (10% of land under culture; J. C. van Lenteren 2005, unpublished) and has very favourable cost–benefit ratios of 1 : 20–500. As soon as a natural enemy has been released and becomes effective, it contributes annually to benefits, while costs are minimal. As with natural biological control, the continuously increasing benefits of classical biological control programmes are often overlooked once a pest disappears as a result of the release of an efficient natural enemy. The comparative estimate for area usage of augmentative biological control is 16 Mha (0.046% of land under culture, table 3; van Lenteren & Bueno 2003), with a cost–benefit ratio of 1 : 2–5, which is similar to chemical pest control. More than 5000 introductions of approximately 2000 species of non-native arthropod biological control agents have been made over the past 120 years in classical biological control programmes targeted against arthropod pests in 196 countries or islands; and more than 150 species of natural enemies (parasitoids, predators and pathogens) are currently commercially available for augmentative forms of biological control (van Lenteren *et al*. 2006*a*).

(a) *Modern biological control in sustainable agriculture: restoring the ecosystem function of pest management*

Before the large-scale application of chemical pesticides, biological control was one of the main pest management methods embedded in a 'systems approach' to pest prevention and reduction, covering animals, weeds and pathogens. A farmer had to think about pest prevention before designing the next season's planting scheme and choice of crops. This concept generally made use of three methods of pest management: cultural control, host-plant resistance and biological control. Cultural methods such as crop rotation, cover crops and manipulation of sowing and harvesting dates were used to prevent the build-up of pest numbers (Delucchi 1987). Plants that had a high degree of resistance or tolerance to pests were another cornerstone of pest prevention, and the third was natural, classical, inundative and conservation biological control.

From around 1950, these methods became redundant as almost all pests could be easily managed by the newly discovered pesticides. As a result, pest control research became a highly reductionist activity, and changed from an important decision-making exercise in pest management to a routine but initially successful fire brigade activity. Another effect was that plants were no longer selected for resistance to pests, but only for the highest production of biomass (food) or cosmetic appearance (flowers), produced under blanket applications of pesticides. This, in turn, has led to the current situation in which crops have become 'incubator plants', unable to survive without frequent pesticide applications and agro-ecosystems that have few, if any, natural enemy populations.

However, now that chemical pesticides are no longer seen as the major solution for sustainable pest management, it is not possible to simply return in a year or so to

Table 3. Worldwide use of major augmentative biological control programmes. (After van Lenteren & Bueno (2003).)

natural enemy	pest and crop	area under control (ha)
Trichogramma spp.	lepidopteran pests in vegetables, cereals, cotton	3–10 million, Russia
Trichogramma spp.	lepidopteran pests in various crops, forests	2 million, China
Trichogramma spp.	lepidopteran pests in corn, cotton, sugar cane and tobacco	1.5 million, Mexico
Trichogramma spp.	lepidopteran pests in cereals, cotton, sugar cane and pastures	1.2 million, South America
AgMNPV	soya bean caterpillar in soya bean	1 million, Brazil
entomopathogenic fungi	coffee berry borer in coffee	0.55 million, Colombia
microbial agents	lepidopteran pests and others	1 million, Russia
Cotesia spp.	sugar cane borers	0.4 million, South America, China
Trichogramma spp.	lepidopteran pests in cereals and rice	0.3 million, South East Asia
egg parasitoids	soya bean stink bugs in soya bean	0.03 million, South America
Trichogramma spp.	*Ostrinia nubilalis* in corn	0.1 million, Europe
Orgilus sp.	pine shoot moth, pine plantations	0.05 million, Chile
5 spp. of nat. enemies	Lepidoptera, Homoptera, spider mites in orchards	0.03 million, Europe
more than 30 spp. of nat. enemies	many pests in greenhouses and interior plantscapes	0.015 million, worldwide

pre-pesticide methods of control: crops are too weak to survive without pesticides, natural enemy faunas are absent, and many farmers remain 'pesticide-addicted'. So, first there is a need to invest in the development of new crop cultivars with resistance to pests and diseases, and there is evidence that this is happening in some countries. For example, the Dutch plant breeding industry now invests 35% of its research funds in the development of pest resistance compared with only 5%, 20 years ago (J. C. van Lenteren 2005, unpublished). At the same time, there is a need to restore previously used natural, classical, inundative and conservation biological control (e.g. control of spider mites and insect pests in apple orchards in several European countries; table 2 in van Lenteren 1993*b*). Further, several other alternatives to conventional chemical pest control can also be implemented such as mechanical, physical, genetical, pheromonal and semiochemical control. Also, the environment can be manipulated to make it more attractive and favourable for natural enemies. This strategy involves a range of methods, from manipulation of biotic and abiotic components of the environment such as modifying the climate (e.g. greenhouses and wind shields), to the application of chemicals that stimulate the activity of natural enemies. If natural enemies fail to establish (either due to agricultural practices or lack of adaptive ability in the natural enemy) or, if once established, fail to control the pest, manipulation of the natural enemy or its environment may lead to greater control. The local habitat may lack certain key requisites, which when provided may allow natural enemies to establish or become more effective. Manipulation of the environment is currently applied on a limited scale though there are many opportunities for implementation (see van Lenteren (1987) and Landis *et al.* (2000) for reviews).

The successful introduction (or more accurately, 're-introduction') of these 'new' pest management strategies will require retraining of the extension and advisory service and of growers. This is easier said than done, because it is difficult to simply replace a certain pesticide with an alternative method of control. Instead, there is a need to return to the systems approach, where the influence of all factors affecting pest abundance is considered. An example of a successful systems approach is seen with the optimization of fertilizer use, where a considerable reduction in fertilizer application reduced the development of several pests including aphids, whiteflies and leaf miners. The aim of this approach is to create a system that is inherently resistant to many pests and, thus, requires fewer or no treatment with conventional pesticides. Here, it is important to recognize that maximizing net income is not synonymous with maximizing yield. High yields are obtained with excessively high inputs of fertilizers and pesticides. Reducing the level of inputs may lead to somewhat lower yields, but as the financial inputs are also lower, the net income may be the same or higher. In general, integrated farming takes a more complete account of the impacts of agriculture on ecosystems (pesticide and fertilizer pollution of soil and water, preservation of flora and fauna, quality and diversity of landscape, conservation of energy and non-renewable resources), as well as sociological considerations (employment, public health and well-being of persons associated with agriculture), than is the case with conventional farming practices (Vereijken *et al.* 1986; Wijnands & Kroonen-Backbier 1993).

