Chapter 5
Management of Unwanted Organisms

5.1 Weed Management

Suppression of the growth of weeds in agroecosystems can be accomplished in numerous ways. The measures used are either intended to give the crop a favourable starting position in the competition with other species or to keep the crop stand free from weeds, as far as possible.

5.1.1 Herbicides

Herbicides are chemical compounds that serve for management or elimination of unwanted plants. In the nineteenth century, such inorganic compounds as copper(II) sulfate, iron(III) sulfate, or sodium chlorate were first used to combat weeds. Today's herbicides are mostly organic compounds from a variety of chemical groups. Currently, there are more than 200 substances with approximately 20 different mechanisms of action. In most cases, the herbicides impair the metabolism of the plant by inhibiting enzyme activity. The most important processes in which herbicides interfere are:

- photosynthesis (e.g. by impairing electron transport in the photosystems);
- carotenoid synthesis (by preventing the production of carotenoids, which are important as protective pigments of chlorophyll);
- cell respiration (by impairing the acquisition of energy from stored organic compounds);
- fatty acid metabolism (e.g. by impairing the formation of waxes and cutins on the plant's surface and thus disturbing the plant's water balance);
- amino acid synthesis (by which the formation of various proteins and enzymes is prevented);

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- cell growth (by herbicides which correspond in their effect to the natural plant hormone auxin and lead to uncontrolled growth of the plant); and
- cell division (by disturbance of the processes of mitosis).

Herbicides are usually applied in the liquid form and are taken up by the plant either through the roots (soil herbicides) or through the leaves (leaf herbicides). Herbicides can be further differentiated into contact herbicides, which are only effective at the sites at which they come into contact with the plant, and systemic herbicides, which are transported inside the plant to the locations in which they are effective.

Another criterion used for classification of herbicides is the selectivity of their impact. Non-selective or broad-spectrum herbicides are effective against a wide range of different plant species. In agroecosystems, they are often applied before sowing or germination of the crop (the so-called pre-emergent herbicides). In contrast, selective herbicides are only effective against certain types of plants and can therefore be used against individual weeds in a crop stand without significantly damaging the crop (post-emergent herbicides). The active agents to be applied are selected according to the respective crop and weed species. The selectivity of a herbicide is often not only determined by the physiological and morphological characteristics and the stage of development of a plant, but also by the quantity of herbicide applied, the time of application, and different environmental factors (e.g. weather, soil properties).

As protection against the effects of specific herbicides, so-called safeners or antidotes were developed for several cereal species. They selectively protect crop plants from herbicide damage without reducing activity in target weed species. Safeners consist of additional ingredients in herbicides which are taken up by the crop and suppress the activity of the herbicides in different ways (e.g. by breakdown or deactivation of the active agent of the herbicide during crop metabolism). Safeners do not impair the desired effect in the target species (primarily grasses), because these have physiological properties different from those of the crop species.

5.1.2 Herbicide-Resistant Crops

Genetic engineering of crop plants is another means of creating biochemical selectivity against herbicides. By transfer of appropriate genes from another organism (primarily bacteria), it has been possible to bestow crop species with resistance to specific active agents. Such transgenic plants are capable of synthesizing enzymes that enable them to degrade the active ingredient in a herbicide, rendering it harmless.

Fig. 5.1 Common barnyard grass (*Echinochloa crus-galli*)

The most important crops with such properties are varieties of soybean, rapeseed, maize, and cotton resistant to glyphosate or glufosinate. Both of these substances are non-selective herbicides which impair the synthesis of amino acids in plants and can thus only be applied to stands of resistant varieties as post-emergent herbicides. Farmers can thereby easily control weeds during the entire growing season and have more flexibility in choosing times for spraying.

In chemical weed management of such crops, however, the farmer is dependent on herbicides that contain the compound to which the particular crop variety being grown is resistant. This relationship is called a herbicide resistance system, which consists of the resistant variety and the so-called complementary herbicide, which does not damage the respective crop variety. The important advantage of this method is that a non-selective herbicide can be applied to a crop stand and chemical or mechanical weed management is thus no longer necessary before sowing. It is also possible then to mostly or entirely give up soil cultivation because the disadvantages of no-till methods (conservation soil tillage and direct seeding; Box 4.2), in relation to weed management are eliminated. Whether the herbicide resistance system is generally a more environmentally friendly method of weed management than the application of selective herbicides cannot be estimated. There is always a threat that with the repeated application of herbicides with the same active mechanisms, which is necessarily the case in the herbicide resistance system, resistant populations of weeds will develop. Such weeds are already a problem in various production systems, having developed as result of continuous application of specific active compounds. Examples of weed species with herbicide-resistant populations include the slender meadow foxtail (*Alopecurus myosuriodes*) and the common windgrass (*Apera spica-venti*) in cereal production in Europe, common barnyard grass (*Echinochloa crus-galli*; Fig. 5.1), white goosefoot (*Chenopodium album*), and other species in corn and soybean production in North America.

5.1.3 Cultivation Measures

The growth and development conditions of weeds can be affected by a variety of measures in the design and management of cultivation systems. These include:

Crop rotation. The importance of individual weed species in an agroecosystem is essentially determined by the respective crop species, because the cultivated species and varieties differ in their competitive ability against different weed species. When production is conducted in the form of monocultures, then the populations of the respective problematic weeds can increase from year to year. For example, the repeated production of winter cereals promotes such grass species as foxtail grass and common windgrass, which primarily germinate in autumn. Such developments can be limited by appropriate crop rotation (e.g. by switching between cereals and root crops). Although such crop rotation promotes a diverse assemblage of weeds, dominance of specific weed species in one of the crop stands can be avoided.

Undersown crops. The stands of such plants can suppress the growth of weeds by shading (Sect. 4.4.1.1) and in some cases also as a result of allelopathic effects (Sect. 4.4.2).

Sowing date. For many crop species, the choice of the sowing date has a substantial effect on the competitive ability of the crop against some weed species.

Examples: With an early spring sowing date of summer cereals or beet, such weed species as common wild oat and sticky weed develop almost simultaneously with the crop. With a later sowing date, the germinating weeds can be eliminated during seed bed preparation.

An early sowing date for winter cereals in autumn favours the development of weed species that germinate during this time, but leads to a suppression of the growth of annual species that emerge in the following spring. At that time, the cereal stand is already so closed that the plants cast substantial shade.

The incidence of the parasitic weed *Orobanche crenata*, and the biomass produced on the host plant, are reduced with decreasing soil temperature (Fig. 5.2). This situation can be used in the production of such species as lentils, by moving the sowing date from October to December.

Soil cultivation. Reduction in the density of weeds can be achieved by mechanical soil cultivation with a variety of equipment (e.g. hoe, weeding harrow, cultivator, plough). Depending on the method, growing plants are cut into pieces, rooted out, or buried. This is primarily accomplished by the plough, whereby seeds are also transferred into lower soil layers. In many weed species, the germination can thus be reduced. However, previously buried seeds can also be brought back to the surface by ploughing.

Variety selection. The varieties of a crop species can vary in their ability to compete with weeds. This is based on characteristics which include height, leaf size, leaf position, and growth rate and are important in, primarily, competition for light (Sect. 4.4.1.1).

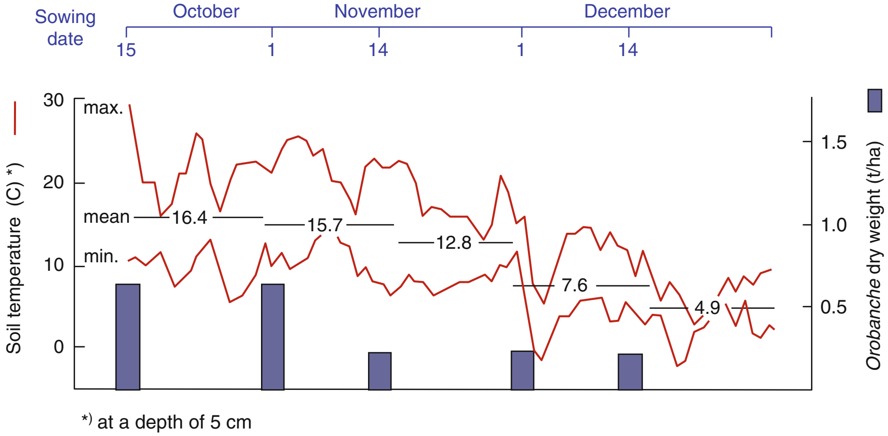


Fig. 5.2 Effect of sowing date of lentils and soil temperature on the dry mass production of *Orobanche crenata* in Tel Hadya, northwest Syria (Based on Sauerborn 1989)

5.1.4 Additional Methods of Weed Management

In addition to the methods of weed management described above, other measures exist that, depending primarily on technical and financial feasibility, can be applied as either complementary or alternative measures:

Seed cleaning. Often the seeds of weeds are gathered during harvesting of crops and can find their way back to the fields in the course of the next sowing. With modern methods of seed cleaning, this means of dispersal can be strongly limited, but this can also contribute to the loss of biodiversity of wild plants (Sect. 3.3.2).

Manual labour. Manual removal of weeds and use of simple tools (hoes) are the most labour-intensive methods of weed management. In small-scale agricultural systems in the tropics, these methods are often of great importance because of the lack of alternatives (cf. Sect. 2.4.1). Because of the high labour input, manual weed management can become a factor limiting the amount of land cultivated. Even in intensively managed agroecosystems, primarily in field vegetable production, manual weeding can make an important contribution to securing yields.

Thermal methods. By use of a variety of methods it is possible to manage weeds by temperature treatment. The methods used include flaming with tools that produce an open flame or release infrared radiation, as well as microwave treatment. Another technique is solarization, which is primarily successful in regions with high insolation (e.g. in the Mediterranean region). In this method, areas of cultivation are first irrigated and then covered with foil through which light can pass. This results in a substantial increase in the surface temperature of the soil and thus causes the seeds and shoots of many weed species to die off.

Application of thermal methods is limited in agroecosystems because of cost and effectiveness. However, flaming techniques can be an alternative to manual weed management, especially in field vegetable production.

Biological methods. In contrast with biological control of pests (Sect. 5.2.4), management of weeds in agroecosystems by use of organisms (phytophages and phytopathogens) is not currently significant. It is rarely possible to control weeds with bioherbicides, i.e. with phytopathogens applied to fields as spore suspensions. On the basis of the classical principles of biological control (Sect. 5.2.4.7), in many cases it has been possible to repress plant species on continents to which they were introduced from other continents (e.g. some grassland weeds and aquatic plants).

5.2 Pest Management

The most important objective of pest management in agroecosystems is the prevention of economically significant yield losses of crops. Means by which this is achieved primarily include application of chemical substances, cultivation of pest-resistant varieties, use of specific means of cultivation, and use of antagonists of the pests.

5.2.1 Chemical Pest Control

The most common type of management of animal pests in agroecosystems is the application of **pesticides**, i.e. chemical compounds that are designed to counter different groups of target organisms (Box 2.2). Pesticides can be classified as either synthetic or natural, the latter being derived from plants, animals, or microorganisms. The substances either act as contact poisons, i.e. they enter the organism through the body surface or as stomach poisons, the latter by ingestion during feeding. Because the insects are the largest and most important group among the animal pests, the following sections focus on insecticides.

5.2.1.1 Synthetic Insecticides

Today, almost all synthetic insecticides are organic compounds; inorganic compounds, for example arsenic or hydrogen cyanide (prussic acid) are no longer used or are banned. Most synthetic insecticides belong to the following groups of compounds:

Organochlorine compounds. These compounds impair the transmission of impulses in the nervous system by blocking the ion channels of the axon.

One of the first insecticides of this group, DDT (dichlorodiphenyltrichloroethane) was used during and after the second World War in the military hygiene sector against lice, fleas, and bed bugs, later also in the fight against malaria and its vector (*Anopheles* mosquitoes) and against agricultural pests. DDT is difficult to break down, can enter the food chain, and accumulates in the fat tissues of organisms. For these reasons, its production and use in have been prohibited in most countries. Other substances from this group are e.g. hexachlorocyclohexane (HCH) and endosulfan.

Organophosphates. These compounds (esters of phosphoric acid) include not only insecticides but also chemical weapons, for example the nerve gases tabun and sarin. They have neurotoxic effects by inhibiting the enzyme acetylcholinesterase and thus disrupting the transmission of nerve impulses. Most of the insecticides from this group, with some exceptions, for example parathion (E 605), have low toxicity to mammals but are highly toxic to aquatic organisms (fish and shellfish). Some of these substances are also taken up by plants and distributed within their transport systems. As a result of this systemic effect, they also work against sucking insects and mites. Other organophosphates enter the plant via leaf and stem tissues. Examples of this type of compound include chlorpyrifos, malathion, and phosphamidon.

Carbamates. This group consists of derivatives of carbamic acid, which have a neurotoxicological effect by inhibition of acetylcholinesterase, similar to the organophosphates. This group also includes substances that are taken up by plants and distributed in their tissues. Pirimicarb acts systemically via the roots and is regarded as safe for some aphid antagonists, for example ladybirds and green lacewing larvae. Other examples of carbamates are methiocarb and carbofuran.

Pyrethroids. These synthetic compounds are chemically related to the pyrethrins which occur naturally in the flowers of some *Chrysanthemum* species. The pyrethroids have a greater efficacy and lower light sensitivity than the natural plant substances and can be produced more easily. They are contact poisons that do not enter the plant and have a neurotoxicological effect similar to that of the organochlorine compounds. Active agents used in agriculture include deltamethrin, cypermethrin, and fenvalerate.

Chloronicotinyls. This group of substances was developed in the 1980s. As neurotoxins, they inhibit the acetylcholine receptors and are thus similar to nicotine in their effect. They act as contact poisons, but are also taken up by the plant and act against a wide range of insects. The most important substance is imidacloprid.

Benzoyl ureas. In contrast with most of the other synthetic insecticides, these compounds (e.g. diflubenzuron) are not neurotoxins, but instead block chitin biosynthesis and thus the development of arthropods. Because their effect is not immediately lethal to animals, the possibilities of use of these substances in agriculture are limited. They are primarily used against pests in the forestry sector.

5.2.1.2 Natural Insecticides

Substances derived from organisms that are used to manage pests largely include secondary plant metabolites (Sect. 4.5.5.2), which the plants produce to protect themselves from feeding enemies. Some of these plant-based insecticides have been used for thousands of years in the management of pests, but many have lost most of their importance since the development of synthetic insecticides. Worldwide, approximately 2,400 plants are known that can be used against pests, but only a few are produced commercially. Nevertheless, some of these species are of regional importance and can serve small-scale farmers in the tropics, especially, as an alternative to (expensive) synthetic insecticides. In the search for new substances, natural insecticides are also of interest to the chemical industry, because they can potentially be the source of initial compounds or models for more effective synthetic compounds. An example of this has already been given above—the pyrethrins were the basis for the development of the pyrethroids. Other examples of plant-based insecticides are:

Nicotine. Extracts from tobacco plants (*Nicotiana* species) have a neurotoxicological effect and were, before the development of DDT, among the most important agents in insect management. However, nicotine is also highly toxic to warm-blooded animals (endotherms) and other organisms, for example earthworms.

Quassin. This substance is derived from the South American tree species *Quassia amara*. Until the 1940s it was used to control aphids and caterpillar pests in Europe and North America.

Rotenone. This neurotoxin comprises a variety of substances found in tropical legumes of the genera *Derris*, *Lonchocarpus*, and *Tephrosia*. They act not only on insects but also on fish and other aquatic organisms.

Azadirachtin. This substance is found in the seeds, leaves, and bark, of the neem tree (*Azadirachta indica*), which originates from the Indian subcontinent. It is an antifeedant for many species of insects and also has an inhibitory effect on their metamorphosis. Neem leaves are traditionally used against storage pests. Neem extracts (primarily from the seeds) are also suitable for use in agroecosystems and are gaining increasing importance not only in tropical regions, but also in Europe and North America.

