

TEACHING TOOLS IN PLANT BIOLOGY™: LECTURE NOTES

Plants and Arthropods: Friends or Foes?

Arthropods, the largest animal phylum, make up perhaps 80% of known animal species and include insects, arachnids, and crustaceans. The interactions between arthropods and plants are diverse and complex but can be simplified into a basic conflict and two uneasy alliances. The basic conflict is that plants are the most abundant terrestrial food source and arthropods their most abundant consumers. For this reason, plants are heavily defended by thick impervious coverings and extraordinary toxins. However, plant fitness also depends upon alliances with arthropods, such as with pollinators. These interactions are mediated in part by an enormous diversity of plant chemical products, many of which have resulted from pressures to deter and attract other organisms. Understanding the conflicts and alliances between plants and arthropods will help plant farmers, breeders, and growers to decrease the impact of herbivorous arthropods on crop yields without impinging upon the beneficial arthropods.

PLANTS AND ARTHROPODS: A LONG-TERM, COMPLICATED RELATIONSHIP

Plants and arthropods began to live on land more than 400 million years ago. Four-hundred-million-year-old fossils are rare but reveal a fairly simple, homogeneous early ancestry for each group, as well as clear signs of plant herbivory by arthropods (including plant tissues in fossilized arthropod excrements, also known as coprolites). Over time, arthropods developed increasingly sophisticated mouthparts that enabled them to pierce and bite through tough plant material and specialized digestive systems that enabled them to use plant material as food and to neutralize dangerous plant substances.

The basic conflict between plants and animals is about food. Plants can do a trick that animals cannot, photosynthesis, and animals are hungry and have to eat to grow, develop, and, especially, to reproduce. Hence, ~50% of the known arthropod species (over one million) are plant eaters. However, animals can do also tricks that plants cannot do; they are mobile and often eat other arthropods (carnivory). Plants and arthropods have sometimes evolved a mutualism (i.e., an interaction in which different species become allies since they both derive a fitness benefit from interacting). Two such alliances are common in nature: (1) an alliance in which plants accommodate hungry carnivores such that these liberate them from herbivores and (2) an alliance in which plants feed mobile hungry arthropods via floral nectar to establish pollination. These alliances, however, are extremely tense since each of the participants has been selected to maximize its own fitness and not that of other

organisms. Natural selection causes the genotypes of the individuals with the highest reproductive success (i.e., the highest fitness) to become increasingly abundant during the consecutive generations. This implies that natural selection will be hard on groups of reproductive organisms that display forms of optimal resource management since these groups are prone to invasion by selfish genotypes that maximize rather than optimize their fitness. As a consequence, arthropod pollinators and natural enemies of herbivores were not selected to be friendly; they are in competition with other arthropods and were selected to try to get as much as they can. For this reason, flowering plants have to control the behavior of beneficial arthropods. Otherwise, these arthropods may continue eating plant tissues after the herbivores are consumed or plunder and destroy flowers during nectar feeding. Like any relationship, those between plants and arthropods can require a lot of effort to maintain.

THE BASIC CONFLICT: PLANT DEFENSES AND HERBIVORE ADAPTATIONS

Plant fitness is maximal when nutrient loss to herbivory is minimized, so plants are under selection to restrict herbivore feeding as cost-efficiently as possible. Plant defenses to herbivory include physical and chemical deterrents, often toxins, and indirect defenses that entail the recruitment of predators and parasitoids of arthropods. These plant defenses in turn select for counteradaptations in herbivorous arthropods. Plants produce constitutive defenses, which are always present, but also induce additional defenses when attacked; it is thought that this combination may provide an optimal defense strategy without unnecessary, wasteful resource expenditure.

Herbivore Nutritional Requirements and Feeding Styles

Many herbivorous arthropods are specialist feeders (mono- or oligophagous), whereas others are more generalized (polyphagous). Herbivorous arthropods are dependent on plants to meet their nutritional requirements, including water, phytochemicals, vitamins, lipids, and an appropriate ratio of protein-to-digestible-carbohydrates. Monophagous species are highly dependent upon their host plant. Although insects that undergo incomplete metamorphosis (like scale insects, grasshoppers, etc.) use similar food throughout their life, the different stages of insects that undergo complete metamorphosis (like butterflies) may require different foods. In addition, plant nutritional quality and particularly protein levels may vary depending on varying and fluctuating environmental conditions.

Arthropods eat all parts of the plant, including roots, leaves and stems, flowers, pollen, seeds, and fruits. They have evolved

a wide variety of feeding styles, which can be broadly classified as chewing or piercing. The chewing insects have jaws and include beetles, caterpillars, and stem or fruit borers; some are leaf miners that eat the tender mesophyll cells within the leaf. Piercing arthropods include aphids and mites and have needle-like stylets that pierce tissues and suck nutrients out from phloem, xylem, or parenchyma tissues.

Chewing insects have salivary glands that secrete saliva into the oral cavity, which comes into contact with damaged leaf tissues during chewing. Moreover, some chewing insects regurgitate (i.e., they mix the plant material with gut enzymes and then digest the mixture in the oral cavity and outside the body). By doing so, larger volumes of food can be digested while toxins are kept away from the gut until they are detoxified. Chewing causes extensive mechanical damage to plant tissues, and often these feeding sites are entries for opportunistic pathogens. Stylet-feeding arthropods have mouthparts that during the course of evolution have been modified into needle shapes and usually comprise separate canals for saliva and food ingestion. Upon insertion of the stylets, saliva is injected into the plant tissue where it may predigest the plant tissue and interfere with local defenses. Stylet feeders usually cause only minor damage to plant tissues, although some species can be very damaging to the tissues they pass when drilling for phloem. Among the arthropod lineages, piercing-sucking and chewing may have evolved more than once.

