Chapter 12
Herbivorous Insects—A Threat for Crop Production

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Abstract It is estimated that, in spite of plant breeding and pest control efforts, 15 % of crop yield is worldwide lost to herbivory by insects. Examples demonstrate how insect pests have developed in the past and why they will develop in the future. The evolutionary potential of insects to become new pests is considered for traditionally and genetically modified crop varieties. The immune system of plants is presented step by step. Generalist herbivores can be effectively repelled, but specialist herbivores are much harder to repel. They use plant defenses as cues for host plant recognition. Next to direct defense, indirect defense by attracting natural enemies of (specialist) herbivores is explained. Finally, the interactions of plants and insect herbivores with microbial symbionts—and their consequences—are discussed.

12.1 Introduction

Probably not a single wild plant will complete its life cycle without being victim of herbivory by one or usually many more insect species during some stage of its life. Without special treatment, like the application of insecticides, the release of natural enemies and/or modification of their immune system, crop plants are even more vulnerable than their wild relatives. The worldwide loss of crop yield to insects is estimated to be 15 % (Maxmen 2013). Loss of crops has been familiar to man as long as he has been growing them. Locust pests were already well known in ancient Egypt. Especially the Migratory locust (*Locusta migratoria*) belongs to the most voracious pests and at the same time to the most difficult pests to control. A high local juvenile population density stimulates individuals to adapt their physiological development. They grow into adults with effective wings and lightweight energy reserves. These individuals start migrating (Fig. 12.1) in search for new food sources. During their flight they mix with other groups of the same species and eventually these swarms may become incredibly large. Swarms have been observed with an estimated number of 70 billion individuals, ten times as many individuals as the total human world

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B. Lugtenberg (ed.), *Principles of Plant-Microbe Interactions,*
DOI 10.1007/978-3-319-08575-3_12

Fig. 12.1 A swarm of locusts is landing, an insect pest develops. (Reproduced with permission by FAO (©FAO/Yasuyoshi Chibam))

population. Locusts feed on *Sorghum*, maize and wheat and other grass species. A recent outbreak led to 42 % reduction in farmland grass production of 36,000 ha in Northern China in 2003 (Tanaka and Zhu 2005).

Interestingly, already long ago (2500 BC) Sumerians used sulphur compounds to control insects and mites (Dent 2000). Recent control methods include warning systems with drones, insecticides, resistant plant varieties and biological control with predators, parasitoids or insect pathogens. Despite immense scientific efforts, plagues continue to affect plants and consequently human food supply. It may be argued that we will probably never get completely rid of insect (and other) pests (Chaps. 9, 10, 11, and 13). What makes insects such outstanding guerilleros? Their short generation time (relative to that of their food sources) and their extremely high fecundity (their potential number of offspring), make them evolutionarily extremely successful. They can often adapt to insecticides and to new resistance genes within a few generations. Moreover, for each plant species probably several hundreds of insect herbivore species exist that may grow into effective pest species.

To demonstrate how insect pests work, how they develop and how some pests are in the waiting room to develop, I will give some examples. This continuous battle is probably best illustrated by one of the most important crop plants worldwide, maize. Maize (*Zea mays*) originates from Central America and has been grown for more than 6000 years. Today maize is grown all over the world. By far the largest part of the maize crop is fed to livestock; smaller amounts serve as human food or are turned into ethanol. Economically, maize is extremely important but it is vulnerable to insect feeding. In the U.S. more than 100 different insect species were reported to cause important pest damage. Some of these can be dealt with by using insecticides. Others—like the European corn borer (*Ostrinia nubilalis*)—feed inside the stem, in immature kernels, or inside the roots. In these cases insecticides are less effective. Alternative measures are biological control by insect parasitoids, viruses or microorganisms. Another alternative is the development of resistant varieties by genetic modification. Products containing the soil bacterium *Bacillus thuringiensis* (Bt) have been known to be effective insecticides since the first half of the last century. More recently, several toxic proteins were detected and the coding genes were identified (Chap. 40). Maize is now one of the crop plants for which varieties have been developed which harbour Bt-genes. They produce the Bt-proteins, which make them resistant to several butterfly, moth and beetle pests such as the European corn borer. These genetically modified varieties have become very popular in some countries, like the USA and Spain. It must be stressed however, that similar to natural varieties of wild plants and varieties of crop plants that have been developed with traditional breeding techniques, these phenotypes are prone to loss of their resistance by natural selection and evolution of their insect herbivores. Counter resistance is especially expected to develop when host plants are grown in large monocultures over longer periods of time. In 2012, Gassmann reported the first examples in which the European corn borer broke through the resistance of Bt-maize in fields in Iowa that had been grown with this variety for 3 to 6 years. Right now it has become an urgent question how to deal with these economically extremely important plant resistance characteristics. This makes future pest control one of the most urgent and at the same time most exciting fields of the biological sciences.

