SECTION V

Biological Control
CHAPTER 7

Biological Control of Insects

James Robert Hagler

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7.1 INTRODUCTION

Throughout history, a relatively small number of insect species have threatened human welfare by transmitting disease, reducing agricultural productivity, damaging forests and urban landscapes, or acting as general nuisances. Humans have attempted to eradicate, control, or manage these pests using a wide variety of methods including chemical, biological, cultural, and mechanical control (National Academy of Sciences, 1969). The main strategy used in the second half of the 20th century for controlling pests has been the use of chemical pesticides (van den Bosch, 1978; Casida and Quistad, 1998).

The pesticide revolution began in the early 1940s with the development of synthetic pesticides. These pesticides showed a remarkable ability to kill pests without any apparent side-effects. The early success of synthetic pesticides led many experts to believe that they had discovered the “silver bullet” for pest control. As a result, biological, cultural, and mechanical controls were often underutilized or disregarded as viable pest management strategies. Although pesticides provided a short-term solution for many pest problems, the long-term negative effects of using pesticides did not begin to surface until the late 1950s. In 1962, Rachel Carson’s book *Silent Spring* provided the general public with the first warning that many pesticides produced undesirable side-effects on our environment (Carson, 1962). Further consequences of overreliance on pesticides became apparent over the next few decades. For example, prior to the 1940s, it was estimated that insects destroyed 7% of the world’s crops. By the late 1980s, crop destruction due to pests had risen to 13% (Wilson, 1990). This doubling of crop damage since the pesticide revolution occurred despite a 12-fold increase in pesticide use (Poppy, 1997). The increase in crop destruction is due, in part, to increased incidence of pesticide resistance, secondary pest outbreaks, and natural enemy destruction. These problems, coupled with increasing environmental concerns and pesticide costs, have forced growers to seek more environmentally safe and cost-effective pest control strategies. One of the most promising, yet underused, pest control strategies is biological control.

This chapter will provide readers with a general review of the fundamental principles of biological control, including the history, the methods, and the agents used for biological control. Central to this review is discussion of the key issues surrounding implementation of biological control in the new millennium.

7.2 DEFINITION OF BIOLOGICAL CONTROL

Entomologists have struggled with a definition for biological control for almost a half-century. In 1919, the eminent biological control researcher H. S. Smith defined
biological control simply as “the control or regulation of pest populations by natural enemies” (Debach and Rosen, 1991). He defined a natural enemy as any biological organism that exerts the control. His definition only included the use of predators, parasitoids, and pathogens as biological control agents.

Biological control is the deliberate exploitation of a natural enemy for pest control. In other words, biological control is an activity of man. This differs from natural control, which is unassisted pest regulation due to biotic (e.g., predators, parasites, and pathogens) and abiotic (e.g., weather) forces (Debach and Rosen, 1991). Recently, a working group from the National Academy of Sciences broadened the definition of biological control beyond living organisms to include the use of genes or gene products to reduce pest populations (National Research Council, 1987). In 1995, the U.S. Congress, Office of Technology Assessment defined “biologically based technologies for pest control” (BBTs). BBTs included the use of predators, parasitoids, pathogens, pheromones, natural plant derivatives (e.g., pyrethrums, nicotine, etc.), insect growth regulators, and sterile insect releases as biological control agents (U.S. Congress, 1995).

Variations in the definition of biological control might seem trivial, yet those who prefer the more narrow definition are concerned that these other pest management approaches might garner most of the research dollars at the expense of the traditional biological control approaches. For this review, I will use the strictest definition of biological control and consider only predators, parasitoids, and pathogens as biological control agents. Pheromones, natural plant compounds, insect growth regulators, sterile insect releases, and genetic manipulations will be regarded here as parabiological control agents (Sailer, 1991). Although I do make a distinction between biological control and parabiological control, it is important to understand that parabiological control tactics will be of the utmost importance to enhancing the future success of the traditional biological control approaches. It is likely that parabiological control tactics will be included in the definition of biological control more frequently in the years to come because they are usually selective and environmentally benign.

### 7.3 HISTORY OF BIOLOGICAL CONTROL

One of the oldest-known methods used to control pests is the deliberate exploitation of their natural enemies. The first documented evidence of the use of natural enemies to control pest populations came from China and Yemen. Hundreds of years ago, ant colonies were moved between fields for controlling pests in tree crops (Coulson et al., 1982). Linnaeus made written reports of the use of predators to control pests in 1752 (Van Driesche and Bellows, 1996). In 1762, the first planned successful international movement of a natural enemy was undertaken. The mynah bird was introduced from India to control the red locust, *Nomadacris septemfasciata* in Mauritius. By 1772, this bird was credited for successfully controlling a locust pest (Debach & Rosen, 1991).

The so-called “modern age of biological control” began in 1888 when natural enemies were collected in Australia and imported to California to control the cottony-cushion scale, *Icerya purchasi* Maskell. This project is considered one of the major
milestones in the history of entomology. The cottony-cushion scale was discovered in Menlo Park, California in 1868. This scale was not native to California, therefore it lacked any co-evolved natural enemies. The scale population exploded and within 20 years it had destroyed the citrus industry in California. In 1886, C.V. Riley (Chief of the Division of Entomology of the USDA), Albert Koebele, and D.W. Coquillett (and many others), initiated a classical biological control program targeted at the cottony-cushion scale. It was believed that this scale originated in Australia, so that is where the researchers searched for its natural enemies. The cottony-cushion scale was difficult to locate in Australia because the native natural enemy complex there was very effective at suppressing the pest population. However, a few scales were discovered that were either parasitized by a fly, Cryptochetum iceryae (Williston) or being eaten by a lady bird beetle, Vedalia cardinalis (later named Rodolia cardinalis [Mulsant]). These two natural enemies were shipped from Australia to California and placed into screened cages in citrus orchards for further evaluation. The lady beetle had a voracious appetite specifically for cottony cushion scale and within a couple of months had completely devoured all of the scales within the cages. The beetles were then distributed to a few growers in California and released into open citrus orchards for their establishment. By the end of the decade, the cottony cushion scale was fully controlled by the lady beetle. To date, this is perhaps the greatest example of a successful biological control program (Caltagirone and Doutt, 1989).

Ironically, the overwhelming success of this effort proved to be a problem for subsequent biological control programs, because every subsequent research program was expected to yield equally impressive results. Over the past 110 years there have been dozens of successful biological control programs initiated. Unfortunately, there have also been many failures. A database has been developed by the International Institute of Biological Control (IIBC), called BIOCAT, that is accessible on the World Wide Web. This database summarizes both successful and unsuccessful classical biological control programs (Greathead and Greathead, 1989). It also provides interesting insights into the patterns that exist between successful and unsuccessful programs.

### 7.4 BIOLOGICAL CONTROL — ITS ROLE IN IPM

Integrated pest management, or IPM, is a pest management approach that incorporates several different management strategies into one overall program (Stern et al., 1959). Ideally, IPM programs are designed to provide environmentally friendly and sustainable pest control. Ironically, before the insecticide revolution, the fundamental principles of IPM were being readily used for pest control. There was an enormous amount of effort dedicated to studying insect pest biology and non-chemical pest control strategies (Kogan, 1998). During this time, there were no “silver bullets” for pest control, so entomologists were forced to “integrate” biological, cultural, physical, and mechanical controls. Biological control is only one of the components of IPM. Biological control was a popular pest management strategy because it complemented many of the other IPM tactics. However, in the late 1940s, synthetic pesticides became the dominant method for pest control. Pesticides were
not only incompatible with most other IPM tactics, but they were used without any regard to those alternate approaches.

The “re-invention” of IPM originated in the late 1950s when researchers began to realize that chemical pest control was not an effective strategy. The development of resistance to pesticides, the occurrence of secondary pest outbreaks, along with the harmful effects of pesticides on natural enemies and on the environment forced us to reexamine the fundamental concepts of IPM. Today, the frequency that IPM is being used as it was originally defined is rising (Kogan, 1998).