At least seven different groups of arthropods, usually stylet feeders, are able to induce galls on plant tissues. Galls are localized regions of cell proliferation, and in some cases, the arthropod manipulates plant hormone levels to produce the tissue proliferation. The arthropods lay their eggs in the gall tissues, which form a shelter for the developing larvae. Gall shape, size, and chemistry are extremely diverse. Some studies have found that the level of nutrients within the gall is high, and the level of defense compounds is low in the gall interior but high in the outer layers. In some cases, plant cells are manipulated to produce nourishment for the developing arthropods via formation of specialized feeding cells.

Plant Defenses: Overview

Plant defenses can be roughly divided in direct and indirect defenses. Direct defenses are established by the plant via morphological or chemical changes that directly affect the plant eater. Indirect defenses are morphological or chemical changes that facilitate foraging by natural enemies of plant eaters. Interactions between plants (first trophic level) and herbivores (second trophic level) via carnivores or parasitoids (third trophic level) are also referred to as tritrophic interactions. Both direct and indirect defenses can be constitutive (always present) or induced.

Plants and plant tissues vary in their degree of defensiveness. Large, long-lived plants are often more highly defended than small, short-lived plants that may be variable in their time and place of emergence. Nutrient-rich species, or tissues such as seeds, are often more highly defended than less nutritious ones. Plants defend their resources mainly via decreasing resource

palatability as described below but also can reallocate resources to roots for storage or directly into reproductive tissues. Moreover, when infestations persist (i.e., when plant defenses are inefficient), plants often initiate emergency actions, such as senescence and cell death of infested tissues to isolate the attacker from the remaining healthy tissues and to deprive it of food. Let it be noted that, despite all defenses, plants are often not fully successful in eliminating an attacker.

Constitutive Plant Defenses and Herbivore Countermeasures

The plant surface provides many barriers against herbivory. The surface texture and composition of the cuticle affects herbivores' ability to move on the plant surface; slick, slippery surfaces are more difficult to adhere to or hamper movement. Some arthropods use silk or sticky secretions to move about on the plant. Thorns are obviously obstacles but may be more effective against larger herbivores than against arthropods. Trichomes (epidermal hairs) are similar to thorns but smaller and so effective as barriers against smaller animals. Some arthropods are able to avoid damage from barbed or hooked trichomes by covering these over with silk meshes or biting off the ends. Specialized glandular trichomes are not only physical barriers but also produce defensive chemicals, such as fast-acting sticky substances that trap the herbivore, or toxic, repellent, or deterrent substances that reduce or prevent further herbivory. As examples, a damaged glandular trichome of wild potato releases terpenoid substances identical to aphid alarm pheromones, motivating other aphids to stay away, and the sugars ingested by caterpillars on *Nicotiana attenuata* are hydrolyzed and released as volatiles that attract predatory ants.

Approximately 10% of angiosperms produce latex or resin or similar exudates. Latex is usually rich in toxic chemicals and has been compared with animal venom. Among the compounds found in latex are toxic alkaloids (for example, morphine in poppy latex) and Cys proteases. Latex-producing plants include the rubber tree (*Hevea brasiliensis*), poppy (*Papaver somniferum*), papaya (*Carica papaya*), and milkweed (*Asclepias* spp). Latex is stored under pressure in vein-associated lactifers. When lactifers are bitten, latex is extruded. Arthropods that feed on latex-producing plants can avoid the latex by biting through veins, often via leaf trenching at an upstream point, causing the lactifer to empty. Downstream of the cuts, the herbivore can feed unmolested by latex. Vein cutting and trenching are behavioral countermeasures.

Plants constitutively produce many antiherbivorous chemicals, but because many of these compounds, such as nicotine, are induced to accumulate more abundantly in response to herbivory, they will be discussed further below.

INDUCED DEFENSES AND INSECT COUNTERMEASURES

Perception of Herbivory

Venus flytraps (*Dionaea muscipula*) have tiny hairs that when touched trigger trap closure. Even without these specialized

hairs, plant surfaces are sensitive to touch, probably through touch-sensitive ion channels; plants have been shown to react to the pressure of insect footprints. Plants can also perceive secretions from arthropod oral and reproductive tissues. Feeding behavior is recognized through physical damage as well as the chemical components (elicitors) produced as a result of herbivory, which include insect saliva-derived chemicals but also partially digested plant materials. Volicitin was isolated from the oral secretions of beet armyworm (*Spodoptera exigua*) and is a plant-derived fatty acid conjugated to Gln in the insect midgut before regurgitation. Upon recognition of volicitin, plants upregulate the formation and release of volatile compounds that attract parasitic wasps that parasitize the herbivores. Another class of lipid-based elicitor, the caeliferin, seems to be limited to the *Caelifera* (grasshoppers). A plant-derived peptide elicitor, inceptin, has been identified. Inceptin is a proteolytic cleavage product of a chloroplastic ATP synthase (i.e., it is of plant origin but formed by the insect) and can be perceived by the plant when the insect regurgitates its food. Like volicitin, caeliferin, and inceptin are herbivore-derived signals that induce plant direct and indirect defenses.

Plants respond defensively to arthropod egg laying (ovipositing). Plants sense physical damage as well as insect compounds exuded during ovipositing. Examples include bruchins, which have been isolated from reproductive secretions of the pea weevil (*Bruchus pisorum*) and antiaphrodisiac substances transferred by the male insect to the female insect during mating, of which trace amounts come into contact with the plant after the female has deposited her eggs. Plants respond to oviposition by producing substances that harm the larvae after egg hatching and volatile compounds to attract parasitoids.