The most important natural insecticides originating from microorganisms are the toxins of the bacterium ***Bacillus thuringiensis*** **(Bt)**. For approximately 100 years it has been known that this soil-living species produces proteins with toxic effects on insects. After oral ingestion and enzymatic activation, these so called δ-endotoxins destroy the intestinal mucosa of insects, which subsequently die. More than 140 such proteins are known; they are produced by different subspecies of *B. thuringiensis* and each affects a specific group of insects. These primarily include butterflies, beetles, and diptera (flies and mosquitoes), but not all representatives within these orders. The Bt proteins are not dangerous to mammals and other vertebrates.

Bt formulations have been used as bioinsecticides since the 1930s and consist of dried bacteria spores or crystallized toxins. They are primarily used in maize, potato, fruit, and vegetable production. They are of greatest importance in organic agriculture. Another way of using Bt toxins is to transfer the respective genes into crop species (Sect. 5.2.2.1).

5.2.1.3 Pheromones

Substances that are released by organisms and have an attractive or repulsive effect on individuals of the same species are called **pheromones**. As sexual attractants, pheromones are important for numerous insect species. They are released by the females and have an attractive effect on the males. Many of these substances, which are usually specific to particular species, can be produced synthetically and used, e.g., in the management of pest caterpillar species in fruit and grape production. However, pheromones, usually applied in insect traps, are not usually suited to direct control, because the number of individuals caught usually makes up only a small portion of the total population. The traps primarily help to identify the start of the flight period of the pest butterflies and enable estimation of population density. Thus, they are used to determine the optimum time period and method with which to manage the pests. Against some species, for example the codling moth (*Cydia pomonella*) or the European grapevine moth (*Lobesia botrana*), sources of pheromones are placed among the crops to confuse the males. When concentrations of the attractive substances in the air are high, the males are no longer able to locate the females, whereupon reproduction, and thus the number of offspring, are reduced.

Another strategy which makes use of pheromones is the development of genetically modified crops that produce pheromones that are repellent to a pest. This approach has been realized in the development of a wheat variety which releases the sesquiterpene (*E*)-beta-farnesene, an alarm pheromone for many aphids. Such pheromones are released by aphids when they are attacked by their enemies, for example ladybirds, and causes them to disperse. This wheat variety was created by transformation of an (*E*)-beta-farnesene synthase gene from peppermint (*Mentha* × *piperita*) and is expected to repel aphids from the crop plant by emission of their alarm pheromone (Rothamsted Research 2012).

5.2.1.4 Unwanted Effects of Insecticides

With the exception of the Bt toxins, most synthetic and natural insecticides are unspecific, which means they usually affect a wide range of insect species. Furthermore, the neurotoxic substances not only affect insects and other arthropods, but almost all organisms with a nervous system. Nevertheless, it is possible to use insecticides in such a manner that not all species of the agricultural community are affected in the same way. Such selectivity is not usually based on fundamental changes in the mechanism of the applied substance but is essentially because of the following factors:

Dose-dependent effects. Some insects are more harmed than others by the same quantity of an insecticidal compound. Such differences are dependent on such factors as the size of the species, the development stage (egg, larva, pupa, adult), morphological characteristics, for example the structure of the cuticles, or physiological differences in the ability to detoxify harmful substances. By application of small quantities of the substances it is therefore possible to successfully manage some pests while at least some of the other insects survive. However, the latter can be harmed by sub-lethal effects. Sub-lethal insecticidal effects do not lead to the immediate death of the individuals but can, instead, reduce fertility, delay metamorphosis or impair metabolism and thus have a negative effect on the development of the population. Such disturbances can be found among predators and parasitoids when they feed on phytophages contaminated with insecticides.

Contact-dependent effects. Another way to limit the effects of insecticides to specific target groups is to avoid contact between the substances and some organisms. With treatments adjusted to the presence or the phases of activity of specific species or their developmental stages, it is possible to limit effects on organisms other than the pests. For example, pollinators, for example bees or parasitoids, can be protected when application of insecticides is avoided during the flowering stage of a crop. Effects on other organisms can be avoided, or at least reduced, by use of active agents that are taken up by the plant and primarily act as toxins when ingested by herbivores.

Use of methods to limit the impact range of insecticides requires detailed knowledge of the application of the products. Even humans can be harmed by inappropriate application of insecticides, for example by application of excessive quantities or by too frequent application. Approximately 90% of cases of illness or death that are caused worldwide by synthetic pesticides occur in developing countries. This can be primarily attributed to a lack of education and insufficient protection when working with the substances.

The insecticides and other pesticides applied to crop stands often end up in the environment in large quantities. As a result of water and wind, the substances also reach ecosystems far from the areas of application (Bedos et al. 2002).

Insecticide-Induced Pest Resurgence

There have been instances when the population density of some pests has not been reduced by application of an insecticide but has, instead, increased substantially. This phenomenon, known as insecticide-induced pest resurgence, has been observed in many production systems, for different pest species, and after application of different active agents. The causes of this are complex and not usually

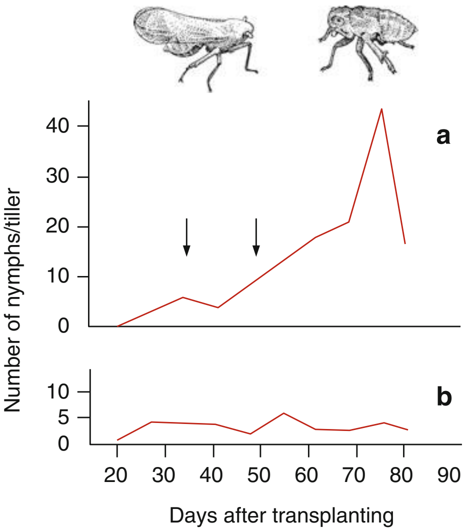


Fig. 5.3 Population development (number of nymphs) of the brown planthopper (*Nilaparvata lugens*) on rice plants that (**a**) were treated with the insecticide deltamethrin on two occasions (*arrows*) and (**b**) were not treated (Based on Heinrichs et al. 1982)

attributable to a single factor. The following mechanisms may be involved (Hardin et al. 1995):

- The applied substance, or the quantity applied, has a stronger effect on natural enemies of the pest than on the pest species itself. As a result, the effect of the antagonist on the pest population decreases, and the latter subsequently increases. In addition, other specific insecticidal effects, for example those affecting alternative prey species of the antagonist (Sect. 5.2.4.2) or competitors of the pest, can also be involved.
- In many cases, it has been shown that the insecticide affects the physiological processes of plants. Such changes can have a positive effect on the herbivores via the uptake of food and may improve their ability to detoxify insecticidal substances or increase their fecundity.

Example: For some rice varieties, the concentration of free nitrogen compounds in the transport tissues increased after application of the pyrethroid deltamethrin. As a result, the quality of food of the brown planthopper (*Nilaparvata lugens*) improved, and was believed to be the main reason for the observed resurgence of the pest (Heinrichs et al. 1982; Fig. 5.3).

Insecticide Resistance

Another factor resulting in reduced susceptibility of some insect pests is explained by insecticide resistance. In contrast with the mechanisms of insecticide-induced pest resurgence, insecticide resistance is an evolutionary process based on mutation

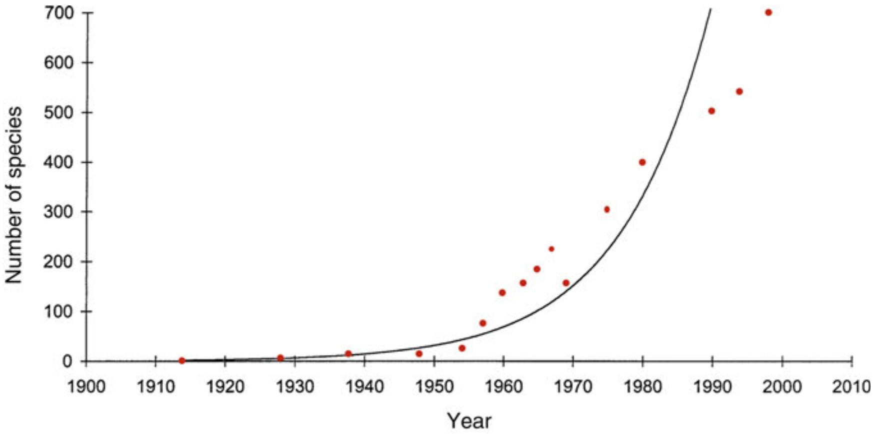


Fig. 5.4 Increase in the number of arthropod species resistant to at least one insecticide in the course of the twentieth century (Based on Thacker 2002)

and selection (cf. Box 2.1). Mutations can, in some individuals of a pest population, lead to the development of a resistance to a specific insecticide. These properties are generally based on biochemical mechanisms, for example the synthesis of specific enzymes with which the toxic substances are broken down, or on changes in the physiological characteristics of the organism as a result of which the toxic compounds no longer have their effects. The repeated application of insecticides acts as the selection factor through which susceptible individuals of the population become eliminated while the resistant individuals continue to exist and reproduce.

The number of arthropod species that have developed resistance to one or more insecticidal compounds has significantly increased in recent decades (Fig. 5.4) and is likely to continue to increase in the future.

Chemical control of such pests is then only possible with substances against which the respective populations have not yet developed resistance. In response to pesticide resistance, farmers often try to achieve success by increasing the applied quantities of already ineffective substances. However, the resistance that has developed in a population cannot be reversed. Development of insecticide resistance can be delayed by avoiding unnecessary insecticide applications and, if necessary, using the lowest concentrations possible. In other words, adopting the approach of integrated agriculture (Sect. 2.3.6) contributes to resistance management. This may include the application of other measures in pest management, which are the subject of the following sections.

Insecticides not only have toxic effects on specific organisms, but also affect the interactions of the species and other processes in the agricultural community in complex ways.

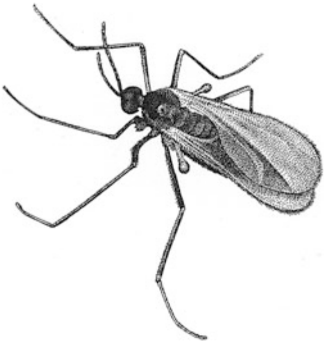


Fig. 5.5 Hessian fly or barley midge (*Mayetiola destructor*). The larvae of this species attack the wheat plant at the point of attachment of the leaf sheath to the stem

5.2.2 Pest-Resistant Crops

One way of managing pests without application of insecticides is the breeding and cultivation of resistant crop varieties. In the context of the definition of plant resistance against herbivores (Sect. 4.5.5), it has already been pointed out that the different mechanisms of plant defence are based on genetic properties of the plants. During the process of domestication and selection, many of the varieties of the different crop species grown today lost the genes that provide resistance, because the breeding was usually primarily directed toward high yields. The objective of **resistance breeding** is improvement of the genetic performance of a crop, to increase its ability to defend itself against the organisms that cause damage.

The phenomenon of pest resistance has been known for a long time. As early as 1792, the wheat variety “Underhill” was produced in North America which, in contrast with other varieties, is rarely attacked by the Hessian fly or barley midge (*Mayetiola destructor*; Fig. 5.5). However, the directed breeding of resistant varieties only began at the beginning of the twentieth century, with increasing knowledge of genetics.

In conventional resistance breeding, the objective is crossing of a desirable but pest or disease-susceptible plant variety with another variety that is a source of resistance. Often the respective resistance genes are found in old landraces or in wild forms from the centre of origin of the crop. By crossing, initially undesirable characteristics are also transferred into the breeding lines, which means that the previously selected characteristics of modern varieties (e.g. high yield) are partially lost. It is therefore necessary, by repeated back-crossing with the modern variety, to regain these characteristics, without losing the crossbred resistance.

Crossbreeding of a resistant variety can take up to 15 years and is undertaken with knowledge of the risk that the pest or disease can overcome the resistance in a shorter period than was required for the breeding.

5.2.2.1 Transgenic Pest-Resistant Crops

The insect resistance of transgenic crops (Sect. 2.3.4) is based, almost always, on the presence of genes of *Bacillus thuringiensis*. At the beginning of the 1980s, the first transfers of Bt-endotoxin genes into the genomes of plants succeeded. Subsequently, these plants were able to produce the toxins by themselves and were thus resistant to some herbivores. Compared with the application of insecticides, use of **transgenic Bt crops** has the following **advantages**:

- Bt plants have systemic protection that is present at all stages of growth and thus over the entire cropping period.
- Bt plants are also protected against some endophagous consumers (e.g. stem borers); this is difficult to achieve by application of many insecticides.
- Bt plants can be used against insects that have become resistant to some insecticides.
- Overall, the frequency and quantity of application of conventional insecticides can be substantially reduced by use of Bt plants, which reduces costs for the farmer and effects on the environment.

In addition to these advantages, cultivation of Bt crops is also accompanied by **problems and risks**:

- The relatively high specificity of Bt toxins is a disadvantage when economic damage is caused by different insect groups, which is usually the case. Pest species that are not affected by the Bt toxins (e.g. representatives of the true bugs, aphids, spider mites, and thrips) can still only be managed by use of insecticides.
- Insects may not only become resistant to synthetic insecticides, but also against Bt toxins, which has already occurred in some species as a result of application of Bt formulations. This process can be accelerated by use of transgenic Bt crops, because the herbivores are constantly subject to a selection pressure as a result of the systemic effect of the toxins. If insects acquire systemic resistance against transgenic Bt crops, they can also no longer be managed by use of Bt formulations. This would be particularly disadvantageous for organic agriculture, in which such products are used.
- Negative effects of Bt crops against non-target organisms cannot be definitively ruled out. They might affect animals (primarily antagonists of the pests; Sect. 5.2.4.1) and plants. By gene flow via pollen transfer, introgression of Bt genes to non-transgenic plants of the same species (e.g. maize) or to closely related wild forms might occur. In the extreme case, transgenic wild plants acting as weeds can therefore become more serious. As a result of their resistance against specific insects, these wild plants would have an advantage which would not only promote their dispersal but also harm insect species other than pests as a result of their toxic effects. By incorporation of harvest residues of Bt crops into the soil, microorganisms could also be affected. It is also possible that the genes of Bt toxins could be transferred to related *Bacillus* species.

Overall, the complexity of ecological systems is a substantial challenge to experiments to assess the risks, benefits, and inevitable uncertainties of genetically engineered plants. Collectively, current studies emphasize that these can vary spatially, temporally, and according to the trait and cultivar modified (Wolfenbarger and Phifer 2000).

In principle, genes other than those of *Bacillus thuringiensis* can be transferred to plants and provide them with increased resistance to insects. Most attempts are concentrated on the development of transgenic plants that synthesize proteins (e.g. protease inhibitors) that are harmful to the pests.

Example: A trypsin-inhibitor gene that is found in the winged bean (*Psophocarpus tetragonoloba*) has been produced synthetically and transferred into rice. In the transgenic plants, caterpillars of the stem borer *Chilo suppressalis* developed more slowly than in non-transgenic control plants (Mochizuki et al. 1999). In this case, and in many similar cases, the effects on the target organisms have, so far, been not sufficient enough to enable the use of such plants commercially.

5.2.3 Cultural Methods of Pest Management

By use of a variety of agricultural methods, the environmental conditions of the agroecosystem can be changed such that colonization by pests or the increase of current populations can be limited. Such measures include modifications in time (crop rotation and sowing date) and space (plant density, soil cultivation).

5.2.3.1 Crop Rotation

Most pest species are feeding specialists and feed on specific plant species only (cf. Sect. 4.5.2). By crop rotation in which a crop species that affected by pests is followed by another crop species that is not used by these pests, development of pest populations can be interrupted.

Example: A measure used to manage the western corn rootworm (*Diabrotica virgifera*) and the northern corn rootworm (*Diabrotica barberi*) in North America is annual rotation of maize and soybean. The larvae of these beetles feed on the maize roots and develop into adults at the end of the season. The females lay their eggs in the soil that same autumn and the larvae of the next generation then emerge in the following spring. The species are then confronted with soybean, on which they are unable to feed, instead of maize. However, in some areas *D. barbari* has adapted to the annual rotation by expanding the larval development stage to 2 years. Some populations of *D. virgifera* now also lay their eggs in soybean fields, which means that the larvae that emerge the following year can then feed on maize (O’Neal et al. 2002). In both cases, the regular rotation of crops as a method of reducing the population of the beetle became ineffective.

