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Plants and Arthropods: Friends or Foes? (TTPB 18) – Teaching Guide

Overview – Plants are the most abundant terrestrial food sources, and arthropods (insects and arachnids) their most abundant consumer. Plants defend against herbivory through physical and chemical, constitutive and induced defenses. However, herbivores have evolved many ways to circumvent plant defenses. The relationship between plant and arthropods is made more complicated by two alliances. Arthropods provide mobile vectors to transfer gametes from plant to plant, and plants entice and reward them through various measures. Some arthropods are carnivorous and eat herbivorous insects, or parasitize them; the arthropods respond to signals produced by infested plants. These alliances are uneasy and can break down and re-emerge repeatedly. This lecture introduces some of the secondary metabolites involved in plant – arthropod interactions, and case studies of well-known plant – arthropod pairs.

Learning objectives

By the end of this lecture the student should be able to:

- Identify the ongoing conflict and two types of alliances between plant and arthropod, and provide specific interactions of each
- Describe four ways that arthropods can evade plant defenses
- Describe some of the roles of plant volatile compounds in their interactions with arthropods
- Identify each of the levels of a tritrophic interaction
- Describe two ways that flowers attract pollinators, and two mechanisms that minimize nectar theft
- Give examples of specific interactions between plant and arthropod the include arthropod tolerances to plant defenses, carnivorous arthropods, and pollinators
- Describe the short and long term consequences on population of plants, herbivores and carnivores when a plant begins to "cry wolf" by emitting volatile compounds that indicate the presence of herbivores when no herbivores are present.

Study / exam questions (*understanding and comprehension*)

- What are two constitutive ways that plants defend themselves against herbivory?
- How do plants detect the presence of herbivory? How do they differentiate herbivory from wounding?
- Name three functions that trichomes can have in defending against herbivory.
- What is trenching behaviour?
- What is ovipositing, how do plants detect and respond to it?
- What hormones are involved in defenses against herbivory?
- What are secondary metabolites?
- Secondary metabolites involved in defense include nitrogen-containing compounds, phenolics, and isoprene-derived compounds. Give an example of each.
- How do herbivore-induced volatile compounds contribute to indirect defense mechanisms?
- True or False: Pollination services by arthropods are a behaviour that evolved after flowering plants appeared on the earth.
- What are three mechanisms by which a plant restricts damage and herbivory by its pollinators?
- What are three ways that plants attract pollinators?
- What organism would you predict would pollinate a highly fragrant, white flower that stores nectar at the base of a long tube?
- A plant that emits herbivore induced plant volatiles all the time attracts "bodyguard" arthropods that protect it from damage. Given that this plant has an enhanced fitness, why is this trait not more abundant?

Discussion questions (*engagement and connections*)

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- Could plants have evolved independently of animals? How might they be different if they had never encountered an animal?
- It is widely assumed that the origins of pollination lie in pollen herbivory. What are some of the ways plants minimize pollen herbivory and maximize pollen transfer?
- The relationships between plants and pathogens or pests are often described as “arms races”. Is this an appropriate metaphor? Why or why not?
- The diversity of plant defense compounds is amazing and largely unexplored. Many scientists are examining the chemical compositions of plants from threatened environments, before it’s too late. How would you go about screening for “useful” chemicals? Should the countries in which these plants are abundant (mainly tropical and developing) share rights to any products?
- Many gardeners introduce ladybugs into their gardens – why?
- Increasing atmospheric CO_2 levels are likely to alter the carbon-nitrogen balance of plant metabolism. How might this affect their production of defense compounds?
- Some plants produce phytoecdysteroids that are exact replicas of insect molting hormones. How might these compounds benefit the plant?
- Many compounds that produce to deter herbivory are toxic or unpleasant to humans. During the course of selection of plants for food, toxin production has been eliminated, in many cases making our crop plants more vulnerable to herbivory than their wild relatives. Do you think it would be possible to reintroduce these defensive compounds into plants without harming the consumer?
- The case studies of monarch and *Heliconius* butterflies describe two types of mimicry; how do they differ?
- In what ways do plant defenses against piercing insects (such as aphids or whiteflies) differ from those against chewing insects?
- Plants produce many types of volatile compounds for defensive purposes. Choose one to investigate further. What plants produce this compound, and under what conditions. What signals trigger its production, or is it produced constitutively. Is its synthesis tissue-specific? What organisms perceive and respond to this compound?
- Some herbivores including mites and whiteflies are able to interfere with the plants defense responses. Find a research article that describes these herbivore countermeasures. Do we fully understand these adaptations? How might a plant adapt to overcome them?
- How did von Frisch study bee vision? Why is it important to understand arthropod perception of olfactory and visual cues? How would you go about identifying a volatile herbivore repellent that could be used in crop protection?
- Genetically amenable plants like Antirrhinum and petunia are important tools in our understanding of pollinator preferences. In what ways do these studies differ from studies of pollinator preferences using diverse wild populations? Find a research article that examines pollinator preferences using genetic tools and discuss it with your classmates. Would it be possible custom-design flowers to attract different species of pollinators? Could you design a flower that deterred all pollinators, for example to prevent pollen from GM plants from being moved by arthropods?
- Find another example of a mutualistic relationship in which one or both partners can gain a fitness advantage by cheating.
- Plants expressing an insecticidal protein from *Bacillus thuringiensis* (Bt) are highly resistant to herbivory. What efforts are being used to delay herbivore tolerance to Bt? How does the Bt protein affect pollinators and the natural enemies of herbivores?
- Is it reasonable to imagine that we can produce an herbivore-resistant crop plant?