Induced Defense Responses

Induced plant defenses are primarily produced at and near the tissues that are damaged by the herbivore (referred to as the local response) but can also occur in distal, undamaged tissues of the same plant (referred to as the systemic response). (For more on the molecular bases of plant systemic signaling, see Teaching Tools in Plant Biology articles on small RNAs, jasmonates, and salicylates.) Induced responses to herbivory include the induction of genes involved in synthesis of terpenes, alkaloids, and other defense compounds as described below, genes involved in damage repair, including callose synthase and peroxidases, and increased trichome density. Herbivory also induces the accumulation of proteins or compounds with antinutritive properties, including proteinase inhibitors that interfere with gut enzymes that herbivores need for nutrient absorption.

Many induced plant defense responses are mediated by the phytohormones jasmonate, ethylene, and salicylate. In a first approximation, jasmonates and ethylene accumulate in response to wounding or to chewing herbivores, whereas a cocktail of jasmonates and salicylates are induced in response to piercing herbivores. Jasmonate is particularly important in combating herbivory. Its most active form is an amino acid conjugate, JA-Ile, which derepresses transcription factors and induces defense gene expression. Some antiherbivore defenses also depend on

salicylate-related signaling, but the active form of this hormone is not yet known. (The signal transduction pathways downstream of these hormones have been described in other Teaching Tools in Plant Biology.) The induction of system-wide defenses involves hormones and other systemic signals. The volatile compounds ethylene, methyl jasmonate, and methyl salicylate accumulate in response to wounding and herbivory and are thought to contribute to systemic defense signaling and also to participate in indirect defense responses.

Herbivore adaptations to plant defenses include interference with the biosynthesis of toxins and the plant's signal transduction pathways. For example, an enzyme in insect saliva (glucose oxidase) that produces H₂O₂ interferes with jasmonate-mediated induction of nicotine synthesis in *Nicotiana* species, and whiteflies and mites disable the plant's ability to establish defenses via jasmonate signaling. Through these countermeasures, the plant becomes a better food source so the mites and insects develop faster and produce more offspring, and the plant ceases the release of volatiles that could attract natural enemies.

Constitutive and Induced Secondary Metabolites and Herbivore Countermeasures

Plants are amazing chemical factories. At least 80% of all known natural compounds have a botanical origin, and collectively plants are estimated to produce more than 100,000 different compounds. One function of secondary metabolites may be to balance carbon and nitrogen assimilation. However, much of this diversity is believed to have arisen for defensive purposes, with the acquisition of herbivore (or pathogen) tolerance being a significant force driving diversification. Tolerance is due to reduced sensitivity to the defensive phytochemicals, which occurs very frequently. Mechanisms of tolerance include a modification of the toxin's target enzyme, enzymatic degradation of the toxin, sequestration of the toxin, or rapid excretion.

The biochemical pathways involved in defense compound synthesis are considered components of plant's secondary metabolism, which augment the core pathways of primary metabolism that are essential for growth, development, and reproduction. (However, there can be considerable overlap between primary and secondary metabolism.) Among other roles, secondary metabolic pathways contribute to direct plant defenses, indirect defenses, and plant-pollinator interactions. In a landmark article, Fraenkel (1959) identified "the raison d'être of secondary plant substances" as "to repel and attract insects," which laid the foundation for the study of plant chemical ecology. Most secondary compounds can be structurally categorized as nitrogen containing, phenolic, or isoprene derived but can also occur as conjugates of these.

Nitrogen-Containing Compounds

Nitrogen-containing compounds can be directly toxic, like alkaloids, or toxic after enzymatic modification, like glucosinolates and cyanogenic glucosides. Alkaloids affect diverse tissues and functions, including the animal nervous system, and can decrease the appetite. Many are toxic to humans as well as

arthropods. Familiar alkaloids are nicotine (*Nicotiana* spp), morphine (*P. somniferum*), caffeine (*Camellia sinensis* and *Coffea* spp), and cocaine (*Erythroxylum coca*).

Glucosinolates are characteristic for the Brassicaceae (cabbage) family and sometimes called mustard oil glucosides. The tingling sensation that accompanies eating mustard (made from seeds of various members of the Brassicaceae), horseradish (*Armoracia rusticana*), and wasabi (*Wasabia japonica*) comes from the glucosinolates. They are nontoxic until acted upon by a myrosinase enzyme, the action of which produces thioglucose, sulfate, and an unstable intermediate, which rearranges spontaneously to produce several toxic and unpalatable degradation products, including isothiocyanates. The myrosinase enzyme is stored in different plant cells than the glucosinolates, and they only get mixed when herbivores start chewing on these tissues. This glucosinolate-myrosinase defense system is referred to as the mustard oil bomb. Although many arthropods avoid glucosinolate-containing plants or plant parts, the ability to defuse the mustard oil bomb has arisen several times in specialist species. As examples, the diamondback moth (*Plutella xylostella*) produces an enzyme that modifies the glucosinolate substrate, making it resistant to hydrolysis by myrosinase, and the Pieridae butterflies produce a protein that shifts the hydrolysis to release nitriles instead of the more toxic isothiocyanates. Cyanogenic glycosides are similarly nontoxic secondary metabolites that upon damage-mediated cellular mixing are hydrolyzed to produce toxic cyanide. Cassava tubers are important staple foods in much of the world but contain a high level of cyanogenic glycoside and require careful processing to render them nontoxic. Both the glucosinolate metabolic process and cyanogenesis lead to the release of distinct volatiles, thiocyanates, and oximes and nitriles, respectively. Their formation can be induced by jasmonate, and some of these substances are attractive to several natural enemies of herbivores.