A very ancient but yet illustrative example of loss of resistance comes from the grape vine. Wine production has been of great economic importance for ages, probably even before the Greek and Roman cultures. In 1864 a disease was observed among grape vines in Southern France that eventually affected most European vineyards. It took quite some time before it was realized that the disease was in fact caused by sap sucking on leaves and roots by the Grape phylloxera. This small, aphid-related, insect may even kill vines. In France the total production of wine between 1875 and 1889 was reduced by three quarters. The insect, which is native to North America, must have been accidentally introduced in France. Native vines in North America, however, were not seriously affected by this herbivore. The solution to control the Grape phylloxera in Europe has been to graft native varieties onto phylloxera-resistant North American rootstocks (Campbell 2006). However, be careful. Also the grape phylloxera is continuously evolving and is presently causing disasters in Northern California.

Each year crop failures due to insect herbivores take place worldwide, sometimes only locally, sometimes on a very large scale. All major and minor crops are vulnerable. Rice, the second most important crop plant with its main areas of production in China and Thailand, is frequently subject to crop losses of 30 % due to pest insects like the Rice brown plant hopper. Cassava, an important crop of Africa, is frequently subject to large-scale destruction by the Cassava mealy bug, the Cassava green mite, the whitefly *Bemisia tabaci*, locusts and other insects. *Bemisia* is not only a serious threat itself, it is also a vector for the Cassava mosaic virus (CMV). Yield losses in Africa by CMV have been estimated up to 50 %.

The climate of our planet will change in the future as it did in the past. There are several indications that global warming takes place. Will warming affect the influence of insects on human crops? Population dynamics of insects are usually affected to a great extent by weather conditions. Weather can have direct and indirect effects. Especially drought conditions may lead to insect pest development (a. o. White 1969). Under drought conditions that are limited in duration, sap-feeders may benefit from stress-induced increases in plant nitrogen. If our climate continues to change towards higher temperatures and periods of drought, it is very likely that we will be faced with more insect outbreaks all over the world in all kinds of crops from timber to food crops like wheat, maize and potato (Maxmen 2013).

12.2 Pest and Beneficial Insects

The overwhelming variety of insect species that feed on plants may be challenging for an entomologist, but is an absolute threat for plant growers. There are more than a million different insect species and it is estimated that more than 360,000 species are plant feeders.

Insects of some orders undergo complete metamorphosis. Larvae turn into pupae, and pupae into adult insects. The larval stage is usually the most voracious life stage. This is typical for beetles (Coleoptera), butterflies and moths (Lepidoptera) and flies (Diptera). In other groups, like the bugs, whiteflies, leafhoppers and aphids (Hemiptera), locusts and grasshoppers (Orthoptera) and thrips (Thysanoptera) there is so-called incomplete metamorphosis during which immature stages (called nymphs) already resemble the mature stage.

Beetle larvae, with chewing mouthparts, often feed on or inside plant roots or stems, or behave as leaf-miners. Adult beetles feed on leaves of trees, shrubs or herbs. Some species are specialized on seeds. Lepidopteran larvae are mainly leaf chewers. Leaf chewers can have very different feeding patterns; some start eating at the leaf rim, some make feeding holes, and others skeletonise leaves. Hemiptera have piercing mouthparts that enable them to feed from the vascular system of plants or even from individual cells. In this way they can avoid feeding contact with particular (less palatable) tissues. Locusts and grasshoppers are leaf chewers; thrips suck from epidermis cells. Although all insects may be vectors of plant diseases by transmission of bacteria, fungi or viruses from one plant to another, especially the groups with piercing mouthparts bring along this extra threat for plants. Because they feed with their mouthparts inside plants, they may be difficult to control with insecticides.