The future of IPM relies on our ability to get back to the basics of pest management. Emphasis needs to be replaced on studying the ecology of pests and their natural enemies and using IPM tactics that are compatible with biological control. In order for biological control to achieve wide-scale success, it is critical that environmentally benign, area-wide IPM tactics are used in concert with biological control. The principles of the IPM approach to pest management are discussed in greater detail elsewhere in this edition.

### 7.5 TYPES OF BIOLOGICAL CONTROL

The three basic types of biological control are conservation, introduction, and augmentation (Waage and Mills, 1992). Conservation involves preserving and/or enhancing natural enemies that are already present in the environment. Introduction involves importing and releasing exotic (non-indigenous) natural enemies against foreign and indigenous pests. Augmentation involves mass-rearing natural enemies in the laboratory and releasing them into the environment. These strategies are not mutually exclusive. For example, conservation should also be practiced when augmentation and introduction are employed.

#### 7.5.1 Conservation of Natural Enemies

Conservation of natural enemies means enhancing or protecting the environment for natural enemies. It differs from natural control in that it is a conscious management decision. Conservation is achieved by using pest control tactics that preserve or enhance natural enemies (e.g., planting refuge crops) or by avoiding pest control tactics that are harmful to them (e.g., broad-spectrum pesticides). Conservation of natural enemies is a biological control tactic that should be a component of every pest management program, but, unfortunately, is underutilized due to the planning and effort required. Some of the methods used for conserving natural enemy populations include: avoiding the use of broad-spectrum insecticides; planting cover crops or refuge crops; and providing food supplements for natural enemies (see Van Driesche and Bellows, 1996 for more detail).

The use of broad-spectrum chemical insecticides is the major reason that the potential for conservation has not been reached. Most predators and parasitoids are vulnerable to insecticides. Unfortunately, the application of broad-spectrum insecticides is far too often the first and only method used for pest management (van den Bosch, 1978). Recently, more selective insecticides have been developed that are
more compatible with conservation. Some examples of selective insecticides include the use of genetically engineered crops (e.g., Bt cotton), insect pathogens, and chemical formulations that contain pest-specific substances that interfere with the pest’s endocrine system (i.e., insect growth regulators) (U.S. Congress, 1995). The use of pest-specific insecticides should decrease pest populations while conserving natural enemy populations. Before applying any insecticides, the applicator should be aware of the chemical’s effect on non-target natural enemies (Jones et al., 1998).

Another tactic for conservation is to provide cover crops or refuge crops for predators and parasitoids. Cover and refuge crops, planted within and adjacent to high cash crops, serve to help attract, maintain, or increase predator and parasitoid populations by providing them with a more suitable habitat to survive. Growers can conserve predators and parasitoids in their orchards (e.g., pecans and apples) by planting leguminous cover crops (e.g., clover), which attract numerous natural enemy species and sometimes replenish the soil with nutrients (e.g., nitrogen) (Bugg et al., 1991). However, some cover crops may increase the cost of production because they require extra maintenance, water, or fertilizer beyond that required for the cash crop.

Refuge crops can also be planted adjacent to other crops in order to provide predators and parasitoids with a supplemental food source. For example, many parasitoid species rely on nectar-producing plants for energy. Sometimes, plants that are known to yield a high volume of nectar are planted near other crops to serve as an “energy source” for foraging parasitoids. Similarly, pollen is an excellent food supplement for many predator species. Sometimes pollen-rich plants (e.g., sunflowers) are planted near crops to enhance predator populations. Additionally, refuge crops can provide natural enemies with an insecticide-free habitat when adjacent fields are being treated with insecticides. Insecticide-free areas can serve as an invaluable refuge for natural enemies that might be otherwise exposed to harmful insecticides (Van Driesche and Bellows, 1996).

7.5.2 Introduction of Natural Enemies
(Classical Biological Control)

Insects are often introduced into new areas either accidentally or purposefully. Sometimes these introduced insects (also known as exotic or non-indigenous insects) find a suitable host plant(s) in the new habitat in which they can survive and reproduce. When an exotic insect is introduced into a new area, it often does not have any co-evolved natural enemies to suppress its population. As a result, the exotic insect soon becomes a pest. The cottony-cushion scale scenario described above is a perfect example of an insect that was accidentally introduced into an area in which it did not have any co-evolved natural enemies. As a consequence, the cottony-cushion scale, which is not a pest in its native land of Australia, became a destructive pest in California (Caltagirone and Doutt, 1989).

The gypsy moth is another example of an introduced insect becoming a significant pest. In 1869, a scientist attempting to develop the silk industry in America purposefully brought gypsy moths into the U.S. from Europe (Debach and Rosen, 1991). Unfortunately, a few of the captive moths escaped and reproduced. In a very short period of time, with no native natural enemies to control them, the gypsy moth
became (and continues to be) the major forest pest in the United States (Elkinton

When an exotic insect establishes itself in a new area as a pest, the first place
to search for potential biological control agents is in the pest’s native habitat. Often,
an introduced insect has co-evolved natural enemies in its native habitat that kept it
from becoming a pest. If the origin of the pest is known, then natural enemies can
be imported from its homeland and introduced into the new habitat. Importing and
introducing an exotic natural enemy is also known as classical biological control.
Classical biological control is probably the most successful, yet controversial type
of biological control (U.S. Congress, 1995; Waage, 1996). Classical biological
control requires more forethought and research than conservation or augmentation.
Great care must be taken when attempting to establish non-indigenous natural
enemies into a new region in order to minimize the chance of creating further
unforeseen ecological problems (Waage and Mills, 1992).

Classical biological control is researched and implemented by scientists and is
usually funded by federal or state governments. It is not unusual for a classical
biological control program to take five to ten years to complete. However, the
economic benefits derived from a successful classical biological control program
are usually impressive. The benefit-to-cost ratio can range from 10:1 to 100:1
(Tisdell, 1990).

Several basic principles should be followed when selecting a classical biological
control agent. The single greatest characteristic is that the agent must have a narrow
host range, both to increase the effect on the target pest and to minimize any possible
effects on non-target organisms (Debach and Rosen, 1991; Waage and Mills, 1992).
It is for this reason that specialist parasitoids are generally regarded as better can-
ididates for classical biological control than generalist predators. The natural enemy
should also originate from a region with a climate similar to the one in which it is
being introduced. Obviously, if the exotic natural enemy cannot survive and repro-
duce, it will not be an effective biological control agent. Additionally, the exotic
organism should be (although not always) easy to capture in large numbers in its
native habitat or be easy to rear (Debach and Rosen, 1991). The chances of estab-
lishing an exotic natural enemy are greatly increased if thousands or even millions
of individuals can be released over a period of several years. Finally, every precaution
needs to be taken to ensure that the exotic natural enemy itself does not become a
pest. Before any classical biological control agent is introduced into a new area it
must be extensively studied as an individual and as part of its new environment (see
Waage and Mills [1992] and Van Driesche and Bellows [1993] for thorough reviews
of the scientific protocols used for classical biological control).

7.5.3 Augmentation of Natural Enemies

Another type of biological control is augmentation, which consists of augmenting
existing populations by producing natural enemies in the laboratory and releasing
them into the field. The augmentation of natural enemy populations is the biological
control equivalent to insecticide applications (Table 7.1). Unlike conserved or intro-
duced natural enemies, augmented natural enemies are not necessarily expected to
survive into the next year. However, when augmentation is combined with effective conservation, natural enemy populations may increase over time.

The most widely used augmentative biological control agents are insect pathogens. Currently, several pathogens are commercially available for controlling a wide variety of pests. In many cases, predators and parasitoids are not viable augmentative biological control agents because they are not practical or economically feasible to mass-produce (Grenier et al., 1994). There are several logistical difficulties that must be overcome before predators and parasitoids become widely used for augmentative biological control. Currently, most predator and parasitoid species are being reared on their prey (host) at high cost. Inexpensive artificial diets might make the mass production of predators and parasitoids economically feasible (Grenier et al., 1994).