Phenolic Compounds

Phenolic compounds include hydroxylated aromatic rings and are derived from carbohydrates. Plants produce thousands of different phenolic compounds that have many diverse roles in plant defense and protection. As many phenolics do not contain nitrogen, they are particularly important defense compounds for plants growing in a nitrogen-limited environment. Defense-related phenolic compounds include cell wall components, pigments, flavonoids, feeding deterrents, and noxious compounds. Furthermore, plant phenolics give flowers their color through flavonoids (e.g., anthocyanins that are red-purple) and their smell through benzoates, and these compounds are derived from the same pathways and regulated by similar transcription factors. Like phenolics, floral nectar and extrafloral nectar are also products of carbohydrate metabolism.

Isoprene-Derived Compounds

Terpenes are hydrophobic compounds derived from five-carbon isopentane units that originate from fatty acids. Low molecular weight terpenes, such as limonene, menthol, and

pinene, are volatile and contribute to direct and indirect defense responses. Plant essential oils are rich in terpenes and while many of these have antiherbivore or antipathogen properties, some are used by people as flavoring agents and scents. Larger terpenes include diverse feeding deterrents and toxins, including the widely used natural insecticide pyrethrin. Terpenes, together with benzoates, are constituents of flower odors but are also typically released as volatiles from damaged green plant tissues during herbivory and can influence the behavior of arthropods. For example, (*E*)- β -farnesene can repel aphids, and β -caryophyllene can attract entomopathogenic nematodes, which are endoparasites of plant-eating nematodes.

Case Studies: Tolerance and Detoxification, Sequestration, and Mimicry

Cardenolides, also known as cardiac glycosides, are steroids conjugated to sugars. In vertebrates, cardiac glycosides affect the heart muscle through interfering with the action of the Na^+ , K^+ -ATPase. They are highly toxic but in very low doses can correct cardiac arrhythmias; digitoxin is a cardiac glycoside derived from foxglove (*Digitalis purpurea*). Milkweed (*Asclepias* spp) produces the cardiac glycoside ouabain, an efficient defense compound. The larvae of monarch butterflies (*Danaus plexippus*) are able to eat milkweed leaves and are specialized on the milkweed family. The monarch's ouabain tolerance is conferred by a single amino acid substitution in the ouabain binding domain of their Na^+ , K^+ -ATPases. Phylogenetic studies show that some unrelated milkweed feeders have acquired the same substitution (convergence), but other mechanisms for ouabain-tolerance have also arisen. Interestingly, monarch butterflies actually accumulate ouabain within their own bodies, which in turn protects them from being eaten by carnivores. However, two major predators are able to eat monarch butterflies, black-backed orioles (*Icterus galbula abeillei*) and black-headed grosbeak (*Pheucticus melanocephalus*). This ability involves behavioral adaptations (eating the less toxic parts and preferentially eating males that accumulate less cardiac glycoside than females), and the grosbeak additionally may have developed a resistance to the toxin. Unrelated nontoxic viceroy butterflies (*Limenitis archippus*) mimic the coloration of the monarchs, allowing them to escape predation.

Heliconius butterfly larvae are specialist feeders of *Passiflora* passion flowers and are insensitive to their wide variety of metabolites, including cyanogenic glycosides and alkaloids. Most *Heliconius* butterflies are toxic or unpalatable to predators because they sequester the *Passiflora* toxins. The observation that the unpalatable *Heliconius* butterflies share a strong resemblance with the also unpalatable *Melinaea* butterflies contributed to the ideas that mimicry (i.e., unpalatable organisms looking alike or palatable organisms looking like unpalatable ones) could be advantageous. Moreover, *Heliconius* larvae are cannibalistic, and female butterflies are very careful to avoid laying their eggs on an already occupied leaf. Many *Passiflora* produce egg mimics, structures that

resemble *Heliconius* eggs and that effectively deter butterflies from ovipositing.

Case Studies: Aphids and Whiteflies – Phloem-Feeding Insects

Phloem-feeding insects, such as aphids and whiteflies, are major agricultural pests. They remove photosynthate from the plant, but they also are vectors of viral disease, and their sweet honeydew excrement drips onto plant tissues and provides a substrate for proliferation of pathogenic fungi. Because they insert slender stylets into plant tissues, wounding can be minimized, making it more difficult for the plant to detect their presence than chewing herbivores that inflict open wounds. Phloem tissue has a wound-healing response that includes aggregating protein bodies and deposition of the polysaccharide callose. Some, yet unidentified, components of the saliva of phloem-feeding insects suppress defenses, for example, the phloem-specific defenses so that the insect is able to feed continuously from the same free-flowing vascular bundle. These arthropod compounds that interfere with the plant's defenses are often called effectors, by analogy to effectors produced by pathogenic microorganisms.

Many facets of the plant's response to aphids and whiteflies more closely resemble the defense responses to microorganisms than to chewing insects. For example, as mentioned before, the hormonal response of plants to stylet feeders is reminiscent of that to pathogens. Furthermore, an *R* gene (*Mi-1.2*) that confers resistance to aphids, whiteflies, and a nematode has been identified that is similar to the *R* genes that confer resistance to microbial pathogens. A related *R* gene confers resistance to another phloem-feeding insect, the brown planthopper pest of rice.