Beneficial insects are found in the orders of Diptera (flies) and Hymenoptera (bees, wasps and ants). Both orders have pollinators and parasitoids of herbivorous insects. These parasitoids may be extremely important in controlling pest species. Several companies, (like Koppert: http://www.koppert.com/) are specialized in breeding parasitoids for crop protection and pollinators for glasshouse environments. Among the beetles, the bugs and the ants, several species are specialized as predator of herbivorous insects. Because they immediately kill their prey upon finding it, their herbivory-reducing effect may be considerable.

12.3 Which Characteristics Make Insects Dangerous?

For each individual plant, the immune system provides protection against by far the largest majority of 360,000 potential herbivore species. However, they are quite vulnerable to a much smaller group, the so-called specialists. These specialists (a few to more than a hundred different insect species per plant species) have apparently penetrated the plant's immune system during their (co)evolution. These particular plants have become their specific food plants. Specialist insects often use the defense substances of their food plants to recognize and locate these plants. This phenomenon will be illustrated with an example of *Brassica* species and their herbivores. *Brassica* species like Cabbage and Oilseed rape (Fig. 12.2) contain a large group of specific chemical substances, the glucosinolates. We are all familiar with these substances because of their distinct "cabbage smell". Specialist insect herbivores like the Diamondback moth (*Plutella xylostella*), the Cabbage white butterflies (*Pieris* spec.) and the Crucifer flea beetle (*Psylliodes chrysocephala*), all important pest species of *Brassica* on a worldwide scale, use these glucosinolates to find their food plants and to start feeding. Generalist feeders (other insects, birds and slugs, etc) on the other hand, are effectively repelled by the same substances (Fig. 12.2). Alkaloids constitute another group of plant substances that is highly toxic to generalist herbivores (like horses and cattle) but not to specialists. Small amounts of alkaloids spread on pieces of filter paper are sufficient to attract individuals of the specialist Cinnabar moth (Macel and Vrieling 2003). This leads to an awkward dilemma for plant breeders and plant protection in general. The use of these plant substances as insecticides may increase the level of defense of crop plants towards generalist herbivores. At the same time it makes them more attractive to the specialists.

All insects of crop plants are potential pest species. If they can multiply fast, they will soon cause damage. Under natural circumstances the low number of food plants available and the presence of natural enemies, like parasitoids, will (often) keep numbers low. However, under agricultural circumstances large monocultures provide them with excess of food. Development of populations of natural enemies large enough for control can only follow after a time lag of at least one generation. That means after at least one season of crop growth. A special group of insects that may cause crop pests are the so-called invaders. We have seen examples of the Grape phylloxera (*Daktulosphaira vitifoliae*), colonizing Europe from the United States, and the European corn borer colonizing the United States. These species enter a new continent without their natural enemies which under natural circumstances might control them. This clearly gives them a head start in their new environment.