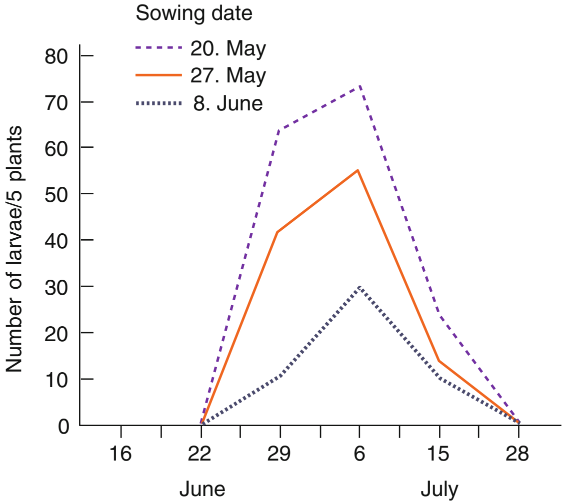


Fig. 5.6 Relationship between the sowing date of sunflowers in North Dakota and subsequent pest incidence of the larvae of the sunflower beetle *Zygogramma exclamationis* on the plants (Based on Charlet and Knodel 2003)

5.2.3.2 Sowing Date

The sowing or planting date of a crop can be chosen so that it does not coincide with the period of migration or with the highest density of a pest population. This measure is therefore based on minimizing the temporal coincidence (cf. Sect. 5.2.4.2) between the appearance of a pest species and the stage of crop development susceptible to the pest.

Examples: Larvae and adults of the sunflower beetle (*Zygogramma exlamationis*) specialize on sunflowers and feed on the plant leaves. The species is the major defoliating pest of sunflower in North America. A study conducted in North Dakota showed that numbers of adults and larvae decreased as planting date was delayed. Even a planting delay of only 1 week was sufficient to significantly reduce feeding on the sunflower plant and thus the extent of damage (Charlet and Knodel 2003; Fig. 5.6).

The females of the wheat stem sawfly (*Cephus cinctus*) lay their eggs in wheat stalks, on which the hatched larvae feed. The wheat plants are vulnerable only after stem elongation has begun and before grains begin to fill. A delay of the sowing date by 2–3 weeks in spring is sufficient in Montana (USA) in some years to completely avoid infestation of the larvae. At that time, the phase of oviposition has already passed (Morrill and Kushnak 1999).

5.2.3.3 Plant Density

The number of individuals of some pest species is affected by the number of plants per area and the distance between rows in the field. But, on manipulation of plant stand density, the yield is often affected more by intraspecific competition of the plants than by the pest incidence.

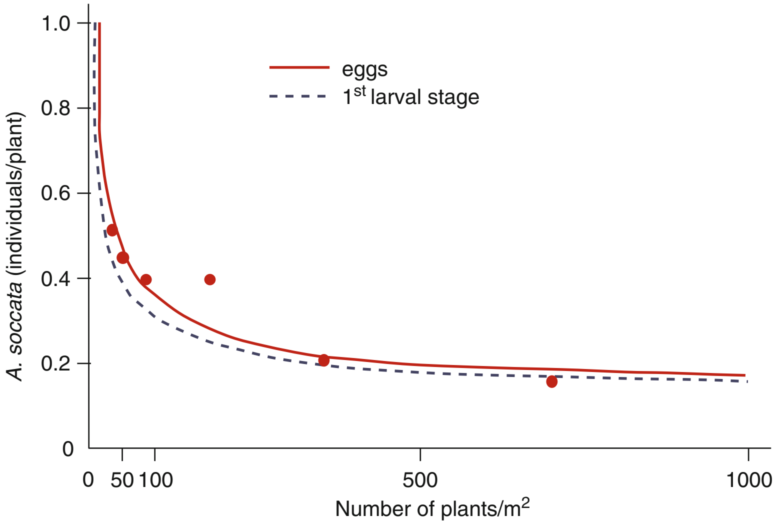


Fig. 5.7 Relationship between the number of individuals of different development stages of the sorghum shoot fly (*Atherigona soccata*) and plant density of sorghum plants in the field (Based on Delobel 1982)

Examples: The incidence of the sorghum shoot fly *Atherigona soccata* on sorghum decreases as plant density increases (Fig. 5.7). However, although an increase in the plant density reduced the damage caused by *A. soccata* an increase in yield was not achieved. The reason is intraspecific competition between the plants, which acts as a yield-limiting factor (Delobel 1982).

The opposite conditions were found in the cabbage root fly (*Delia radicum*), whose larvae feed on the roots of Brassicaceae. The higher the density of their host plants (different cabbage crops), the higher was the number of pupae in the soil (Finch et al. 1976; Fig. 5.8).

5.2.3.4 Soil Cultivation

In soil cultivation, soil-conserving practices (conservation tillage and direct seeding) can be distinguished from conventional ploughing (Box 4.2). Many pest species have development stages that are found in the upper layers of the soil and whose habitat is destroyed by ploughing. The pests then reach either the unprotected soil surface, where they may dry out and are threatened by predators (e.g. birds that often follow the plough), or deeper soil layers where they can no longer complete their development. Furthermore, soil management in agroecosystems may affect the soil arthropod fauna in different ways.

Examples: The number of eggs of cabbage flies (*Delia* species) and the root damage caused by their larvae in rapeseed was lower in ploughed fields than in no-till systems (Dosdall et al. 1998). On the other hand, some pest species occur at

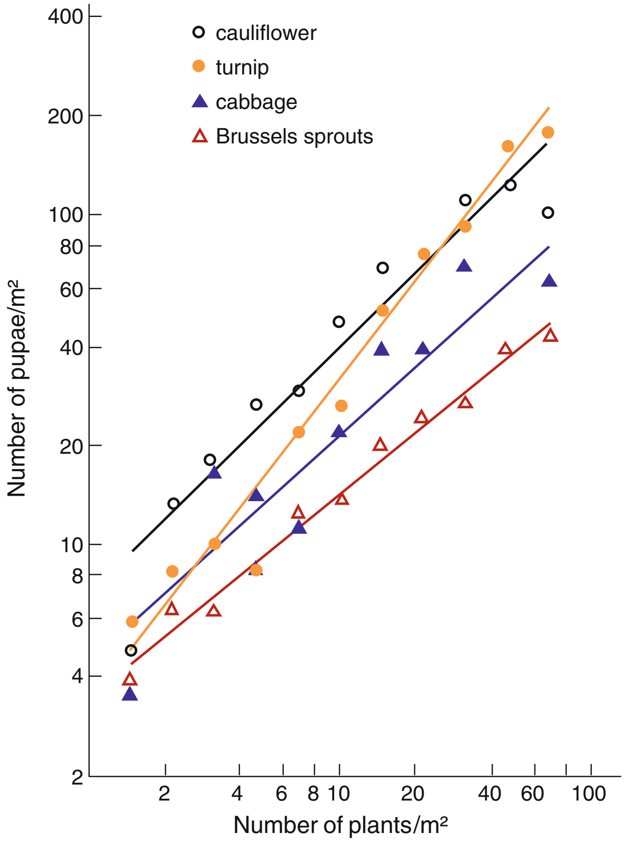


Fig. 5.8 Relationship between the number of pupae of the cabbage fly or maggot (*Delia radicum*) in the soil and the plant density of different Brassicas (Based on Finch et al. 1976)

lower densities on directly sown fields, which was found to be the case for the crucifer flea beetle (*Phyllotreta crucifera*) in rapeseed (Milbrath et al. 1995). Conventional ploughing had a negative effect on antagonists that live at the soil surface, primarily ground beetles and spiders (Holland and Reynolds 2003).

5.2.4 Biological Pest Control

The use of living organisms to limit the populations of phytophages, with the objective of reducing or preventing damage to specific plants, is called **biological pest control**. According to this definition, measures that are biological in the broadest sense, for example breeding for resistance, and application of natural substances and pheromones, are not regarded as biological pest control, because they are not based on the use of living organisms.

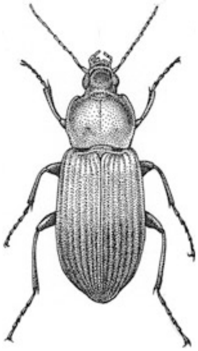


Fig. 5.9 *Poecilus cupreus* is a common ground beetle species in agroecosytems of Central Europe

5.2.4.1 Main Groups of Antagonists

The organisms that are of importance in biological pest control are primarily predators, parasitoids, and animal pathogens. They occur in agroecosystems as **natural enemies** of the pests and are termed **antagonists**. In specific cases, plants can also be used in biological pest management (Sect. 5.2.4.8). The most important groups of antagonists of phytophagous pests in agroecosystems are discussed in the following sections.

Ground Beetles (Carabidae)

In Europe there are approximately 2,700 ground beetle species, but only a few of these are found in agroecosystems (Fig. 5.9). In the fields of Central Europe, 20–30 species are found on average. In tropical cultivation landscapes, the diversity of the Carabidae is usually substantially lower. Most ground beetle species are polyphagous predators but some occasionally feed on plant material (e.g. seeds) also. Some species even occur as pests. The corn ground beetle (*Zabrus tenebriodes*), primarily found in eastern Central Europe, feeds on the ears and milk-ripe grains of cereals and grasses. Normally, however, ground beetles find their food and prey primarily on the soil surface and only occasionally visit plants. The larvae of ground beetles develop in the soil and are also mainly predators. In the temperate latitudes, one generation usually develops per year. Depending on the species, the larvae develop in summer and the adults overwinter, or vice versa.

Rove Beetles (Staphylinidae)

In Central European agroecosystems, the number of rove beetle species is often greater than the number of ground beetle species. The biology of both families is similar in many respects. The rove beetles also live primarily on the soil surface in fields, where most of the species are predators. Because most of the species are only

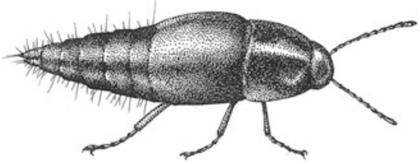


Fig. 5.10 Rove beetles of the genus *Tachyporus* climb on the stems of wheat and prey on aphids

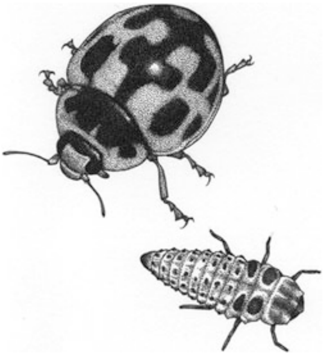


Fig. 5.11 The 14-spotted ladybird beetle (*Propylaea quatuordecimpunctata*) with larva

a few millimetres in size, their range of prey includes correspondingly small organisms, for example springtails (Collembola), mites, nematodes, and some insects.

Species of the genus *Tachyporus* (Fig. 5.10) have a preference for aphids in their prey selection. In cereal stands, they are counted among the most important consumers of these pests, because the beetles are able to climb on the plant stalks. The larvae of the genus *Aleochara* are parasitoids that attack the pupae of different fly pests of the Brassicaceae, notably *Delia* species.

Ladybird Beetles (Coccinellidae)

The ladybirds are a family of beetles with approximately 5,000 species worldwide, many of which occur in agroecosystems (Fig. 5.11).

Approximately 90% of all species are predatory and primarily feed on sap-sucking herbivores, for example aphids, scale insects, whiteflies, nymphs of leafhoppers, and spider mites. Most of the Coccinellidae are more or less specialized on one of these groups. Many species have a preference for aphids and are therefore termed aphidophages. Often, particular species within the aphids are preferred. The seven-spotted ladybird (*Coccinella septempunctata*) primarily feeds on aphid species that attack cereals. The ladybird species *Semiadalia undecimnotata* has a preference for the black bean aphid (*Aphis fabae*), a pest of many vegetable crops. When there is a lack of prey, ladybirds also utilize nectar, honeydew, or pollen as a food source. The larvae of Coccinellidae usually have the same type of prey as the adults.

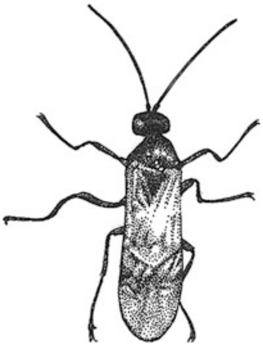


Fig. 5.12 Parasitoid wasp of the genus *Cotesia* from the family of the braconid wasps (Braconidae)

In the temperate latitudes, aphidophagous species develop one generation per year, usually in spring. Other species can reproduce several times per year. The aphidophagous species are characterized by high mobility.

Wasps (Apocrita)

The suborder wasps (Apocrita), which belongs to the order Hymenoptera (sawflies, wasps, bees, and ants) comprises numerous families, including many parasitoids and predators.

Parasitoid wasps. This group includes approximately 50,000 known species overall, which are assigned to at least 36 families (Fig. 5.12). The adults are predominantly small to tiny animals, some of which are even smaller than 0.3 mm. Most of the members of the Ichneumonidae (ichneumon wasps), however, reach a size of more than 5 mm. The larvae of the parasitoid wasps attack insects almost exclusively. The adults usually feed on nectar and pollen.

Predatory wasps. Important predator families of the Apocrita are the wasps (Vespidae) and the sphecid wasps (Sphecidae). The latter are primarily found in the tropics. In both families, prey animals (insects and spiders) primarily serve to feed the larva whereas the adults primarily feed on sugar-containing plant products (nectar, fruit). Whereas the Vespidae, which include the common wasp (*Paravespula vulgaris*) and the hornet (*Vespa crabo*), only use their stinger in self-defence, the sphecid wasps use it to paralyze their prey with poisons.

Ants (Formicidae)

Most ant species, which, similar to the wasps, belong to the Hymenoptera, are omnivores and feed on plant products, for example nectar and seeds, and on a wide range of living and dead arthropods and other invertebrates. The South and Central American leaf-cutter ants have another strategy, they practise fungal cultivation (Sect. 1.1). Some ant species also use the honeydew secreted by aphids and scale

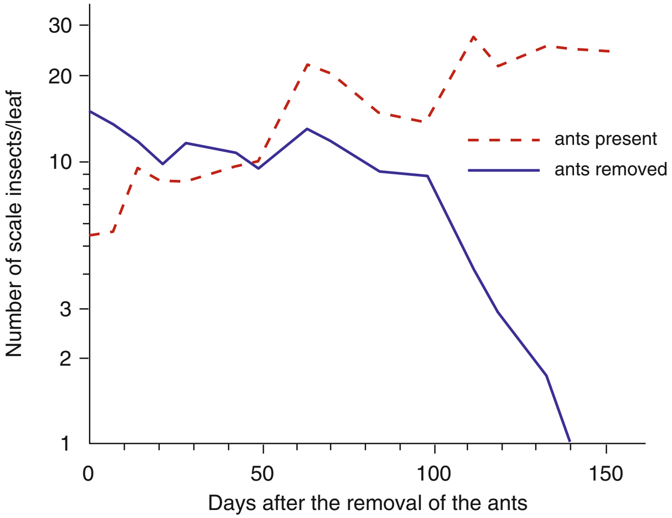


Fig. 5.13 Effect of the removal of the ant species *Pheidole megacephala* on the population of the scale insect species *Coccus viridis* on coffee shrubs of a plantation in Hawaii (Based on Reimer et al. 1993)

insects as a component of their diet, and so they also protect these animals from their enemies. In most agroecosystems of the temperate regions, ants are relatively rare. They reach their highest diversity in the tropics (cf. Table 3.1), where they can have quite different effect on agricultural systems. An example of a species acting as a predator and a serious pest is the red fire ant (*Solenopsis invicta*), an invasive species of North America originating from South America (details are given in Sect. 3.3.3).

The Asian weaver or green ants *Oecophylla smaragdina,* which inhabit trees, are traditionally used as antagonists of pests in fruit production in China and Vietnam. However, other ant species often have negative effects in such systems, because they utilize the scale insects as sources of honeydew and simultaneously eliminate their antagonists. In Australian citrus plantations, outbreaks of these pests were attributed to the presence of the ant *Iridomyrmex rufoniger* (James et al. 1999). In coffee plantations on Hawaii, the scale insect species *Coccus viridis* disappeared after the ants (*Phediole megacephala*) were experimentally removed from the plants (Reimer et al. 1993; Fig. 5.13).