Once the difficulties of developing artificial diets are overcome, then quality control studies are needed to test the efficacy of the biological control agents in the field (Hoy et al., 1991). Predators and parasitoids reared for successive generations on artificial diet in the laboratory might not perform as well as their native counterparts (i.e., they might become domesticated) (Hagler and Cohen, 1991; van Lenteren et al., 1997). Additionally, the production, distribution, and application of augmented biological control agents needs to be standardized so that their full potential is realized (Hoy et al., 1991; Smith, 1996; Obrycki et al., 1997; O’Neil et al., 1998; Ridgway et al., 1998). Augmentative biological control is not just a matter of ordering a package of natural enemies, releasing them into the field, and waiting for the control to happen. Both the suppliers and users of natural enemies need to have an understanding of how to apply the agent properly and of its limitations. End-users need to apply the agent in sufficient quantities to ensure effective pest management when the target pest is most vulnerable (Smith, 1996). For example, it would not be practical to release an egg parasitoid when there were no pest eggs present in the field. Also, it is important that the biological control agent is applied in a manner to minimize its mortality. For example, most parasitoids should be released during the cool part of the day and away from direct sunlight.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Predators</th>
<th>Parasitoids</th>
<th>Pathogens</th>
<th>Conventional Pesticides</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Host Range</strong></td>
<td>Moderate/Wide</td>
<td>Narrow</td>
<td>Narrow</td>
<td>Wide</td>
</tr>
<tr>
<td><strong>Commercial Availability</strong></td>
<td>Low</td>
<td>Low</td>
<td>Medium</td>
<td>High</td>
</tr>
<tr>
<td><strong>Shelf Life</strong></td>
<td>Short (days)</td>
<td>Short (days)</td>
<td>Short/Moderate</td>
<td>Long (years)</td>
</tr>
<tr>
<td><strong>Cost</strong></td>
<td>High</td>
<td>High</td>
<td>Moderate</td>
<td>Low</td>
</tr>
<tr>
<td><strong>Ease of Application</strong></td>
<td>Difficult</td>
<td>Difficult</td>
<td>Easy</td>
<td>Easy</td>
</tr>
<tr>
<td><strong>Effectiveness</strong></td>
<td>Low</td>
<td>Low/Moderate</td>
<td>Low/Moderate</td>
<td>High</td>
</tr>
<tr>
<td><strong>Compatibility with Pesticides</strong></td>
<td>Low</td>
<td>Low</td>
<td>High</td>
<td>High</td>
</tr>
<tr>
<td><strong>Environmental Impact</strong></td>
<td>None</td>
<td>None</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td><strong>Occurrence of Resistance</strong></td>
<td>Low</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
</tr>
</tbody>
</table>
Whereas predators and parasitoids have been used sparingly for augmentative biological control, there are circumstances where they have been used successfully (Hoffmann et al., 1998). They are often used for controlling pests on high cash crops that are grown in small fields (e.g., strawberries) (Hoffmann et al., 1998). Additionally, predators and parasitoids are often released into barnyards, interior landscapes, greenhouses, and home gardens where insecticide applications are impractical because of the proximity to large numbers of humans and livestock.

The concept of augmentative biological control has generated an enormous amount of public interest over the past decade. Many small businesses have begun to market predators, parasitoids, and pathogens as “environmentally friendly” and “natural” alternatives for pest control. Currently, there are over 100 companies in North America that are dedicated to selling beneficial organisms (i.e., predators and parasites) for augmentative biological control use (Hunter, 1994). Although probably environmentally safe, these biological control agents might be serving only as a placebo to the end-user (Harris, 1990). More thorough field studies are needed to evaluate the efficacy of augmentative biological control agents before they are sold to consumers (Hagler and Naranjo, 1996). Additionally, the quality of predators and parasitoids reared for successive generations in captivity need further examination (Hopper et al., 1993).

### 7.6 GROUPS OF NATURAL ENEMIES

Natural enemies are classified into three major groups; predators, parasitoids, or pathogens. Predators and parasitoids are often collectively referred to as macrobiological control agents and pathogens are often called microbiological control agents, or simply microbials. A fourth classification of natural enemies, that of parabiological control agents (Sailer, 1991), is often included when the broadest definition of biological control is used (U.S. Congress, 1995).

Natural enemy communities are often large and complex, with a wide array of interactions occurring at any given time (e.g., predator-prey interactions, hyperpredation, competition, etc.). An excellent review of the types of natural enemy interactions that can occur is provided by Sunderland et al. (1997).

#### 7.6.1 Predators

Insect predators, including representatives from most of the major orders in the class Insecta, are abundant in agroecosystems, urban environments, and aquatic habitats (Table 7.2). Most insect predators feed on a wide variety of prey, consume many prey throughout their immature and adult life stages, rapidly devour all or most of their prey, and prey on insects and mites smaller than themselves (Sabelis, 1992; Lucas et al., 1998). Although predators are regarded as a major biological control force, remarkably little is known about their prey choices in the field. Complex interactions among predators and prey make each predator assessment unique and difficult to describe (Hagler and Naranjo, 1996; Sunderland, 1996; Naranjo and Hagler, 1998).
Table 7.2  A Listing of Some of the Common Predators Found in Agroecosystems

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Predator</th>
<th>Prey*</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthoptera</td>
<td>Mantidae</td>
<td>Praying mantids</td>
<td>Large and small insects</td>
<td>Van Driesche and Bellows, 1996</td>
</tr>
<tr>
<td></td>
<td>Labiduridae</td>
<td>Earwigs</td>
<td>Caterpillars, many others</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Aleolothripidae</td>
<td>Predaceous thrips</td>
<td>Spider mite eggs</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Anthocoridae</td>
<td>Minute pirate bugs</td>
<td>Insect eggs, soft-bodied insects, small</td>
<td>Hagler and Naranjo, 1996</td>
</tr>
<tr>
<td></td>
<td>Lygaeidae</td>
<td>Big-eyed bugs</td>
<td>Insect eggs, soft-bodied insects, small</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Miridae</td>
<td>Plant bugs</td>
<td>Insect eggs, soft-bodied insects, small</td>
<td>Hagler and Naranjo, 1994</td>
</tr>
<tr>
<td></td>
<td>Nabidae</td>
<td>Damsel bugs</td>
<td>Insect eggs, small insects</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Reduviidae</td>
<td>Assassin bugs</td>
<td>Small insects, caterpillars</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Pentatomidae</td>
<td>Predaceous stink bugs</td>
<td>Caterpillars</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>Chrysopidae</td>
<td>Lacewings</td>
<td>Aphids, soft-bodied insects</td>
<td>Flint and Driestadt, 1998</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Coccinellidae</td>
<td>Lady beetles</td>
<td>Aphids, soft-bodied insects, insect eggs</td>
<td>Flint and Driestadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Carabidae</td>
<td>Ground beetles</td>
<td>Insect eggs, soft-bodied insects, small</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Staphylinidae</td>
<td>Rove beetles</td>
<td>Small insects</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Melyridae</td>
<td>Soft-winged flower bees</td>
<td>Insect Eggs, soft-bodied insects, small</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td>Diptera</td>
<td>Cecidomyiidae</td>
<td>Predaceous midges</td>
<td>Aphids</td>
<td>Flint and Driestadt, 1998</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>Formicidae</td>
<td>Ants</td>
<td>Insect eggs, soft-bodied insects, small</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Vespidae</td>
<td>Hornets, yellow jackets</td>
<td>Caterpillars, small insects</td>
<td>Flint and Driestadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Sphecidae</td>
<td>Digger wasps, mud</td>
<td>Caterpillars, small insects</td>
<td>Flint and Driestadt, 1998</td>
</tr>
</tbody>
</table>

* Virtually all of the predators listed here are generalist predators and feed on many types of prey.
Most predators are generalist feeders that can and will feed on a wide variety of insect species and life stages (Whitcomb and Godfray, 1991). Some predators, such as lady beetles and lacewings may prefer certain prey (e.g., aphids) (Obrycki and Kring, 1998), but they will attack many other prey that they encounter. Unfortunately, many important predator species are cannibalistic and/or feed on other beneficial insects (Sabelis, 1992). For example, green lacewings and praying mantids are notorious for preying on younger and weaker members of their own species. Most predators have a host range that also includes other beneficial insects. It is not uncommon for higher-order predators to feed on other predators or parasitoids (Polis, 1994; Sunderland et al., 1997; Rosenheim, 1998). Additionally, some predator species can be pests. Perhaps the best example of an insect possessing the characteristics of both a pest and a predator is the fire ant, Solenopsis spp. The fire ant is a voracious predator on the eggs of many lepidopteran pests. However, the fire ant is also a major pest because it inflicts painful stings to animals and constructs nests that are detrimental to landscapes (Lofgren et al., 1975; Way and Khoo, 1992).

