Chapter 6

Kinds of Natural Enemies

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Successful biological control requires knowledge of the organisms used and their biology. Growers, scouts, and consultants can use such information to choose which natural enemy to use for a particular situation and to predict the level of control possible to achieve. A variety of predators, parasitoids, pathogens, and entomopathogenic nematodes are used to manage pest arthropods. In this chapter, we list the principal species in current use and describe their biologies. Basic references for further reading on natural enemies include Burges and Hussey (1971), Huffaker (1971), Van den Bosch, Messenger, and Guitierrez (1982), and Van Driesche and Bellows (1996) and can be helpful to developing a broader knowledge of the topic.

Predators

How They Work

Predators are free-living organisms for which the adults and most of the immature stages must kill and eat prey for their survival. Predators are usually larger than their prey, and many prey are often needed for complete development. Commercially available predators include predatory insects and mites (see tables 6.1 and 6.2), such as thrips (Thysanoptera), true bugs (Hemiptera, *Orius* spp.), green lacewings (Neuroptera, *Chrysoperla* spp.), beetles (Coleoptera, various ladybird beetles), flies (Diptera), and phytoseiid mites.

The biologies of predators are quite diverse. Some feed by chewing up the prey's tissue with their mandibles; others pierce the prey's body and suck out body fluids. A visible sign of the action of predators may be dead prey, particularly in the case of sucking predators, which often leave remnants of prey attacked on plants. Others, such as *Delphastus* spp., may deposit brightly colored frass droplets on the foliage as signals of their activity.

Predators are generally released when pest densities are relatively high, because low densities of prey are not sufficient for predators to sustain themselves. For example, two coccinellid predators of whiteflies, *Nephaspis oculatus* (Blatchley) and *Delphastus catalinae* (Horn), feed on all stages of *Bemisia argentifolii* Bellows and Perring, but both species must eat many whiteflies to be able to lay eggs. Adult female *D. catalinae*, for example, must find and eat a minimum of 167 *B. argentifolii* eggs per day (Hoelmer, Osborne, and Yokomi 1993), whereas adult females of *N. oculatus* need to find and eat only 78 eggs per day (Liu et al. 1997) to maintain oviposition. Immature *N. oculatus* must consume 700 whitefly eggs to develop from a second instar to an adult (Ibid.), but *D. catalinae* requires 1,000 eggs for complete larval development (Hoelmer, Osborne, and Yokomi 1993).

Issues of prey density occur both in the mass production of predators and in their subsequent release into protected crops. Because predators have large food requirements, they are often expensive to mass rear, and these costs are passed on to the end user. In addition, some predators are cannibalistic if underfed, making their mass rearing more difficult and costlier because they must be reared individually. In an attempt to reduce production costs, numerous research projects have focused on the development of artificial diets to feed to predators during the mass-rearing process in place of normal prey (Thompson 1999). Unfortunately, the demand for this technology still far outweighs the successes made by researchers.

Once released, some predators can sustain themselves on alternate foods such as pollen or by feeding on the crop if prey is scarce. Many predatory mites eat pollen, and some species can develop on a diet of pollen alone. Green lacewing adults (*Chrysoperla* spp.) will lay eggs if fed on honeydew (sugars produced by aphids and other homopteran insects). Pollen and sugars are used in some mass-rearing systems to lower production costs.

The selection of predators for release is often based on the target crop and pest species. For example, the predatory mite *Neoseiulus californicus* (McGregor) is used for crops typically infested with the pest mites *Tetranychus urticae* Koch and *Polyphagotarsonemus latus* (Banks). In contrast, *Phytoseiulus persimilis* Athias-Henriot is the preferred predatory mite for release onto palms because *T. urticae* is often the only important pest mite. Occasionally, a release of

Neoseiulus fallacis (Garman) will be made on palms to manage species such as *Tetranychus tumidus* Banks, which *P. persimilis* will not eat.

Knowledge of predator mobility is important to obtain maximum benefit in terms of pest suppression from a natural-enemy release, especially when pest outbreaks are distributed as isolated patches within a crop. Predatory mobility is a function of development stage as well as of the species in question. The immature stages of most predators used in protected culture are mobile, but their abilities to locate prey over large distances are limited. For insects, the adults fly and can search larger areas to find patches of prey and lay their eggs. Their offspring, then, need to search only the local area for prey. Wingless predators, in contrast, must search plants by walking in both immature and adult stages, limiting their ability to cross barriers between plants and benches. Insects such as the fly *Feltiella acarisuga* (Vallot)[2] can easily move through an entire crop after its release. It feeds on several species of mites, and it does so under high temperature and low humidity, which are unfavorable to *P. persimilis*. Other anecdotes prevail, but in at least in one case the importance of movement to biological control has been demonstrated experimentally. The parasitoid *Aphidius colemani* Viereck is capable of dispersing almost 150 ft. (46 m) per day due to its ability to fly. As a result, this wasp is capable of locating and parasitizing many more green peach aphids (*Myzus persicae* [Sulzer]) infesting potted chrysanthemums than are larvae of the green lacewing, *Chrysoperla rufilabris* (Burmeister), which is incapable of dispersing to pots located 1 ft. (0.3 m) from their point of release (Heinz 1998). Spacing *A. colemani* release points within greenhouses appropriately greatly increases the level of aphid suppression obtainable (see chapter 16).

The food requirements of a natural enemy can also affect the release strategy employed. If the goal of a release is establishment, then most predators need dense prey populations to reproduce successfully. If, however, the aim is to utilize multiple releases of a predator as a biological insecticide, then any pest population density can be targeted. If the predators are relatively inexpensive, as with predatory mites, releases are often initiated early within a crop cycle and continue until harvest to prevent pest outbreaks. If the predators are relatively expensive, as with beetles, mirids, and anthocorids, then predators may be used locally to reduce high-density host patches, or they may be used temporarily throughout a crop to reduce a pest outbreak to an acceptably low density (Heinz and Parrella 1994a).

Predatory mites vary in their biologies, most importantly in their choices of food or prey (McMurtry and Croft 1997), which may significantly influence their effectiveness as biological control agents. Several species are highly specialized predators of select pest species. As examples, *P. persimilis* feed only on *T. urticae* and a few other tetranychids. *Neoseiulus californicus, N. fallacis*, and *Galandromus occidentalis* (Nesbitt) feed on *Tetranychus* spp. that produce webbing. Other species, such as *Iphiseius degenerans* (Berlese), *Neoseiulus cucumeris* (Oudemans), and *Neoseiulus barkeri* Hughes[3], are generalist predators and feed on mites, thrips, whiteflies, mealybugs, and scale crawlers, although the last three groups are not preferred prey. These predatory mites can also develop if fed only pollen. A final group of predators, *Euseius* spp., are specialized pollen feeders that also act as generalist predators, but none are currently being used in protected culture. Releasing predators with different dietary specializations in combination, such as *P. persimilis* and *Neoseiulus longispinosus* (Evans), can provide better control than either species used alone (Mori, Saito, and Nakao 1990). In contrast, combining two species with the same dietary specialization (*N. fallacis* and *G. occidentalis*) may provide the same level of pest suppression as releasing either alone (Strong and Croft 1995).

Predators Sold for Use in Protected Culture

Species of predators sold commercially vary between countries. Tables 6.1 and 6.2 list thirty-three species that are currently available in North America and are recommended for use in greenhouses (Hunter 1997). Although commercially available, many of these species have not been critically evaluated for efficacy, and few experiments are available to support claims made by some retailers.

[table 1]

Table 6.1. Common Predatory Mites Sold for Control of Greenhouse Pests.

Predator Species (all Phytoseiidae)	Prey
Galandromus (= *Metaseiulus* = *Typhlodromus*)	spider mites

occidentalis (Nesbitt)	
Hypoaspis aculeifer Canestrini	fungus gnats and western flower thrips
Hypoaspis (= *Geolaelaps*) *miles* (Berlese)	fungus gnats and western flower thrips
Iphiseius (= *Amblyseius*) *degenerans* (Berlese)	western flower thrips and pest mites
Mesoseiulus (= *Phytoseiulus*) *longipes* (Evans)	spider mites
Neoseiulus (= *Amblyseius*, = *Phytoseiulus*) *barkeri* (= *mckenziei)* Hughes	thrips
Neoseiulus (= *Amblyseius*) *californicus* (McGregor)	spider mites
Neoseiulus (= *Amblyseius*) *cucumeris* (Oudemans)	thrips, cyclamen, and broad mites
Neoseiulus (= *Amblyseius*) *fallacis* (Garman)	European red and two-spotted spider mites
Phytoseiulus macropilis (Banks)	spider mites
Phytoseiulus persimilis Athias-Henriot	spider mites

[end table]

[table 2]

Table 6.2. Common Predatory Insects Sold for Control of Greenhouse Pests.