True Flies (Diptera)

Some families of flies are predatory species that feed on other insects. Examples include the adults, and usually also the larvae, of the robber flies (Asilidae), several members of the gall midges or gall gnats (Cecidomyiidae), which feed on aphids and scale insects, and the larvae of many hoverflies (Syrphidae), which are more or

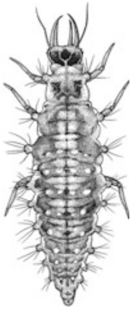


Fig. 5.14 Larva of a green lacewing of the genus *Chrysopa*

less specialized on aphids. Numerous species of different families of the Diptera are parasitoids. These include the big-headed flies (Pipunculidae) that attack leafhoppers and are important in rice production, amongst other systems.

Net-Winged Insects (Neuroptera)

From this order, the most important representatives are the green lacewings (Chrysopidae). Their larvae (Fig. 5.14) feed on smaller arthropods, which primarily include the aphids. The adults of these species are herbivores, predators, or omnivores.

True Bugs (Heteroptera)

Predatory true bugs include some representatives of the minute pirate bugs or flower bugs (Anthocoridae), capsid bugs (Miridae), damsel bugs (Nabidae), chinch bugs (Lygaeidae), and assassin bugs (Reduviidae). The last are primarily found in the tropics. Like many phytophagous bugs, the predatory representatives of the true bugs also have piercing-sucking mouthparts and feed on the body fluid of their respective prey.

Species of the genus *Nabis* (Nabidae) and *Geocoris* (Lygaidae; Fig. 5.15) are common predators in many crops in North America (e.g. cotton and soybean). Flower bugs of the genus *Orius* are used in the control of thrips in greenhouses. *Cyrtorhinus lividpennis* (Miridae) is an important antagonist of the brown planthopper (*Nilaparvata lugens*) in rice production in Southeast Asia (cf. Fig. 3.2).

Dragonflies (Odonata)

Both damselflies (Zygoptera) and dragonflies (Anisoptera; Fig. 5.16) are predators. Their adults capture their prey mainly while flying. Because their larvae develop in water, the agroecological importance of dragonflies is largely limited to paddy rice production.

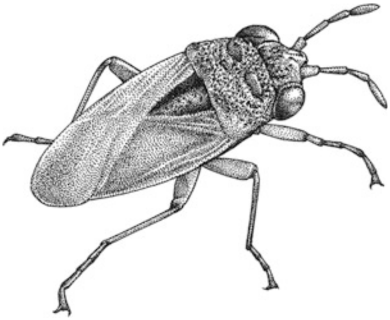


Fig. 5.15 A predatory true bug of the genus *Geocoris*

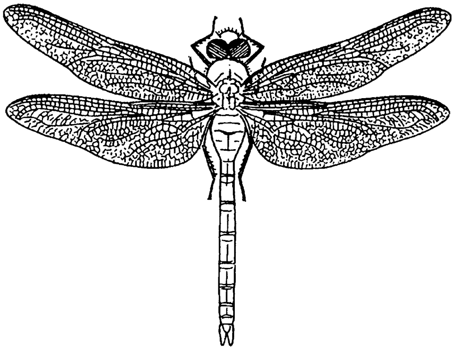


Fig. 5.16 A dragonfly (suborder Anisoptera of the order Odonata). Drawing by W. Lang

Spiders (Araneae)

All spiders, which are divided into approximately 60 families, are predators. Most species are generalists and feed on a broad range of arthropods (primarily insects). Measured by the number of individuals, they are the most common predators in many agroecosystems. Two main groups can be identified: species that construct webs to catch prey and species that hunt their prey.

The composition of the spider fauna in an agroecosystem is essentially affected by the geographic location, the crops that are produced, and by the type of management. In the production systems of Central and Northern Europe, primarily Linyphiidae (dwarf or money spiders) species are found. These species construct horizontal webs in which they catch mostly small insects (e.g. aphids). In most regions of the tropics and subtropics, a more diverse spider fauna can be found, e.g. in the production systems of southern North America. There, hunting species dominate; their range of prey includes caterpillars and phytophagous bugs. They are primarily represented by the lynx spiders (Oxyopidae), crab spiders (Thomisidae), and wolf spiders (Lycosidae; Fig. 5.17). The net spiders of this region are predominantly the long-jawed orb weavers or long jawed spiders (Tetragnathidae); the Linyphiidae are relatively rare (Nyffeler and Sunderland 2003).

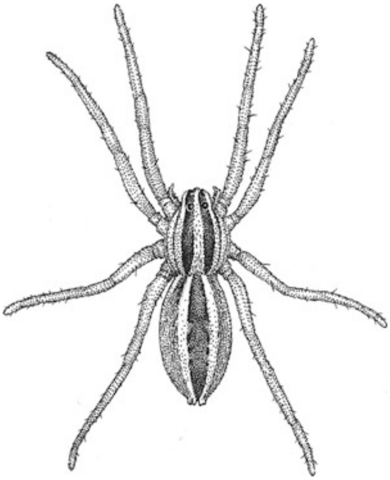


Fig. 5.17 A wolf spider (family Lycosidae)

The composition of spider communities can be markedly different in different crop stands. For example, in peanut, soybean, and alfalfa fields, ground-dwelling spiders (primarily Lycosidae) are the most common species, whereas plant-inhabiting spiders (both net-building and hunting species) predominate in stands of maize, cotton, sugarcane, and sorghum. Such differences are based primarily on factors such as structure of the crop stand, microclimate, prey availability, and disturbance frequency (Uetz et al. 1999).

Mites (Acari)

Several families of mites include predaceous species. These are more or less specialized and feed on small arthropods, for example phytophagous mites, thrips, whiteflies, and scale insects. As antagonists of phytophagous mites in agroecosystems and greenhouses, members of the family Phytoseiidae are important.

Roundworms (Nematoda)

Predatory nematodes generally live in the soil and prey on other nematodes, and/or insects. The latter primarily include the larvae and pupae of flies, beetles, and butterflies. Members of the genus *Steinernema* and *Heterorhabditis* enter the body openings of insects. Symbiotic bacteria live in the colon of these nematodes, and are released into the host organism. The bacteria fluidify the internal tissues of the insect and thus kill them. The fluidified tissue serves as food for a new generation of nematodes, which later live in the soil.

Pathogenic Microorganisms of Arthropods

Pathogens of arthropods may include bacteria, fungi, protozoa, and viruses. Some of these disease agents, especially viruses and protozoa, colonize the cells of their host and reproduce there. Most bacteria and fungi feed and reproduce extracellularly in or on the host organism. Among the bacteria, *Bacillus thuringiensis* has the greatest importance in agroecosystems. The effects of this pathogen occur as a result of release of toxic proteins in the digestive tract of insects (Sect. 5.2.1.2).

Many fungi that attack insects enter the host via the cuticula. The spores form a germ tube that develops into mycelia in the host organism. The insect dies as a consequence of the destruction of its tissues and/or the effect of toxins. Subsequently, the fungus grows out of the dead animal and forms new spores on its surface. An example of an entomopathogenic fungus is *Beauveria bassiana*, which attacks numerous insect species from various orders, as do most entomopathogenic fungi.

5.2.4.2 Relationships Between Antagonists and Pests

It is expected that antagonists in agroecosystems limit the number of pests and thus keep yield losses of crops to a minimum. This is only possible when they exert a control over the pest population, which means that the antagonists must be the factor that determines the upper limit of the growth of the pest population. The criterion for this is **predation rate**, in other words the portion of the pest population that is killed by the antagonists within a specific period of time. To limit the population density of the pests (in the ideal case before reaching the damage threshold), the predation rate must be at least as high as the growth rate of the pest population. When the number of pests increases either by reproduction or immigration of individuals, the number of individuals killed must also increase, which means that predation rate must increase appropriately. The precondition for this is an increase in the number of antagonists by reproduction or immigration.

The following sections examine more closely important factors, particularly the predation rate, that can affect the relationships between populations of antagonists and populations of prey species in agroecosystems.

Prey and Host Specificity of Antagonists

Similar to phytophages, there are specialists and generalists among the predators and parasitoids. The specialists feed on a limited range of animal species from specific taxonomic groups (usually genus, family, or order). Monophagous specialists, which only utilize a single species, are the exception among both predators and parasitoids. Generalists are species that feed on members of different orders. The factors that affect prey or host selection by antagonists are more complex than the factors involved in selection of host plants by phytophages, and are less well understood.

Prey selection by predators. An important criterion in food selection by predators is the body size of the potential prey. Most predators can only prey on animals that are smaller than themselves, but the prey must also be more than a minimum size to be attractive to the predator. Thus, the optimum body size of the prey of many spiders is approximately 50–80% of the spider's body size (Nentwig 1987). This is not true for ontogenesis, and there is a very wide range of sizes of prey organisms for individual spider species.

The range of prey utilized can also be related to the strategy of food acquisition. Most specialist predators are active hunters in their search for prey and may be aided in this by odorants or other characteristics of the prey or the host plant of the prey. Predators with a sit-and-wait strategy and predators that use traps (e.g. spider webs) are predominantly generalists.

Host selection by parasitoids. Most species of parasitoids are relatively specialized, both in terms of host species and the host's stage of development (egg, larva, pupa, adult). The host range of parasitoids is usually limited to members of a specific family and only in rare cases comprises different orders. In their search for hosts, parasitoids that attack phytophagous insects can be attracted by volatile compounds released by damaged plants (Sect. 5.2.4.3).

Defence Strategies of Prey Species

Animals have numerous options to defend themselves and/or to escape from predators, including the following strategies:

- Many arthropods have mechanisms of **chemical defence** against attackers. These are based on the release of secretions from glands or urticate hairs, for example those of some caterpillars. The defence substances utilized by phytophages are often secondary plant metabolites that they ingested with their food and that deter or harm the attacker.
- **Camouflage** can occur by way of blending in with their habitat and/or by imitation of objects that are of no interest to predators, for example twigs and leaves (Fig. 5.18).
- Discovery can also be hindered or prevented by finding hiding spots or by leading a furtive lifestyle, for example, in rolled-up leaves or in plant stems.
- Another way of preventing contact with feeding enemies is **flight**.

In individual species, defence is often based on a combination of different strategies. A specific reaction can also depend on the situation and change in relation to the predator species, which, in turn, affects predation success.

Example: The pea aphid (*Acyrthosiphon pisum*) is an important pest of alfalfa in North America. The most common antagonists of this species are the ladybird beetle *Coccinella septempunctata* and three predaceous bug species. The main

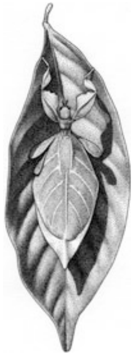


Fig. 5.18 The "walking leaves" (order Phasmida), found mainly in tropical Asia, which imitate living or dead leaves or twigs both in form and colour

strategy used by the aphids to escape from their predators is to drop from the plant. In the absence of predators, fewer than 7% of the aphids dropped. Dropping more than doubled (14%), when one of the predaceous bugs was present. Nearly 60% of the aphids dropped when the ladybird beetle was present.

The different reactions of the aphids are probably primarily because the ladybird is recognized as a predator from the vibrations it produces on the plant. Because the ladybird is significantly larger than the bug species, the disturbance caused by it is also greater. In reaction to this, the aphids release an alarm pheromone that elicits the dropping response in conspecifics (Losey and Denno 1998a).

Coincidence of Antagonists and Pests

The precondition for the occurrence of interactions between antagonists and pests is their temporal and spatial coincidence. The extent of the overlap of the respective populations also has substantial effect on predation success.

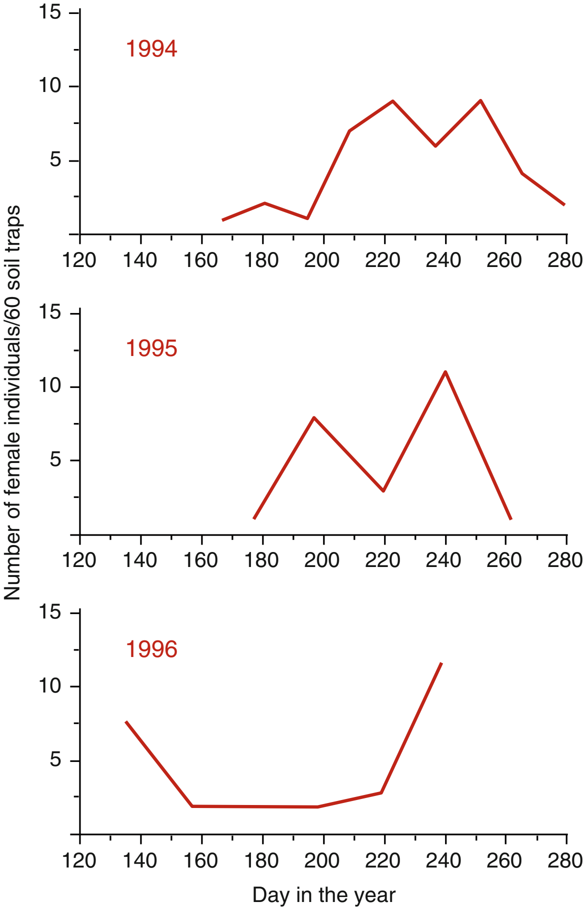
Temporal coincidence. This depends on the life cycles and phenology of the species. The presence and the abundance of pests and their antagonists in an agroecosystem is affected by a variety of factors. These include the duration of development and reproduction success, and environmental factors (especially climate and weather). The timing of the appearance of the species in the course of the year (phenology), the number of generations, and the temporal changes in abundance are also related to these factors.

Example: Development of the cockchafer (*Melolontha melolontha*), which is found in large parts of Europe, takes 4 years, on average. During this time, the larvae (grub) live in the soil and feed on roots. In warm regions, development is complete in 2–3 years whereas in colder regions it can take up to 5 years.

An example of seasonal and annual variations in the abundance of pest species is shown in Fig. 5.19.

Spatial coincidence. The environmental conditions that prevail in an agroecosystem and its surroundings can affect the colonization behaviour of

Fig. 5.19 Densities of female individuals of the wolf spider species *Hogna helluo* in a soybean field in Ohio (USA) in 3 consecutive years. The causes of the differences are unclear. It is possible that this species only produces one generation every 2 years (Based on Marshall et al. 2002)



antagonists and pests, and thus their population density. The factors of primary importance for this are:

(a) The **microclimatic conditions**, which are affected by plant density and the structure of the soil surface, are important to the presence and abundance of many species in a system. For soil-dwelling predators, which include most of the ground beetles, many rove beetles, and some spiders (e.g. wolf spiders), soil cover, either plants or mulch, is important (Sect. 5.2.4.5).

(b) The species and variety-dependent growth form and habitus of a crop, and the plant density, shape not only the microclimate but also the **spatial structure** of a plant stand. For example, these factors are of crucial importance in the colonization of agroecosystems by web-building spiders that require appropriate structures on which to attach their webs. The mobility of some species can also be impaired by spatial barriers that can result from dense vegetation.

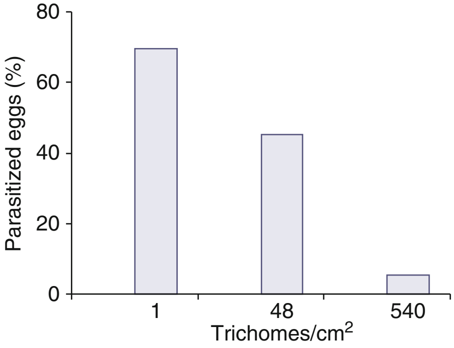


Fig. 5.20 Parasitization of eggs of the butterfly *Helicoverpa zea* by the ichneumon wasp *Trichogramma pretiosum*, on cotton, in relation to variety-specific trichome density on the leaves of the plants (Based on Treacy et al. 1986)

(c) The different animal species found in an agroecosystem colonize **different habitats**. These are essentially the soil, the soil surface, and the vegetation layer, but also specific parts of plants (e.g. the interior of the stalk, the flower, or the lower surface of leaves). Depending on where the pest and antagonist species primarily live, the probability of their encountering each other will vary.