Although research on integrated farming is still limited, this approach is gaining impetus in Europe. The practices which can be manipulated in integrated farming programmes are crop rotation, cultivation, fertilization, pesticide use, cultural control measures, biological control and other alternatives to conventional chemical control. The practical results obtained in a large, long-term project in The Netherlands indicate that environmental pollution can be reduced through a decrease in fertilizer use and the replacement of chemical pesticides by non-chemical measures. In integrated farming, artificial fertilizers tend to be replaced by organic manure, reducing the total amount of freely available nitrogen (N) in the system, and hence the crop is less attractive or suitable for pest and disease development. Weed, pest and disease problems are reduced in integrated farming through the use of weed-competitive or disease- and pest-resistant varieties, reduction of N-fertilization, adoption of specific sowing

dates and plant spacing, mechanical weed control and natural control. Chemical pest control in integrated farming is based on accurate sampling of pest population densities linked to economic thresholds. Using this approach, a consistent reduction of more than 90% in pesticide use can be achieved with the same economic return as conventional farming (van Lenteren 1997a). The generally lower yields from the integrated system are compensated by reductions in cost from the lower input of pesticides and fertilizers.

Biological control will be a key feature of future sustainable crop production (van Lenteren 1998). The landscape in which agriculture currently takes place is characterized by (i) low species diversity, (ii) plants with little architectural complexity, and (iii) plants and animals that are short-lived with high fecundity, relatively good dispersal but poor competitive ability (Bukovinszky 2004). Further, many agro-ecosystems are dominated by weeds, insects and pathogens that are highly adapted for rapid colonization and population increase. Plants with simple architectures have fewer associated species of insects (pests and beneficials) than diverse and architecturally complex plant communities (Landis & Marino 1997). As a consequence of these low-diversity plant and herbivore communities, agro-ecosystems often have strongly impoverished natural enemy communities when compared with natural ecosystems (Landis et al. 2000). However, the areas adjacent to crop fields are usually less disturbed and architecturally more complex, with a richer and more stable natural enemy fauna that can provide source populations of beneficial arthropods to promote pest management. But it should be realized that these extra-field communities may also act as a reservoir for pest species (Winkler 2005).

Sustainable pest management must, therefore, be based on an appreciation of how the structure of the agricultural landscape can influence the interactions between extra-field and within-field processes. An understanding of the interchange of organisms between areas of the landscape, and the influence of landscape structure on these interchanges, is critical for predicting and managing pest populations in agricultural fields (Lewis et al. 1997). However, as a starting point, it might be more efficient to first concentrate on changes within cropping systems that could increase natural pest control. One approach would be the use of multi- or poly-cropping systems with (i) two or more crop species, (ii) a crop with an undersowing of an economically unimportant plant, or (iii) a multi-crop consisting of a crop species and herbaceous field margins. Although there are many publications which state that the natural enemy fauna is richer in multi-crops, and that natural biological control is greater than in monocultures, there is very little experimental, quantitative data to support this view (see Vandermeer (1989) for a review). There is, for example, hardly any information on how natural enemies search for prey in multi-crop systems compared with searching behaviour in monocultures. However, one of the most frequently cited reasons for multi-cropping (which is applied on 60% of the world area used for food production) is protection from pests (Vandermeer 1989). Pest pressure is usually lower in multi-crops, though not always. The presence of associated plants in a multi-crop can reduce the damage to the main crop species in three ways, all involving a lower population growth rate of the pest. In the first situation, the associated plants are more attractive hosts for the pest than the crop (*host-plant quality hypothesis*). In the second response, the associated plants interfere directly with activities of the pest (*disruptive crop hypothesis*); and in the third, the associated plants change the environment to favour natural enemies of the pests (*natural enemies hypothesis*).

A series of studies have tried to identify the mechanisms by which the numbers of insect herbivores are reduced in multi-crop systems and concluded that in most cases the disruptive crop hypothesis is the best explanation for the data, but that the natural enemies hypothesis could often be supported (Risch et al. 1983). Some recent experimental studies indicate that all three hypotheses for pest reduction, the host-plant quality hypothesis (see Theunissen et al. 1995), the disruptive crop hypothesis (see Visser 1986; Finch & Kienegger 1997) and the natural enemies hypothesis (see Coll & Bottrell 1996) may be valid. Other reviews reveal similar results and data clearly show that plant diversity often results in higher natural enemy populations (e.g. Andov 1983).

An analysis of 51 recent studies of habitat manipulation to enhance conservation biological control (Gurr et al. 2000) showed that in the vast majority of cases there were significant benefits for natural enemies. However, a significantly beneficial effect on natural enemies did not always result in a greater reduction of pest populations or higher yields. Owing to the empirical approach that typifies many of these studies, the effects of agro-ecosystem diversification on the searching behaviour and success of arthropod natural enemies remains poorly understood. Studies in this area are a priority to inform the design and fine-tuning of farming schemes aimed at pest prevention.

4. BIOLOGICAL CONTROL AND GM CROPS
The estimated global area of commercially grown GM crops in 2004 was 81 Mha, equivalent to approximately 5% of the global area available for cultivating crops and 3.2 times the total land area of the UK (James 2004). Four major GM crops (soya bean, cotton, maize and oilseed rape) were grown by 8.25 million farmers in 17 countries in 2004, and approximately 90% of the farmers were resource poor from developing countries. GM herbicide tolerance in these four crops occupied 58.6 Mha (72% of the total GM area), while GM insect resistance in maize and cotton was grown on 15.6 Mha (19%). Stacked genes for herbicide tolerance and insect resistance in maize and cotton occupied 6.8 Mha (9%). GM crops containing genes of *Bacillus thuringiensis* (Bt) expressing truncated Cry proteins which are toxic to specific insect groups (e.g. Lepidoptera, Coleoptera) are currently the only commercial insect resistant GM plants and are grown on 22.4 Mha (28%). Bt Cry1-expressing maize and cotton are protected from attack by lepidopteran pests including corn borers (mainly *O. nubilalis*) in maize and the budworm–bollworm complex (*H. virescens*, *Helicoverpa* spp., *Pectinophora gossypiella*) in cotton

(Shelton *et al.* 2002). In 2003, Bt maize for control of *Diabrotica* spp. (corn rootworms) was commercialized, expressing the coleopteran-specific Cry3Bb toxin.

An advantage of insect-resistant transgenic Bt plants is the reduced need for conventional insecticides, providing benefits for human health and the environment (Shelton *et al.* 2002). For example in US cotton, the average number of insecticide applications used against the budworm–bollworm complex decreased from 4.6 in 1992–1995 to 0.8 in 1999–2001, largely due to the introduction of Bt cotton (FAO 2004). In China, the introduction of Bt cotton has led to a 60–80% decrease in the use of foliar insecticides (Fitt *et al.* 2004).

Detailed analysis of potential effects of GM crops on the environment and the crop ecosystem is crucial prior to commercial release (Dale *et al.* 2002). Key concerns are potential ecological consequences on non-target organisms, including the natural enemies of pests. For Bt toxin, direct effects can be expected only if it is ingested and the parasitoid/predator is susceptible. This requires that the toxin is acquired through direct plant feeding (e.g. pollen), or that it is passed on in a biologically active form by the host/prey. Indirect, host/prey-quality mediated effects can be expected if susceptible herbivores ingest the toxin. Affected herbivores are often smaller, develop slower, behave differently and/or have an altered tissue composition compared to healthy individuals. Such changes may influence the quantity of prey and their nutritional quality for the next tropic level. Effects on natural enemies include death, sublethal effects (e.g. prolonged development, reduced weight), altered behaviour (e.g. reduced parasitization rate, changes in prey choice), or species may be unaffected.