Predator Species	Common Name and Prey
Aphidoletes aphidimyza (Rondani),[4] Cecidomyiidae (gall midge)	Predator for aphids
Chrysoperla (= *Chrysopa*) *carnea* (Stephens),[5] Chrysopidae (common green lacewing)	General predator
Chrysoperla (= *Chrysopa*) *comanche* Banks, Chrysopidae (Comanche lacewing)	General predator
Chrysoperla (= *Chrysopa*) *rufilabris*	General predator

(Burmeister), Chrysopidae (green lacewing)	
Coleomegilla maculata (De Geer),[6] Coccinellidae (pink-spotted ladybeetle)	Predator for aphids
Cryptolaemus montrouzieri Mulsant, Coccinellidae (mealybug destroyer)	Predator for various scales and mealybugs
Delphastus catalinae (Horn), Coccinellidae	Predator for whiteflies
Deraeocoris brevis (Uhler), Miridae (true bug)	Predator for whiteflies
Feltiella acarisuga (Vallot)(= *Therodiplosis persicae* Kieffer), Cecidomyiidae (gall midge)	Predator for mites
Geocoris punctipes (Say), Lygaeidae (big-eyed bug)	General predator
Harmonia axyridis (Pallas), Coccinellidae (ladybeetle)	Predator for aphids
Hippodamia convergens Guérin-Méneville, Coccinellidae (convergent ladybeetle)	General predator
Macrolophus caliginosus Wagner, Miridae	Predator of whiteflies
Orius insidiosus (Say), Anthocoridae (insidious flower bug)	General predator
Orius majusculus (Reuter),[7] Anthocoridae (minute pirate bug)	General predator
Orius laevigatus (Fieber), Anthocoridae (minute pirate bug)	General predator
Orius tristicolor White,[8] Anthocoridae (minute pirate bug)	General predator
Podisus maculiventris (Say), Pentatomidae (spined soldier bug)	Predator for caterpillars
Rhyzobius (= *Lindorus*) *lophanthae* (Blaisdell),	Predator for various scales

Coccinellidae	
Rhyzobius (= *Lindorus*) *ventralis* (Erichson), Coccinellidae	Predator for various scales
Scolothrips sexmaculatus (Pergande), Thripidae (six-spotted thrips)	Predator for mites and thrips
Stethorus punctillum Weise, Coccinellidae	Predator for mites

[end table]

Predators of Aphids

Hippodamia convergens (convergent lady beetle)

Both adults and larvae are generalists that feed on aphids, mites, mealybugs, and scales. Beetles may consume twenty-five to 170 melon aphids (*Aphis gossypii* Glover) per day when on potted chrysanthemum (Dreistadt and Flint 1996). This species may either be mass reared or collected from large natural aggregations occurring within the field. Unless physically confined by a greenhouse structure, aggregation-collected beetles disperse from plants one to three days after release. This tendency to disperse can be reduced by prefeeding and preflying beetles for seven to ten days prior to their release (Ibid.). Also, insectary-reared beetles disperse more slowly than aggregation-collected beetles stored at 39 to 50°F (4 to 10ºC) until their release. A single release of thirty-four to forty-two beetles per pot (of chrysanthemums) can result in 25 to 84% melon aphid control (Ibid.).

Coleomegilla maculata (the pink-spotted lady beetle)

This beetle is able to efficiently reduce aphid populations in corn (Wright and Laing 1982) and wheat (Rice and Wilde 1991). It has recently become obtainable from commercial insectaries, thus making it available for use in augmentation programs. At the present, its abilities to control aphids infesting crops within protected culture have not been evaluated.

Harmonia axyridis (Asian multicolored lady beetle)

The larvae and adults of this species are semiarboreal in nature and feed on a wide range of aphid species (Lamana and Miller 1996[9]). Eggs of this predator occur in groups of ten to fifty on the bottoms of aphid-infested leaves. Larvae are black with orange-yellow spots, and development from egg to the last (fourth) larval stage takes two to three weeks. Larvae are the stage usually sold by commercial insectaries. They may eat 150 aphids per day, and because they can tolerate low temperatures, they may be useful in unheated greenhouses located in temperate climates. Larvae pupate on the foliage. Adults can live for months and lay more than 3,000 eggs during their life. This natural enemy has been best evaluated for biological control of arboreal pests (McClure 1987, LaRock and Ellington 1996), and thus it may prove useful in controlling aphids and mites infesting interiorscape trees. Evaluations of its effectiveness at controlling pests occurring on plants grown in protected culture are still needed.

Aphidoletes aphidimyza (gall midge)

Adults of this fly are not predacious, but rather feed on plant nectars and aphid honeydew. The adults resemble fungus gnats, but are smaller (0.08 to 0.12 in. [2 to 3 mm]). They are weak fliers and are most active at dawn and dusk. A female can lay 100 to 300 eggs during her life, the actual number depending on the number and types of prey consumed by the larva. Eggs are laid near aphids, and in two to three days (at 70°F [21°C]) hatch into small reddish larvae that feed on aphids. Larvae eat three to fifty aphids per day and kill more aphids than they consume. After seven to fourteen days at 70°F (21°C), larvae drop to the soil and pupate. Fourteen days later, adults emerge and then mate. *Aphidoletes aphidimyza* (Rondani) work well in combination with parasitoids, and use of this species is important for control of *A. gossypii*. These flies are used in pepper, tomato, cucumber, and ornamental crops. They are sold as pupae, which are sprinkled on moist substrates. *Aphidoletes aphidimyza* do poorly in greenhouses with plastic or concrete on the floor because there is little substrate for pupation. Repeated releases are necessary when establishment is not possible (as is the case in Florida). These predators are released in three different ways: trickle, inundative, and use of banker plants. Some strains enter diapause under short, cool days.

Chrysoperla carnea, C. comanche, and *C. rufilabris* (green lacewings)

Lacewing larvae eat aphids, mealybugs, and whiteflies and will attack other species of beneficial organisms. Adults are delicate, light-green insects with golden eyes and long, transparent wings with very fine venation. Adults feed on honeydew, nectar, and pollen (Hagen 1964). The larvae consume over 400 aphids during their development; older larvae consume 30 to 50 aphids per day. Green lacewings have given excellent control of mealybugs in interior landscapes. High release rates for control of *Bemisia* sp. infesting poinsettia have yielded promising results in small-scale greenhouse trials (Nordlund and Legaspi 1996), but results from trials conducted in commercial greenhouses have been erratic (Osborne unpublished data[10]). Because reproduction and establishment within the crop are seldom achieved, inundative releases are necessary for achieving biological control. Lacewing eggs are produced and sold cheaply, and equipment has been developed for mechanical application of eggs to plants. Lacewings are also sold as young larvae that have been given some food before release (*prefed* larvae). These have performed better than eggs in interior landscapes but are more expensive to rear because larvae are cannibalistic. Larvae of *C. rufilabris* can sustain themselves in the absence of insect prey by limited feeding on plants. Developmental times depend on both temperature and prey. Development from egg to adult requires twenty-eight days at 75°F (24°C) and eighteen days at 81°F (27°C).

Predators of Mites

Of the natural enemies known to attack mites, most are other predatory mites. More than 1,000 species of predacious mites have been described, and many have potential for use in plant protection. During the period of 1970 to 1985, about 500 scientific papers were published on the role of one group of mites, the phytoseiids, as predators of spider mites (Chant 1985). Consequently, most of our attention will be directed toward the biologies of predacious mites important to biological control within protected crops. Several insect species (in the taxonomic groups containing beetles, flies, and thrips) may also be important predators of pest mites.