Example: Pests with below ground stages in their life cycles, for example Diptera, whose larvae feed on plant roots, rarely come into contact with antagonists living on the soil surface, for example as ground beetles. The females of the cabbage fly (*Delia radicum*) lay their eggs on the root hairs of the host plant or in adjoining cracks in the soil. Most of the ground beetles are not able to find such deposits under the soil surface and their predation success is correspondingly low. This also applies to the eggs of the Western corn rootworm (*Diabrotica virgifera*), which are laid in the soil of maize stands and are not detected by ground beetles (Kirk 1982).

(d) **Morphological characteristics of the plant**, for example growth form and structure of their surfaces, can effect search behaviour and likelihood of the antagonist acquiring prey on the one hand and the distribution and chances of prey individuals taking flight or hiding on the other.

Example: The larvae of the parasitoid *Trichogramma pretiosum* develop in the eggs of the butterfly *Helicoverpa zea*, whose caterpillars, as polyphagous pests, are found on many crop species. In cotton, the success of predation is highly affected by the variety-specific trichome density on the leaves. The denser the hairs, the lower the number of eggs attacked (Fig. 5.20). The reason for this is primarily the limited mobility of ichneumon wasp females on hairy leaves.

(e) The prerequisite for colonization of agroecosystems by animal species that can only exist there during the cropping period is the presence of suitable **habitats in the surroundings**, which often serve for hibernation. The more suitable the living conditions and the higher the chance of survival outside the system, the greater is the potential of the respective populations to reach high densities in crop stands. This applies not only to many antagonists but also to some pest species. For example, the cereal aphid species

Metopolophium dirhodum has very specific requirements and uses roses (*Rosa* species) for overwintering.

Prey Availability

The prey available to antagonist species can be of importance from a variety of perspectives with regard to interactions between pests and predation success. The factors which primarily affect this are:

Pest density. For many antagonists, agroecosystems become attractive predation sites only when the pest density is high. However, at that point they no longer exert a regulatory effect on the development of the pest population, because they arrive at a time when the greatest crop damage has already occurred.

Example: Ladybird beetles (Coccinellidae) often act as antagonists of aphids but have little importance in agroecosystems (e.g. in cereal stands) in the control of populations of these pests. Most often, the number of ladybirds is too low at the beginning of the cropping period to be able to prevent an increase in the density of the aphids. Only with a relatively high prey availability does the number of ladybirds also increase (e.g. Dean 1974; Honěk 1982).

When the number of aphids in the crop stand reaches a specific threshold, the ladybirds also oviposit their eggs. The emerged larvae then encounter a high availability of prey. This relationship was shown in experiments by Hemptinne and Dixon (1997) in a wheat field in Belgium (Fig. 5.21). Both the larvae and the adults of the ladybirds profit from the large number of aphids, which are present near the end of the growing season in such crop stands. Even when predation success high, yield losses can no longer be prevented.

The dwarf or money spiders (Linyphiidae) commonly found in cereal fields of Europe also usually have no significant effect on limitation of the aphid population below the damage threshold. The number of spiders usually increases only in the course of the cropping season, which is the time the aphid population has already reached its highest density (Fig. 5.22). Thus, cereal fields also are attractive to dwarf spiders only when they provide sufficient prey (Sunderland et al. 1986; Harwood et al. 2001).

Availability of alternative prey species. Most predator species that appear as antagonists of pests in agroecosystems are not highly specialized and can, therefore, also feed on arthropods that are not pests. Such alternative prey species can determine the number of antagonists, and their influence on pest populations in various ways:

(a) In some agroecosystems, large populations of alternative prey species are present before an increase of pests occurs. Such prey availability can be attractive to predators and thus lead to an increase in their population density, even at an early stage of cropping. When the density of the pest increases, their antagonists are already present in large numbers.

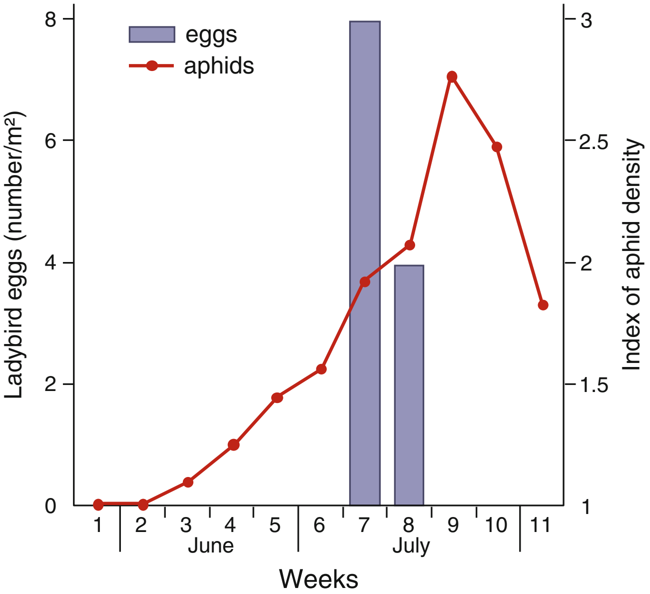


Fig. 5.21 Development of a population of the cereal aphid species *Sitobion avenae* and number of eggs of ladybirds (Coccinellidae) in a wheat field in Belgium (Based on Hemptinne and Dixon 1997)

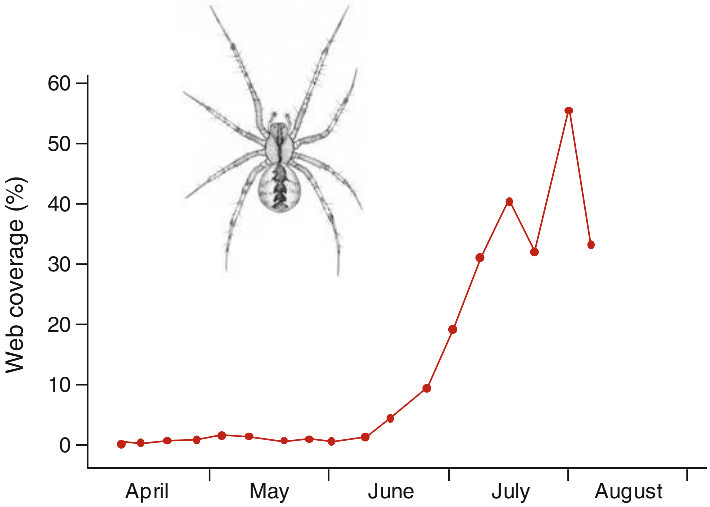


Fig. 5.22 Population development of dwarf or money spiders (Linyphiidae), measured by the degree of coverage of the horizontal webs in a wheat field in England (Based on Sunderland et al. 1986)

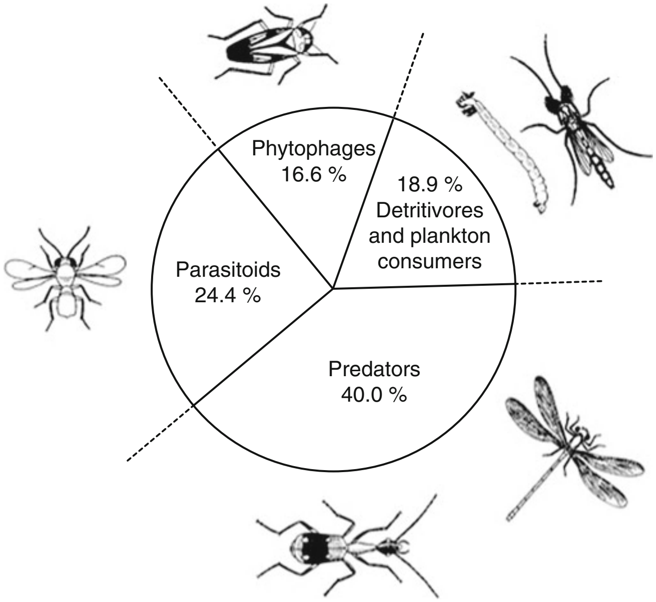


Fig. 5.23 Proportion of the different trophic groups of the arthropod species recorded in paddy rice fields of Java, Indonesia (Based on Settle et al. 1996; drawing by W. Lang)

Example: In the growing season, rice paddies are usually flooded with several centimetres of water. In this aquatic habitat, a variety of insects that feed on the detritus or plankton are present. Many of these species are larvae of Diptera, primarily non-biting midges (Chironomidae) and shore flies (Ephydridae). The adults of these species hatch at the water surface and appear on rice plants, but are not phytophagous. They become the prey of many predator species that are also antagonists of rice pests. In an experiment in Indonesia, it was found that the adults of these Diptera reached their highest abundance approximately 30 days after the rice was transplanted. Subsequently, the density of predators also increases. The number of rice pests only increases approximately 50–60 days after transplanting. At this time, a relatively high density of their antagonists is already present in the fields. Overall, approximately 19% of all arthropod species of the rice field community are detritus and plankton feeders. The proportion of the total community of these alternative prey species is thus even higher than that of the phytophagous pests (Settle et al. 1996; Fig. 5.23).

(b) Another situation occurs when antagonists colonize a crop stand on which high densities of pests and alternative prey species are present simultaneously. If the antagonist does not have a high preference for the pest, then the alternative prey species can make up a large portion of the antagonist's diet and, thus, the number of pests consumed is correspondingly lower than it would otherwise be.

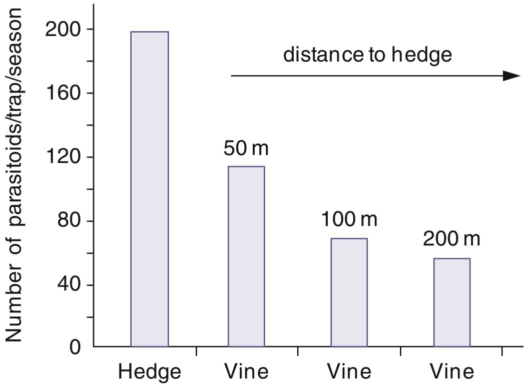


Fig. 5.24 Number of individuals of dwarf wasps of the Mymaridae family (egg parasitoids of the grape leafhopper) in the area of a hedge and in an adjoining parcel of vineyard in eastern Switzerland. The insects were collected by use of yellow traps over the course of one season (Based on Remund and Boller 1996)

(c) The presence of alternative prey or host species outside the agroecosystem can also be of importance to interactions between the antagonist and the pest:

- When crop stands have lower prey availability than habitats in the surroundings, they are less attractive to mobile predators.
- In phases or seasons in which there is no crop present and thus there are no pests, the antagonists require alternative sources of food, assuming this time is not a resting period of the antagonist. Species that act as alternative hosts during the absence of the utilized pests are important to parasitoids.

- **Example:** The grape leafhopper (*Empoasca vitis*) is a pest in European viticulture. Parasitoid wasps from the Mymaridae family act as antagonists of the grape leafhopper and develop in their eggs. The grape leafhopper hibernates outside the vineyards as an adult, which means that the eggs of this species are not available during this time. However, because the parasitoid also produces larvae during this time, it requires an alternative host. Some species of leafhoppers which overwinter in the egg stage on hedge plants are candidates for this. In a study in Switzerland, it was found that eggs of the leafhopper genus *Ribautiana* serve the parasitoids as a winter host and are frequently found on wild roses and on blackberry. In spring, when the grape leafhoppers return to the grape vines and deposit their eggs, these are again utilized by the parasitoids. At the same time, further generations of parasitoids develop in the hosts of the hedge plants, from where the adults also fly into the vineyards. There, the number decreases with increasing distance from the adjoining hedges (Fig. 5.24; Remund and Boller 1996).

Development stage of the prey. For many groups of insects (e.g. butterflies, saw fly, gall midges), only the larvae are pests; the adults usually only use the crop stands to deposit their eggs. Because of their short stay and high mobility, they are rarely found by predators in the crop stand. The predatory activity of antagonists in agroecosystems is therefore limited to specific stages of development of pest species, which are only a part of the total population of a species.

Whether a reduction in the number of eggs, larvae, or pupae in agroecosystems affects the development of such pest populations in the long term depends largely on the living conditions of the adults, i.e. the factors that cause their mortality. When the survival and reproductive success of the adults is high, a correspondingly high incidence of the larvae on the crop can result.

5.2.4.3 Relationships Between Antagonists and Crop Plants

Many predators and parasitoids have relationships, in various ways, with plants, which can also effect their interactions with their prey or host species.

Induced Indirect Plant Defence

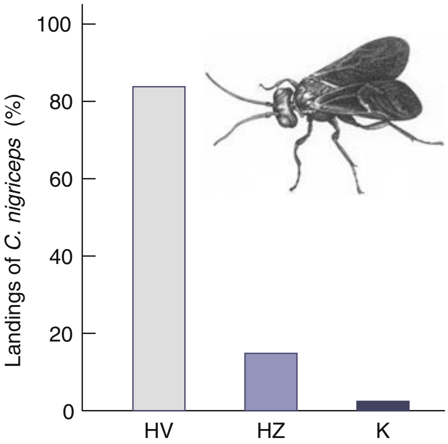
In addition to the various mechanisms of direct defence against herbivores presented in Sect. 4.5.4.3, plants have mechanisms that attract natural enemies of herbivores after damage of plant tissues. This type of interaction between plants and antagonists of plant enemies is called **induced indirect plant defence**. Its underlying mechanism is release of volatile substances as reaction to an attack, leading to so-called herbivore-induced plant volatiles (HIPVs) in the air, which are then perceived by antagonists, for example parasitoids or predators. The HIPVs mainly comprise mixtures of terpenoids, but also include such other substances as green leaf volatiles (alcohols and aldehydes), which are responsible for the odour of damaged leaves (e.g., the odour of freshly mown grass). They are emitted either at the site of damage or systemically from undamaged parts of the affected plants. The blends can be complex, comprising hundreds of compounds, some of which are not produced by intact or artificially damaged plants and others of which are newly synthesized in response to herbivore attack (Dicke and Baldwin 2010).

The quantity and the composition of HIPVs released by the plants vary depending on the type of herbivore that causes the damage. As for direct induced defence, indirect defence is initiated by elicitors originating from the organism causing the damage. Overall, the blends of volatiles released from damaged plants are frequently specific, depending on the type of herbivore and its age, abundance, and feeding guild (specialist or generalist). Antagonists not only detect individual compounds of herbivore-induced blends, but also respond to the blend as a whole depending on the ratios of the components present (Clavijo McCormick et al. 2012).

It also has been shown that antagonists can differentiate between different HIPV mixtures. Thus, they are able to identify whether a plant has been attacked by a suitable host or by another species.

Example: In a field experiment, two groups of tobacco plants were established, one with caterpillars of the tobacco budworm (*Heliothis virescens*) and another with caterpillars of the cotton bollworm (*Helicoverpa zea*). Both species are members of the owlet moths (Noctuidae), and both are generalists. A third group

Fig. 5.25 Proportion of landings (in percent) of females of the ichneumon wasp *Cardiochiles nigriceps* on different tobacco plants in the field: plants attacked by *Heliothis virescens* (*HV*), plants attacked by *Helicoverpa zea* (*HZ*), and undamaged plants (*K*) without herbivores (Based on De Moraes et al. 1998)



of plants was kept free from herbivores and served as a control. The parasitoid ichneumon wasp *Cardiochiles nigriceps* (Braconidae) uses the caterpillars of *H. virescens* as hosts for the development of its larvae, but does not attack the caterpillars of the *H. zea*.

In field trials, *C. nigriceps* females distinguished between the odours emanating from tobacco plants infested by their host, *H.virescens*, and those from plants infested by *H. zea* or from undamaged plants. Females selected host over non-host infested plants in approximately 83% of plant visits (Fig. 5.25). Thus, this parasitoid is able to identify infestations of its host on the basis of chemical cues involving either quantitative or qualitative differences in the composition of volatile compounds produced and emitted by the plant.

Other studies have revealed that parasitoids are attracted by the volatile plant substances, and not by substances released by the caterpillars. When cotton was used instead of tobacco as the food plant for the two caterpillar species, *C. nigriceps* again showed a pronounced preference for plants with caterpillars of *H. virescens*. Thus, the parasitoids recognize their host even on different plant species, even though these plants release different mixtures of terpenoids in reaction to the same herbivore species (De Moraes et al. 1998).