There is still a lot to learn about how arthropods manipulate their host and evade its defense responses. The green-peach aphid (*Myzus persicae*) is a generalist feeder that feeds on plants in more than 50 families, including *Arabidopsis thaliana*, whose outstanding genetic resources are contributing to an understanding of plant responses to phloem-feeding insects. In 2010, the genome sequence of the pea aphid was completed. We are on the threshold of a new understanding of plant–arthropod interactions facilitated by the power of genetics and genomics.

PLANT–ARTHROPOD ALLIANCES

The diversity of plant defense mechanisms and herbivore countermeasures is huge, but these interactions are complicated and enriched further by the mutualistic alliances arthropods form with plants, as allies against herbivores and as mobile vectors to carry their pollen.

Alliance #1: Plants and Carnivorous and/or Parasitoid Arthropods

The first major mutualistic alliance is formed when plants are attacked by herbivores and is mediated primarily via the pro-

duction and aerial release of herbivore-induced volatile chemical compounds. Predatory arthropods seeking prey, or parasitoid arthropods seeking hosts for reproduction, can use these odors to locate plants infested with herbivorous arthropods. Through this indirect defense, the plant rids itself of the herbivores because the carnivorous arthropods can eat the herbivores, or the parasitoid arthropods can lay eggs within them, leading to their ultimate death. This alliance is precarious because other undesirable arthropods can be attracted to these odors as well. For example, the odors can attract still other carnivores that may eat the beneficial carnivores or parasitoids. Furthermore, other food-seeking or mate-seeking herbivores can be attracted to these odors, increasing the attack. Finally, the allied arthropods must be able to withstand the plant's antiherbivory defenses, such as sticky trichomes and slippery surfaces. Some plants form longer-lasting and stable alliances with predatory arthropods by providing them with domatia (homes for the arthropods) and specialized food sources such as extrafloral nectar.

Volatile Compounds

Plants continually broadcast updates about their physiological and reproductive status throughout their ecosystem. Almost 20% of the photosynthetically fixed carbon is released from the plant as volatile compounds, the ecological importance of which is only recently being realized. Much of our understanding of the effects of volatiles on arthropod behavior comes from studies using a Y-tube olfactometer, which provides a foraging arthropod with a choice of two airflows carrying plant odors. Advances in our ability to detect these compounds via analytical techniques that are increasingly easy to use and afford and our ability to experimentally manipulate their production (i.e., via synthetic mimics or through transgenic or mutant plants) are revealing the complexities of this fascinating volatile world. The organic volatiles released from green tissues (leaves) are predominantly 6-carbon-long alcohols, aldehydes and their esters, fatty acid-derived terpenes, and phenolics. Shoot-released volatiles repel herbivores, attract pollinators and seed dispersers, convey information to other plants, and attract predatory or parasitoid organisms. The roles of the volatiles under healthy conditions are diverse and not always well understood: isoprenes are implicated in thermotolerance and some terpenes probably serve as constitutive toxins that are stored in glandular trichomes. Others may function as softeners of resins and evaporate upon wounding to allow resins to harden. Herbivory causes a strong increase in the emission of volatiles, both pre-formed substances released due to tissue damage and also newly synthesized compounds, but jasmonate-deficient tomato (*Solanum lycopersicum*) plants fail to induce herbivore-induced volatile compounds. Plant-produced volatile compounds have many effects on arthropods, a few of which are described below. Furthermore, experiments are underway to determine if crop plants can be made resistant to herbivory through alterations of the volatile compounds they produce.

C₆-Volatiles or Green Leaf Volatiles

The C₆-volatiles are also called green leaf volatiles and constitute the typical smell of damaged grass after the lawn has been

mowed. Green tissues release small amounts of these substances but these amounts increase rapidly upon mechanical damage or herbivory. This increased emission is often of short duration, and since the release is mostly localized to the damaged tissues, the majority may not be produced *de novo*. The C₆-volatiles are produced in two isomeric forms, the *cis*- and the *trans*-forms, and the ratio of these two isomers released from wild tobacco (*N. attenuata*) changes from *cis* to *trans* when the specialist herbivore *Manduca sexta* chews on its leaves. The chemical shift seems to be caused by an enzyme in the insect's saliva. Predatory insects are attracted to the *trans*-form. Thus, the herbivore reveals itself to the predators through the action of its salivary enzymes, and this signal is produced very rapidly, before the production of other herbivore-induced plant volatiles. The question why this property of *Manduca*'s saliva has not been eliminated by natural selection is still open, but the *cis-trans* conversion may have a simultaneous beneficial functions for the caterpillar (e.g., since the *trans*-form is highly toxic to several disease-causing microorganisms).

Terpenoids

Terpenes from tomato are used by parasitic plants (*Cuscuta*, dodder) to locate their host, but most terpenoids appear beneficial to plants as their presence is strongly associated with enhanced plant attractiveness to natural enemies of herbivores. For instance, transgenic *Arabidopsis* transformed with a strawberry terpene synthesis gene produced more nerolidol and became thereby more attractive to predatory mites, while maize varieties supplemented with a gene to make it produce β-caryophyllene became more attractive to entomopathogenic nematodes that kill root-feeding insect larvae.

Phenolics

Most volatile phenolics are produced by flowers to attract pollinators, including the potent attractor methyl benzoate. Methyl salicylate is a volatile phenolic emitted from green leaves. Herbivory leads to increased methyl salicylate emission in a jasmonate-dependent manner. Methyl salicylate can be converted to salicylate to induce defense responses and can be transmitted to other plants, inducing their defense responses. However, many herbivorous and carnivorous arthropods are attracted to methyl salicylate; hence, its effects on plant defenses are complex.