Phytoseiulus persimilis

This is the most widely used predatory mite. It was the first commercially available beneficial species used in greenhouse crops, first sold in 1968 (chapter 1). *Phytoseiulus persimilis* is a voracious predator of the two-spotted spider mite, *T. urticae*, and it cannot survive without *T. urticae*. Consequently, fluctuations in these predator and prey populations require multiple applications of *P. persimilis* to be made throughout the season to achieve biological control. In ornamental crops, biweekly applications are made even when no mites have been detected. Scouting is used to concentrate releases in and around dense patches of mites (areas with 1.9 mites per $ft.^2$ [20 mites per m^2]). This predator does not perform well at relative humidities below 50% or temperatures above 90°F (32°C). Of critical importance are these values at the leaf surfaces (the area occupied by the mites), which can often have higher relative humidities and different temperatures than the ambient values. Strains may be purchased that tolerate higher temperatures or some pesticides. Ornamental plants susceptible to damage from broad mites should be carefully monitored for outbreaks of this pest, as these may become a problem when transitioning from a chemical control program to a biological control program.

Neoseiulus (= Amblyseius) californicus

This species is very mobile and is used to control spider mites in peppers, roses, strawberries, and ornamental crops. Relative to *P. persimilis*, it tolerates lower relative humidity (Osborne et al. 1998), and it can survive longer without food, making preventive releases possible. Even though it attacks all stages of prey mites and it develops twice as fast as *T. urticae* at some temperatures, *N. californicus* reduces dense populations of spider mites more slowly than *P. persimilis*. Many growers use both mites together, *N. californicus* as the primary control agent and *P. persimilis* applied to plants with high mite densities. In Florida, it is also an effective predator of broad mite, *P. latus* (Peña and Osborne 1996).

Neoseiulus (= Amblyseius) cucumeris

This species is the most commonly used agent for control of western flower thrips (*Frankliniella occidentalis* [Pergande]), but will also feed on other mite species, including *Phytonemus pallidus* (Banks) (cyclamen mite) and broad mite. For additional information on this species and *N. barkeri*, see the section on predators of thrips.

Stethorus punctillum

Little is known about the ability of this species to control mites in greenhouses. It commonly feeds on mites outdoors and should be evaluated further (see chapter 11).

Feltiella acarisuga

This species is similar in appearance to *A. aphidimyza*. Larvae feed on all stages of *T. urticae*, but information is lacking on its full host range. For details on the biology of this species, see chapter 11. Larvae are parasitized by *Aphanogmus parvulus* Roberti, which may reduce the ability of this fly to establish and suppress mites. The degree of mortality caused by this predator depends on mite density. Larvae kill more prey than they eat. Adults are excellent searchers, and in Florida are often among the first species to find mite infestations on roses grown outdoors. The optimum relative humidity for this species is around 90%. Development rate increases with increasing temperature to a maximum of 81°F (27°C). *Feltiella acarisuga* (Vallot) requires at least a few high-density patches of mites to establish successfully. Commercial use of this predator has been limited, and results have been inconsistent.

Scolothrips sexmaculatus

Recent studies have shown that this species can be an excellent predator for *T. urticae* in greenhouses and interior landscapes on some ornamental plants (Osborne unpublished[11]). Both larvae and adults are predacious, and they attack all stages of spider mites. In Florida, this predator is among the first predator species to colonize mite-infested plants outdoors. Palm growers in south Florida have found that *Scolothrips sexmaculatus* (Pergande) can help control *T. urticae* on plants grown under shade cloth. Limited numbers of this thrips are commercially available. Adults lay eggs in plant tissue, but no plant damage has been noted.

Predators of Thrips

Orius spp.

These bugs feed on mites, aphids, whiteflies, lepidopteran eggs, pollen, and on plant sap. Nymphs can develop to adults on a diet of pollen, and the adults can sustain themselves on pollen but need animal prey in order to reproduce. *Orius* spp. are sold as adults, primarily for the control of thrips. These bugs attack all stages of thrips, in contrast to predatory mites that mainly attack the very young larvae. All stages feed by inserting their piercing–sucking mouthparts into a prey and removing body fluids. At high prey densities, *Orius* bugs will kill more prey than they consume. Adults fly well and easily find new pest infestations. Eggs are laid in plant tissue and hatch in twelve to twenty days. Nymphs (0.02 to 0.07 in. [0.4 to 1.8 mm] in length) are pear-shaped, yellow to red-brown, and have red eyes and no wings. Adults (0.08 to 0.12 in. [2 to 3 mm] long) are dark purple with white markings, and live three to four weeks. Development from egg to adult takes under three weeks at 77°F (25°C). For *Orius insidiosus* (Say), development does not occur below 59°F (15°C). Often recommended minimum release rates for *Orius* spp. are 0.05 per ft.^{2} (0.5 per m^2) as a preventive measure if pollen is available and to 0.09 to 0.93 ft.^{2} (1 to 10 per m^2) for control of light to heavy infestations.

Neoseiulus (= Amblyseius) cucumeris

This species is used against thrips, but also feeds on various mites. It is light brown, about 0.04 in. (1 mm) long, very mobile, and quite easy to see. Development (egg to adult) takes eight to eleven days at 77 and 68°F (25 and 20°C, respectively). Adults live three weeks if adequate food is available. Adults eat larval stages of thrips and are used in peppers, cucumbers, eggplants, melons, and several ornamental crops. A controlled release formulation (sachet bags hung in crop canopy) allows for continuous release of this predator in the crop for four to six weeks. Sachet bags contain bran and grain mites (which feed on the bran). The predators feed on grain mites, later moving into the crop in search of other prey as predator numbers increase. Control of thrips with this predator has been erratic.

Iphiseius (= Amblyseius) degenerans

Adults are dark brown and slightly larger than *A. cucumeris*. They are very active and easily seen foraging on flowers or undersides of leaves. Eggs are laid in groups along veins on the undersides of leaves. The larva is brown with an X-shaped marking on its back; it is not very active and does not feed. Adults and nymphs search actively for thrips larvae and spider mites, consuming their body fluids. Pollen is also eaten and can support mite populations even if thrips are absent. Mite colonies can be reared on a diet of castor bean (*Ricinus communis* L.) pollen alone. *Iphiseius degenerans* is used primarily for control of thrips in peppers. It is introduced as a preventive application as soon as flowers produce pollen, allowing populations to increase and spread throughout the entire crop and be present when thrips invade the greenhouse. *I. degenerans* can tolerate environments with low relative humidities, and it does not enter diapause. Therefore, it has been successfully used in both summer and winter crops.

Hypoaspis aculeifer and *Hypoaspis miles*

Hypoaspis spp. are soil-dwelling predatory mites that feed on insects found in the top 1.6 in. (4 cm) of soil. Adults (0.04 in. [1 mm] in length) are brown and lay their eggs in soil; egg to adult developmental time is twelve to thirteen days at 77°F (25°C). *Hypoaspis* spp. are active above 10°C (50°F), and their optimum temperature range is 60 to 72°F (16 to 22°C). The influences of warm temperatures on mite biology and effectiveness are unknown. Optimal habitats are moist but not water-logged soils. *Hypoaspis (= Geolaelaps) miles* (Berlese) can live for several weeks without prey. The rates recommended for fungus gnat management (9.3 mites per ft.^{2} [100 mites per m^2] as a preventative to 23 per ft.^{2} [250 per m^2] as a curative) are also the rates used to suppress thrips.

In greenhouses, *Hypoaspis* spp. eat collembolans, thrips pupae, and fungus gnat larvae. They reduce survival of thrips pupating in the soil, but the level of control is insufficient by itself (Brødsgaard, Sardar, and Enkegaard 1996; Gillespie and Quiring 1990; Lindquist, Buxton, and Piatkowski 1994). *Hypoaspis* spp. are best used in combination with other controls. Mites are released onto the moistened soil surface before planting or potting. Mites feed on organic matter or other prey if fungus gnats or thrips are absent, but are compatible with entomopathogenic nematodes. *Hypoaspis aculeifer* Canestrini, which is sold primarily in Europe, has been reported to be better than *H. miles* for thrips control (see chapter 20), and is used for control of bulb mites during bulb storage. Diapause has not been reported in either species, and both can be used all year.

Predators of Whiteflies

Delphastus catalinae

This shiny black beetle is 0.05 to 0.06 in. [1.2 to 1.4 mm] long. Females lay about three eggs per day (about 183 over their lifetime). There are four to five larval instars and a pupa. Development (egg to adult) requires about twenty-one days. This beetle is used against locally dense patches of whiteflies or where parasitoids have been unsuccessful (Heinz and Parrella 1994a), or in crops with high whitefly tolerances. Beetle larvae and adults consume many whitefly eggs, nymphs, and pupae. Adults require one hundred whitefly eggs per day to produce eggs. This beetle is compatible with the use of whitefly parasitoids.