Over the past 10 years, a number of laboratory studies have investigated possible deleterious effects of Bt plants on the mortality, longevity and development of predators and parasitoids. To date, there is no indication of direct effects of Bt transgenic plants on any of the species studied so far, either in direct plant-feeding assays or when the natural enemies had been provided with non-susceptible prey or hosts containing the Bt (Cry) proteins (Romeis *et al.* 2006). Adverse effects have only been reported in studies using herbivores as prey or hosts that ingested the Bt toxin and were susceptible to it (Romeis *et al.* 2006). Such indirect host-quality mediated effects are to be expected because sublethally intoxicated prey or hosts are generally of lower nutritional quality. However, such indirect effects are not unique to Bt toxins, and are known to occur with other insecticides.

On a larger scale, more than 50 studies have been conducted in both experimental and commercial fields to evaluate the impact of Bt crops on natural enemies. Experimental field studies have revealed only minor, transient or inconsistent effects of Bt crops when compared to a non-Bt control. Exceptions were observed with specialist natural enemies which were virtually absent in Bt fields due to the lack of target pests as prey (Riddick *et al.* 1998) or hosts (Pilcher *et al.* 2005). A few studies in Bt crops revealed consistent reductions in the abundance of different generalist predators that were also associated with the reduced availability of sensitive (target)

lepidopteran prey (Daly & Buntin 2005; Naranjo 2005a; Whitehouse *et al.* 2005). Some studies have compared the function of natural enemies (parasitization and predation) in Bt and conventional crops; parasitization rates of naturally occurring or sentinel larvae of sensitive (target) lepidopteran species in Bt crops have been reported to be lower compared to control plots (Siegfried *et al.* 2001; Bourguet *et al.* 2002). This reduction in parasitism is not surprising given that host populations were significantly decreased by the Bt crop. Predation rates on sentinel lepidopteran eggs or larvae did not differ between Bt and untreated non-Bt fields (Musser & Shelton 2003; Sisterson *et al.* 2004; Naranjo 2005b), but were significantly reduced by the application of broad-spectrum insecticides (Musser & Shelton 2003). Studies in commercially managed cotton fields revealed much higher predation rates in Bt cotton compared to non-Bt fields, where more insecticides were applied (Head *et al.* 2005). A 6-year field study in Bt cotton on the abundance of 22 arthropod natural enemy taxa indicated that the exposure to the Bt toxin over multiple generations did not cause any chronic long-term effects (Naranjo 2005a). As yet, there is little evidence that secondary pest outbreaks in Bt crops have emerged as a problem requiring significant use of insecticides. This confirms that overall biological control is not negatively affected by the use of Bt plants (Fitt *et al.* 2004; Naranjo 2005b; Whitehouse *et al.* 2005). The analysis of all published peer-reviewed studies on Bt crops and natural enemies (Romeis *et al.* 2006) has indicated that parasitoid and predator abundance and level of biological control are similar in Bt and untreated non-Bt crops, whereas broad-spectrum insecticides generally lead to a drastic reduction in natural enemy populations as well as a loss of biological control function. It seems, therefore, that in those Bt crops that have been cultivated in commercial production, the Bt technology can contribute to natural enemy conservation and be a useful tool in IPM. Furthermore, it appears that Bt crops and biological control could be used in combination, which may be particularly valuable where the GM-conferred insect resistance is not effective against other key pests. As GM technology evolves, it will be important to evaluate GM traits conferring insect resistance on a case-by-case basis, to identify any adverse effects on the associated natural enemy fauna, and the compatibility of the GM crop with biological control.

5. RISKS, BENEFITS AND REGULATION

Since pest problems in agriculture involve plants, plant-feeding organisms and their natural enemies, the regulation of biological control agents has usually been the responsibility of national plant quarantine services. For this reason, regulation over several decades focused on the need to ensure that introduced natural enemies would not become agricultural pests (Waage 1997). Concern about the risk which introduced biological control agents used against arthropod pests might pose to natural, non-agricultural ecosystems did not become a major issue until much more recently. In contrast, the potential for herbivorous arthropods to become pests when introduced for the biological control of weeds has been recognized for

a long time, and pre-release screening procedures, such as host-specificity testing, have been in place for over 40 years (Harris & Zwoelfer 1968). Pre-release screening of entomophagous biological control agents lagged behind their weed counterparts until the warnings by Howarth (1983, 1991) and Lockwood (1993), which raised concerns about possible impacts on non-target species. Interestingly, an analysis of published and unpublished information found that only 1.5% of entomophagous biological control agents introduced before 1999 had undergone any pre-release host specificity testing (Lynch *et al.* 2001). Yet, despite the fact that non-target effects of entomophagous biological control agents were rarely considered prior to import and release, there are only a few known cases where any adverse effects can be attributed to the release of such organisms (van Lenteren *et al.* 2006*a*).

The increasing popularity of biological control as an alternative to pesticide-based programmes has resulted in more frequent import and release of exotic entomophagous organisms in many countries (van Lenteren 1997*b*). In the past, Europe has generally been a source rather than a recipient of invertebrate biological control agents, in comparison to other countries with greater experience in classical biological control such as Australia, Canada, New Zealand, South Africa and the USA (Greathead 1976). These countries had legislation and testing procedures in place relatively early to regulate imports and analyse the risks of exotic entomophagous biological control agents (Sheppard *et al.* 2003).

Increasing international trade in agricultural products together with accidental introductions of organisms related to tourism and global trade have become important sources for new imports of exotic pests as demonstrated by Bin & Bruni (1997) for Italy. Many of these introduced organisms are candidates for classical biological control, especially if they establish in conservation areas where they may threaten native species and communities. A significant event in the history of regulation of entomophagous biological control agents was the adoption of the Convention on Biological Diversity following the Rio Conference in 1992. Signatory countries have accepted the obligation to prevent the introduction and to control alien species that threaten indigenous ecosystems and habitats. A broad and ongoing discussion within the scientific community and in public fora was initiated by the publication of the Convention, and biodiversity issues made a sudden appearance on the agendas of policy makers. As a consequence, the public perception of threats to biodiversity has changed markedly in recent years. Biological control, which had previously been viewed as an environmentally friendly method of pest control was subjected to a more critical evaluation, the assumed safety was questioned, and the need for regulation of the import and release of non-native species has become a keenly debated issue.

(a) *Harmonization of regulation of entomophagous biological control agents*

Regulation of the introduction and release of entomophagous biological control agents differs between countries, and some have yet to establish guidelines and procedures. International laws and agreements require a harmonized and effective regulatory system between countries. In many cases, introductions of biological control agents are administered under regulations which were established for other purposes, such as plant quarantine, wildlife conservation and GM plants. The application of appropriate regulatory procedures is important in order to maintain public confidence in biological control and to facilitate introduction and use of non-native species.