Predators must eat many prey items during their immature and/or adult stages in order to survive. The number of prey needed for a given predator species to complete its development varies among species. Some predators, such as some lacewing species, are only predaceous during their immature stages. The adults of these lacewings only feed on nectar or water.

The time spent handling prey varies by predator species and life stage. Handling times can vary from a few seconds to several hours (Cloarec, 1991; Wiedenmann and O’Neil, 1991). Most predators are highly mobile, and are only briefly associated with their prey. The predator quickly devours a single prey item and then moves on to feed again. The relatively short period of time that predators are associated with their prey, coupled with the lack of evidence of feeding (i.e., they often totally devour their prey) are two of the many reasons that make it difficult to quantify predation in the field (Hagler et al., 1991).

Generally, predators attack and feed on arthropods that are smaller and weaker than themselves (Whitcomb and Godfrey, 1991; Sabelis, 1992; Lucas et al., 1998). Preying on smaller animals allows them to use brute force to capture and kill prey. Some predators, however, are able to kill and consume prey many times their size by using artifacts such as venoms, traps (pitfall traps, webs, etc.), and modified body structures (raptorial forelegs, body spines, modified mouthparts).

Predators consume their prey in one of two different ways. Some predators (e.g., beetles, dragonflies, praying mantids) use biting or chewing mouthparts for consuming their prey. Chewing predators usually capture smaller prey using their powerful mandibles, and totally devour prey (Figure 7.1). Others (e.g., true bugs) use piercing and sucking mouthparts for consuming prey. Piercing and sucking predators quickly pierce their prey with needle-like mouthparts, inject potent digestive enzymes, and suck up the internal liquefied nutrients from their victims (Figure 7.2). Typically, piercing and sucking predators do not totally devour their prey (Cohen, 1998).

Predators search for their prey using one of two strategies. Some groups of predators actively stalk their prey. Stalking predators are usually very quick and
Figure 7.1  A lady beetle devouring an aphid with its powerful chewing mandibles.

Figure 7.2  A spined soldier bug piercing and sucking nutrients from a Mexican bean beetle larva.
mobile (e.g., lady beetles). Other groups of predators patiently sit and wait for mobile prey to walk into an ambush. Ambush predators are usually well camouflaged (e.g., praying mantids) and use the element of surprise for attacking unsuspecting prey (Cloarec, 1991; Sabelis, 1992).

Predators are important natural agents, and as a group, are usually best suited for conservation because of their generalist feeding habits. Every effort should be made to conserve or enhance indigenous predator populations using one or more of the conservation tactics described previously. If a given predator species is to be considered for classical biological control, extensive research will be needed to ensure that non-target organisms will not be impacted.

The potential for using predators for augmentative biological control has not been fully realized. Mass-producing predators is costly and difficult. Furthermore, research aimed at testing the efficacy of predators reared on artificial diets is lacking (Leppa and King, 1996). For instance, there is always the possibility that predators reared for successive generations on an inanimate artificial diet will become domesticated. Domesticated predators may be unable to perform as efficiently as their native counterparts (Hagler and Cohen, 1991). Hopefully, in the near future, inexpensive and effective artificial diets will be developed that will facilitate the research, mass production, and application of predators as augmentative biological control agents (Grenier et al., 1994).

7.6.2 Parasitoids

Parasitoids are often referred to in the entomology literature as parasites. Although these two terms are often used interchangeably, a distinction should be made between them. A parasitoid ultimately consumes and kills its hosts, whereas a true zoological parasite (e.g., tapeworm) does not. Virtually all arthropod “parasites” are true parasitoids (Godfray, 1994).

Parasitoids are abundant in virtually all agroecosystems and urban environments. However, they are not as widespread in the class Insecta as predators. Almost all of the major parasitoid species occur in the orders Hymenoptera (wasps) (approximately 78% according to Feener and Brown [1997]) and Diptera (flies) (Table 7.3). Almost every insect pest, predator, and parasitoid has one or more parasitoid species that attacks it. Parasitoids that attack insect pests are commonly known as primary parasitoids, while those that attack other parasitoids are known as hyperparasitoids. Obviously, hyperparasitoids are not ideal candidates for biological control (Sullivan, 1987).

Parasitoids have many characteristics that distinguish them from predators (Table 7.1). Generally, parasitoids have a narrow host range; feed on only one host throughout their life span; attack hosts larger than themselves; feed on their host only during their immature stage (although the adults of some species may feed on hosts); and are immobile as immatures and free-living as adults (Sabelis, 1992).

Usually, a parasitoid species will attack a specific life stage of its host. Thus, parasitoids are classified as egg parasitoids, larval (nymphal) parasitoids, or adult parasitoids. Some parasitoid species will oviposit in one life stage, but emerge in a later life stage. Such parasitoids are named accordingly. For example, Chelonus sp. nr. curvimaculatus is an egg-larval parasitoid of pink bollworm (Hentz et al., 1998).
The narrow host range exhibited by parasitoids makes them ideal biological control agents. Most parasitoids only attack one species or a group of related species. Therefore, parasitoids are well suited for conservation, augmentation, and classical biological control. To date, parasitoids are the most important of the macrobiological control agents used for classical biological control programs. Because most parasitoids are species- and stage-specific, it is critical that they are present in the habitat when their host is at its vulnerable stage of development. Therefore, the timing of a parasitoid release is of utmost importance. It would not be effective to release an egg parasitoid if only the larval stage of the targeted pest was present in the field.

Parasitoids have evolved a much more intricate relationship with their hosts than predators have with their prey. Adult parasitoids are free-living and usually feed on honeydew, nectar, pollen, or water in order to survive. However, some adult species are predaceous and will prey on their hosts by piercing soft-bodied prey (i.e., whiteflies and aphids) with their ovipositor or mouthparts and eating the juices that leak out of the wounded host. This type of behavior, known as “host feeding,” leads to the death of the host and usually enhances the impact of the parasitoid on the host population (Jervis and Kidd, 1986; Heimpel and Collier, 1996).

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Host</th>
<th>Internal/External</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diptera</td>
<td>Tachinidae</td>
<td>Beetles, butterflies, and moths</td>
<td>Internal</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Nemestrinida</td>
<td>Locusts, beetles</td>
<td>Internal</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Phoridae</td>
<td>Ants, caterpillars, termites, flies, others</td>
<td>Internal</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Cryptocheilidae</td>
<td>Scale insects</td>
<td>Internal</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>Chalcididae</td>
<td>Flies and butterflies (larvae and pupae)</td>
<td>Internal or External</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
<tr>
<td></td>
<td>Encyrtidae</td>
<td>Various insects eggs, larvae or pupae</td>
<td>Internal</td>
<td>van Driesche and Bellows, 1996</td>
</tr>
<tr>
<td></td>
<td>Eulophidae</td>
<td>Various insects eggs, larvae or pupae</td>
<td>Internal or External</td>
<td>van Driesche and Bellows, 1996</td>
</tr>
<tr>
<td></td>
<td>Aphelinidae</td>
<td>Whiteflies, scales, mealybugs, aphids</td>
<td>Internal or External</td>
<td>van Driesche and Bellows, 1996</td>
</tr>
<tr>
<td></td>
<td>Trichogrammatidae</td>
<td>Moth eggs</td>
<td>Internal</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Mymaridae</td>
<td>True bugs, flies, beetles, leafhoppers eggs</td>
<td>Internal</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Scelionidae</td>
<td>Insects eggs of true bugs and moths</td>
<td>Internal</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Ichneumonidae</td>
<td>Larvae or pupae of beetles, caterpillars and wasps</td>
<td>Internal or External</td>
<td>Flint and Dreistadt, 1998</td>
</tr>
<tr>
<td></td>
<td>Brachonidae</td>
<td>Larvae of beetles, caterpillars, flies and sawflies</td>
<td>Internal (Mostly)</td>
<td>Knutson and Ruberson, 1996</td>
</tr>
</tbody>
</table>
Unlike predators, parasitoids are only (highly) mobile and able to seek out their host during the adult stage. Typically, adult females lay one or more eggs in (endoparasitoid) or on (ectoparasitoid) a host (Figure 7.3). When the egg hatches, the larva begins to feed on its host. Parasitoids do not immediately kill their hosts. The immobile larvae utilize the host as food and shelter throughout their development. The parasitoid-host relationship is more efficient than a predator-prey relationship, requiring far less food for survival (Hassell and Godfray, 1992).