Macrolophus caliginosus

This bright green bug (0.11 to 0.14 in. [2.9 to 3.6 mm] in length) inserts eggs into plant tissue. The bugs develop through five nymphal stages, requiring twenty-nine to ninety-five days at 77 to 59°F (25 to 15°C) before becoming adults with red eyes and long legs and antennae. Adults and nymphs move rapidly in search of prey, feeding on spider mites, whiteflies, and other insects. Adults lay 100 to 250 eggs in their lifetime, depending on temperature and availability of food. When prey are unavailable and *Macrolophus caliginosus* Wagner densities high, some tomato varieties are damaged when these predators feed on plant sap. Because this insect can cause damage to plants, it probably will not be approved for importation into some countries, including the United States.

Inoculative releases of this predator are common in Holland, France, Belgium, Scandinavia, Poland, and Germany. A seasonal inoculative approach is typically employed, whereby two releases are made two weeks apart. Sometimes moth eggs (*Ephestia* sp.) are provided as food to facilitate establishment. Release rates vary greatly depending on the crop and expected pest pressure. For example, recommended release rates range from 0.05 to 0.5 predators per ft.^{2} [0.5 to 5.0 per m^2]; at higher rates, predators should be concentrated in whitefly-infested areas. *Macrolophus caliginosus* are often used together with *Encarsia formosa* Gahan when greenhouse whitefly is the most important pest within a complex of pests attacking a crop. In these cases, *E. formosa* release rates often need to be increased to achieve the desired level of biological control, since *M. caliginosus* does not distinguish between parasitized or unparasitized whitefly nymphs as does *D. catalinae*. Populations of this predator may become infected in late summer by a naturally occurring *Entomophthora* sp. fungus, thus greatly reducing their densities.

Chrysoperla carnea, C. comanche, and *C. rufilabris*

These green lacewings are sold as aphid predators, but they also eat whiteflies. See the section Predators of Aphids for details on the biology and use of these species.

Predators of Other Pests

Cryptolaemus montrouzieri

This predator is often used for control of the citrus mealybug, *Planococcus citri* (Risso), or the longtailed mealybug, *Pseudococcus longispinus* (Targioni-Tozzetti), infesting interior landscapes. *Cryptolaemus montrouzieri* Mulsant does not reproduce well on species of mealybugs that do not produce masses of eggs protected by waxy filaments. Both larvae and adults of this predator feed on all mealybug stages but require large prey populations to sustain a population. Consequently, releases are often made in combination with parasitoids (see the section Other Parasitoids) to achieve the greatest level of success.

Eggs (about 500 per female per lifetime) are laid in mealybug aggregations and hatch in about five to six days. The larvae (up to 0.5 in. [13 mm] long) are covered with copious amounts of white wax, and to the uneducated eye look like large, active mealybugs. Larvae eat about 250 young mealybugs before pupating. Adults (0.2 in. [4 mm] in length) are brownish black, with an orange-brown head and thorax. The life cycle requires thirty-one to forty-five days at 81 to 70°F (27 to 21°C). This beetle is not active below 61°F (16°C) or above 91°F (33°C), and it may enter diapause in winter.

Parasitoids

General Biology of Parasitoids

Insect parasitoids (a term frequently but incorrectly interchanged with *parasites*) develop inside (endoparasitoids) or outside (ectoparasitoids) their hosts, depending on the parasitoid species.

Immature parasitoids are closely associated with their hosts and do not move from one host to another. Parasitoids are generally smaller than their hosts and are free-living only as adults. Parasitoids used most commonly in greenhouses are wasps (Hymenoptera), including *E. formosa*, *Eretmocerus eremicus* Rose and Zolnerowich, *Aphelinus abdominalis* (Dalman), *A. colemani*, *Aphidius ervi* Haliday, *Dacnusa sibirica* Telenga, *Diglyphus isaea* (Walker), and *Leptomastix dactylopii* Howard (table 6.3).

[table 3]

Table 6.3. Common Parasitoids Sold for Control of Greenhouse Pests.

Parasitoid	Host
Aphelinus abdominalis (Dalman), Aphelinidae	Aphids
Aphidius colemani Viereck, Braconidae	Aphids
Aphidius ervi Haliday, Braconidae	Aphids
Dacnusa sibirica Telenga, Braconidae	Leafminers
Diglyphus isaea (Walker), Eulophidae	Leafminers
Encarsia formosa Gahan, Aphelinidae	Greenhouse whitefly
Eretmocerus eremicus Rose and Zolnerowich, Aphelinidae	Silverleaf and greenhouse whiteflies
Leptomastix dactylopii Howard, Encyrtidae	Citrus mealybug

[end table]

Adult parasitoids have wings and are active fliers. Some kill hosts by puncturing them with an ovipositor and feeding on body fluids. This process is called host-feeding and can be very important in pest population suppression. When adults parasitize a host rather than feed on it, they lay one or more eggs near, on, or within the host insect. These eggs hatch, and the wormlike larvae feed on the host. Because parasitoid eggs are placed within or very near to hosts, which are often immobilized during the attack by the adult wasp, immature parasitoids do not have forage for prey, as do immature predators. Parasitoid larvae pupate near the host (as in the case of *D. isaea* on leafminers) or inside of the host (as in the case of parasitoids of aphids and whiteflies).

Parasitoids have evolved many specialized characteristics due to their close associations with their hosts. Many of these characteristics are associated with parasitoid reproduction and host location, which are directly associated with the abilities of parasitoids to establish or to suppress a target pest after their release. In the following sections, we discuss several of these characteristics and relate the importance of each to the implementation of biological control.

Parasitoid Reproduction

Parasitoids are described as egg, larval, nymphal, pupal, or adult parasitoids, depending on which life stage of the host they attack. Due to these host-stage specializations, parasitoid releases should be synchronized with the availability of hosts suitable for parasitoid attack. The occurrences of host stages tend to change dramatically with time within a pest infestation cycle. Early within an infestation cycle, one life stage of the pest tends to predominate at a time. But if the pest population persists, then the abundances of all life stages tend to be equal at any one time. Thus, the abundances of parasitoid-suitable hosts need to be monitored and parasitoid releases carefully coordinated to achieve success.

The patterns of egg production and deposition within the lives of parasitoids may vary significantly. Female wasps of *pro-ovigenic*[12] species emerge from their pupae with their full complement of mature or nearly mature eggs. Consequently, pro-ovigenic wasps begin ovipositing eggs almost immediately after emerging. The number of eggs they oviposit is determined by the conditions experienced by the preceding larval stage rather than the conditions experienced by the ovipositing wasps (Jervis and Kidd 1996). Pro-ovigenic wasps tend to be short-lived, surviving for only a few days, and they may feed for maintenance purposes (Ibid.). *Synovigenic*[13] parasitoids emerge with none or part of their total mature egg complement and develop eggs throughout their adult life. These wasps need to feed (on hosts, honeydew, or flowers) to maintain and maximize egg production, but they also tend to be relatively long-lived.

Few parasitoids have been shown to be pro-ovigenic. One such group consists of the whitefly parasitoids in the genus *Amitus*. Several releases of these species, or high synchronization of each release with their susceptible host stage, may be needed to obtain their establishment. Because they can lay eggs rapidly without having to wait for more to mature, they may be best used in inundative approaches. The majority of parasitoids, including species within the genera *Diglyphus* and *Encarsia* (Heimpel and Rosenheim 1998), appear to be synovigenic (Jervis and Kidd 1986). To achieve the maximum benefit from releases of synovigenic species, sufficient food supplies must be available to reach maximum egg production and reproduction. Parasitoids with this method of egg production can be used in all forms of biological control, but they may be particularly well suited to situations where long-term control is desired.

Hymenopteran parasitoids exhibit several modes of reproduction important to the ratio of male to female offspring produced by a single wasp. Because female wasps are the only sex capable of attacking pestiferous hosts, parasitoid sex ratios are critical to biological control. Most parasitoids reproduce through *arrhenotoky*, in which unfertilized eggs become males and fertilized eggs produce females. The female controls the sex of her offspring when ovipositing by selectively controlling fertilization of each egg passing through her reproductive tract. Such species are termed *biparental* since both a mother and father are necessary for the production of daughters. A minority of parasitic Hymenoptera reproduces in other, entirely parthenogenic ways termed *thelytoky* and *deuterotoky*. With thelytoky, there are no males, and unfertilized eggs give rise to daughters. With deuterotoky, either male or female progeny may be produced from unfertilized eggs, but the males are nonfunctional. In both of these latter cases of parthenogenic reproduction, these species are referred to as *uniparental*, and all functional wasps are female. Mass rearings and releases of thelytokous and deuterotokous species are simpler and less expensive than those of arrhenotokous species, since only females must be included in all facets of biological control when using completely parthenogenic forms.