Case Studies: Plant–Carnivore Alliance

Spider Mites and Predatory Mites

Spider mites (*Tetranychus urticae*) are stylet-feeding generalist herbivores on over 900 plant species in 124 plant families and are notorious pests on tomato. An infestation usually kills the plant because the mite population increases so rapidly; adult female spider mites produce over 50% of their body weight in eggs per day. Hence, spider mites are a well-known pest species in agriculture and horticulture. Some plants are resistant to spider mites, and these usually are plants or plant varieties

with a high density of trichomes, especially glandular trichomes, that interfere with the ability of the tiny, 0.5-mm-long mite to move around on the plant.

Spider mites feed from the leaf mesophyll, predominantly parenchyma cells, by piercing the cells and consuming their contents. Plants activate jasmonate and salicylate defenses rapidly after feeding starts, but spider mites frequently become insensitive to these direct defenses. Mite infestation also causes plants to induce the production of volatile compounds, including the terpenes linalool and ocimene and methyl salicylate, which are attractive to the specialist predatory mite *Phytoseiulus persimilis*. As described earlier, plant volatile signals can be quite variable due to abiotic conditions and plant age, but the predatory mites appear to rapidly learn to associate host plant odors with the absence or presence of prey, making them flexible in environments where signals can change over time.

Studies show that there is considerable phenotypic variation within natural spider mite populations. Within such populations, some individuals are resistant to direct defenses, while others are not, and some induce while others suppress the plant's direct or indirect defenses. The genetic diversity and the ability to suppress host responses contribute to the ability of the species to adapt to a very broad host range.

Acacia and Ants

Some plants form ongoing mutualistic partnerships with predatory arthropods, employing them as bodyguards in advance of any attack. Over 100 genera of plants live mutualistically with ants and are known as myrmecophytes (ant plants). The most well known and classically studied example of this form of plant mutualism is that of the acacia (*Acacia* spp) and the *Pseudomyrmex* ant. The plant provides the ants with food from extrafloral nectaries and also specialized lipid-rich food bodies (Beltian bodies) for which no function other than to feed the ants has been found. The ants live within swollen thorns they have hollowed out, their domatia, and protect their host from herbivory by arthropods as well as vertebrates and from encroachment by other plants.

Alliance #2: Plants and Pollinators

The second major mutualistic alliance between plants and arthropods concerns pollination, in which plants harness arthropods' ability to move freely to enhance the distribution of their gametes and progeny. The origins of pollination are found in herbivory and precede the emergence of flowering plants and their major pollinators; spores, seeds, and pollen are abundant in arthropod coprolites much older than angiosperms. In this alliance, the plant enhances its reproductive success via targeted pollen distribution by rewarding visiting arthropods with nectar. The plant-pollinator alliance is primarily controlled by the plant. The plant controls the absence or presence of open flowers, the signals to advertise them, and the distribution of nectar, which plants usually provide only in small amounts to keep the pollinators moving between flowers. Plants must work hard to keep the interaction net-beneficial since arthropods may try to rob the

nectar without loading pollen, may continue to eat nectar also after pollination, may transmit the pollen to an inappropriate host, may damage the flower or cause infections, or they or their offspring may eat the plant since many pollinators also lay their eggs on the plants they pollinate.

Flowers affect the searching behavior of arthropod pollinators through visual and olfactory-gustatory cues. Visual cues include size, shape, symmetry, colors, and patterns. Olfactory cues include flower fragrances, and gustatory cues are provided by nectar, mainly its sugars and amino acids. After pollination, most flowers quickly induce petal senescence and stop producing nectar and volatile odors to put an end to their attractiveness. Hence, from the perspective of a single flower, the plant-pollinator alliance is a brief encounter, not a long-term relationship, and, as described below, a plant may even “divorce” a favorite pollinator if its behavior starts to degenerate toward herbivory.

Plants and Pollinators Have Evolved Physiological Compatibility

Visual Cues That Attract Pollinators

The size, shape, symmetry, colors, and patterns of flowers attract and facilitate the interaction with pollinators. The color of a flower is correlated with the visual field of its pollinators. For example, bee vision is shifted to shorter wavelengths than human vision, meaning that they can see UV light, but their ability to see longer-wavelength red light is limited. Color vision of bees was discovered by Karl von Frisch using artificially colored cards and sugar water, and who in 1973 received a Nobel Prize for his work on vision, olfaction, and orientation behavior of bees. Most species of moths are nocturnal, and many flowers pollinated by nocturnal moths are white or pale yellow and heavily scented. Hummingbird-pollinated flowers are often red. Many flowers produce patterns of spots and stripes called nectar guides to help the pollinator identify the position of nectar sources. The surface texture of the petals not only helps the pollinator to grip onto the flower, but also affects the perception of the flower color. Some orchids have evolved extremely specialized shapes, including those shapes that mimic the female of pollinating insect and stimulate mating behavior from the males; this has become known as sexual deception.

Olfactory-Gustatory Cues That Attract and Repel Arthropods: Scents and Nectars

Flowers produce scents and sweet nectar to attract and reward pollinators. Volatile flower compounds include predominantly benzenoids (e.g., methyl benzoate) and terpenoids [e.g., isoprene, (S)-linalool]. Many scent compounds that attract pollinators are synthesized in petal epidermal cells. Although we associate flowers with sweet smells, some flowers attract pollinators by producing odors we find repellent. For example, *Arum* lily pollinators are attracted to their rotting-flesh smells,

and ammonia and sulfur-containing compounds attract carrion-eating beetles and flies.