The mode of life adapted by parasitoids has greatly limited their freedom of action; they have become highly adapted to certain niches. In particular, the larval stages of parasitoids have become intimately connected to and dependent on their hosts both for their shelter and food. Consequently, parasitoids are usually smaller than their host. To this end, biological control by parasitoids is subtler than a population of pests being devoured by predators. However, it is usually easy to detect parasitism. For example, immature whitefly parasitoids can be readily seen within large whitefly nymphs; many caterpillar egg parasitoids cause their host to turn black; and aphid parasitoids turn the aphids black and “mummified.”

Searching is vital to the success of parasitoids. Parasitoids are much more efficient than predators at searching and locating their hosts. They have an uncanny ability to locate prey, even at very low host densities, using chemical cues (Vet and Dicke, 1992; Godfray, 1994). For example, some parasitoids locate their host by homing in on long-range chemical cues produced by undamaged plants (Udayagiri
and Jones, 1993) and plants that have been damaged by caterpillars (Paré and Tumlinson, 1997). Once the plant has been located, the female wasp then begins to use short-range chemical cues produced directly by the pest (Tumlinson et al., 1993). Good searching capacity allows parasitoids to control pest populations more efficiently than predators.

Parasitoids as a group are commonly used for all types of biological control. Every effort should be made to conserve or enhance native parasitoid populations. Parasitoids are particularly susceptible to broad-spectrum pesticides, therefore applications of these materials should only be used as a last resort (Theiling and Croft, 1988; Jones et al., 1998).

The narrow host range exhibited by most parasitoid species makes them ideal candidates for classical biological control. As with predators, the full potential for using parasitoids for augmentative biological control has not been fully realized. Mass production of parasitoids is easier and less expensive than the mass production of predators, but research is still needed to further develop rearing procedures. To date, the greatest use for parasitoids as augmentative biological control agents has been in the greenhouse industry (van Lenteren and Woets, 1988). An enormous amount of progress has been made over the past decade in developing parasitoids for augmentative biological control (van Lenteren et al., 1997). In the near future, the application of parasitoids will be a common pest control tactic.

### 7.6.3 Pathogens

Just like vertebrates, insects are susceptible to a variety of pathogens. The pathogens used for biological control of insects include bacteria, fungi, viruses, protozoans, and nematodes. Within each of these groups, there are hundreds or thousands of species that are known to attack insects. However, only a few have been used for pest control. Naturally occurring pathogens commonly attack insects, causing illness and sometimes death (Figure 7.4). Often the sub-lethal effects of pathogens can alter insect behavior to prevent insect reproduction.

Dozens of pathogens have been mass-produced and marketed as “biological insecticides” (Cook et al., 1996). These pathogens, mainly bacteria (*Bacillus thuringiensis*), have been used for controlling a wide variety of pests. Most pathogens are applied directly to crops using standardized pesticide sprayers or dispersed through irrigation water (Chapple et al., 1996). Commercially available pathogens are attractive biological control agents because they usually have a narrow host range, are environmentally safe, and are biodegradable (Table 7.1). Unfortunately, microbials only account for about 2.0 to 5.0% of the world pesticide market (Payne, 1989; Ridgway and Inscoe, 1998). Currently, there are numerous other pathogen species that show promise as biological insecticides. However, more progress is needed toward developing better mass production systems and more stable formulations (Roberts et al., 1991).

Most types of pathogens share some of the pitfalls associated with chemical insecticides. For example, insects can develop resistance to pathogens if they are constantly exposed to them (McGaughey and Beeman, 1988; McGaughey, 1994;
Additionally, the development and registration of pathogens is often difficult and costly. Some pathogens have a short shelf life or field life. Improved formulations for pathogens may increase shelf life and field persistence, and ensure that the pathogens rapidly move from infected individuals to uninfected ones, killing the hosts.

Ironically, the narrow host range exhibited by most pathogens, which is a desirable quality for biological control, has limited commercial pathogen development. The pesticide industry is reluctant to invest in products that have a narrow host range, and thus, a narrow sales market (Waage, 1996).

The basic approaches used for exploiting pathogens are mainly by conservation and augmentation. Classical biological control of insects is only rarely attempted with pathogens, since most diseases are distributed worldwide (Milner, 1997). Naturally occurring pathogen populations are usually conserved through some form of microhabitat manipulation (Fuxa, 1987; Roberts et al., 1991) in order to create favorable conditions for pathogen reproduction. Most pathogens thrive in warm, moist habitats. Augmented pathogens, like predators or parasitoids, can be applied by either inoculation or inundation. For inoculation, the pathogen is released in low numbers where it maintains and spreads itself throughout the pest population. For inundation, the pathogen is applied in large quantities just like a chemical pesticide. In this case, the pathogen is not necessarily expected to spread throughout the pest population (Fuxa, 1987).
7.6.3.1 **Bacteria**

Many different insect species are infected and killed by bacteria. Bacterial pathogens are the most common type of pathogen used for biological control. Currently, there are several formulations that are registered for commercial pesticide use.

*Bacillus thuringiensis* or Bt, is the most widely applied biological control agent (Cook et al., 1996). Bt exerts its toxicity only after phytophagous insects have ingested it. The Bt toxin is a high molecular weight protein crystal that causes paralysis of the insect’s gut, followed by a general paralysis and insect death (Gill et al., 1992). The major advantages of using Bt (and most other bacterial pathogens) for pest control are that it is specific, effective, environmentally safe, and rapidly kills its host. Additionally, Bt has a short residual period so it is an ideal candidate for pest control on fruits and vegetables, in urban areas (parks), and near streams and ponds (Pinnock et al., 1977).

Several different formulations and varieties of Bt exist. Early Bt products only controlled lepidopteran larvae. These products continue to be used successfully to control lepidopteran pests. Subsequently, Bt products have been developed specifically for controlling pests (e.g., Colorado potato beetle and elm leaf beetle).

Recently a second generation of Bt products has been developed. Bt has been incorporated into plant tissue (e.g., cotton, potato, tomato, and corn) using genetic engineering technology. The use of crops that have been genetically modified to contain Bt have generated an enormous amount of scientific and ethical debate. On the one hand, crops that contain Bt have automatic and specific pest protection. Therefore, the labor and costs associated with applying conventional insecticides are eliminated. Additionally, natural enemies are conserved because the Bt toxin does not affect them (Meeusen and Warren, 1989). On the other hand, pests are constantly exposed to Bt, even when control is not needed. This constant exposure will undoubtedly increase the incidence of pest resistance to Bt (Meeusen and Warren, 1989; Tabashnik, 1994; Gould, 1994). Additionally, the incorporation of an “automatic” pest control tactic means that consumers must pay for the pest control even if it is not needed. The development and application of genetically engineered crops will be the focus of much more research and scientific and ethical debate in the years to come (U.S. Congress, 1995; Rice and Pilcher, 1998).