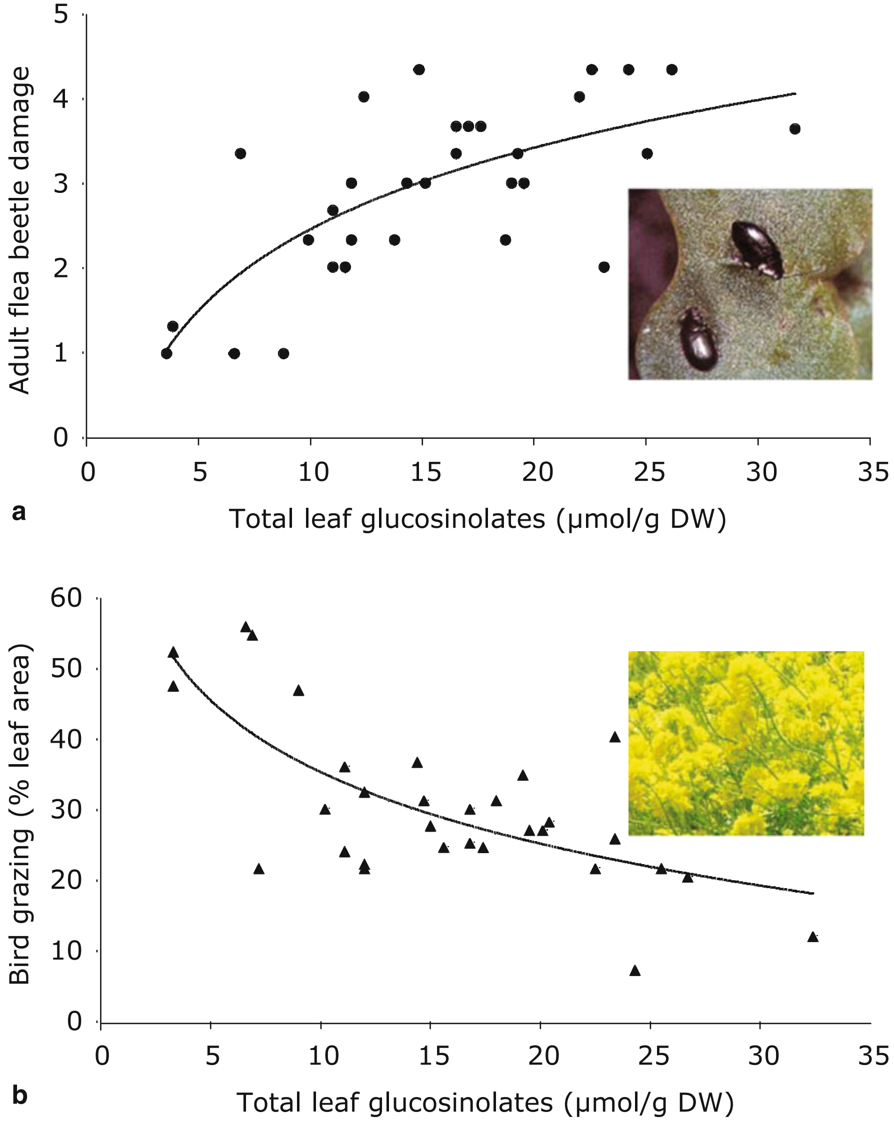

Fig. 12.2 **a** Relationship between (specialist) Crucifer flea beetle damage and total leaf glucosinolates in Oilseed rape (*Brassica rapa*). (Inserted photograph of Crucifer flea beetle by Richard Mithen). **b** Relationship between (generalist) bird feeding and total leaf glucosinolates in Oilseed rape. (Inserted photograph of oilseed rape by Eddy van der Meijden. Figures redrawn from Giamoustaris and Mithen (1995) by permission of the publisher)

12.4 The Plant's Immune System, Step by Step

Firstly, each plant produces a blend of volatile chemicals. These substances pass through the stomata and cuticle and surround the whole plant. Such a cloud may contain a few dozens to several hundreds of different compounds. Undamaged plants emit leaf volatiles. Upon damage the blend of compounds may change considerably. The production of some new substances is induced by herbivore damage. They are plant-species specific and their composition sometimes also depends on the particular herbivore. Leaf volatiles constitute the outer layer of a plant's immune system. They provide information to the majority of herbivores that can smell that a particular plant is not their host plant and is consequently unsuitable to feed or lay eggs upon. As was mentioned earlier, each plant has also some specialist herbivores that are not repelled by the plant's immune system, and these use these volatiles to find their particular host plant. Insects have advanced olfactory organs in their antennae that enable them to sense particular volatile substances and blends in extremely low concentrations (Schoonhoven et al. 2005).