Knowing which natural enemies attack which hosts is essential to manipulating parasitoid complexes within biological control programs. Parasitoids can be grouped based on the kind of hosts they attack; some kinds of natural enemies may not be beneficial to biological control. A *primary parasitoid* attacks hosts that are not parasitoids themselves. Provided they target the pest species as their host, primary parasitoids are frequently used in biological control programs. In selecting an appropriate parasitoid for release, it should be remembered that some parasitoids may attack and kill other nonpestiferous insects. In these cases, releases of natural enemies may not provide the level of biological control desired, or they may draw the ire of other groups with special interests in nonpestiferous species affected by the releases.

Parasitoids that attack other parasitoids are termed *hyperparasitoids* or *secondary parasitoids*. Yet another type of parasitism, called *adelphoparasitism*[14] or *autoparasitism*, occurs when a species is parasitic on individuals of its own species. Some whitefly parasitoids, for example, lay unfertilized eggs (destined to become males) in or on female larvae of their own species inside parasitized whiteflies. Male eggs hatch and larvae feed on females within the body of the whitefly host. Fertilized eggs, destined to become females, are laid within the unparasitized whitefly. Typically, hyperparasitoids and autoparasitoids are not used in biological control programs aimed at protected culture. However, parasitoids with these lifestyles commonly occur in nature and may invade greenhouses and interfere with ongoing biological control programs. There is some evidence from Spain to suggest that the autoparasitoid *Encarsia pergandiella* (Howard) may invade tomato greenhouses and interfere with the primary parasitoid *E. formosa* released for control of greenhouse whitefly (Gabarra et al. 1999).

One additional form of parasitoid-to-parasitoid interaction occurs most commonly in mass-rearing systems and hence may influence augmentation biological control programs. If more than one egg is laid in a host by a single species of parasitoid, and if not all of the eggs are able to develop to maturity, competition for the host results. This condition is called *superparasitism.* Superparasitism may lead to the production of small-sized parasitoids of inferior quality, the overproduction of male wasps, and a general decline in the supply of wasps available for an augmentation biological control project.

Host Finding and Selection

The methods parasitoids use to find and choose hosts to attack are important in understanding their effectiveness (see Van Driesche and Bellows 1996 for an overview). These mechanisms can be complex, and often involve behavioral responses to a series of odors, tastes, or other cues. In augmentative biological control, we release natural enemies into the pest's habitat (i.e., the crop), but the parasitoid must still find the individual pests. A few species of parasitoids find hosts by chance encounter, but most species use airborne or contact chemicals, visual features, or vibrations to detect hosts. These stimuli can be produced by the host, the plant eaten by the host, or the interaction of pest and plant. Once a parasitoid locates a host, similar or other stimuli (e.g., size of the host, chemicals on its body, and whether or not it is already parasitized) may elicit oviposition, host-feeding, or host rejection behaviors (Heinz and Parrella 1989, Van Driesche and Bellows 1996). Pesticide applications, cultivar selections, and cultural practices that influence plant or environmental characteristics can modify these host-finding and host-acceptance stimuli.

E. formosa, once released into a greenhouse, searches randomly for whiteflies (van Lenteren, van Roermund, and Sütterlin 1996; Hoddle et al. 1998). When *E. formosa* wasps detect a host, honeydew, or other whitefly remains, they are stimulated to stay in a local patch and search longer for more hosts. Encounters with whitefly nymphs or waste products can stimulate wasps to increase the length of time on a patch two- to tenfold. Some natural enemies find host patches by following physical trails formed by excrement, webbing, cast skins, or feeding marks on the plant caused by the host (Turlings et al. 1993).

Encounters with hosts by searching parasitoids can be influenced by many environmental factors. Light, temperature, host plant architecture, and presence of honeydew can affect the walking speed of some parasitoids, which in turn has a marked influence on the rate and efficiency of host location. *E. formosa*, for example, prefers to walk rather than fly at temperatures below 64°F (18°C), and does not remain long in patches with copious amounts of honeydew, which interferes with the wasps' searching and causes them to spend more time cleaning their legs. Many studies have demonstrated that high densities of leaf trichomes reduce searching parasitoid efficiency (Heinz and Parrella 1994b, van Lenteren et al. 1995, Sütterlin and van Lenteren 1996).

Once a host is found, the natural enemy must decide what to do with it. Depending on the stage of whitefly encountered and the nutritional state of the adult, *E. formosa* may oviposit in it or may pierce the nymph with its ovipositor and feed on the host's body fluids to obtain nutrition to develop additional eggs. Such host-feeding is a significant source of mortality in many pest populations (Debach 1943). Sometimes a wasp will use its ovipositor to pierce a potential host, but will neither oviposit nor host-feed on it. Depending on the amount of damage caused by this probing, the host may die. If neither host-feeding nor death from probing occur, the host is likely to receive an egg, and a new parasitoid will develop on the host and eventually emerge, increasing the population of parasitoids in the greenhouse. Superparasitism occurs infrequently within biological control programs since hosts that have previously been parasitized are often rejected. *E. formosa*, for example, rejects parasitized whitefly nymphs (van Roermund and van Lenteren 1992).

Species of parasitoids sold commercially vary between countries. Table 6.3 lists eight species that are currently available in North America and are commonly used in greenhouses (Hunter 1997). Although commercially available, several of these species have not been critically evaluated for efficacy, and experiments may be lacking to support or refute claims made by some retailers.

Parasitoids of Aphids

Aphelinus abdominalis

This synovigenic parasitoid attacks large-sized aphids such as *Macrosiphum euphorbiae* (Thomas) (potato aphid) and *Aulacorthum solani* (Kaltenbach) (glasshouse and potato aphid). The adult (0.12 in. [3 mm] long) is black with a yellow abdomen. The female oviposits inside aphids. Larvae grow through four instars and, after one week, pupate inside mummified aphids, which turn black. Upon emergence, mating occurs within the first twenty-four hours. It takes about two weeks to complete the entire life cycle. Wasps parasitize ten to fifteen aphids per day, and they will kill other aphids not accepted for oviposition by host-feeding. Previously parasitized hosts are not attacked. Hyperparasitoids of *A. abdominalis* are known to occur. Although this species does best in well-lighted, warm greenhouses, release of *A. abdominalis* by themselves does not result in successful biological control. To achieve satisfactory levels of aphid suppression in sweet pepper, tomato, eggplant, beans, gerbera, rose, chrysanthemums, and *Lisianthus*, aphid predators must also be released.

Aphidius colemani

This species has replaced *Aphidius matricariae* Haliday as the most commonly used aphid parasitoid in many southern greenhouses. This parasitoid will attack *M. persicae*, *Myzus nicotianae* Blackman, and, most importantly, the melon aphid, *A. gossypii*. In contrast, *A. matricariae* can only be used against *Myzus* spp. The adult (0.08 inch [2 mm] long) is black with brown legs. Because the adult is not long-lived, this species is shipped as pupae (inside mummies). Most of the female's eggs are laid in four to five days, inserted inside aphids or nymphs. After seven days (at 70°F [21°C]), the parasitoid larva attaches the aphid to the leaf and pupates in the dead aphid, forming a cocoon that makes the aphid swell and become brown and leathery. At this stage, the dead aphid is often called a mummy. After three to four days, the adult parasitoid chews a round circular hole in the mummy and emerges.

Adults of *A. colemani* can find aphid colonies from a long distance by using odors from honeydew (an adult food source) and possibly odors produced by aphid-infested plants. In some situations, this wasp eradicates the aphid population and thus fails to establish. When long-term control is desired, the failure of the parasitoid to establish leaves the crop unprotected against future aphid infestations. Therefore, continuous releases of *A. colemani* may be achieved using a banker plant system (based on the use of barley plants infested with a nonpest aphid *Rhopalosiphum padi* [L.]). Alternatively, *A. colemani* may be released weekly in low numbers. Other release strategies used include seasonal inoculative, preventive, and inundative releases. Typical release rates are 0.01 wasps per ft.^{2} [0.15 per m^2] each week (preventive), 0.05 wasps per ft.^{2} [0.5 per m^2] each week for at least three weeks (curative), and 0.05 wasps per ft.^{2} [0.5 per m^2] twice weekly for six weeks (for infestations). Dense infestations should be managed with other tactics (compatible pesticides, predators) either in combination with or before releasing this wasp.