7.6.3.2 **Fungi**

It has been estimated that over 700 species of fungi infect insects; however relatively few (approximately 17) have been developed and used for insect control (Roberts et al., 1991; Fuxa, 1987; Jaronski, 1997). Compared to most other types of pathogens, fungi have a relatively wide host range. For example, *Beauveria bassiana* has been identified as a potential biological control agent of many different arthropod pests (e.g., beetles, ants, termites, true bugs, grasshoppers, mosquitoes, and mites). The wide insect host range of some fungi has caused concern regarding safety to non-target organisms. Honey bees are susceptible to *Beauveria* and *Metarhizium* (Roberts et al., 1991). Clearly, thorough research needs to be conducted on
the host specificity of entomopathogenic fungi and methods need to be developed
that will minimize adverse effects on non target organisms.

Fungi differ from most of the other types of insect pathogens in that they do not
have to be ingested in order to invade their host (Hajek and St. Leger, 1994). Fungi
can enter their host through natural openings in the insect cuticle and spread to the
hemocoel (Ferron, 1978). Because fungi infect insects by penetrating the cuticle,
direct contact between the fungi and the insect host is necessary. The time required
to kill an insect by fungal infection can be from only a few days to several weeks
(generally 3 to 7 days), depending on the fungus (Jaronski, 1997). The ability of
fungi to infect the insect’s external integument makes them good candidates for
controlling piercing/sucking herbivores, which are usually immune to other patho-
gens due to their feeding behavior (Roberts et al., 1991).

Most entomopathogenic fungi have many biotic and abiotic limitations that limit
their wide-scale development and application. The biotic limitations are poorly
understood, but they are primarily associated with the penetration of the fungus into
the host’s integument (i.e., the degree of contact and infectivity). A better under-
standing of the factors that affect the ability of a given fungus to penetrate and invade
its host are of paramount importance in the future development of fungi as viable
biological control agents. Also, better fungal formulations are needed to improve
their overall shelf life, virulence, infectivity, and persistence (Milner, 1997; Fuxa,
1987; Jaronski, 1997).

Many abiotic factors also limit the use of fungi for controlling insect pests. Most
fungi require a cool and moist environment (>90% humidity) to germinate (Ferron,
1978). Once they germinate, then their efficacy can be maintained at moderate
humidity (i.e., approximately 50%) and temperatures between 20 to 30°C. However,
there are a few strains of fungal pathogens that are effective in arid environments
(Bateman et al., 1993).

Unlike other pathogens, fungi grow well on simple and inexpensive media. This
characteristic, coupled with their relatively wide host range, makes many fungal
pathogens potentially good candidates for commercial production.

7.6.3.3 Viruses

For the most part, viruses have been used for classical and augmentative biolog-
ical control (Roberts et al., 1991). Nuclear polyhedrosis viruses (NPVs) comprise
the major group of viruses that attack insects. Most NPVs attack and infect young
lepidopteran larvae that have ingested virus particles. Death by viral infection usually
takes several weeks. The relatively slow speed at which viruses kill their host has
hindered their acceptance as a widely used biological control tactic (Bonning and
Hammock, 1996).

The efficacy of most viruses is heavily influenced by prevailing environmental
factors. The transfer of a virus to a host usually requires the virus to survive in soil
litter and on plant surfaces, before they are moved passively by abiotic and biotic agents.
Additionally, the efficacy of many viruses is adversely affected by direct sunlight.

The major advantages of using viruses for insect control are that they are host
specific and environmentally safe (Bonning and Hammock, 1996). Again, their
narrow host specificity makes them desirable candidates for biological control, but limits their commercial development (Roberts et al., 1991).

### 7.6.3.4 Protozoa

Many indigenous protozoans infect and kill insects. The most common group of protozoans is microsporidia (Brooks, 1988; Henry, 1981). Over 250 species have been described; however, it is believed that thousands of additional species probably exist (Maddox, 1987). There is a lack of research documenting the effectiveness of protozoans as biological control agents because they are difficult to diagnose and identify (Hazard et al., 1981).

Most microsporidia are transmitted to insects by oral ingestion of spores. However, some species are transmitted transovarially via the egg or by parasitoids (Andreadis, 1987; Siegel et al., 1986). In most instances, insects infected with indigenous microsporidia go unnoticed because they kill their host so slowly that it is difficult to differentiate between disease-caused mortality and natural mortality. It is for this reason that the sub-lethal effects of microsporidia infections may cause the most significant reductions in pest populations. For example, insects that are infected with sub-lethal amounts of microsporidia may have reduced fecundity and reduced mating. This ultimately results in lower pest populations over subsequent generations (Canning, 1982; Maddox, 1986). The sub-lethal effects of microsporidia infections on pest populations is a research area that needs to be more thoroughly examined.

Protozoans have not been developed as microbial insecticides because they do not cause rapid mortality. Additionally, because they are obligate parasites and cannot be grown on artificial media (they must be produced in living host cells), commercial development of protozoans is impractical. It is probably more realistic to consider protozoans as natural control agents.

### 7.6.3.5 Nematodes

Entomophagous nematodes are probably among the most potentially useful and commercially attractive type of pathogen. Nematodes (the name is derived from the Greek word for thread) are slender, tubular (non-segmented) worm-like organisms that can be found throughout the world inhabiting both soil and water. Many of the species are barely visible to the naked eye.

The class Nematoda contains a wide variety of species. Most species are free-living and feed on bacteria, fungi, and algae. Many nematode species are pests that parasitize animals (including humans) and plants. Nearly 40 families of nematodes are known to exclusively parasitize and feed on arthropods. To date, the most beneficial nematodes are found in the families Heterorhabditidae and Steinernematidae (Georgis, 1990). Both of these families are obligate parasites that have evolved a symbiotic relationship with pathogenic bacteria (e.g., *Xenorhabdus* and *Photorhabdus*) (Poinar, 1990). The nematodes provide the “transportation” for the bacteria by penetrating the insect through the mouth, anus, or spiracles (heterorhabditids can also penetrate the cuticle) (Georgis, 1992). Once in the host, the nematodes release...
the bacteria, which quickly multiply and kill the host. In turn, the nematodes use
the bacteria and the insect cadaver as a source of food and shelter (Kaya and Gaugler,
1993). The nematodes then mature, mate, and reproduce in the host tissue. Infective-
stage juveniles emerge from the cadaver and search for a new host (Georgis, 1992).

Nematodes have characteristics that make them outstanding candidates for all
types of biological control (e.g., conservation, augmentation, and classical) and
potentially competitive with insecticides for marketability. Nematodes are highly
mobile, and can find and kill a new host in just a few days (Gaugler, 1988). Several
nematode species are easily mass-produced \textit{in vitro} and applied into the field using
standardized pesticide sprayers or irrigation systems (Georgis and Hague, 1991).
Additionally, nematodes and their bacterial symbiots are safe to higher order animals
and plants. Finally, nematodes have a relatively wide host range which makes them
more likely to be developed commercially (Georgis, 1992).

One major drawback associated with nematodes is their susceptibility to desic-
cation and ultraviolet light (Georgis, 1992; Gaugler et al., 1992). As with most other
groups of pathogens, most nematode species prefer a cool and moist environment
to survive. Additionally, their relatively wide host range suggests that non-target
organisms might be impacted by nematode applications (Akhurst, 1990). However,
a recent study suggests that non-target effects of nematodes on predators and para-
sitoids is minimal (Georgis et al., 1991).

Nematology as a science is still in its infancy. However, discoveries over the
past two decades have shown that they have enormous potential for controlling many
types of insect pests under certain environmental conditions (Webster, 1998). Major
barriers to overcome before they are widely accepted as viable biological control
agents include storage and shipping of large-scale supplies of nematodes. Increased
effort is needed to search and screen for more virulent strains of the nematode/bac-
terium complex that can survive under a wider variety of environmental conditions
(Georgis, 1990).