The second component of the plant's immune system that an insect has to deal with is the outer surface, the epidermis. It provides protection by its toughness caused by lignin and cellulose. Grasses in general, are three times tougher than herbs (Schoonhoven et al. 2005). The epidermis is covered with a wax layer which contains a great variety of molecules that play an essential role in plant defense. Insects can sense these substances with their antennae and with the sense organs in their tarsae. The maintenance of the chemical composition of these compounds in the wax layer is an active process. Trichomes on the leaf surface are penetrating through this layer. They may be glandular or non glandular. In the first case they may secrete repelling or even toxic substances.

The insects that have not been stopped by leaf volatiles and other external defenses are subsequently confronted by a world that is dominated by an incredible variety of complicated chemical substances within the plant. These chemicals do not play an important role in the primary activity of growth, and are therefore called secondary metabolites. Up till now about 200,000 of these substances have been detected. Many of them reduce herbivory by particular insect species. This is the *constitutive defense system* of plants. These metabolites may be toxic or just repelling. Some act as digestibility reducers. For instance, saponins inhibit enzymes in the gut of insects that digest proteins. Some even act as attractors of pollinators. Some of these compounds clearly have several different functions within a plant. Most of the substances in the cloud of leaf volatiles are also secondary metabolites.

The glucosinolates or mustard oil glucosides are characteristic for the Brassicaceae, a plant family with more than 3500 species. All the cabbage varieties—Black mustard, Indian mustard and Oilseed rape—belong to this family, but also the model species for molecular research, *Arabidopsis thaliana*. About 120 different glucosinolates have been identified and each different species usually contains twenty or more of them, providing a specific fingerprint for that particular species. Typical is that they contain at least one glucose residue, one sulphur and one nitrogen atom.

Some other groups of secondary metabolites are the alkaloids (16,000) that occur in, for instance, the Solanaceae (a. o. potato, tomato) and the sesquiterpenes (6500) of the Asteraceae (a. o. sunflower and artichoke).

Not all plant parts contain the same concentration of secondary metabolites. Hound's tongue (*Cynoglossum officinale*) is a poisonous plant with a high concentration of pyrrolizidine alkaloids. However, young leaves may have a ten- to fifty-fold higher concentration than old leaves. Specialist herbivores and generalist herbivores that were fed on these leaves demonstrated a totally different preference. Specialists fed predominantly on the younger leaves; generalists avoided these leaves and fed on the older leaves with much lower concentrations (Van Dam et al. 1995; Fig. 12.3).

In general, much higher concentrations of secondary metabolites are found in the reproductive organs of plants and in younger leaves that are important for future photosynthesis, than in older leaves. The former plant parts are thus better protected (against generalist herbivores). The Hound's tongue example demonstrates that less important plant parts (from the plant's point of view) with low concentrations may be attacked by generalist herbivores. Significantly different patterns in secondary compounds were even detected among cell layers, like epidermis and mesophyll (Nuringtyas et al. 2012).

Insect herbivore-challenged plants do not only act passively with their constitutive defenses, but also respond to herbivory with the production of toxins and defensive proteins that target physiological processes in insects (Howe and Jander 2008). This is the extremely important *inducible defense system*. Contrary to the constitutive defenses, induced responses follow upon particular damage cues and may thus be more directed towards defense against the specific herbivore that is causing the damage. To respond in this specific way, plants should be able to recognize herbivore species. Such recognition has been earlier found in several plant-pathogen studies (Chap. 14). During the past 20 years many experimental studies have demonstrated differences in plant physiological responses to mechanical damage and insect herbivory. These are the result of differences in induced gene expression patterns and transcriptional responses.

There is strong evidence from experimental studies that plant defense is induced by the oral secretions of insects (Howe and Jander 2008). The presence of fatty acid-amino acid conjugates (FACs) in insect oral secretions was found to be an important induction elicitor. These substances are derived from moieties from both insect and host plant. There are indications that plants have specific FAC receptors. Other insect and plant derived substances with similar functions are being studied. This field of research is very actively developing right now. Signal transduction pathways from insect signals to induced plant responses are still relatively unknown. What we do know, is that especially the jasmonates play a crucial role in signalling and regulating defense responses to insect herbivory. Many studies have demonstrated that jasmonate mutants lack the ability to induce defenses against a wide variety of insect species, whereas experimentally application of jasmonate to leaves increases the level of defenses (Howe and Jander 2008).