To fully understand the significance of a plant’s olfactory cues, we need to know something about the arthropod’s olfactory perception. Compared with vertebrates, arthropods seem to have fewer olfactory receptor cells, but some of these are highly sensitive to specific compounds. As examples, the fruit fly *Drosophila melanogaster* is quite sensitive to compounds produced in rotting fruit (on which it lays its eggs), and moths are particularly sensitive to some terpenoids produced by the plants they pollinate. Interestingly, the attractiveness of a compound depends on the total composition of perceived compounds. As an analogy using human taste perception, the repellent bitterness of chocolate becomes attractive when combined with sweetness. Although a few chemical compounds serve as attractants or repellents for arthropods on their own, others seem to only elicit a response when provided in very specific combinations.

Nectar is a sugar-rich liquid produced in floral nectaries (although some gymnosperms also produce nectar as an enticement for pollinator services). Floral nectaries have evolved independently several times and are highly diverse in their structure and position. Nectar can be produced in epidermal tissues such as trichomes or secreted from subepidermal tissues, and some nectaries secrete nectar through modified stomata. Many flowers accumulate nectar at the base of a long spur. The length of the spur correlates with the length of the pollinators tongue; short-tongued bumblebees pollinate short-spurred columbine flowers, whereas long-tongued hawkmoths pollinate long-spurred columbine. Darwin famously predicted that the very long-spurred orchid *Angraecum sesquipedale* would be pollinated by a moth with an equally long tongue; 40 years later, the pollinating moth (with a 22-cm tongue) was identified. The chemical composition of nectar is quite diverse. All nectar contains sugar, but nectar can also include amino acids, volatile compounds, defensive compounds, antimicrobial compounds, and defense proteins. Volatile nectar compounds can act as attractors, repellants, or as selective filters for pollinators.

Case Studies: Plant–Pollinator Interactions

The garden snapdragon (*Antirrhinum majus*) has well-developed genetic resources and has been a model organism for studies of evolution and development as well as interactions with arthropods. *Antirrhinum* flower petals are formed so that the stamen and pistil are inaccessible to most insects, but the weight of a heavy bumblebee landing on the lower petals opens them. The availability of mutants with diverse floral characteristics has allowed for studies of pollinator preferences between flowers that differ in a single gene or trait. Through this approach, it has been found that pigmentation patterns and intensity affect pollinator visits and that the shape of epidermal cells affects the bee’s perception of the underlying colored cells. Surface texture is also important in pollination; for example, experimental studies show that bumblebees need a rough petal texture to grip onto as they sip nectar.

In petunia (*Petunia* spp), different species are specialized to attract different pollinators. For example, *Petunia axillaris* flowers are white, strongly scented, and store their nectar at the base of a long tube, making them well suited for pollination by moths. *Petunia integrifolia* are purple, with little fragrance, and store their nectar at the base of a short tube, making them well suited for pollination by bees. *Petunia exserta* are red, produce abundant nectar, and have exerted sexual organs perfectly placed to dust with pollen the head of their pollinating hummingbirds. Because these are closely related species, it has been possible to use genetic approaches to identify loci that correlate with specific pollinator cues and to create hybrid lines that send mixed messages. Not only are these experimental studies useful in determining which pollinator cues are most important, but they provide excellent opportunities to experimentally test our assumptions about plant–pollinator coevolution.

Figs (*Ficus* spp) and fig wasps of the family Agaonidae need each other for reproduction. Their obligate mutualism seems to have arisen ~90 million years ago, through a single event in each partner's lineage. It has often been said that each species of fig is pollinated by a unique species of wasp, but there are exceptions to this generalization. Figs need specialized pollinators because their flowers are held within an enclosed inflorescence called a syconium. The fig wasps need to crawl through a small hole into the syconium where they pollinate the flowers (some syconia contain both male and female flowers, whereas others contain only male or female flowers). The female wasps lay their eggs in the female flowers, and the emerging wasp offspring pick up pollen from the male flowers while leaving the syconium that they then transmit to other female flowers.

M. sexta (tobacco hornworm) larvae feed on wild tobacco (*N. attenuata*) and are able to sequester and secrete nicotine and so avoid its toxicity. *Manduca* is also the major pollinator of *N. attenuata*, leading to a situation in which the plant must deter the larval form but attract the adult form of this insect. The chemical ecology of this interaction has been under scrutiny for many years and has revealed the extent to which plants can fine-tune their chemical signals. For example, as a moth-pollinated plant, *N. attenuata* flowers open and produce the strong moth attractant benzyl acetone at night. At the site of a long-term field study, there was a particularly fierce attack of *Manduca* caterpillars one year, which coincided with a large number of the flowers opening in the morning, but the timing of benzyl acetone production was unchanged. Thus, by being open in the morning, the flowers were less accessible to their nocturnal pollinators and also less attractive to them (we described this earlier as “divorcing” the pollinator). Nevertheless, these flowers were pollinated by an opportunistic hummingbird. By being less attractive to the adult moths, the plants escaped egg deposition and reduced their ensuing losses to larval herbivory. This study indicates that sometimes corrections and realignments are needed to maintain a balanced relationship between organisms.

Further studies of this system revealed another mechanism by which the plant controls the outcomes of its pollinators. Nicotine deters herbivory, even by tolerant *Manduca*. Through study of plants in which nicotine biosynthesis was blocked by RNA

interference, nicotine was also shown to restrict the consumption of floral nectar by *Manduca* and hummingbirds as well as nectar-robbing insects that eat nectar without moving pollen. Because nicotine in nectar causes the pollinators to spend less time visiting each flower, the pollinators visit more flowers. Thus, although it is a deterrent to pollinators, nicotine is essential for maximum reproductive success; nicotine ensures that the plant gets the maximal pollination service for minimal nectar production.