A number of regulatory documents for the import and release of invertebrate biological control agents have been produced by international organizations; for example, the Food and Agricultural Organization of the United Nations (FAO 1996, 2005), the European and Mediterranean Plant Protection Organization (EPPO 1999, 2001, 2002) and the Organization for Economic Co-operation and Development (OECD 2004). More recently, guidance on procedures and methods for environmental risk assessment (ERA) of non-native invertebrate biological control agents has been proposed (van Lenteren *et al.* 2003; Babendreier *et al.* 2005; van Lenteren *et al.* 2006*b*; Bigler *et al.* 2006). The biological control industry was concerned when the OECD guidance document was published, as the information requirements were considered to be too stringent, and manufacturers feared that national authorities would establish their own regulatory systems. As a consequence, the International Biocontrol Manufacturers Association proposed that the International Organization for Biological Control of Noxious Animals and Plants/West Palaearctic Regional Section (IOBC/WPRS) should coordinate the harmonization of the various regulatory documents. This resulted in the establishment of a Commission of the IOBC/WPRS in 2003 with the aim of offering a platform to scientists, regulators and industry to develop coordinated guidelines for European countries. The recommendations of this Commission were recently published (Bigler *et al.* 2005), and can now be adopted and implemented by national authorities.

The regulatory guidelines propose a two-step procedure in which the first stage is to license the import of an organism for research under contained conditions. This enables researchers to identify the key biological characteristics of the organism, such as host range and climatic requirements, which determine the ability of species to establish in new environments. This phase of the regulatory process should provide sufficient information for judgements to be made on the safety and efficacy of the organism. In the second step, companies submit an application for a licence to release the organism, with a dossier of information compiled in line with the guidelines, and including an evaluation of the risks and benefits arising from the proposed release. The risk–benefit analysis should include both positive and negative effects to the economy (farmer, producer and public), human/ animal health and the environment (ERMA NZ 2000).

In contrast to pesticides, biological control agents usually lack the potential to adversely affect human and animal health. There have been some rare cases of adverse effects on human health in allergic reactions to some organisms (for example, to wing scales of Lepidoptera) among personnel working in production

facilities. Environmental risks and benefits of biological control extend to a comparative evaluation (with pesticides) of effects on water, soil, air, biodiversity and ecosystem functions. Invertebrate biological control agents do not pollute water, soil or air (Greathead 1995), and thus the assessment of potential environmental effects have focused on biodiversity issues. However, it is difficult to assign monetary values to the damage or loss of species or ecosystem functions (Simberloff & Stiling 1996; Thomas & Willis 1998), such that environmental effects have to be considered in a qualitative manner. As a generalization, a strong case can be made for the view that biological control contributes to a reduction in pesticide use with corresponding benefits to the environment. While it should not be assumed that introduced biological control agents pose no risk to native species and ecosystems, history suggests that there have been remarkably few problems, even through the many decades when regulation was virtually non-existent (Lynch *et al.* 2001; van Lenteren *et al.* 2006a). The recently published regulatory guidelines (Bigler *et al.* 2005) are intended to produce a careful analysis of the establishment potential of an imported species in a new environment and any adverse effects on non-target organisms and ecosystem functions that may then arise.

(b) Consequences of regulation for the use of biological control agents in sustainable agriculture

Stakeholders in the area of biological control include scientists, industrial producers, retailers, growers, consumers, environmentalists and government regulators. Different stakeholders may have overlapping or conflicting interests; for example, the biological control industry and national organizations with responsibility for protecting the natural environment. It can be a time-consuming exercise to find a consensus between these differing views, with the net effect that innovative products are kept off the market for a long time, or that some species are never released. The costs of delaying product introduction to the market or the failure to licence a species at all can be calculated in terms of the economic loss for producers, retailers and growers, whereas the benefits of effective regulation can be expressed as 'public goods', like environmental protection. When seen in these terms, it is clearly difficult to make direct comparisons between the costs and benefits of regulation.

Markets for biological control products are usually small and cannot support or justify high levels of expenditure on the evaluation of environmental risks and preparation of the dossiers that are required for registration. The procedure is not only costly but also time consuming; the dossier for the registration of the bacterium *Pseudomonas chlororaphis* used for seed treatment against seed-borne diseases of barley and wheat was submitted in January 1996 under European Union (EU) directive 91/414 and was finally approved in April 2004. The regulatory process can be very costly and therefore may prevent small and medium-sized enterprises from developing biological control products. Only larger companies have the necessary finance to conduct research, produce a dossier and enter into the

iterative discussions that are part of the registration procedure. As a consequence of overly stringent regulations, small and medium-sized businesses may be discouraged or prevented from identifying and assessing new species as potential biological control agents. Unnecessary over-regulation thus inhibits the development and introduction of innovative products for sustainable agriculture, and also impacts on start-up and spin-off companies in the biological control sector, as venture capital becomes even more scarce in the light of reduced returns on investment.

The current dilemma is not whether to regulate biological control agents, but how to regulate without introducing negative trade-offs which prevent innovation and limit the introduction of novel biological control agents in sustainable crop protection systems. In essence, the regulatory framework, and therefore associated costs, should be set at the minimum level that does not compromise environmental safety and human health.

An efficient and low-cost regulatory system is likely to be characterized by a number of key features: (i) applicants and regulators should establish contact at an early stage in the regulatory process and exchange information openly thus preventing unnecessary data generation; (ii) harmonized regulation among countries (e.g. across Europe) will be cost-effective because companies will be able to submit the same (or slightly modified) risk assessment dossier in different countries; (iii) governments should support public–private partnership to gather information on risks and benefits of candidate agents; and (iv) when previous releases in other countries or ecoregions with similar climatic conditions have proved to be effective and environmentally safe, a light-touch process of notification rather than regulation should be applied.

There have been a number of recent developments that hold out the prospect of a harmonized regulatory system in Europe. Firstly, scientists and representatives of the biological control production industry collaborated in an EU-funded project (ERBIC, 'Evaluating Environmental Risks of Biological Control Introductions into Europe') to develop a structure for a general ERA, consisting of (i) characterization and identification of the biological control agent, and determination of (ii) risks to human health, (iii) environmental risks, and (iv) efficacy. The ERA was proposed to focus on five risk factors of natural enemies: host/prey range, establishment, dispersal, and direct and indirect effects of releases (van Lenteren *et al.* 2003). It was recognized that the design and application of an ERA depends crucially on the availability of appropriate methods that are both realistic and cost-effective for the industry to apply. In this respect, the recent discovery that the outdoor winter survival (and hence establishment potential) of a number of insect and mite agents used in greenhouses is strongly correlated with their low-temperature survival under laboratory conditions (Hatherly *et al.* 2005 and references therein) is an important contribution to a risk assessment protocol.