In general, HIPVs have been interpreted as being indirect defences. However, given that it is so far unknown whether HIPVs benefit the fitness of a plant, their defensive function remains to be verified. Moreover, herbivores, pathogens, pollinators, and competitors also respond to HIPVs. In addition, neighbouring plants also emit volatiles that provide a background odour. These considerations enrich the evolutionary context of HIPVs and complicate predictions regarding their adaptive value. HIPVs have more functions than solely as carnivore attractants and should be seen in the context of an infochemical web that overlays the food webs of a community (Dicke and Baldwin 2010).

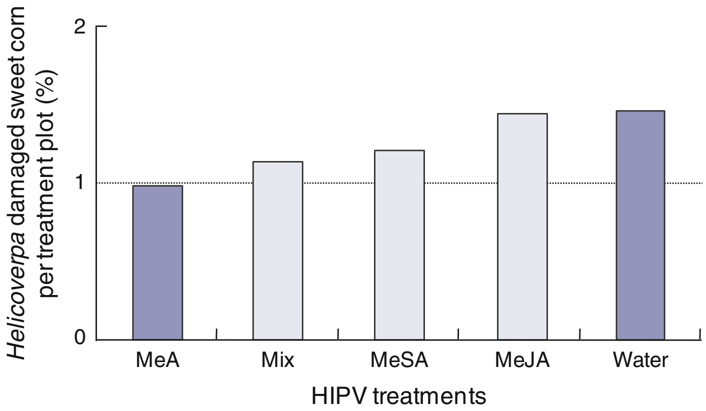


Fig. 5.26 Proportion of *Helicoverpa* spp. damage to sweet corn cobs for different HIPV treatments as attractants and for control (water) in plots with buckwheat (*Fagopyrum esculentum*) as reward plant (Based on Simpson et al. 2011)

Nevertheless, the principle of herbivore-induced plant defence can be of use in pest control, adopted to attract natural enemies into crops from surrounding habitats.

Example: Simpson et al. (2011) conducted field studies to test a novel biological control approach, the "attract and reward" method. It uses synthetic HIPVs to improve immigration of beneficial taxa into crops (attraction) and nectar plants to maintain their populations in the field (reward). This approach was tested for sweetcorn, broccoli, and wine-grapes with several HIPV formulations, using methyl anthranilate (MeA), methyl jasmonate (MeJA), methyl salicylate (MeSA), and a mixture of these. Buckwheat (*Fagopyrum esculentum*) was used as reward. Increased predator and parasitoid abundance (assessed by use of non-attractive sticky traps) were demonstrated for several of the HIPV treatments. Nectar plant reward increased catches of parasitoids in all three crop species tested and increased predators in sweet corn and broccoli. Increases in natural enemy numbers were correlated with effects at the first and second trophic levels. Significantly fewer larvae of pest caterpillars (*Helicoverpa* spp.) were found on sweetcorn plants from plots with reward. Furthermore, significantly less *Helicoverpa* damage was evident on cobs for one of the HIPV treatments (MeA, Fig. 5.26). The overall results of this study suggest that application of synthetic HIPVs can enhance recruitment of natural enemies and buckwheat was a suitable resource subsidy plant for increasing abundance and residency.

Indirect Effects of Plants on Antagonists

Plants can have effects on antagonists that occur indirectly via the herbivorous prey. Herbivores ingest secondary plant metabolites while feeding, which can

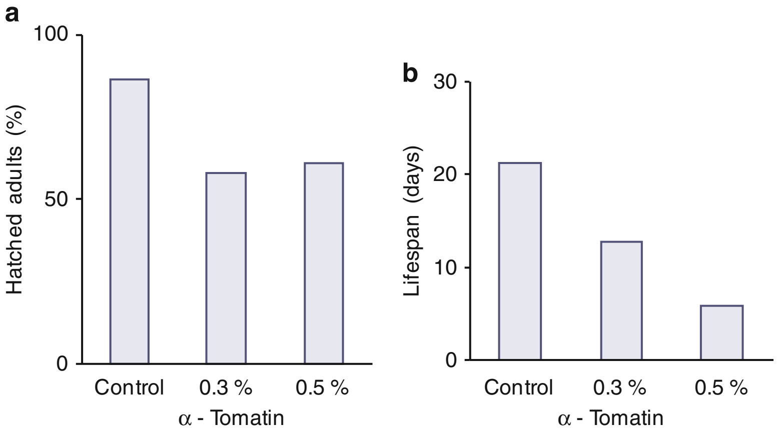


Fig. 5.27 Effects of the alkaloid α-tomatin on (**a**) the number of hatched individuals and (**b**) the lifespan of adults of the ichneumon wasp *Hyposoter exiguae*. The percentage values refer to the concentration of α-tomatin in the food of the caterpillars of *Heliothis zea*, which served the parasitoid larvae as hosts (Based on Campbell and Duffey 1979)

accumulate in their body tissues. In some cases, concentrations can be reached that are harmless to the herbivore, but that have negative effects on antagonists that feed on the herbivore species.

Examples: The cabbage aphid (*Brevicoryne brassicae*) is specialized on crucifers (Brassicaceae). The plants of this family contain glucosinolates (cf. Sect. 4.5.5.2), which are found in different quantities depending on the species and variety. Consumption of *B. brassicae* by the larvae of the ladybird beetle, *Adalia bipunctata*, increases mortality. Cabbage aphids that were captured on rapeseed (*Brassica napus*) had a lethal effect on 40% of the ladybird larvae. Of the larvae that captured this prey on yellow mustard (*Sinapsis alba*) or on black mustard (*Sinapsis nigra*), all died. The toxic effect is a result of isothiocyanate, which is formed by enzymatic breakdown of glucosinolate during food uptake by the aphids. Rapeseed contains lower quantities of glucosinolate than the two mustard species. Therefore, the concentrations of these compounds found in the aphids vary and finally result in different mortality among ladybird larvae. In contrast with *A. bipunctata*, the cabbage aphids are adapted to high concentrations of glucosinolate and isothiocyanate and are not harmed by these substances (Francis et al. 2001).

Such effects are also found among parasitoids. The caterpillars of the cotton bollworm (*Helicoverpa zea*) ingest the alkaloid α-tomatin when feeding on tomato plants. An antagonist of *H. zea* is the ichneumon wasp *Hyposoter exiguae* whose larvae develop in the caterpillars and are harmed by the alkaloid. The substance affects the number of adults that hatch (Fig. 5.27a) and their lifespan (Fig. 5.27b). The caterpillars of *H. zea* are not very sensitive to α-tomatin (Campbell and Duffey 1979).

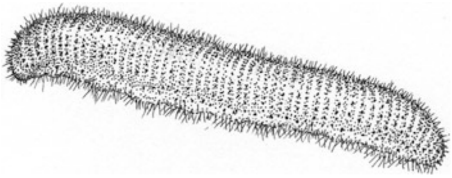


Fig. 5.28 Caterpillar of the small cabbage white (*Pieris rapae*)

Not only secondary plant metabolites but also other factors that affect the quality of food can have an effect on the relationship between antagonists and pests.

Examples: On nitrogen-poor cabbage plants, a larger proportion of the caterpillars of the small cabbage white (*Pieris rapae*; Fig. 5.28) was captured by predators than on plants fertilized with nitrogen. The explanation for this is that the time required for the development of caterpillars increases with decreasing nitrogen concentrations in the food and therefore, there is a higher probability that the larvae fall victim to a predator. Parasitoids prefer caterpillars on nitrogen-rich plants. A possible reason for this is the improved nutrient status for the parasitoid larvae of such host individuals (Loader and Damman 1991).

Seven-spotted ladybirds (*Coccinella septempunctata*) were fed with pea aphids (*Acyrthosiphon pisum*) which had been reared on two different food plants (alfalfa and faba bean). Faster larval development, greater survival, and larger size were observed for the offspring of beetles that consumed aphids from alfalfa than for those that received aphids from faba beans. This can be explained by the different nutritional value of the plant species. Aphids reared on alfalfa take up greater quantities of fatty acids than those reared on faba beans and thus provide a more energy-rich source of food for the ladybirds (Giles et al. 2002).

It has occasionally been shown that the δ-endotoxins produced by transgenic Bt crops (Sect. 5.2.2.1) have a negative affect on antagonists that capture their prey on such plants.

Example: The ichneumon wasp *Parallorhogas pyralophagus* is a parasitoid of the caterpillar of the butterfly *Eoreuma loftini*, which appear as stem borers in maize in America. Mortality was significantly higher for larvae of the ichneumon wasps that utilized hosts on Bt maize than for those that attacked caterpillars on conventional maize (Fig. 5.29a). The surviving larvae developed more slowly and had a shorter lifespan as adults (Bernal et al. 2002). Similar effects have also been observed for larvae of the green lacewing *Chrysoperia carnea* that were fed with the caterpillars of two different pest species. When the prey animals contained Bt toxins from transgenic maize plants, mortality of the green lacewing larvae was approximately one-third higher than for those that received their prey from maize plants without Bt genes (Fig. 5.29b; Hilbeck et al. 1998).

In contrast with these results, no negative effects on survival and reproduction success were observed for a ladybird species (*Hippodamia convergens*) that consumed aphids (*Myzus persicae*) fed on Bt potatoes (Dogan et al. 1996).

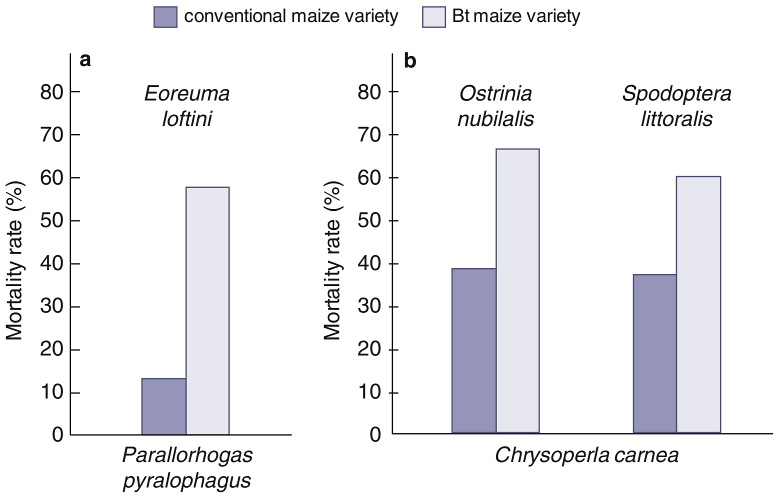


Fig. 5.29 Mortality of antagonists that fed on herbivores of transgenic Bt maize and on conventional maize varieties: (**a**) larvae of the ichneumon wasp *Parallorhogas pyralophagus* in the caterpillars of the stem borer *Eoreuma loftini* (Based on Bernal et al. 2002); (**b**) larvae of the green lacewing *Chrysoperla carnea* fed with caterpillars of *Ostrinia nubilialis* and *Spodoptera littoralis* (Based on Hilbeck et al. 1998)

5.2.4.4 Relationships Between Antagonist Species

In agroecosystems, there are generally several species of antagonist present at the same time and these can have direct or indirect relationships with each other. This variety of interactions can result in very different effects on the populations of pest species.

Feeding Relationships

Some predators and parasitoids are not, or not only, natural enemies of pests, but may also prey on other antagonists. Two situations can be identified in this context:

1. Two antagonist species (A and B) have a pest species as common prey, but antagonist B also feeds on antagonist A (Fig. 5.30a). Sometimes the two antagonist species feed on each other (Fig. 5.30b). Both situations can result in fewer pests being preyed upon in the presence of both antagonists than in the presence of one antagonist species alone.

   Example: In California, the larvae of green lacewings (*Chrysopidae*) are important consumers of pests of cotton, primarily aphids (*Aphis gossypii*). A variety of predaceous bug species also occur in the fields; these prey on both aphids and green lacewing larvae, and some also use plant sap or cotton pollen as a food source. Some development stages of the bugs also serve as prey for green

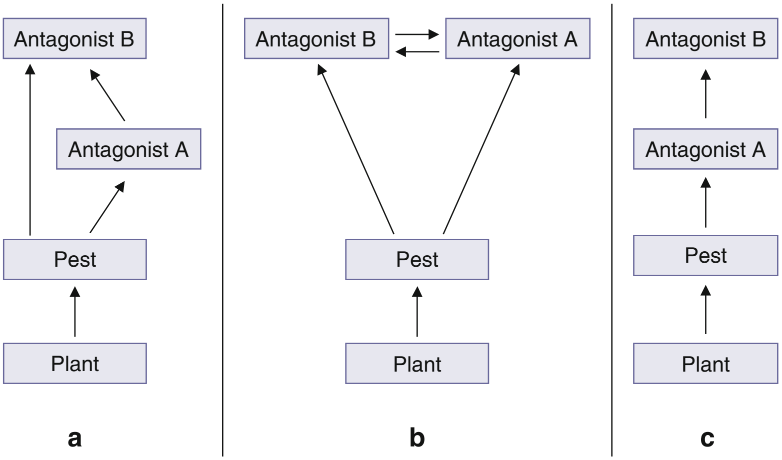


Fig. 5.30 Possible feeding relationships between two antagonist species and a pest species. (**a**) two antagonists (A and B) have a pest species as common prey, and antagonist B also feeds on antagonist A. (**b**) Both antagonist species have a common prey species, but also feed on each other. (**c**) Antagonist A has a pest species as prey, antagonist B only feeds on antagonist A and is thus a second order antagonist

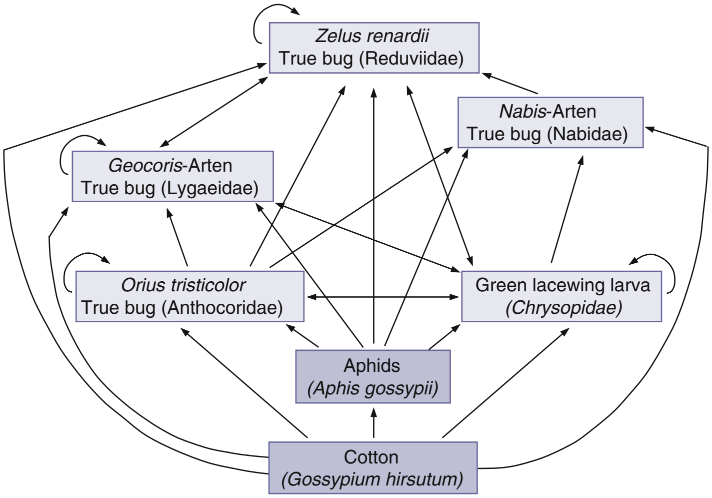


Fig. 5.31 Feeding relationships between the antagonists of aphids in cotton fields in California (Based on Rosenheim et al. 1999)

lacewing larvae, however. Overall, very complex feeding relationships exist between these species (Fig. 5.31). In comparative experiments it has been shown that green lacewing larvae can significantly reduce the number of aphids in the absence of other predators. In contrast, the total community of predators has little effect on the aphid density. The reason for this is the reduction in the number of green lacewing larvae by the bugs. At medium aphid density, approximately 94% of the green lacewing larvae were preyed upon by the bugs; at high aphid density, the proportion was approximately 60% (Rosenheim et al. 1999; Rosenheim 2001).

2. Antagonist A has a pest species as prey. Antagonist B feeds only on antagonist A and is thus a second-order antagonist (Fig. 5.30c). This type of interaction can occur both among predators and parasitoids. In the latter case, the second-order antagonist is termed a hyperparasitoid.

   A special situation occurs when predators feed on prey animals that have already been attacked by parasitoid larvae. Sometimes the predators then have a stronger effect on the population of parasitoids than on the prey species. In Australia it has been shown that caterpillars of the small cabbage white (*Pieris rapae*) that are parasitized by the ichneumon wasp *Apantele glomeratus* are more vulnerable to predation by ants of the genus *Iridomyrmex* than are unparasitized larvae. Presumably, the parasitized individuals are easier to capture because of their impaired condition (Jones 1987).

   Not only pests, but also predatory insects, for example ladybirds, serve as hosts for some parasitoid species. In northern Germany, parasitization of the adults of the ladybird *Coccinella septempunctata* by the ichneumon wasp species *Dinocampus coccinellae* in the hibernating sites in spring can reach 33%. In cereal fields, up to 12.5% of the individuals were attacked (Triltsch 1996).