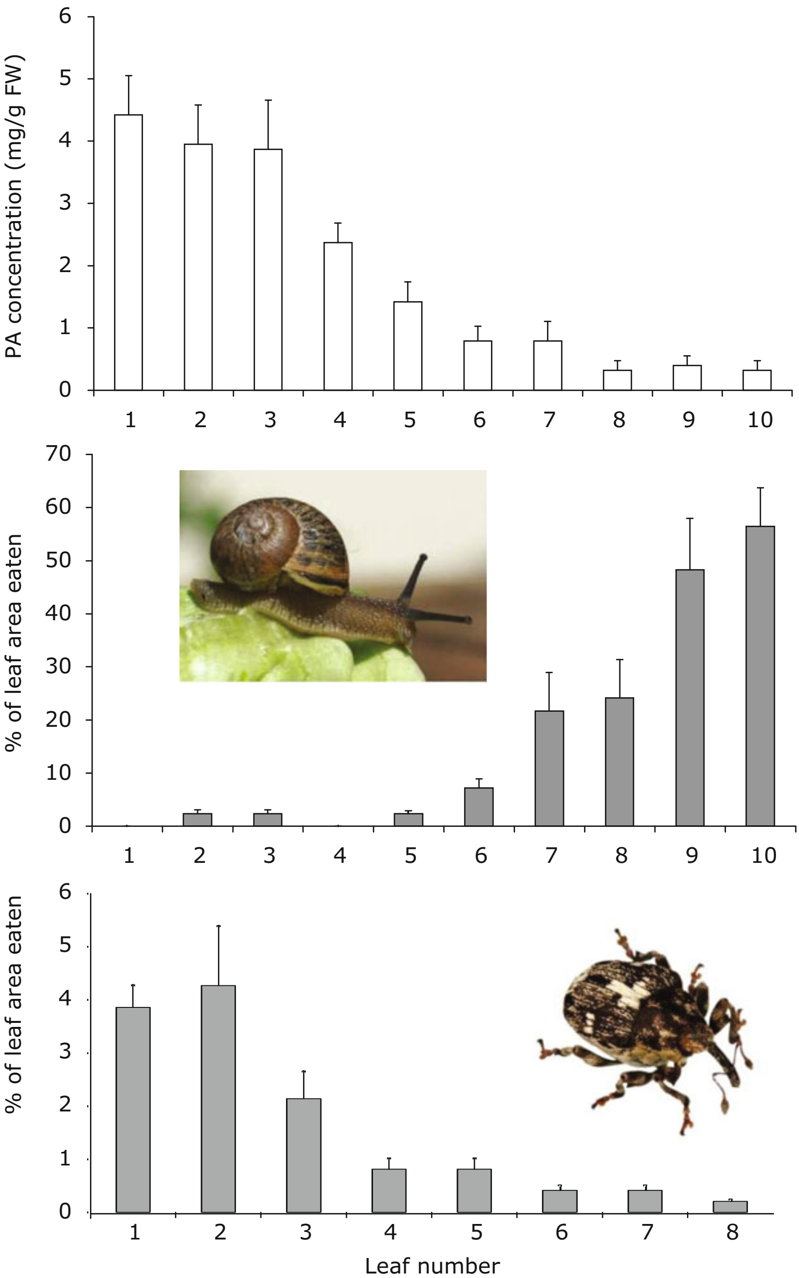

Fig. 12.3 **a** Pyrrolizidine alkaloid concentration in leaves of Hound's tongue (1 is the youngest leaf). **b** Fraction of leaves eaten by the generalist *Helix Aspersa*; (Inserted photograph of *Helix aspersa* by Eddy van der Meijden.) **c** Fraction of leaves eaten by the specialist *Mogulones cruciger*. (Inserted photograph of *Mogulones cruciger* by Henri Goulet, Agriculture and Agri-Food Canada. Figures redrawn from Van Dam et al. (1995) by permission of the publisher)

How Specific is the Plant Immunity System? The impression that one gets today from a wide variety of studies on different species from feeding guilds like leaf chewing caterpillars to phloem feeding aphids, is that the type of defense reaction is more related to feeding guild than to individual insect species (Howe and Jander 2008).