The requirements of an ERA for non-native biological control agents have recently been addressed by Bigler *et al.* (2006), with detailed background

information and methodologies for the determination of host ranges (Kuhlmann *et al.* 2006; van Lenteren *et al.* 2006*b*), establishment (Boivin *et al.* 2006), dispersal (Mills *et al.* 2006), and direct and indirect effects of releases on non-target organisms (Albajes *et al.* 2006; Messing *et al.* 2006). Concurrently, the IOBC established a commission to review and amalgamate various risk assessments documents (from FAO, OECD and EPPO) and produce a harmonized regulatory framework for Europe (Bigler *et al.* 2005). The current state of affairs with regard to the risks of releasing exotic natural enemies, variation in regulatory systems in different countries worldwide, and proposals for both comprehensive and quick-scan methods for ERA have been reviewed by van Lenteren *et al.* (2006*a*). The EU has recently expressed the view that the application and success of biological control (with macrobial and microbial agents, and semiochemicals) has been lower in Europe than in other parts of the world, and questioned whether this relative lack of success is attributable to a fragmented or over-cautious regulatory process in different European countries. A new EU project (Registration of Biological Control Agents, REBECA) will address these issues and bring forward recommendations for a Europe-wide regulatory framework for these different types of control agents.

6. FUTURE PERSPECTIVES AND CONCLUSIONS

It may not be an easy task at the present time to convince farmers worldwide to adopt a systems approach to pest management and make greater use of biological control. Yet in an agricultural industry that is still dominated by pesticides, biological control has found its place in the form of augmentative releases, particularly for the management of pests that are difficult to control with insecticides. Each pest species has tens to hundreds of associated natural enemy species (parasitoids, predators and pathogens), and thus thousands of natural enemies still await discovery. During the past 40 years, the identification and pre-release evaluation of natural enemies—including ERAs—has improved greatly (van Lenteren & Manzaroli 1999; Bigler *et al.* 2006), with more than 150 species of natural enemy now commercially available for augmentative biological control (van Lenteren 2003). Based on the criteria of current evaluation methods, inefficient or hazardous natural enemies can be identified quickly, and thus avoid unnecessary expenditure on further research. Improvement of networking among the world's biological control community and construction of easily accessible databases containing information on all studied natural enemies (with appropriate evaluation) will help to increase the rate of identification of new and efficient control agents. Once a good natural enemy has been found, it is important to train the extension service and farmers in its use, an aspect of biological control that is often neglected. The FAO Farmers Field School (FFS) projects in Asia and Africa have shown that, as a result of self-learning and experimenting, farmers are capable of quickly selecting the most appropriate pest management strategy for their crops, and rapidly move away from chemicals to cultural methods and biological control (Ooi & Kenmore 2005). An adaptation of the FFS approach might be considered as a means of achieving sustainable pest management in the developed world as well. But biological control practitioners will also have to spend time creating societal awareness about the benefits of sustainable and environmentally friendly pest management, otherwise conventional chemical control will continue to dominate control options.

Though it is evident that biological control programmes have been successfully implemented in a wide range of crop environments in all parts of the world, and the potential to increase the role of biological control is great (including in IPM), it remains the case that the adoption and implementation of this method of control is slow. Owing to technical and economic, but mainly attitudinal barriers, ecologically sound pest management has not been used for a wide variety of pests and diseases. Although the funding for research on biological control is limited, it is our conviction that the main constraints are related to the attitudes of advisory personnel and farmers, combined with the disinterest in anything other than chemical control among the pesticide industries, and the hollow endorsement of alternative methods made by policy makers in which words are yet to be matched by a realistic investment in research and development. We are confident, however, that future pest management will depend strongly on biological control because it is the most sustainable, cheapest and environmentally safest system of pest management (table 1), with additional benefits for growers and consumers. Biological control is expected to account for a significantly increased proportion of all crop protection methods by the year 2050.

REFERENCES

Albajes, R., Castañé, C., Gabarra, R. & Alomar, O. 2006 Risks of plant damage caused by natural enemies introduced for arthropod biological control. In *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (eds F. Bigler, D. Babendreier, U. Kuhlmann), pp. 132–144. Wallingford, UK: CAB International.

Andov, D. A. 1983 Plant diversity and insect populations: interactions among beans, weeds and insects. PhD thesis, Cornell University, Ithaca, NY.

Babendreier, D., Bigler, F. & Kuhlmann, U. 2005 Methods used to assess non-target effects of invertebrate biological control agents of arthropod pests. *BioControl* **50**, 821–870. (doi:10.1007/s10526-005-3633-3)

Bellows, T. S. & Fisher, T. W. (eds) 1999 *Handbook of biological control*. San Diego, CA: Academic Press.

Bigler, F. 1986 Mass production of *Trichogramma maidis* Pint, Et Voeg. and its field application against *Ostrinia nubilalis* Hbn in Switzerland. *J. Appl. Entomol.* **101**, 23–29.

Bigler, F., Bale, J. S., Cock, M. J. W., Dreyer, H., Greatrex, R., Kuhlmann, U., Loomans, A. J. M. & van Lenteren, J. C. 2005 Guidelines on information requirements for import and release of invertebrate biological control agents in European countries. *Biocontrol News Inform.* **26**, 115N–123N.

Bigler, F., Babendreier, D. & Kuhlmann, U. (eds) 2006 *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment*. Wallingford, UK: CAB International.

Bin, F. & Bruni, R. 1997 Evaluating one century of classical biocontrol in Italy. *EPPO Bull.* **27**, 53–59.

Boivin, G., Kölliker-Ott, U. M., Bale, J. S. & Bigler, F. 2006 Assessing the establishment potential of inundative biological control agents. In *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (eds F. Bigler, D. Babendreier & U. Kuhlmann), pp. 98–113. Wallingford, UK: CAB International.

Bourguet, D., Chaufaux, J., Micoud, A., Delos, M., Naibo, B., Bombarde, F., Marque, G., Eychenne, N. & Pagliari, C. 2002 *Ostrinia nubilalis* parasitism and the field abundance of non-target insects in transgenic *Bacillus thuringiensis* corn (*Zea mays*). *Environ. Biosafety Res.* **1**, 49–60.

Bukovinszky, T. 2004 Tailoring complexity: multitrophic interactions in simple and diversified habitats. PhD thesis, Wageningen University.

Brodsgaard, H. F. & Enkegaard, A. 1997 Interactions among polyphagous anthocorid bugs used for thrips control and other beneficials in multi-species biological pest management. *Recent Res. Dev. Entomol.* **1**, 153–160.

Coll, M. & Bottrell, D. G. 1996 Movement of an insect parasitoid in simple and diverse plant assemblages. *Ecol. Entomol.* **21**, 141–149.

Costanza, R. *et al.* 1997 The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260. (doi:10.1038/387253a0)

Dale, P. J., Clarke, B. & Fontes, E. M. G. 2002 Potential for the environmental impact of transgenic crops. *Nat. Biotechnol.* **20**, 567–574. (doi:10.1038/nbt0602-567)

Daly, T. & Buntin, G. D. 2005 Effects of *Bacillus thuringiensis* transgenic corn for lepidopteran control on non-target arthropods. *Environ. Entomol.* **34**, 1292–1301. (doi:10.1603/0046-225X(2005)034[1292:EOBTTC]2.0.CO;2)

DeBach, P. 1964 *Biological control of insect pests and weeds*. London, UK: Chapman and Hall.