Aphidius ervi

This parasitoid resembles *A. colemani*, but is much larger and attacks different species of aphids. This species is used against *M. euphorbiae* and *A. solani* on such crops as tomato, pepper, eggplant, gerbera, rose, cucumber, strawberry, and *Lisianthus*. *Aphidius ervi* develops from egg to adult in twelve to twenty-six days at 75.5 and 57°F (24 and 14°C, respectively). The mummy is yellowish brown in color. One female wasp can lay over 300 eggs. This species is most frequently used as a preventative measure by making weekly introductions of less than one wasp per 108 ft.^{2} [1 per 10 m^2] or by using a banker plant system of barley plants infested with the nonpest aphid *Metopolophium dirhodum* (Walker). In suppressing existing aphid infestations, this species is recommended for use with *A. aphidimyza* and *Harmonia axyridis* (Pallas).

Parasitoids of Whiteflies

Encarsia formosa

This is the most commonly used and best-studied parasitoid in protected culture. In this thelytokous species, virtually all individuals are females (0.02 in. [0.6 mm] long) with black bodies and yellow abdomens. Eggs are laid preferentially in third- and early fourth–instar whiteflies. At 73.4°F (23°C), the larva pupates inside the host in ten days, and the adult emerges twenty days after oviposition by chewing a circular hole in the dead whitefly. The duration of this life cycle varies from fifteen to thirty-two days at 79 to 64°F (26 to 18°C). Parasitized *Trialeurodes vaporariorum* (Westwood) (greenhouse whitefly) last-instar nymphs become melanized and turn black. In *B. argentifolii*, however, parasitized nymphs remain transparent enough to allow one to see the parasitoid inside. *E. formosa* prefers to attack *T. vaporariorum* rather than *B. argentifolii*. Adults of *E. formosa* eat honeydew and host-feed on first and second instars. *E. formosa* can parasitize between 250 and 400 whiteflies and host-feed on thirty to seventy nymphs in a lifetime. Additional details on the biology and use of this species are reviewed by Hoddle et al. (1998).

Eretmocerus eremicus

This wasp, formally referred to as *Eretmocerus* sp. near *californicus* Howard, is a common, lemon-colored parasitoid of *B. argentifolii* and *T. vaporariorum* in the southern United States. *Eretmocerus* spp. differ from *Encarsia* spp. in several ways. In contrast to *Encarsia* wasps, which lay eggs inside hosts, *Eretmocerus* species lay their eggs underneath the whitefly nymph. The first instar larva of *E. eremicus* burrows into the host, where it completes its development. *E. eremicus* will develop on younger instars than *E. formosa* will. Second- and early third–instars are *E. eremicus*'s preferred hosts for oviposition. The egg hatches three days after oviposition; two weeks later, a yellow pupa is visible inside the host. The total life cycle takes seventeen to twenty days, depending on temperature and the stage of whitefly attacked. *E. eremicus* kills many whiteflies by host-feeding, and in commercial poinsettia, most host suppression is due to host-feeding, not parasitization. In this arrhenotokous species, males comprise about 50% of pupae received from commercial producers.

Parasitoids of Leafminers

Dacnusa sibirica

This endoparasitoid parasitizes all larval stages of its *Liriomyza* hosts. Adults (0.08 in. [2 mm] long) are dark brown to black, with long antennae (in contrast to *D. isaea*, which has short antennae). Eggs are laid preferentially in young host larvae (first or second instars), which continue to feed and to pupate. The parasitoid larva develops within the later developmental stages of the leafminer and the wasp emerges from the leafminer pupa. The developmental time (egg to adult) varies from seventeen to twenty days at 68°F (20°C), but it also varies according to the leafminer instar parasitized by the wasp. This species does not host-feed, and adults do not attack parasitized larvae. As the temperature increases from 15 to 77°F (59 to 25°C, respectively), the average number of eggs laid per female declines from more than two hundred to less than fifty. Consequently, both inundative and inoculative releases of this species are used predominantly during the winter season or in northern climates to suppress early infestations of leafminers (Minkenberg and van Lenteren 1986). This wasp will parasitize *Liriomyza bryoniae* (Kaltenbach), *Liriomyza huidobrensis* (Blanchard), *Liriomyza trifolii* (Burgess), and *Phytomyza syngenesiae* (Hardy).

Diglyphus isaea

This synovigenic ectoparasitoid causes significant mortality by host-feeding, which the female must do to support the production of her eggs. The adult (0.08 to 0.12 in. [2 to 3 mm] long) is slightly larger and has shorter antennae than *D. sibirica*. Female wasps are larger than males, and both are black and metallic green. When attacking a leafminer larva, a female first paralyzes the second or third instar with her ovipositor and then reinserts it into the mine to lay an individual egg on or near the host. The parasitoid larva feeds externally on the paralyzed leafminer larva, eventually pupating inside the leaf mine. Upon emergence, the adult wasp escapes the leaf mine by chewing a small exit hole through the leaf cuticle. The optimum temperature for oviposition by this species is 77°F (25°C), and the developmental time (egg to adult) ranges from thirteen to thirty-three days at 77 and 61°F (25 and 16°C). Under laboratory conditions, the female may lay between 200 and 300 eggs during her life span, which ranges from between ten to thirty-two days at 77 to 68°F (25 to 20°C). Oviposition rates and adult life spans are likely to be significantly lower in conditions typical of protected culture (Heinz 1996, Heinz and Parrella 1990a). The abilities of this parasitoid to increase rapidly and to be effective at warm temperatures are its most important advantages compared to *D. sibirica*. Inundative or seasonal inoculative releases of this species have been used to manage *L. bryoniae, L. huidobrensis, L. trifolii,* and *P. syngenesiae* (Minkenberg and van Lenteren 1986, Johnson and Hara 1987, Heinz and Parrella 1990b).

Other Parasitoids

Leptomastix dactylopii

This encyrtid parasitoid can be used to manage citrus mealybug, *P. citri*, infesting interior landscapes. This wasp does not parasitize other mealybugs commonly found in protected culture. The adult wasp (0.12 in. [3 mm] long) is yellow-brown and parasitizes large female citrus mealybug nymphs and adults. One egg is usually laid inside each host, and the larva develops through four instars before pupating. Once the parasitoid pupates, the mealybug mummy becomes brown and swollen, resembling a grain of brown rice. To emerge, the parasitoid adult chews a circular hole in the mummy. Each wasp can parasitize fifty to one hundred mealybugs and can live relatively long if given food and high humidity. The life cycle ranges from twelve to forty-five days at 95 to 64°F (35 to 18°C), respectively. *Leptomastix dactylopii* is most effective when the mealybug density is very low, provided it is released directly into areas where mealybugs occur (due to the parasitoid's poor dispersal ability). Dense mealybug populations should be treated with selective pesticides prior to making parasitoid releases, or *L. dactylopii* should be used in conjunction with other mealybug natural enemies such as *C. montrouzieri*, *Anagyrus pseudococci* (Girault), and *Leptomastidea abnormis* (Girault).

Pathogens

Insect pathogens, generally applied as commercially formulated biopesticides in protected culture, include bacteria, fungi, viruses, and protozoa. These biopesticides contain either the living microbe or its chemical byproducts, and they are regulated as pesticides in most countries. Such products must meet criteria concerning safety, purity, and, in some countries, efficacy.

Because of the cost of such registrations, the number of products available for use in protected culture is limited (see tables 6.4, 6.5, and 6.6). Consequently, we discuss only species that are commercially available. We will discuss nematodes separately.

[table 4]

Table 6.4. Commercially Available Bacterial Pathogens and Their Target Pests.

Bacterial Pathogen	Target Pests
Bacillus thuringiensis Berliner *kurstaki*	Lepidopteran larvae
B. thuringiensis aizawai	Lepidopteran larvae, especially those that are not susceptible to *B. thuringiensis* var. *kurstaki*
B. thuringiensis israelensis	Diptera larvae (mosquitoes, black flies, and fungus gnats)
B. thuringiensis tenebrionis	Coleoptera (esp. Colorado potato beetle)
B. thuringiensis japonensis strain buibui	Soil-inhabiting beetles
B. thuringiensis aizawai encapsulated delta-endotoxins	lepidopteran larvae
B. thuringiensis kurstaki encapsulated delta-endotoxins	Lepidopteran larvae and some beetles
Bacillus sphaericus Neide	Mosquito larvae

[end table]

[table 5]

Table 6.5. Commercially Available Viral Pathogens (All Baculoviridae) and Their Target Pests.