CHEATERS, DECEIVERS, AND THIEVES

Organisms evaluate their biotic and abiotic environment on the basis of cues. Some of these cues are signals: they are produced by other organisms to establish an interaction. These signals contain information as, for example, some plant volatiles signals say to a carnivorous arthropod or a potential pollinator “you can find food here.” It is convenient to describe some of the interactions between plants and arthropods as alliances, but as stated earlier, most organisms are functioning purely in their own self-interest due to natural selection. Hence, it could be beneficial for a plant to produce flowers that signal the presence of nectar while actually not containing nectar since the energy saved could be used for reproduction. Therefore, dishonest individuals producing false signals, cheaters, can emerge occasionally and be successful within honest communities albeit only temporarily when their frequencies still are relatively low. Natural selection also selects for signal honesty in interactions in which different species are mutually dependent because dishonesty of one will cause the other to either go extinct or abort the interaction. When cheaters or freeloaders have a higher fitness than noncheaters, their frequency in the population will increase over the generations, but as honesty becomes rarer, the benefits of cheating will decrease proportionally. Moreover, if the organism that is cheated upon has the ability to learn, as arthropods do, it may rapidly begin avoiding the cheater, thereby equivalently rapidly selecting against it.

As an example, in a plant–carnivore alliance, herbivore-induced volatile compounds are effective protection against herbivores as long as the carnivore responds to them. If a plant produces these compounds in the absence of herbivores (i.e., it “cries wolf”), it may gain in the short term by recruiting bodyguards that prevent any damage from herbivores. However, the cheating plant also weakens the alliance; ultimately, the carnivores learn to ignore these signals or their response will no longer be selected for. In principle, cheaters will not necessarily destroy the alliance; ultimately, new signals should evolve that honestly and effectively recruit the carnivores, until they themselves are eroded again by cheaters. Hence, in the majority of cases, cheaters and freeloaders will occasionally emerge and disappear over the generations of the species in a frequency-dependent manner. This is one of the reasons why large-scale improvement of crop protection via transgenic plants that “cry help” all time, even when not infested, is often questioned since natural enemies may rapidly learn to avoid these plants or be selected to do so.

The plant–pollinator alliance is also fragile and susceptible to thieves and deceivers, the latter referring to species that mimic

signals from other species to their own benefit. Some flowers recruit pollinators deceptively, either by mimicking a female arthropod or by mimicking a nectar-producing flower species but not themselves providing nectar. However, it was found that a honeybee's sensitivity to nectar rewards with different qualities can bias its response to floral scent. Doing so, the bee may select for flowers that produce odors that reliably indicate the presence of nectar and select against flowers releasing detectable scents when no nectar is present. As described above, cheaters may benefit in the short term but erode the effectiveness of these signals over the long term and ultimately lead to the development of new, honest signals. Arthropods and other animals do not always play fair and regularly steal nectar or pollen without providing a pollination service, which has led to the production of toxin- or deterrent-containing nectar and complex, inaccessible nectaries. And of course, the ultimate deceivers and sources of pleasure to all budding botanists are the carnivorous plants, some of which mimic flowers as a way of attracting their victims; instead of getting a meal, the unsuspecting arthropod comes to be a meal.

AGRICULTURAL APPLICATIONS AND ONGOING STUDIES

The interactions between arthropods and plants have fascinated naturalists and aggravated farmers for millennia. Arthropod-mediated crop loss is a persistent problem. In recent years, Australia has faced the destructive power of huge swarms of herbivorous locusts, and the California wine industry has been crippled by the tiny phylloxera aphid, which has caused millions of dollars of economic losses. The need to protect crops from arthropod herbivory has fueled the development of broad spectrum insecticides, but the outcomes from this approach are decidedly mixed. Pest control measures that harm carnivorous predatory organisms or pollinators are not sustainable or sensible approaches, as pests often develop rapidly insensitivities due to the power of natural selection. Declining honeybee populations have raised awareness of the fragility of the ecosystem in which plants, even crop plants, live. Scientifically and ecologically informed approaches, such as integrated pest management, work within the ecosystem rather than against it or attempt to outsmart it. Our increasing understanding of the relationships between plants and arthropods is allowing us to develop new approaches to control of arthropod herbivory that are sustainable.

Open questions include: What are the long-term environmental effects of plants modified to express Bt toxin constitutively and how will this effective antiherbivory tactic affect predatory arthropod populations? Can we harness the power of plant volatile compounds as repellents to herbivory? Plants that constitutively emit herbivore-induced volatile compounds show reduced damage to herbivory, but will this tactic remain effective over several generations? More fundamental questions include: What are the mechanisms by which some herbivores are able to reduce the effectiveness of plant defense responses? For example, how do aphids interfere with the sealing of vascular bundles or mites and whiteflies with phytohormone production? We have only begun to explore chemical compounds involved

in plant defense, herbivore recognition, and ally attraction; certainly as we explore these further we will identify new candidates for development as pesticides as well as new mechanisms of arthropod resistance and plant–arthropod communication. How are climate changes, including global warming and the increasing concentrations of CO₂ in the atmosphere, affecting plant–insect dynamics in crop fields and natural environments? Finally, given our understanding of the constantly changing nature of plant–arthropod interactions, is it reasonable to imagine we can produce an herbivore-resistant crop plant, or are we, like plants and arthropods, committed to a never-ending cycle of innovations?

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RECOMMENDED READING

(This is a representative list of sources to help the reader access a huge body of literature. We apologize in advance to those whose work is not included.)

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