DeBach, P. & Rosen, D. 1991 *Biological control by natural enemies*, 2nd edn. Cambridge, UK: Cambridge University Press.

Dent, D. 2000 *Insect pest management*. Wallingford, UK: CAB International.

Delucchi, V. (ed.) 1987 *Integrated pest management: quo vadis?* Parasitis 1986 Symposium book. Geneva, Switzerland: Parasitis.

EPPO 1999 Safe use of biological control: first import of biological control agents for research under contained conditions. EPPO Standard PM6/1(1). *EPPO Bull.* **29**, 271–272.

EPPO 2001 Safe use of biological control: import and release of biological control agents. EPPO Standard PM6/2(1). *EPPO Bull.* **31**, 33–35.

EPPO 2002 List of biological control agents widely used in the EPPO region. EPPO Standard PM6/3(2). *EPPO Bull.* **32**, 447–461. (doi:10.1046/j.1365-2338.2002.00600.x)

ERMA NZ 2000 *Preparing information on risks, costs and benefits for applications under the Hazardous Substances and New Organisms Act 1996 (ER-TG-03-1 7/00)*. See http://www.ermanz.govt.nz/resources/publications/pdf/ER-TG-03-1.pdf.

FAO 1996 *Code of conduct for the import and release of exotic biological control agents. International standard for phytosanitary measures, no. 3*. Secretariat of the International Plant Protection Convention, FAO, Rome, pp. 21. See http://www.ippc.int.

FAO 2004 *The state of food and agriculture*. Rome, Italy: Food and Agriculture Organization of the United Nations.

FAO 2005 *Guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms*. International standard for phytosanitary measures, no. 3. Secretariat of the International Plant Protection Convention, pp. 14. Rome, Italy: FAO. See http://www.ippc.int.

Finch, S. & Kienegger, M. 1997 A behavioural study to help clarify how undersowing with clover affects host-plant selection by pest insects of brassica crops. *Entomol. Exp. Appl.* **84**, 165–172. (doi:10.1023/A:1003082529819)

Fitt, G. P., Wakelyn, P. J., Stewart, J. M. D., James, C., Roupakias, D., Hake, K., Zafar, Y., Pages, J. & Giband, M. 2004 Global status and impacts of biotech cotton. Report of the second expert panel on biotechnology of cotton. International Cotton Advisory Committee, Washington, DC.

Greathead, D. J. 1976 *A review of biological control in western and southern Europe*. Technical communication, no. 7, p. 182. Farnham Royal, UK: Commonwealth Institute of Biological Control.

Greathead, D. J. 1995 Benefits and risks of classical biological control. In *Biological control: benefits and risks* (eds H. M. T. Hokkanen & J. M. Lynch), pp. 53–63. Cambridge, UK: Cambridge University Press.

Gruys, P. 1982 Hits and misses. The ecological approach to pest control in orchards. *Entomol. Exp. Appl.* **31**, 70–87.

Gurr, G. M., Wratten, S. D. & Barbosa, P. 2000 Success in conservation biological control of arthropods. In *Measures of success in biological control* (eds G. Gurr & S. Wratten), pp. 105–132. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Gutierrez, A. P., Neuenschwander, P. & van Alphen, J. J. M. 1994 Factors affecting biological control of cassava mealy bug by exotic parasitoids: a ratio-dependent supply-demand driven model. *J. Appl. Ecol.* **30**, 706–721.

Harris, P. & Zwoelfer, H. 1968 Screening of phytophagous insects for biological control of weeds. *Can. Ent.* **100**, 295–303.

Hatherly, I. S., Hart, A. J., Tullett, A. G. T. & Bale, J. S. 2005 Use of thermal data as a screen for the establishment potential of non-native biocontrol agents in the UK. *BioControl* **50**, 687–698. (doi:10.1007/s10526-005-6758-5)

Head, G., Moar, W., Eubanks, M., Freeman, B., Ruberson, J., Hagerty, A. & Turnipseed, S. 2005 A multi-year, large-scale comparison of arthropod populations on commercially managed Bt and non-Bt cotton fields. *Environ. Entomol.* **34**, 1257–1266. (doi:10.1603/0046-225X(2005)034[1257:AMLCOA]2.0.CO;2)

Hokkanen, H. M. T. & Pimentel, D. 1984 New approach for selecting biological control agents. *Can. Entomol.* **116**, 1109–1121.

Howarth, F. G. 1983 Biological control: panacea or Pandora's box? *Proc. Hawaii. Entomol. Soc.* **24**, 239–244.

Howarth, F. G. 1991 Environmental impacts of classical biological control. *Annu. Rev. Entomol.* **36**, 485–509. (doi:10.1146/annurev.en.36.010191.002413)

James, C. 2004 *Preview: global status of commercialized biotech/GM crops: 2004*. ISAA brief, no. 32. Ithaca, NY: International Service for the Acquisition of Agri-Biotech Applications.

Kuhlmann, U., Schaffner, U. & Mason, P. G. 2006 Selection of non-target species for host specificity testing. In *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (eds F. Bigler, D. Babendreier & U. Kuhlmann), pp. 15–37. Wallingford, UK: CAB International.

Landis, D. A. & Marino, P. C. 1997 Landscape structure and extra-field processes: impact on management of pests and beneficials. In *Handbook of pest management* (ed. J. Ruberson), pp. 79–104. New York, NY: Marcel Dekker.

Landis, D. A., Wratten, S. D. & Gurr, G. M. 2000 Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* **45**, 175–201. (doi:10.1146/annurev.ento.45.1.175)

Lewis, W. J., van Lenteren, J. C., Pathak, S. C. & Tumlinson, J. H. 1997 A total systems approach to sustainable pest management. *Proc. Natl Acad. Sci. USA* **94**, 12 243–12 248. (doi:10.1073/pnas.94.23.12243)

Li, L.-Y. 1994 Worldwide use of *Trichogramma* for biological control on different crops: a survey. In *Biological control with egg parasitoids* (eds E. Wijnberg & S. A. Hassen), pp. 37–53. Wallingford, UK: CAB International.

Lockwood, J. A. 1993 Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environ. Entomol.* **22**, 503–518.

Luck, R. F. & Forster, L. D. 2003 Quality of augmentative biological control agents: a historical perspective and lessons learned from evaluating *Trichogramma*. In *Quality control and production of biological control agents: theory and testing procedures* (ed. J. C. van Lenteren), pp. 231–246. Wallingford, UK: CAB International.

Lynch, L. D. *et al.* 2001 Insect biological control and non-target effects: a European perspective. In *Evaluating indirect ecological effects of biological control* (eds E. Wajnberg, J. K. Scott & P. C. Quimby), pp. 99–125. Wallingford, UK: CAB International.

Messing, R., Roitberg, B. & Brodeur, J. 2006 Measuring and predicting indirect impacts of biological control: competition, displacement, and secondary interactions. In *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (eds F. Bigler, D. Babendreier & U. Kuhlmann), pp. 64–77. Wallingford, UK: CAB International.