Indirect Relationships

Different species of antagonist are interdependent not only because they feed on each other, but also because they feed on the same prey species. With regard to the effects on a pest in agroecosystems, they can either hinder each other in this activity or they can complement each other. Depending on the situation, this can have different effects on the total number of pests that are captured:

- In instances of interference, i.e. the encounter of individuals of different antagonist species in search of prey, the situation may often result in direct competitive interaction (e.g. local displacement of one species by another). As a consequence, predation success of individual antagonist species can be lower than it would be in the absence of the other species.
- An additive effect occurs when the total number of prey individuals captured by two or more antagonist species in a specific period of time is as high as the sum of the number of prey individuals that is captured by each of these antagonists alone.
- A synergistic effect exists when the total number of prey individuals captured by two or more antagonists is higher than the sum of the number of prey individuals that is captured by each of these antagonists alone.

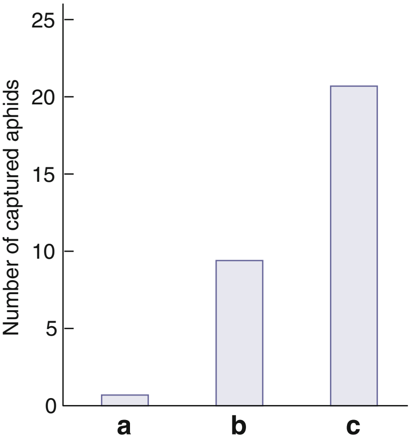


Fig. 5.32 Number of pea aphids (*Acyrthosiphum pisum*) captured by predators over the course of 24 h on alfalfa plants in different experimental setups: (**a**) by the ground beetle *Harpalus pennsylvanicus*, which captures its prey on the ground, (**b**) by the ladybird *Coccinella septempunctata*, which preys on the plants, and (**c**) by both predator species together (Based on Losey and Denno 1998b)

The occurrence of additive and synergistic effects is most likely when the individual antagonist species forage in different habitats within an agroecosystem, and/or have different forage strategies.

Example: In experiments, the effects of two predator species on the number of pea aphids (*Acyrthosiphum pisum*) on alfalfa plants were examined. The predators were the seven-spot ladybird (*Coccinella septempunctata*), which forages on the plants, and the ground beetle *Harpalus pennsylvanicus*, which captures its prey on the ground. Over time periods of 24 h each, the effects of each predator species on the aphids were first observed individually in systems that consisted of one plant, 30 aphids released on to the plant, and one individual of the predator species. The ground beetles alone did not have a significant effect on aphid density on the plants (Fig. 5.32a). The ladybird alone captured approximately one-third of the prey individuals present (Fig. 5.32b). When both predators were present together, the number of aphids was reduced by approximately two-thirds, i.e., combined predation by both predators was substantially higher than would have been expected on the basis of adding their individual consumption (Fig. 5.32c). This synergistic effect is explained by the dropping behaviour of the aphids. In the presence of the foliar-foraging ladybird beetle, aphids fall to the ground where they become vulnerable to attack by the ground-foraging ground beetle. Some aphid individuals are therefore killed before they are able to return to the plant (Losey and Denno 1998b).

5.2.4.5 Conservative Biological Pest Management

The fact that antagonists in an agroecosystem kill pests is, alone, not sufficient to draw any conclusions about the resulting effects. Predators and parasitoids only exert effective pest control when they limit the densities of pest populations and thus, in the end, reduce damage to the crop. Often, however they are unable to

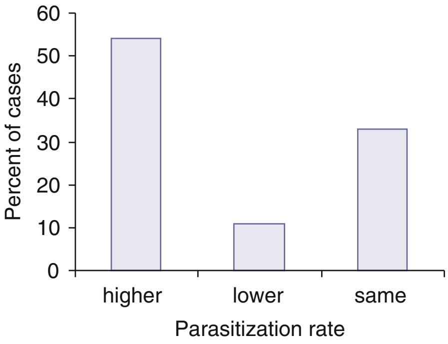


Fig. 5.33 Percentage of cases in which parasitization of pest species in mixed cropping was higher than, lower than, or approximately the same as in sole cropping. The data are based on analysis of 26 individual studies (Based on Coll 1998)

achieve this, because they occur in insufficient numbers or because they appear in the agroecosystem at the wrong time (Sect. 5.2.4.2).

With appropriate measures to protect or promote antagonists, attempts can be made to increase their numbers in the agroecosystem and thus to achieve more effective pest management. This approach is called **conservative biological pest management** and is essentially based on modification of the habitat structure of the cultivation system or its environment.

Mixed Cropping

Numerous experiments have dealt with the question of whether and how the numbers of species and individuals of antagonists in mixed cropping systems differ from those in one-crop systems. Analysis of more than 200 studies showed that for approximately half (53%) of all predator species and three-quarters (75%) of all parasitoid species numbers of individuals in mixed cropping were higher than in one-crop systems. Furthermore, approximately half (52%) of the phytophagous species in mixed crops were present in lower numbers than in sole crops (Andow 1991).

The results of this analysis show that establishment of mixed cropping can contribute to promotion of the populations of antagonists and to reduction of pest densities. However, the question of whether the lower individual densities of the phytophagous species in the mixed cropping systems can always be attributed to the effect of antagonists remains unanswered.

Similar analysis has been conducted for studies based solely on parasitoids (Coll 1998). Not only were the numbers of individuals in different production systems compared but also the success of parasitization. In more than half of the cases, the latter were higher in mixed crops than in sole crops (Fig. 5.33)

In most cases in which the number of antagonists in mixed crops was higher than the number in the one-crop system, this can be attributed to the greater structural diversity of the mixed cropping system (Langellotto and Denno 2004). How this factor improves the living conditions of the species cannot always be clearly stated.

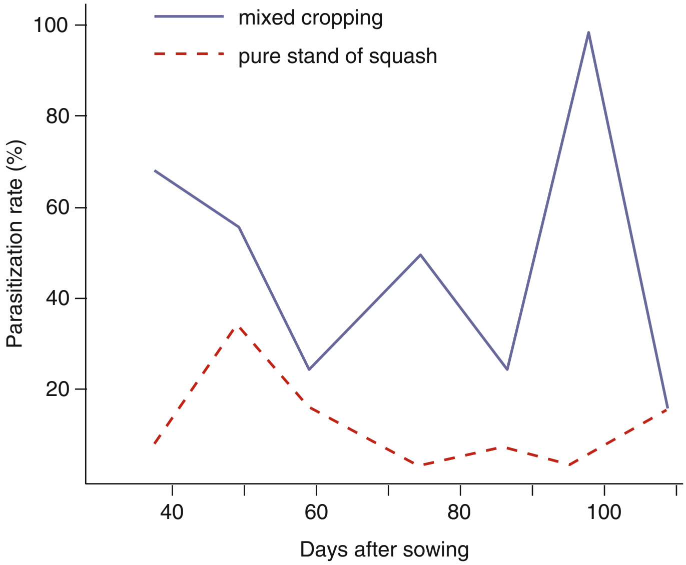


Fig. 5.34 Parasitization of the eggs of the butterfly *Diaphania hyalinata* in pure squash stands and in traditional mixed system of squash, maize, and cowpea in Mexico (based on Letourneau 1987)

It might, for example, be related to the greater availability of alternative prey species, to more suitable forage conditions, or to the availability of nectar and pollen as additional sources of food. Among the antagonists that utilize flowers as resources are the ladybirds, hoverflies, and some green lacewing species, in addition to the adults of parasitoids. Generally valid explanations of the different numbers of individuals of antagonists in mixed and one-crop systems cannot be made, because the species and varieties of the crops used, their patterns of cultivation, and the species of antagonist are very diverse. It is also often observed that different antagonist species do not react in the same way to modifications in the production system.

Examples: The caterpillars of the butterfly *Diaphania hyalinata* occur as pests in cucurbit crops in Central America. A study in Mexico examined whether antagonists in a traditional mixed cropping system of maize, cowpea, and squash had a greater effect on the density of the caterpillar population than in pure squash stands. Parasitization of the eggs and caterpillars of *D. hyalinata* (Fig. 5.34) by different species of ichneumon wasps was significantly higher in the mixed cropping system than in the pure stand of squash. However, the responses of natural enemies to vegetational diversity were not uniform. Most predators were not significantly affected by cropping patterns, and some were more abundant in pure squash stands than in the traditional system (Letourneau 1987).

A study in Uganda examined how the number of individuals of antagonists varies between one-crop of cowpea and mixed crops (cowpea with sorghum, and cowpea with mung bean). Although the densities of ladybirds and hover fly larvae

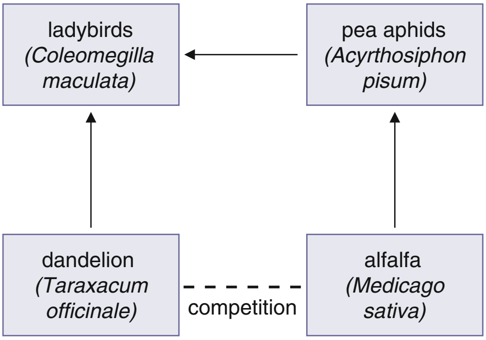


Fig. 5.35 Feeding and competition relationships between different species in an alfalfa field in Wisconsin, USA (Based on Harmon et al. 2000)

were not affected by the cultivation system, those of spiders and predaceous bugs of the genus *Orius*, were more abundant in the one-crop of cowpea than in both mixed crops (Nampala et al. 1999).

Establishment of mixed cropping systems often contributes to management of pests. However, it cannot be assumed that this method will always be successful, because not all antagonist species react to modifications of the production system in the same way.

Integration of Wild Plants

The natural growth or sowing of wild plant species, which do not serve as crops, can promote antagonist populations in a similar way to the establishment of mixed cropping systems.

Examples: In many alfalfa fields in the United States, dandelion (*Taraxacum officinale*) occurs a wild plant. A study showed that the density of these plants was positively correlated with the number of ladybirds (*Coleomegilla maculata*), which feed on the pollen of the dandelion flower as an additional source of food. At the same time, there was a negative correlation between the number of ladybirds and the number of pea aphids (*Acyrthosiphon pisum*). The latter are found as pests in alfalfa but are not found on dandelions. The stands of dandelion thus indirectly reduce pest density. However, in this study by Harmon et al. (2000) it remained unclear how aphid density on the one hand and competition between the dandelions and alfalfa on the other affects yields. The relationships between the species are shown in Fig. 5.35.

In an apple orchard in Switzerland, strips of wild plants were established between the rows of trees. In the flowering phase of the wild plant species, different predators (primarily spiders, bugs, ladybirds, and green lacewings) appeared in greater numbers on the apple trees than in control areas without wild plant strips. The rosy apple aphid (*Dysaphis plantaginea*) and the apple aphid (*Aphis pomi*) were found in lower densities in the area with wild plants than in the control areas. This can be attributed to the activities of the antagonists. The positive effect of the

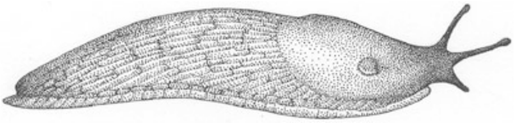
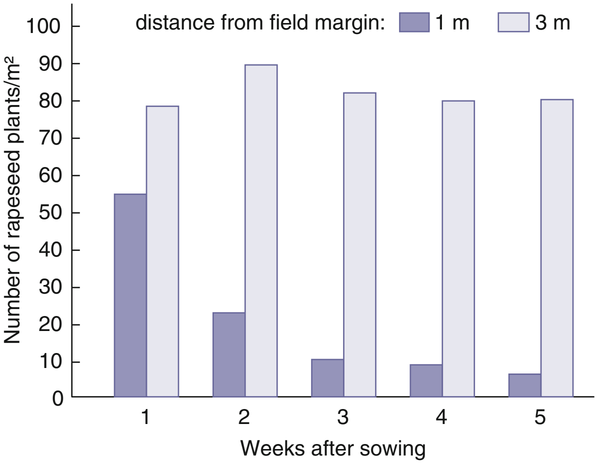


Fig. 5.36 Spanish slug (*Arion lusitanicus*). This species probably originates from the Iberian Peninsula and is today found in large parts of Central Europe

Fig. 5.37 Number of rapeseed plants per square meter at different distances from the field margin, from which different slug species (primarily *Arion lusitanicus*) invade the field (Based on Frank 1998)



wild plant stands on these species is based essentially on the additional availability of food (nectar, pollen, and aphids) found on the wild plants (Wyss 1995).

Natural or sown stands of wild plants in or around agroecosystems may be attractive not only to antagonists but also to pests that attack crop plants.

Example: Field margins are an ideal habitat for slugs because of the shady and moist microclimate of the soil surface. A study in Switzerland showed that the Spanish slug (*Arion lusitanicus*; Fig. 5.36) and other snail species invade adjoining rapeseed fields from these edge habitats, predominantly at night. Up to approximately 1 m inside the field, young rapeseed plants were often completely eaten by the snails whereas no damage occurred 3 m from the field edge (Fig. 5.37; Frank 1998).

Soil Cover

The extent of coverage of the soil surface by stands of wild plants or undersown crops is primarily of importance for soil-dwelling antagonists, for example ground beetles and some spider species. It has often been shown that the number of individuals of such antagonists is higher on soil with dense plant cover than on bare surfaces (Fig. 5.38). However, not all species react similarly to the plant cover

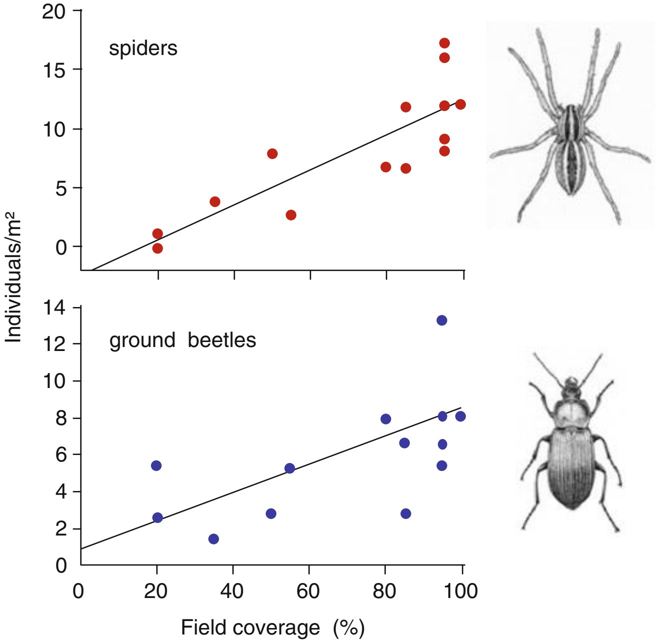


Fig. 5.38 Relationships between soil coverage by wild plants and the density of individuals of spiders and ground beetles in a soybean field in Ohio, USA (Based on Halaj et al. 2000)

density. Ground beetles include species that are mainly found in shaded areas and others that prefer bare ground.

An increase in the density of antagonists may also be achieved by covering the soil with mulch (harvest residues or other organic material).

Example: By covering the soil with straw after planting of potatoes in a field in North America, yield losses caused by Colorado potato beetles were significantly reduced. This pest produces two generations per season. The most important antagonists of the first generation were ground beetle species that climb up the potato plants and primarily prey on the second and third development stages of the potato beetle larvae. With the emergence of the second generation of potato beetles, primarily ladybirds, the larvae of the green lacewing *Chrysoperla carnea*, and the predatory bug *Perillus bioculatus* were present instead of the ground beetles. These species primarily feed on the eggs and on the first larval stage of the pest. The number of different antagonists on the potato plants was higher on straw covered plots than on uncovered plots during the entire growing season (Fig. 5.39). The higher antagonist density resulted in reduction of potato plant leaf area loss by a factor of 2.5 and in potato yields approximately 30% higher than for plots without straw mulch (Brust 1994).