Viral Pathogen	Target Pests
Adoxophyes orana granulovirus	Summerfruit tortrix (*Adoxophyes orana* Fischer von Röslarstamm)
Anagrapha falcifera NPV	Lepidopteran larvae, alfalfa looper[15] (*Anagrapha falcifera* [Kirby])
Anticarsia gemmatalis NPV	*Anticarsia gemmatalis* Hübner and *Diatreae saccharalis* (Speyer)
Autographa californica NPV	Lepidopteran larvae

Cydia pomonella granulovirus	*Cydia pomonella* (L.)
Helicoverpa zea NPV	*Heliothis* and *Helicoverpa* species
Lymantria dispar NPV	*Lymantria dispar* L.
Mamestra brassicae NPV	Lepidopteran larvae
Neodiprion lecontei, NPV	Sawflies
Spodoptera exigua NPV	Beet armyworm (*Spodoptera exigua* [Hübner])
Syngrapha falcifera NPV	*Heliothis* and *Helicoverpa* spp.

[end table]

[table 6]

Table 6.6. Commercially Available Fungal Pathogens (All Deuteromycetes) and Their Target Pests.

Fungal Pathogen	Target Pests
Beauveria bassiana (Balsamo) Vuillemin	Whiteflies, thrips, and soil-inhabiting beetles
Beauveria brongniartii (Saccardo)[16]	Soil-inhabiting beetles
Metarhizium anisopliae Sorok[17]	Coleoptera, Lepidoptera, cockroaches, and termites
Metarhizium flavoviride Gams and Rozsypal	Grasshoppers and locusts
Paecilomyces fumosoroseus (Wize) Brown and Smith	Whiteflies, thrips, and spider mites
Verticillium lecanii (Zimmerman) Viégas	Aphids, thrips, and whiteflies

Bacteria

Many bacteria are associated with insects; however, very little is known about many of them and only a few have been commercialized. The most important, *Bacillus thuringiensis* Berliner (Bt), was first commercialized in 1938. This bacterium has been widely used by gardeners and commercial growers for the control of certain caterpillars. However, commercial Bt products are not truly biological control agents because their activity is the result of a toxin the bacteria produce during the fermentation process. The formulated material contains a protein called a delta endotoxin, which is sprayed on plants or the soil surface to kill worms, beetles, and fly larvae. The toxin must be ingested to poison the target pest. Labels of commercial products indicate the toxin concentration (in international units) and describe how best to use the product.

Products may contain any of several Bt strains: *kurstaki*, *tenebrionis*, *san diego*, *israelensis*, or *aizawai*. Strains differ in the pests they kill. Most strains kill caterpillars, or fly larvae, or some beetles. For example, *B. thuringiensis* var. *kurstaki* kills over one hundred species of caterpillars (Lepidoptera). Disease outbreaks do not occur when these products are applied because transmission between hosts is poor. Genetic engineering of *B. thuringiensis* has added new genes to this species, resulting in products with several toxins. In addition, genes to express Bt toxins have been genetically engineered into many crop plants. This is a very active area of research, as well as a catalyst for debate on the utility and ethics of transforming agricultural plants and animals.

Bacterial products sold commercially for insect control that do not contain live bacteria are not considered to be biological control agents. Rather, these are chemical pesticides based on the endotoxin as the active ingredient. Other biopesticides contain the bacteria *Bacillus papilliae* Dutky, *Bacillus sphaericus* Neide, or *Serratia entomophila* Grimont, Jackson, Ageron, and Noonan.[18] These products, however, are not useful against pests in protected culture.

Viruses

Viruses have not been as widely accepted as bacterial biopesticides, even though insect viruses are highly host-specific and significantly different from those that cause disease in vertebrates and plants. Economically, their high host specificity is a limiting factor because the returns of costs associated with product registrations are low. A product that has activity on a single host, or at best a very limited number of hosts, will, in general, offer limited economic incentives for its commercialization. However, there are some viral pesticides registered in the United States for control of Lepidoptera. Each product contains a nuclear polyhedrosis virus (NPV), consisting of rod-shaped, elongated particles that are enclosed in crystalline protein matrices (called occlusion bodies) that protect virus particles from environmental adversities. Potency of a particular product is expressed in OBs/ml (occlusion bodies/milliliter). In Europe, two products exist that contain members of another group, the granulosis viruses.

Insect viruses attack and multiply within cells located in the hemolymph, trachea, fat bodies, and epithelium. Gypchek[19] is registered for the control of gypsy moth (*Lymantria dispar* [L.]), and Spod-X LC for the control of beet armyworm (*Spodoptera exigua* [Hübner]). These products must be ingested to kill the host insect, but they are somewhat slow to act compared with conventional pesticides (killing in one to seven days, depending on the size of larva attacked). Infected insects often crawl to an upper portion of the plant and die, where they rupture and release virus particles onto the foliage or soil, potentially starting a viral epidemic throughout the pest population.

Fungi

Fungal products have had less commercial acceptance than bacterial products. Because fungal biopesticides contain living cells, conditions such as humidity, temperature, and ultraviolet light levels must be within certain limits if acceptable results are to be achieved (Burges and Hussey 1971). Of hundreds of known entomopathogenic fungi, only a dozen species have been seriously considered for development as biopesticides.

There are several benefits, however, to using fungi. First, some fungi have limited host ranges, allowing them to be used with little harm to beneficial insects. Fungi are considered safer than chemical pesticides for the environment because they do not damage wildlife or contaminate food, soil, or water, as many conventional insecticides do. Second, fungi have the ability, if conditions are favorable, to multiply and cause an epidemic throughout the pest population (Burges and Hussey 1971). Greenhouse crops, which are grown under conditions with controlled temperature, high relative humidity and reduced solar radiation, offer a good physical environment for pest control using entomogenous fungi (van Lenteren and Woets 1988), especially with several species of Deuteromycetes.

Currently, many species of fungi are unsuitable for mass production or formulation into biopesticides, yet the prospect of using other fungi as biopesticides is good. In greenhouses, fungi are primarily used to suppress whiteflies and perhaps thrips. Both *Aschersonia aleyrodis* Webber and *Verticillium lecanii* (Zimmerman) Viégas are common pathogens of whiteflies. Products containing spores of these fungi either have been registered as biopesticides or are currently being evaluated for commercialization. Recent data indicate that *Paecilomyces fumosoroseus* (Wize) Brown and Smith and *B. bassiana* might also play important roles in control of whiteflies and other major pests of vegetable and ornamental plants in greenhouses (Fransen 1990; Osborne 1990; Osborne and Hoelmer 1990; Osborne, Hoelmer, and Gerling 1990; Osborne et al. 1990; Landa et al. 1994; Bolckmans et al. 1995).

Aschersonia aleyrodis

This fungus is specific to whiteflies and occurs naturally in the subtropical region of the Western Hemisphere, causing natural insect epidemics (Berger 1921, Petch 1921, Mains 1959, Fransen 1987).

Verticillium lecanii

This fungus is a common pathogen of aphids, whiteflies, and coccids (Gams 1971, Hall 1976, 1980). It occurs less commonly in Orthoptera, Hemiptera, Thysanoptera, Coleoptera, Lepidoptera, Hymenoptera (Gams 1971; Hall 1980; McCoy, Samson, and Boucias 1988), and mites (e.g., tetranychids and eryiophids) (Gams 1971, Kanagaratnam , Hall, and Burges 1981).

Paecilomyces fumosoroseus

This species is widespread throughout nature and is a pathogen of many different insect hosts. It is most commonly found infecting Lepidoptera, Coleoptera, and Diptera (Poprawski, Marchal, and Robert 1985). A Florida isolate of *P. fumosoroseus* is highly virulent to whiteflies and many other pests, and it causes epidemics that severely reduce whitefly populations in both greenhouses and open shade cloth–protected structures. This strain (PFR 97) is currently registered for use in the United States and Europe and has been evaluated in the laboratory and under greenhouse conditions (Osborne 1990; Osborne and Hoelmer 1990; Osborne, Hoelmer, and Gerling 1990; Osborne et al. 1990; Landa et al. 1994, Bolckmans et al. 1995).