Mills, N. J., Babendreier, D. & Loomans, A. J. M. 2006 Methods for monitoring the dispersal of natural enemies from point source releases associated with augmentative biological control. In *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (eds F. Bigler, D. Babendreier & U. Kuhlmann), pp. 114–131. Wallingford, UK: CAB International.

Musser, F. R. & Shelton, A. M. 2003 *Bt* sweet corn and selective insecticides: impacts on pests and predators. *J. Econ. Entomol.* **96**, 71–80.

Naranjo, S. E. 2005a Long-term assessment of the effects of transgenic *Bt* cotton on the abundance of non-target arthropod natural enemies. *Environ. Entomol.* **34**, 1193–1210. (doi:10.1603/0046-225X(2005)034[1193: LAOTEO]2.0.CO;2)

Naranjo, S. E. 2005b Long-term assessment of the effects of transgenic *Bt* cotton on the function of the natural enemy community. *Environ. Entomol.* **34**, 1211–1223. (doi:10. 1603/0046-225X(2005)034[1211:LAOTEO]2.0.CO;2)

Neuenschwander, P., Borgemeister, C. & Langewald, J. (eds) 2003 *Biological control in IPM systems in Africa*, p. 414. Wallingford, UK: CAB International.

OECD 2004 Guidance for information requirements for regulation of invertebrates as biological control agents (IBCAs). Series on pesticides, no. 21, OECD Environment Directorate, pp. 22. See www.oecd.org/dataoecd/6/ 20/28725175.pdf.

Ooi, P. A. C. & Kenmore, P. E. 2005 Impact of educating farmers about biological control in farmer field schools. In *Proc. Int. Symp. on Biological Control of Arthropods*, *12–16 September 2005, Davos, Switzerland*, pp. 277–289. Washington, DC: USDA Forest Service, Forest Health Technology Enterprise Team-2005–08.

Pickett, C. H., Wilson, L. T. & Flaherty, D. L. 1990 The role of refuges in crop protection, with reference to plantings of French prune trees in a grape agroecosystem. In *Monitoring and integrated management of Arthropod pests of small fruit crops* (eds N. J. Bostanian, L. T. Wilson & T. J. Dennehy), pp. 151–165. Andover, UK: Intercept.

Pilcher, C. D., Rice, M. E. & Obrycki, J. J. 2005 Impact of transgenic *Bacillus thuringiensis* corn and crop phenology on five non-target arthropods. *Environ. Entomol.* **34**, 1302–1316. (doi:10.1603/0046-225X(2005)034[1302: IOTBTC]2.0.CO;2)

Pimentel, D. 1963 Introducing parasites and predators to control native pests. *Can. Entomol.* **95**, 785–792.

Quayle, H. J. 1938 *Insects of citrus and other subtropical fruits*. Ithaca, NY: Comstock.

Ramakers, P. M. J. 1982 Biological control in Dutch glasshouses: practical applications and progress in research. In *Proc. Symp. Integrated Crop Protection*, pp. 265–270. Valence, France: CEC.

Riddick, E. W., Dively, G. & Barbosa, P. 1998 Effect of a seed-mix deployment of Cry3A-transgenic and nontransgenic potato on the abundance of *Lebia grandis* (Coleoptera: Carabidae) and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* **91**, 647–653.

Risch, S. J., Andow, D. & Altieri, M. A. 1983 Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. *Environ. Entomol.* **12**, 625–629.

Romeis, J., Meissle, M. & Bigler, F. 2006 Transgenic crops expressing *Bacillus thuringiensis* toxins and biological control. *Nat. Biotechnol.* **24**, 63–71. (doi:10.1038/nbt1180)

Simberloff, D. & Stiling, P. 1996 Risks of species introduced for biological control. *Biol. Conserv.* **78**, 185–192. (doi:10. 1016/0006-3207(96)00027-4)

Sisterson, M. S., Biggs, R. W., Olson, C., Carriere, Y., Dennehey, T. J. & Tabashnik, B. E. 2004 Arthropod abundance and diversity in *Bt* and non-*Bt* cotton fields. *Environ. Entomol.* **33**, 921–929.

Shelton, A. M., Zhao, J. Z. & Roush, R. T. 2002 Economic, ecological, food safety, and social consequences of the deployment of *Bt* transgenic plants. *Annu. Rev. Entomol.* **47**, 845–881. (doi:10.1146/annurev.ento.47.091201.145309)

Sheppard, A. W., Hill, R., DeClerck-Floate, R. A., McClay, A., Olckers, T., Quimby Jr, P. C. & Zimmermann, H. G. 2003 A global review of risk-benefit-cost analysis for the introduction of classical biological control agents against weeds: a crisis in the making? *Biocontrol News Inform.* **24**, 91–108.

Siegfried, B. D., Zoerb, A. C. & Spencer, T. 2001 Development of European corn borer larvae on Event 176 Bt corn: influence on survival and fitness. *Entomol. Exp. Appl.* **100**, 15–20. (doi:10.1023/A:1019250807782)

Smith, S. M. 1996 Biological control with *Trichogramma*: advances, successes, and potential of their use. *Annu. Rev. Entomol.* **41**, 375–406. (doi:10.1146/annurev.en.41. 010196.002111)

Smith, H. S. & Armitage, H. M. 1920 Biological control of mealybugs in California. *Calif. Dept Agric. Month. Bull.* **9**, 104–158.

Smith, H. S. & Armitage, H. M. 1931 The biological control of mealybugs attacking citrus. *Calif. Agric. Exp. Station Bull.* **509**, 74.

Stern, V. M., Smith, R. F., van den Bosch, R. & Hagen, K. S. 1959 The integration of chemical and biological control of the spotted alfalfa aphid. The integrated control concept. *Hilgardia* **29**, 81–101.

Theunissen, J., Booij, C. J. H. & Lotz, L. A. P. 1995 Effects of intercropping white cabbage with clovers on pest infestation and yield. *Entomol. Exp. Appl.* **74**, 7–16. (doi:10.1007/ BF02383162)

Thomas, M. B. & Willis, A. J. 1998 Biocontrol—risky but necessary? *Trends Ecol. Evol.* **13**, 325–329. (doi:10.1016/ S0169-5347(98)01417-7)

Tisdell, C. A. 1990 Economic impact of biological control of weeds and insects. In *Critical issues in biological control* (eds M. Mackauer, L. E. Ehler & J. Roland), pp. 301–316. Andover, UK: Intercept.