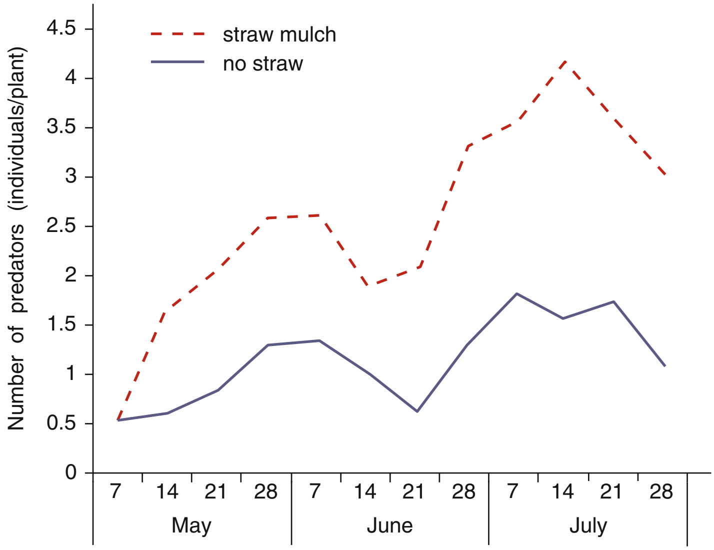


Fig. 5.39 Numbers of individuals of predatory arthropods on potato plants in parcels with straw mulch and in parcels with bare soil in a field in Indiana, USA (Based on Brust 1994)

5.2.4.6 Inundative Biological Pest Control

Antagonists and pests often have different development cycles or phenology; this can result in temporal differences in the appearance and abundance of the respective species (Sect. 5.2.4.2). Even with directed measures to protect or promote antagonists, it is often not possible to increase their numbers at the right point in time, as is necessary for effective control of pests. One solution to this problem is the rearing of specific antagonists under artificial conditions and then releasing them in large numbers into fields or greenhouses. This approach is called **inundative biological pest control**. The principle of this method is to increase the number of antagonists in relation to the pest population to the extent that they are able to reduce the density of a pest significantly within a short period of time. Thus, with this type of management, a similarly strong effect is expected as would result from the application of insecticides. Generally, it is not expected that the respective antagonist species will become established permanently. Depending on the need, they must be released every season or several times during a season. Successful application of the inundative method is based on two necessary preconditions:

- The antagonists selected must, at least, have a preference for the target pest species, to limit their use of other prey or host species, especially other antagonists.
- Both the timing and the number of individuals to be released must be carefully determined. In fields, it must be expected that a small or large portion of the

Fig. 5.40 Ichneumon wasp of the genus *Trichogramma* on the egg of an insect

individuals will either actively or passively (e.g. by wind) disappear from the target area.

Overall, representatives from almost all the antagonist groups described in Sect. 5.2.4.1 are used in the inundative method. Many species are commercially produced and are available for purchase.

Examples: Parasitoid wasps of the genus *Trichogramma* (Fig. 5.40) attack the eggs of different orders of insects (e.g. butterflies, true bugs, and beetles) and are successfully used in inundative pest management worldwide (primarily against caterpillars). For crops such as sugar cane, wheat, maize, or Brassica species, parasitization by *Trichogramma* of 60–80% can be achieved, and thus the yield losses caused by their hosts are substantially reduced (Li 1994).

One of the most important maize pests in Europe is the European corn borer (*Ostrinia nubialis*), whose caterpillars feed inside the maize-cobs and the stems of the plant. From the Mediterranean region, this butterfly species expands to the north and is currently a problem primarily in the south of Germany. *Trichogramma* species (especially *T. evanescens* and *T. brassicae*) are important in corn borer management. They are applied by way of parasitized host eggs that are exposed in the fields on cartons or in capsules, from which the parasitoids hatch. In most years, two applications of approximately 100,000 individuals per hectare are sufficient to reduce pest density so far that the yield losses remain low or are completely prevented.

The predatory bug *Perillus bioculatus* is an important antagonist of the Colorado potato beetle in North America and feeds on the eggs and young larvae of this pest. By directed release of *P. bioculatus*, the number of eggs of the potato beetle in the field can be significantly reduced, as has been shown in experiments by Hough-Goldstein and Whalen (1993; Fig. 5.41).

5.2.4.7 Classical Biological Pest Control

Biological control of pests in a region to which they were introduced from another region is called **classical biological pest control**. The specific characteristic of this method is that management of such pest species is conducted with antagonists that also originate from another region, generally from same region of origin as the pest.

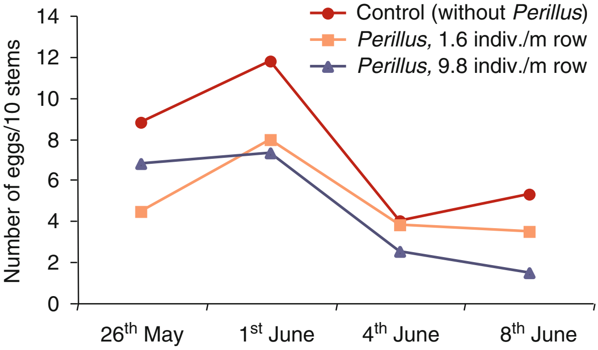


Fig. 5.41 Number of eggs of the Colorado potato beetle (*Leptinotarsa decemlineata*) on potato plants for different densities of the predatory bug *Perillus bioculatus*, which was released in fields in Delaware, USA (Based on Hough-Goldstein and Whalen 1993)

Examples: In 1887, the Californian citrus industry was facing ruin because of a massive attack on the citrus plantations by the cottony cushion scale *Icerya purchasi*. This species, which sucks plant sap, probably originates from Australia, where the search for natural enemies of the pest was subsequently undertaken. These include the larvae and adults of the ladybird *Rodolia cardinalis*. Their release in the citrus plantations led to control of the pest within 1 year. *I. purchasi* was not entirely eliminated, but survived in small and dispersed populations. These were not important to citrus production, but were sufficient to maintain populations of *R. cardinalis*. Problems only emerged in the 1940s, when DDT was applied to the citrus crops and killed not only pests but also the ladybird beetles. For biological control of *I. purchasi*, it was necessary to repeat introduction and rearing of *R. cardinalis*.

St. John's wort (*Hypericum perforatum*) is an herbaceous plant native to the Mediterranean region and was introduced to California in approximately 1900. There, it developed into an invasive weed (cf. Sect. 3.3.3) and, after four decades, covered large areas of pasture land. Not only did it greatly reduce the grazing area for cattle, sheep, and horses, St John's wort also contains the alkaloid hypericin, which is toxic to mammals. Ingestion makes the skin sensitive to sunlight and affects the performance and welfare of the animals. In the 1940s, two leaf beetle species, *Chrysolina hyperici* and *C. quadrigemina* (Chrysomelidae), were introduced from Europe and released in California as biological control agents. Both species are specialist feeders on *H. perforatum*, feeding on shoot tips and leaves (the larvae) and on flower buds (the adults). The species became successfully established and within a few years were able to reduce the area infested by *H. perforatum* to less than 1% of its former extent.

The overwhelming success of such projects is mainly because the introduced antagonist species do not have important natural enemies or competitors in their new habitats, and also because they are highly specialized on the introduced pest species.

There are many examples of classical biological pest control projects in which the desired effects have been achieved; most such approaches have failed. In only approximately 16% of all cases has relevant reduction of the respective pest species

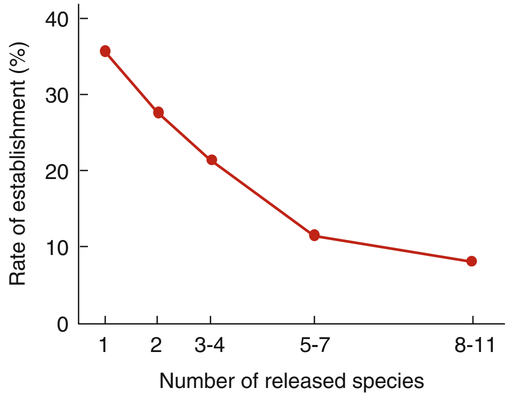


Fig. 5.42 Relationship between rate of establishment and number of simultaneously released antagonist species in classical biological control projects (Based on Ehler and Hall 1982)

been achieved by release of introduced predators or parasitoids (Myers et al. 1989; Waage and Mills 1992). Factors that may explain such failures are primarily:

- Natural enemies of the antagonist: Predators, parasitoids, or animal pathogens can reduce the population density of introduced species and, in extreme cases, lead to extinction of a population.
- The prey or host range of the antagonist: When introduced antagonist species are not highly specialized on the host species, it is possible they also feed on other prey or host species and thus threaten the success of the project.
- The abiotic environment: The climatic conditions that exist in the new habitat of the antagonists are usually not exactly identical with those in their area of their origin. The effects of the climate may, therefore, also impair or prevent establishment or reproduction of the introduced antagonist species whereas the same conditions are tolerated by the introduced pest species.
- Competitors: In many classical biological pest-control projects, not only one but several antagonist species were released in the target area. It has been shown that the rate of establishment of introduced natural enemies is inversely related to the number of species released simultaneously (Ehler and Hall 1982; Fig. 5.42). In many cases, this can be explained by interspecific competition for the common prey or host species, which leads to extinction of the inferior species. When the remaining antagonist species do not have a large effect on the pest population, because of low specialization or other factors, effective control can no longer be achieved.

Overall, the successes and failures of classical biological control projects must be seen against the background of the special situations created by humans (i.e., the accidental introduction of a pest and the intended introduction of antagonist species). It is, therefore, hardly possible to predict the outcome of predator–prey interactions in the area of introduction.

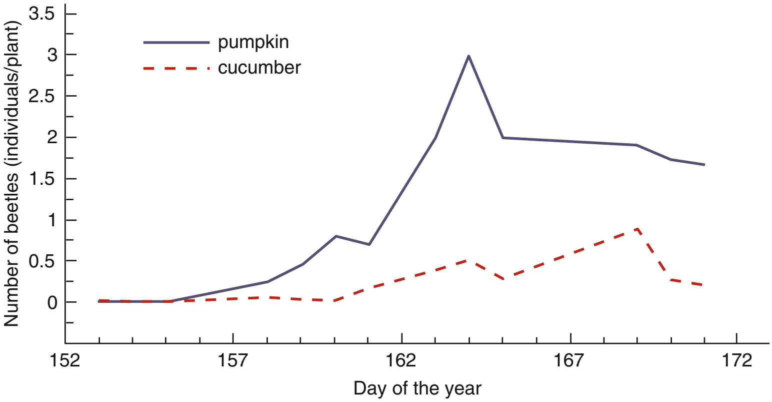


Fig. 5.43 Number of individuals of the striped cucumber beetle (*Acalymma vittata*) per plant in a field (in Maine, USA) which was planted with cucumbers and pumpkin in equal ratio (Based on Radin and Drummond 1994)

5.2.4.8 Biological Pest Management with Plants

Not only antagonists, but also plants can be used for biological pest management. Although conservative biological pest management is intended to promote populations of antagonists, the density of pests on crops can also be directly reduced by specific modification of the plants in agroecosystems. Such measures include the establishment of plant species that are preferred by pests over other food sources (the crop plant) and which therefore serve as **trap crops**. Trap crops have been defined as plant stands grown to attract insects or other organisms, for example nematodes, to protect target crops from pest attack, preventing the pests from reaching the crop or concentrating them in a specific part of the field where they can be economically destroyed (Hokkanen 1991).

Examples: The striped cucumber beetle (*Acalymma vittata*) feeds primarily on cucurbits (Cucurbitaceae) but has different preferences for individual species within this plant family and mainly feeds on pumpkin (*Cucurbita maxima*). This attribute can be used to protect cucumbers (*Cucumis sativus*) from attack by this pest. When half of a crop stand is composed of cucumbers and the other half of pumpkin, at least 70% of the beetles colonize the pumpkin plants (Radin and Drummond 1994; Fig. 5.43).

Lygus bugs (genus *Lygus*) are polyphagous plant sap suckers that occur as pests on many agricultural crops. Because of their wide range of host plants, varieties of wild plant species which are preferred to the crops can be used as trap crops. In the production of lettuce (*Lactuca sativa*) in Sweden, legume species (clover species, alfalfa, common vetch) and mugwort (*Artemisia vulgaris*) have been used for this. Five to thirty times more lygus bugs became established on the legume plants rather than on the lettuce plants. For mugwort the density of the pest was 100 times higher than on the lettuce (Rämert et al. 2001).

Meloidogyne incognita is a root gall nematode that is important as a pest primarily in the tropics and has a wide range of host plants. In experiments in Cuba, lettuce and radish (*Raphanus sativus*) were planted as nematode trap crops and then completely removed from the field after 1 month of growth. By this means it was possible to reduce nematode density in the soil by 50%. For subsequently grown crops, for example tomato, pumpkin, or cowpea, 10–20% higher yield was achieved on the sanitized fields than on plots without previous sanitation with trap crops (Cuadra et al. 2000).

In different situations it has been shown that expectations of the trap crop method were not, or were only partially, fulfilled; insufficient differences between the food preferences of the pests are primarily responsible for this. These are not only related the respective plant species but are also affected by such factors as fertilization or the nitrogen content of the plant (Sect. 4.5.3.2) and pest density.

Example: Use of mustard and rapeseed as trap crops to protect broccoli (*Brassica oleracea*) from attack by the harlequin bug *Murgantia histrionia* in North America was only successful when the pest species appeared in small numbers. At high population density, individuals of the pest population began to move to the broccoli plants (Ludwig and Kok 1998).

5.3 Management of Phytopathogens

In comparison with phytophagous pests, the life strategies of agents of plant diseases are more diverse, which results not only in differences, but also limitations, in the possibilities of control.

5.3.1 Viruses

To reproduce, viruses depend on the host cells they infect. Direct chemical control of phytopathogenic viruses can hardly be achieved, because the agents attack the plant cells and interfere with nucleic and amino acid metabolism. Repression of viral activity by use of chemical inhibitors would also cause significant disorder in the metabolism of the plant. It is, however, possible to limit the spread of viruses, in particular by control of their respective vectors (Sect. 4.6.1) and use of virus-free seeds and plant material. Infected seeds and seedlings are often the primary source of virus diseases.

5.3.2 Bacteria

The most effective way of controlling bacteria is by use of antibiotics. These are substances that are usually produced by bacteria and fungi and have negative effects on the metabolism and the reproduction of other microorganisms (primarily bacteria) and/or their ability to survive. Today, antibiotics also include numerous synthetic compounds. Antibiotics affect either specific groups of microorganisms or a more or less broad range of species.

However, use of such compounds as plant-protection products is problematic for several reasons. First, use of antibiotics can have negative effects on other species in the environment (e.g. soil microorganisms). Second, there is the threat of development of resistance to antibiotics. This is not necessarily limited to the target species, but can also occur in bacteria species that are human and animal pathogens. These can then no longer be controlled by use of antibiotics with a similar mode of action. Nevertheless, antibiotics are sometimes used for plant protection. An example is the use of streptomycin against fire blight (Table 4.9) in pome fruit production. Because of potential ecological and health risks, this antibiotic, which is also used to treat tuberculosis, lost its registration as a plant-protection product in the European Union in 2004. In some countries, for example Germany, streptomycin continues to be used, at least in exceptional cases, against fire blight. Chemical control of phytopathogenic bacteria by use of other substances (e.g. copper compounds) is successful in a few cases only.

5.3.3 Fungi

For control of phytopathogenic fungi, a broad range of fungicides is available. Amongst the longest used of these substances are inorganic copper and sulfur compounds, which were used as long ago as the nineteenth century, primarily in vineyards and orchards. Almost all modern formulations are based on organic substances that interfere with the metabolism of fungi in different ways. Depending on their effect, fungicides can be classified into two groups:

1. **Protective (preventive) substances**, which also include copper and sulfur compounds, are applied to the surfaces of plants or seeds and thus prevent fungal attack. Such substances prevent the germination of spores and/or formation of the germ tubes, for example by impairment of enzyme activity or the mitochondrial respiration chain.
2. **Curative (healing) substances** are usually taken up systemically by the plant and serve to kill the agent of the disease after infection has occurred. This works by impairment of different metabolic processes of the fungus.

Similarly to pest management, there is also a variety of methods used for protection of crops from pathogens (primarily from fungi) that avoid the application of chemical substances. These include the breeding of disease-resistant varieties, which is conducted with the same methods and objectives as in breeding for pest resistance (Sect. 5.2.2). No great progress has yet been made in the development of transgenic varieties with resistance to pathogens. Biological management is also far less important in the treatment of plant diseases than it is for pests. Success has,