Beauveria bassiana

This fungus is reported as a pathogen of many different insect hosts. Most of the host records for *B. bassiana* are from Lepidoptera and Coleoptera, but this pathogen has also been isolated from true bugs (Hemiptera), termites (Isoptera), and ants (Hymenoptera). After the emergence of *B. argentifolii* as a new pest problem in greenhouses in late 1986, isolates of *B. bassiana* able to infect this whitefly were identified and commercialized in the United States. At least one isolate has shown promise for the management of whiteflies. Infection and control of western flower thrips by *B. bassiana* has also been reported, but the levels of control vary substantially by geographic region, season, and crop.

Entomopathogenic Nematodes

Nematode Biology

Entomopathogenic nematodes are small, colorless, and unsegmented cylindrical worms classified into nine taxonomic families, but only those in three—the Steinernematidae, Heterorhabditidae, and Rhabditidae—are reared commercially (or are in development) for use as biopesticides. Many species in these families have wide host ranges, and the infective stages of some species can be easily and economically produced and stored. Their microscopic size makes them very susceptible to desiccation, and consequently they show the most promise for controlling pests residing in soil or inside plant tissues (e.g., borers, leafminers).

Some nematodes actively seek out and penetrate susceptible hosts. These are called cruiser species and include *Steinernema (= Neoaplectana) glaseri* (Steiner)[20] and *Heterorhabditis bacteriophora (= heliothidis)* Poinar. Other nematodes wait for a host to pass near them and then attack. These are called ambush species; examples are *Steinernema (= Neoaplectana) carpocapsae* (Weiser) and *Steinernema scapterisci* Nguyen and Smart. Once nematodes have penetrated a host, death is certain and occurs within twenty-four to forty-eight hours.

Eleven species of Steinernematidae and three of Heterorhabditidae are commercially available for use in protected culture (see table 6.7 for a list of the principal species used in greenhouses). These species are all obligate parasites of insects or slugs and thus are harmless to vertebrates, plants, and other nontarget species.

The effectiveness of nematodes in biological control is due to the presence of mutualistic bacteria within their guts. These bacteria in the genera *Xenorhabdus* (for steinernematids) and *Photorhabdus* (for heterorhabditids) produce antibiotics and toxins that assist in the infection process and in converting host tissues to food usable by the nematodes. Two forms of the bacteria exist. The first form promotes increased growth and reproduction by nematodes and is found in the infective stage of the nematode and in the pest insect during the early stages of infection. This form also produces antibiotics that prevent putrefaction of the host cadaver. The other form is more stable and occurs late in the infection process, but its function is unclear. Once the insects are dead, they turn a characteristic color, depending on which type of nematode is responsible: brownish yellow with the steinernematids, and red with the heterorhabditids.
[table 7]

Table 6.7. Principal Commercially Available Nematode Species and Their Target Pests.

Nematode Species[a]	Target Pests
Heterorhabditis bacteriophora Poinar (H)	Manure flies, caterpillars, weevil larvae, and other soil-dwelling insects
Heterorhabditis megidis Poinar, Jackson, and Klein (H)	Various soil-dwelling insects
Phasmarhabditis hermaphrodita (Schneider) Andrassy[21] (R)	Slugs
Steinernema carpocapsae (Weiser) (S)	Caterpillars, beetle larvae, some flies, and other soil-dwelling insects
Steinernema feltiae (= *bibionis*) (Filipjev) (S)	Various soil-dwelling insects such as fungus gnats and banana moth larvae (*Opogona* spp.)
Steinernema glaseri (Steiner) (S)	Soil-dwelling white grubs

Steinernema riobravis Cabanillas et al. (S)	Corn earworm, mole crickets, and the larvae of citrus weevils

[a] Heterorhabditidae (H), Steinernematidae (S), and Rhabditidae (R)

[end table]

The generalized nematode life cycle consists of an egg, four juvenile stages, and the adult. The third juvenile stage (frequently called a dauer) is the infective stage. All members of this stage contain living bacteria and are free-living and motile. This stage has stored food reserves, and even though it does not feed, it can survive in an active state for several weeks when conditions are favorable.

Once a host is found, nematodes enter through natural body openings such as the mouth, anus, or spiracles. Heterorhabditids have a dorsal tooth that allows them to enter the host directly by penetrating the softer membranes found between insect segments (Bedding and Molymeux 1982, Poinar 1990). Inside the host's body, nematodes enter the hemocoel and release bacteria. The infected insect dies within twenty-four to forty-eight hours from bacterial growth (septicemia). The nematodes feed and develop on the bacteria cells and host body tissues. More than one generation of nematodes can develop within the cadaver of a single host. The life cycle typically requires ten to twenty days at 82.2 to 64.4°F (28 to 18°C) (Martin and Miller 1994).

Steinernematids reproduce sexually in all generations. The number of generations, as well as the number and size of individuals within a generation, are thought to depend on host size and the amount of nutrition available to the nematodes. Small insects will die after being attacked, but they may not support a generation of nematodes.

Due to their microscopic size, nematodes are very susceptible to desiccation, and as a result, moisture has the greatest environmental influence on nematode biology. The activity and infectivity of one of the more commonly used nematodes, *Steinernema* (= *Neoaplectana*) *feltiae* (= *bibionis*) (Filipjev), are greatest at 25 to 40% soil moisture. Low moisture levels, rapid desiccation on leaf surfaces, and exposure to ultraviolet light are believed to limit the ability of nematodes to infect foliage-feeding arthropods. These factors can also significantly affect nematodes that are applied to the soil surface if they are not transported into the soil by ample irrigation immediately after the application.

Temperature also influences nematode biology, although the relationship is not quite as direct as with moisture. The relationships between survival, infection, developmental rate, and temperature all vary between species and strains. Some strains have a narrow range of temperatures over which they are effective. The strain selected for use in a given crop should be effective at the temperatures it will encounter in that crop; *Heterorhabditis marelatus* Liu and Berry, for example, is a cool-temperature species, whereas *H. bacteriophora* is a warm-temperature species.

Commercially Available Nematodes

Heterorhabditis bacteriophora

This species attacks the black vine weevil, *Otiorhynchus sulcatus* (F.), a serious pest of nursery stock. This nematode moves actively through the upper layers of potted soil to find hosts. Several biological factors work against the widespread use of *H. bacteriophora* for biological control within protected culture. The species is sensitive to low temperatures, and control declines when temperatures drop below 68°F (20°C). In addition, it has a poor shelf life, and the infective stages are short-lived in the soil.

Heterorhabditis megidis

This species has also shown efficacy against black vine weevil larvae and pupae. Dependent upon pest densities, recommended release rates vary between 46,500 and 93,000 nematodes per ft.^{2} (500,000 and 1,000,000 nematodes per m^2) of soil surface. *Heterorhabditis megidis* Poinar, Jackson, and Klein is effective in soils where the temperature does not fall below 54°F (12°C) for at least two weeks following treatment. This nematode can remain active for about four weeks, as long as the soil conditions are suitable.

Steinernema carpocapsae

This species has been well studied and is widely used. It has proven effective against many pests, including webworms, cutworms, armyworms, girdlers, and wood-borers. It is an ambush species that waits for its prey to pass by. Therefore, it is most useful against prey that are highly mobile. *Steinernema carpocapsae* products have much better shelf life than do those containing *Heterorhabditis* spp. This is generally the case when comparing *Steinernema* species with *Heterorhabditis* species. *Steinernema carpocapsae* works best at temperatures between 72 and

82°F (22 and 28°C).

Steinernema feltiae

This nematode seeks out its prey in soil and is most often used in greenhouses to control fungus gnats (Sciaridae) and various other flies. It is frequently used in combination with predatory mites (*Hypoaspis* spp.) to control particularly problematic infestations. Effective management programs for sciarid larvae require routine preventative applications of nematodes. *Steinernema feltiae* is most effective in moist soil that is between 59 and 68°F (15 and 20°C). These nematodes become inactive at temperatures below 50°F (10°C) and above 86°F (30°C), and hence applications during these conditions should be avoided. One hindrance to using *Steinernema feltiae* products is their relatively short shelf life.

Other nematodes

Although *Steinernema glaseri* and *Steinernema riobravis* Cabanillas et al. are commercially available, they are currently recommended for managing pests only in turf, citrus, and sugarcane.

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