Vandermeer, J. 1989 *The ecology of intercropping*. Cambridge, UK: Cambridge University Press.

van Driesche, R. G. & Bellows, T. S. 1995 *Biological control*. New York, NY: Chapman & Hall.

van Emden, H. F. 1989 *Pest control*. London, UK: Edward Arnold.

van Lenteren, J. C. 1987 Environmental manipulation advantageous to natural enemies of pests. In *Integrated pest management: quo vadis?* (ed. V. Delucchi), Parasitis 1986 symposium book, pp. 123–166. Geneva, Switzerland: parasitis.

van Lenteren, J. C. 1990 Implementation and commercialization of biological control in West Europe. In *Int. Symp. on Biological Control Implementation, McAllen, Texas 4–6 April 1989*, NAPPO Bulletin 6, pp. 50–70.

van Lenteren, J. C. 1993a Biological control of pests. In *Modern crop protection: developments and perspectives* (ed. J. C. Zadoks), pp. 179–187. Wageningen, The Netherlands: Wageningen Press.

van Lenteren, J. C. 1993b Integrated pest management: the inescapable future. In *Modern crop protection: developments and perspectives* (ed. J. C. Zadoks), pp. 217–225. Wageningen, The Netherlands: Wageningen Press.

van Lenteren, J. C. 1997a From *Homo economicus* to *Homo ecologicus*: towards environmentally safe pest control. In *Modern agriculture and the environment* (eds D. Rosen, E. Tel-Or, Y. Hadar & Y. Chen), pp. 17–31. Dordrecht, The Netherlands: Kluwer Academic.

van Lenteren, J. C. 1997b Benefits and risk of introducing exotic macro-biological control agents into Europe. *EPPO Bull.* **27**, 15–27.

van Lenteren, J. C. 1998 Sustainable and safe crop protection: a reality. Mededelingen van de Faculteit der Landbouwwetenschappen. *Universiteit Gent* **63**, 409–414.

van Lenteren, J. C. 2000a A greenhouse without pesticides: fact or fantasy? *Crop Protect.* **19**, 375–384. (doi:10.1016/S0261-2194(00)00038-7)

van Lenteren, J. C. 2000b Measures of success in biological control of arthropods by augmentation of natural enemies. In *Measures of success in biological control* (eds G. Gurr & S. Wratten), pp. 77–103. Dordrecht, The Netherlands: Kluwer Academic.

van Lenteren, J. C. 2003 Commercial availability of biological control agents. In *Quality control and production of biological control agents: theory and testing procedures* (ed. J. C. van Lenteren), pp. 167–179, ch. 11. Wallingford, UK: CAB International.

van Lenteren, J. C. 2005 Early entomology and the discovery of insect parasitoids. *Biol. Control* **32**, 2–7. (doi:10.1016/j.biocontrol.2004.08.003)

van Lenteren, J. C. & Bueno, V. H. B. P. 2003 Augmentative biological control of arthropods in Latin America. *BioControl* **48**, 123–139. (doi:10.1023/A:1022645210394)

van Lenteren, J. C. & Godfray, H. C. J. 2005 European science in the Enlightenment and the discovery of the insect parasitoid life cycle in The Netherlands and Great Britain. *Biol. Control* **32**, 12–24. (doi:10.1016/j.biocontrol.2004.08.009)

van Lenteren, J. C. & Manzaroli, G. 1999 Evaluation and use of predators and parasitoids for biological control of pests in greenhouses. In *Integrated pest and disease management in greenhouse crops* (eds R. Albajes, M. L. Gullino, J. C. van Lenteren & Y. Elad), pp. 183–201. Dordrecht, The Netherlands: Kluwer.

van Lenteren, J. C. & Woets, J. 1988 Biological and integrated pest control in greenhouses. *Annu. Rev. Entomol.* **33**, 239–269. (doi:10.1146/annurev.en.33.010188.001323)

van Lenteren, J. C. et al. 2003 Environmental risk assessment of exotic natural enemies used in inundative biological control. *BioControl* **48**, 3–38. (doi:10.1023/A:1021262931608)

van Lenteren, J. C., Bale, J. S., Bigler, F., Hokkanen, H. M. T. & Loomans, A. J. M. 2006a Assessing risks of releasing exotic biological control agents of arthropod pests. *Annu. Rev. Entomol.* **51**, 609–634. (doi:10.1146/annurev.ento.51.110104.151129)

van Lenteren, J. C, Cock, M. J. W., Hoffmeister, T. S. & Sands, D. P. A. 2006b Host specificity in Arthropod biological control, methods for testing and interpretation of the data. In *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (eds F. Bigler, D. Babendreier & U. Kuhlmann), pp. 38–63. Wallingford, UK: CAB International.

van Steenis, M. 1995 Evaluation and application of parasitoids for biological control of *Aphis gossypii* in glasshouse cucumber crops. PhD thesis, Wageningen University.

Vereijken, P., Edwards, C., El Titi, A., Fougeroux, A. & Way, M. 1986 In *Proc. Workshop on Integrated Farming*, pp. 34, Bulletin IOBC/WPRS 1986/IX/2.

Visser, J. H. 1986 Host odor perception in phytophagous insects. *Annu. Rev. Entomol.* **31**, 121–144. (doi:10.1146/annurev.en.31.010186.001005)

Waage, J. 1997 Global developments in biological control and the implications for Europe. *EPPO Bull.* **27**, 5–13.

Waage, J. K. & Greathead, D. J. 1988 Biological control: challenges and opportunities. *Phil. Trans. R. Soc. B* **318**, 111–128. (doi:10.1098/rstb.1988.0001)

Wäckers, F. L. 2003 The parasitoids' need for sweets: sugars in mass rearing and biological control. In *Quality control and production of biological control agents: theory and testing procedures* (ed. J. C. van Lenteren), pp. 59–72. Wallingford, UK: CAB International.

Wardlow, L. R. 1992 The role of extension services in integrated pest management in glasshouse crops in England and Wales. In *Proc. Int. Symp. "Biological Control and Integrated Crop Protection: towards environmentally safer agriculture", Veldhoven, The Netherlands, 8–13 September 1992*, (eds J. C. van Lenteren, A. K. Minks & O. B. M. de Ponti), pp. 193–200.

Whitehouse, M. E. A., Wilson, L. J. & Fitt, G. P. 2005 A comparison of arthropod communities in transgenic *Bt* and conventional cotton in Australia. *Environ. Entomol.* **34**, 1224–1241. (doi:10.1603/0046-225X(2005)034[1224:ACOACI]2.0.CO;2)

Wijnands, F. G. & Kroonen-Backbier, B. M. A. 1993 Management of farming systems to reduce pesticide inputs: the integrated approach. In *Modern crop protection: developments and perspectives* (ed. J. C. Zadoks), pp. 227–234. Wageningen, The Netherlands: Wageningen Press.

Winkler, K. 2005 Assessing the risks and benefits of flowering field field edges: strategic use of nectar sources to boost biological control. PhD thesis, Wageningen University.

Winkler, K., Waeckers, F. L., Bukovinszkine-Kiss, G. & van Lenteren, J. C. 2006 Nectar resources are vital for *Diadegma semiclausum* fecundity under field conditions. *Basic Appl. Ecol.* **7**, 133–140.

Yu, X., Heong, K.L., Hu, C., Barrion, A.T. 1996 Role of non-rice habitats for conserving egg parasitoids of rice planthoppers and leafhoppers. In *Proc. Int. Workshop on Pest Management Strategies in Asian Monsoon Agroecosystems* (eds N. Hokyo & G. Norton), pp. 63–67. Kumato, Japan: Kyushu National Agricultural Experimental Station.