7.6.4 Parabiological Control Agents

Although parabiologicals are excluded from the traditional definition of biological
control (Debach and Rosen, 1991), they provide specific pest control and work syn-
ergistically with predators, parasitoids, and pathogens. Parabiologicals include sterile
insect releases, pest-specific pheromones, and insect growth regulators (Sailer, 1991).

7.6.4.1 Sterile Insect Release

Sterile insect release involves exposing \textit{in vitro} reared insects to radiation and
releasing them into the field to mate with native insects. This technique is an
enormously successful pest control tactic for certain pests. The doses of radiation
sterilize the laboratory-reared insects, thus making them incapable of producing any
offspring. In turn, the reproductive potential of the pest can be drastically reduced
over several generations if enough sterile insects mate with normal insects. The
landmark example of a successful sterile insect release was with the screwworm,
\textit{Cochliomyia hominivorax} (Coquerel) in the southwestern U.S. (Bushland, 1974;
Since then, sterile insect releases have been successful for controlling many other pests, particularly fruit flies (Debach and Rosen, 1991). The pest’s biology, natural history, and population dynamics limit the wide-scale use of sterile insect release.

### 7.6.4.2 Pheromones

Pheromones have proven invaluable for monitoring insect pest populations and disrupting the mating behavior of certain pests (Shorey, 1991). Many pheromone-based traps and mating disrupters are commercially available for managing pests. For example, the synthetic sex pheromone, gossyplure, has been an invaluable tool for disrupting the mating behavior of the pink bollworm, *Pectinophora gossypiella* (Saunders) in the southwestern U.S. (Gaston et al., 1967; Flint et al., 1974; Shorey et al., 1974; Gaston et al., 1977; Baker et al., 1990). The use of pest-specific pheromones is highly compatible with biological control (Shorey, 1991). Like many parasitoids and pathogens, pheromones are pest-specific and have no adverse effects on non-target organisms. Additionally, insects do not develop resistance to the pheromones. As with the other parabiologicals, pheromones are designed to be used as one of several components of an overall IPM program. As of 1995, sex pheromones had been formulated for almost two dozen lepidopteran pests (Cardé and Minks, 1995).

### 7.6.4.3 Insect Growth Regulators

Insect growth regulators (IGRs) have become popular for pest management over the past two decades; however, their potential has not yet been fully realized (Staal, 1975).

IGRs interfere with the endocrine system of the pest and affect their normal growth and development (Dhadialla et al., 1998). Most existing IGRs can be categorized into two major groups by their mode of action; juvenile hormone analogs or chitin synthesis inhibitors (Horowitz and Ishaaya, 1992; Plapp, 1991). For the most part, IGRs are thought to be compatible with biological control because they are pest-specific and they generally do not have any adverse effects on natural enemies. However, some recent studies have shown that certain IGRs are toxic to natural enemies (Croft, 1990; Biddinger and Hull, 1995; Delbeke et al., 1997). Additionally, as with the synthetic pesticides, insect pests can develop resistance to IGRs (Plapp and Vinson, 1973; Cerf and Georghiou, 1974; Brown and Brown, 1974; Wilson and Fabian, 1986; Horowitz and Ishaaya, 1994). To this end, IGRs should not be overused and they should be regarded as a single component used to complement an overall IPM program.

### 7.7 LIMITATIONS AND RISKS ASSOCIATED WITH THE VARIOUS BIOLOGICAL CONTROL APPROACHES

In many cases, biological control is a simple, effective, and environmentally sound pest management approach. However, biological control is not a panacea for all pest
problems. Biological control requires patience. Even an effective natural enemy is almost always slower acting than an insecticide (U.S. Congress, 1995). Furthermore, a decision to commit to a biological control program might alter other pest management strategies, such as insecticides or cultural practices harmful to natural enemies. Research on the efficacy of many potential biological control agents is limited, as verification of the efficacy of a biological control agent requires considerable expertise.

Far too often, the efficacy of a biological control agent is compared with a chemical pesticide in terms of its direct capacity to kill a pest (Waage, 1996). Unfortunately, this standard of measurement is unfair because biological control is more difficult to assess. For example, most biological control agents (parasitoids and pathogens) do not immediately kill their hosts. However, they are not only compatible, but synergistic with most of the other IPM tactics. On the other hand, broad-spectrum pesticides rapidly kill pests, but are not compatible with most of the other IPM tactics. A key issue for biological control researchers is to document the long-term efficacy of biological control as a component to an overall area-wide IPM program (Knipling, 1979, 1980; U.S. Congress, 1995, Kogan, 1995, 1998; Wellings, 1996).

There are many reasons that biological control has not been used as frequently as pesticides. Pesticides are easy to apply and they produce rapid and dramatic results. In contrast, biological control is generally more difficult to apply, more expensive, slower acting, and more subtle than pesticides, but has several advantages over chemical pesticides (Debach and Rosen, 1991). For instance, unlike broad-spectrum pesticides, biological control agents are usually pest-specific. Furthermore, many biological control agents need to be applied only once (or a few times) to become established and continue to work effectively. Unfortunately, while pest specificity, single or limited applications, and long-lasting pest control are positive qualities for biological control, these features inhibit their commercial development. Consequently, biological control agents are often unavailable to pest management personnel (Waage, 1996).

There are very few ecological risks associated with conservation or augmentation because they both use indigenous natural enemies (Wellings, 1996). However, the use of classical biological control has received some criticism. Proponents of classical biological control offer convincing arguments for its safety (if done properly), efficacy, and cost effectiveness. Opponents of classical biological control argue that it is not possible to predict if an agent will have any long-term, irreversible affects to non-target organisms (plants and animals). Some fear that a classical biological control agent might alter the composition of entire ecosystems. For example, it has been speculated that the introduction of parasitoids into Hawaii has had a negative impact on native butterfly and moth populations. However, biological control cannot be singled out as the sole cause of the decline in butterfly and moth populations because of habitat destruction, pesticide use, and other environmental problems found in Hawaii (U.S. Congress, 1995).

### 7.8 BIOTECHNOLOGY AND BIOLOGICAL CONTROL

Enormous progress has been made over the past decade toward advancing the role of biotechnology in biological control (Sheck, 1991). Biotechnology has and
will continue to play a major role in biological control. Through genetic engineering, scientists have transferred genetic material from one organism to another. The classical example is with the insect pathogen, Bt. As mentioned above, Bt is a naturally occurring soil bacteria that has been formulated as a biological insecticide against a variety of pests. Scientists have genetically inserted toxic genes from Bt directly into plant tissue. The major advantage of having Bt directly inserted into the plant is that the plant receives continuous protection from certain pests (Kirschbaum, 1985). Additionally, the new growth of the plant is also protected, which is a problem when using spray formulations (U.S. Congress, 1995).

Despite the obvious advantages of using Bt crops, the possibility of their widespread use raises some potential problems. Already, there have been reports that certain pests have developed varying degrees of resistance to Bt crops (Gould, 1998). To this end, extensive resistance monitoring of genetically engineered crops used for pest control will be critical for further development of genetically altered organisms (Gould, 1994).

Insect pathogens are not the only natural enemies that have been genetically modified for biological control. Predators, parasitoids, and nematodes have also been modified to increase their potential for controlling pests (Hoy, 1986; Hokkanen, 1991; Gaugler et al., 1997). The major constraint on improving predators and parasitoids is accurately predicting which trait is helpful to improve (Scheck, 1991; Hopper et al., 1993). In the long history of biological control, it is difficult to pick out any single trait that a natural enemy has that makes it a successful natural enemy (Beddington et al., 1978; Hopper et al., 1993). Assuming that biotechnology advances to a point where we can easily produce genetically modified insects, then the “question” remains about which changes are needed to a natural enemy that will make it a more effective agent (e.g., dispersal capability, fecundity, diet breadth, etc.).

Some predators have been genetically modified so that they are resistant to certain insecticides. The most progress in this area has been breeding insecticide resistance into predatory mites (Hoy, 1985). The major drawback associated with having pesticide-resistant predators is that in order to maintain the resistance in the field, insecticides must be continuously applied to ensure that the selected strain does not breed with native (non-resistant) individuals. Ultimately, this practice could destroy the other natural enemies present in the field (Scheck, 1991). Additionally, pesticide resistant natural enemies are not resistant to all pesticides; therefore, pesticides must be chosen very carefully in order to avoid killing the resistant strain.