12.5 Tritrophic Systems

Why would a plant change its production of leaf volatiles after herbivory? One possibility is that it follows from damage without any particular function. Studies demonstrate an incredible variety of organisms that can perceive these volatile signals. During the last few decades, evidence has been collected that natural enemies of herbivores—parasitoids, predators and pathogens—use this induced blend of compounds to locate their hosts and prey. Insect-eating birds (great tits) are being attracted by volatiles of trees with damage caused by caterpillars. Predatory soil-living nematodes are attracted by volatiles to feeding sites of larvae of the Western corn borer in maize roots. It is tempting to believe that the induction process was the next evolutionary step after the immune system of the plant was hacked by specialist herbivores. Induction of plant volatiles provides information to parasitoids, predators and pathogens that may lead to parasitization or predation of insect herbivores. If this eventually would lead to a reduction of herbivore damage and a higher fitness of individual plants, natural selection would favour this type of induced response. Another function of the production of volatiles by herbivore-damaged leaves might be that they signal other leaves of the same plant to become induced so that further damage can be restricted. An alternative would be to signal through the phloem. Future research will give the answer, but it is clear that rapid reactions are extremely important for limiting herbivore damage.

How fast inducible responses through volatile emission work, is beautifully illustrated by a study of Allmann and Baldwin (2010). Coyote tobacco in the Western U.S. produces nicotine as a constitutive defense substance. Nicotine is toxic to most insects, but not to the Tobacco hornworm, a specialist insect herbivore of tobacco. Mechanically damaged leaves produce a. o. the volatiles hexenal and hexenol. So do Tobacco hornworm-damaged leaves. But there is an important difference. The cloud of volatiles of mechanically damaged leaves is dominated by z-isomers of these substances, whereas the tobacco hornworm-damaged leaves have more or less equal concentrations of z- and e-isomers. The change from the production of e-isomer dominated volatiles to z-e balanced blends takes place within a few minutes after the onset of damage, and is induced by the oral secretion of the specialist herbivore. Oral secretions of two generalist insect herbivores had no such effect. Blends with predominantly e-isomers were much more attractive for an important predator of the tobacco hornworm, the predatory bug *Geocoris*. By producing the induced blend locally in an extremely fast way, predation may start immediately and the search activity of the predator is guided by signals of the damaged leaf to its prey.

12.6 Insect Symbiotic Microbes Hijack Plant Defense Signalling

There are relatively few studies on the role of microorganisms on insect-plant interactions, but that is not a reliable indicator for their impact. Both insects and plants carry microbial pathogens and symbionts. One of the most important functions of this symbiosis is that microbial symbionts provide insects with (essential) amino acids that are not available in their food plants. They also play a role in resistance against natural enemies. Microbial symbionts of plants fulfil the same roles: the uptake of nutrients and the protection against pathogens.

Recent studies suggest that microbial symbionts of herbivorous insects play a crucial role in modifying food plant defenses. Larvae of the Colorado potato beetle produce oral secretions that suppress the induced defenses in tomato and potato. To unravel the mechanism, larvae were fed either antibiotic-treated leaves or non-treated leaves. The first group was not able to suppress the jasmonate regulated defenses. The second group did suppress these defenses. The bacteria in the insect's oral secretion (belonging to the genera *Stenotrophomonas*, *Pseudomonas* and *Enterobacter*) elicit salicylic acid-regulated defenses. This negatively cross-talks with jasmonate signalling, which in turn disables the plant to fully activate its jasmonate-mediated resistance. Apparently the food plant does not recognize the insect herbivore any more, but instead it defends itself against a microbial attack (Chung et al. 2013). Several more or less similar experiments have been published now, which gives support to the idea that we are dealing with an important phenomenon. Further study in this particular field is expected to give information on why plant defense sometimes fails.

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