There are other possibilities for improving natural enemies using biotechnology (Hoy, 1989; Hoy, 1990). Heat or cold tolerance could be increased in certain natural enemies, allowing them to withstand greater climatic extremes and to inhabit a broader region for a greater length of time (Hoy, 1990; Gaugler et al., 1997). Another exciting possibility for genetic improvement on a natural enemy is to alter the venom of a parasitoid in such a way that it causes its host to stop feeding (due to paralysis). This would significantly reduce crop damage by reducing the pest feeding while it is parasitized (Beckage, 1990; Scheck, 1991).

The possibilities of using genetically engineered natural enemies are limitless. Certainly, more genetically altered natural enemies will be developed in the years to come. However, research in this area must proceed with caution. Projects that are
initiated in the future toward genetically altering any natural enemy need to be scrutinized by researchers and the general public. Researchers need to be cautious when selecting desirable characteristics to be sure that these changes will not pose any long term consequences.

### 7.9 FUTURE OF BIOLOGICAL CONTROL

Biological control as a pest management strategy is gaining popularity. For the first time since the beginning of the pesticide revolution, biological control can play a major role in IPM because it is ecologically sound, environmentally benign, self-perpetuating, and inexpensive. These attributes, combined with changing consumer attitudes about food and fiber consumption, have influenced governments throughout the world to change their pest management policies. For instance, some European nations have set a goal to reduce their pesticide usage 50% by the year 2000 (Baerselman, 1995). In the U.S., a government initiative is underway to implement IPM on 75% of crops by the year 2000 (U.S. Congress, 1995). Furthermore, developing countries in Asia have declared IPM as their national crop protection strategy (Ooi et al., 1992). Clearly, biological control will be the backbone of these government initiatives. This global commitment to biological control provides biological control researchers with a unique opportunity to further develop safe, effective and user-friendly pest management.

Classical biological control will be used more than ever because of increased movement of alien pests due to technological advances in transportation and fewer restrictions on international trade. International trade agreements such as Europe’s General Agreement on Trades and Tariffs (GATT) and North America’s North American Free Trade Agreement (NAFTA) will increase the probability that alien pests will inhabit new regions of the world (Waage, 1996).

New information is needed to predict the effectiveness and safety of classical biological control agents. The ecological consequences of introducing an improper biological control agent, one that attacks insects other than the target pest, are irreversible. In the past, biological control researchers have had a difficult time estimating the long-term economic benefits derived from successful natural enemy introductions. Better economic assessments will increase the competitiveness of classical biological control with conventional pest control (i.e., pesticide applications) (Greathead, 1995; Hokkanen and Lynch, 1995).

Augmentative biological control will continue to gain popularity. There are an increasing number of small businesses dedicated to selling biological control agents (Hunter, 1994). Generally, these businesses sell relatively small quantities of macrobiological agents (e.g., predators and parasitoids) to home gardeners and greenhouse operators. Major breakthroughs are still needed toward developing artificial diets for macrobiologials. Until these breakthroughs occur, predators and parasitoids will have limited use in large-scale augmentative biological control programs (Grenier et al., 1994).

The future’s most promising augmentative biological control agents are pathogens, or biopesticides. In the past, many big businesses have developed useful
biopesticides for controlling a variety of pests. This market will continue to grow in the near future. As of 1993, there were over 175 microbial products (mainly Bt products) on the market (Waage 1996). However, biopesticides still only constitute less that 5.0% of the pesticides sold worldwide (Ridgway and Inscoe, 1998).

Industry has been reluctant to invest in biopesticides for many reasons. Biopesticides often have a short shelf-life or are unstable in the field and have an uncertain market demand (Roberts et al., 1991). However, these shortcomings could be overcome with sufficient incentive and investment in research and development. Unfortunately, many of the reasons that biopesticides are not readily available for commercial use are of an economic nature. Many potentially marketable biopesticides have a narrow host range and are self-perpetuating, thus making them less profitable than chemical pesticides. Formulations of Bt and nematodes constitute over 90% of the biopesticide market. These two agents are known for their quick killing capacity, relatively wide host range, and non-persistence in the field. These products are on the forefront of commercial development because they have characteristics that are similar to chemical pesticides (Waage, 1996). Unfortunately, many other potentially useful biopesticides that are self-perpetuating, persistent in the field, and have a narrow host range (e.g., viruses, fungi, and protozoans) are not prime candidates for commercial development. In the future, we need to do a better job of developing biopesticides into useful products (Kirschbaum, 1985). We need to create incentives for industry to invest in the research and development of such products (Waage, 1996). Only then will we be able to develop biological control products that are truly compatible with IPM and not necessarily compatible with traditional pesticide development.

Conserving natural enemies as a pest management tactic needs to be practiced on a far greater scale than it is presently. Many more opportunities exist for conservation than for classical or augmentative biological control combined. Conservation is a pest management strategy that should be applied by everyone. For conservation to reach its full potential, several scientific, social, and economical barriers must be overcome.

Greater resources are needed to research various conservation tactics. Unfortunately, conservation is probably the least studied of the three biological control tactics because it does not lend itself easily to the research and extension activities of most academic institutions. We still lack a basic knowledge of the biology and ecology of most pests and their natural enemies. Moreover, we still do not fully understand the efficacy and economic impact that native natural enemies have on pest populations. Even farmers who use conservation tactics do not have clear-cut instructions on how to apply the tactics. Academic institutions need to design extension programs to educate farmers and the general public on conservation tactics. Extension personnel need to collaborate with entire communities and organize area-wide pest management programs. We need to empower individuals by training them to understand conservation tactics and to participate with scientists in selecting additional interventions when necessary to complement an areawide IPM approach to pest management (Knipling, 1979; Waage, 1996). A weak link in implementing conservation tactics (and the other biological control tactics) is convincing farmers to experiment with them. Area-wide extension programs are needed to provide
farmers with unbiased technical support so that they can make informed decisions (Wearing, 1988). Presently, much of the technical support offered to farmers is from “private consultants” who are provided incentives from chemical companies to sell their products. In the future, we need to provide farmers with financial incentives to try IPM.

Producers of agricultural products will need to change their expectations concerning pest management if conservation is going to reach its full potential. Growers are accustomed to using fast-acting insecticides to “control” their pest problems. This monotactic approach to pest management must change if we expect to achieve environmentally friendly pest control. Conservation (and the other types of biological control) is not only slower acting than pesticides, but usually needs to be used with other environmentally friendly IPM tactics. Conservation of natural enemies is not usually a “silver bullet” approach to pest management, but it is compatible and often synergistic with other pest management tactics.

Consumers will also need to change their expectations concerning the produce they purchase if biological control is to succeed. Consumers’ insistence that their produce must be “perfect” has severely deterred the use of biological control. Growers will require assistance from consumers to wean themselves off the “pesticide treadmill” (van den Bosch, 1978). To this end, consumers should be willing to accept some minor insect damage on their produce.

In summary, production agriculture throughout the world needs to maintain or increase its current level of production while providing the public with environmentally friendly and compatible pest management. The restoration of agricultural productivity by the reduction of pesticide use must be approached by using areawide IPM programs with biological control as their backbone. Ever-changing complexities to our landscape will increase the need for biological control. The enormous growth of urban areas is encroaching on agricultural land. This so-called “urban sprawl” has increased the concern of using insecticides near homes, schools, and commercial buildings. Urban sprawl will increase the attractiveness of biological control for pest management to farmers and suburban homeowners.

Enormous progress has been made toward improving the efficacy of biological control. Now it is critical that researchers engage in more extension activities that apply directly to consumer crops (Allen and Rajotte, 1990). For biological control to continue to prosper into the next millennium, entire communities need to become involved in the pest management decision-making process. This will require a dedicated effort from extension specialists, farmers, pest management regulators, and the general public.

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REFERENCES


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