Lecture synopsis

Introduction (1 – 9)
Arthropods cause crop yield losses of 10 – 30% or more every year. How do arthropods damage plants? How do plants defend themselves against herbivory? How do herbivores cope with plant defenses? How do plants establish mutualistic interactions with arthropods including pollinators and their herbivores' natural enemies? Arthropods have been eating plants for more than 400 million years, during which time they and plants evolved increasingly complex and sophisticated systems for eating and avoiding being eaten.

The ongoing conflict: Herbivory (10 - 63)
Herbivores can be highly specialized or generalists, can eat all plant parts and their feeding styles can be broadly classified as chewing or piercing. Some form galls in which they lay eggs.
<u>Constitutive plant defenses and herbivore countermeasures (14 – 23)</u>
Plants and tissues vary in their degree of defensiveness. Plants have physical and chemical defense mechanisms including thorns and trichomes, sticky substances, toxins, deterrents and venom-like latex. Chemical defenses are described in more detail in slides 35 – 51.
<u>Induced defenses and herbivore countermeasures (24 – 34)</u>
Plants perceive herbivory through physical (touch) but primarily chemical means. Several compounds that are strong elicitors of plant defenses have been identified. Some of these are plant compounds that have been modified by insect digestive enzymes, providing unambiguous cues of herbivory. These elicitors induce defense responses through hormone independent and hormone dependent pathways; jasmonate, salicylate and ethylene are the main hormones in defense signaling. Induced defenses include expression of defense-associated genes and also systemic responses. Some herbivores can suppress induced plant defense responses.
<u>Defense chemicals and herbivore countermeasures (35 – 51)</u>
Plants produce >100,000 chemical compounds, many of which have roles in defense. Many are products of a highly diverse set of secondary metabolic pathways, which augment the core pathways of primary metabolism. Some herbivores have evolved tolerance to plant toxins. Defense compounds are classified as nitrogen-containing, phenolic or terpenoid. Nitrogen-containing compounds include alkaloids (e.g. nicotine) and compounds that become toxic upon enzymatic modification, like glucosinolates and Cyanogenic glucosides. Glucosinolates accumulate in cabbage (Brassicaceae) family. The ability to "defuse the mustard oil bomb" has evolved independently several times.
Case study: Milkweeds and monarch butterflies (52 – 56)
Monarch butterflies have a evolved tolerance to the toxic alkaloid ouabain, and some of the monarch's predators have also. A non-ouabain accumulating butterfly mimics the coloration of the monarchs.
Case study: Heliconian butterflies and passion flowers (57 – 59)
Passion flower butterflies can detoxify and tolerate the cyanogenic glucosides, and some of these toxin-accumulating butterflies mimic each other. Passionflowers sometimes produce structures called egg mimic that resemble *Heliconian* eggs which deter ovipositing.
Case study: Aphids and whiteflies, phloem-feeding insects (60 – 62)
Aphids and whiteflies are phloem feeding insects and major agricultural pests. They spread viral disease, and the honeydew they excrete provides a substrate for the proliferation of pathogenic fungi. The sequencing of the genome of the green pea aphid should enhance our understanding of these complex organisms.

Alliance #1 – Plants and Carnivores or Parasitoids (64 – 86)
Herbivore-induced plant volatiles are recognized by predatory arthropods seeing prey, or parasitiod arthropods seeking hosts for reproduction. Parasitoids spend part of their life as a parasite. Parasitoid arthropods lay their eggs within the bodies of the herbivores, killing or weakening them. Tritrophic interactions involve the plant, the herbivore and the carnivore, and information flows between and amongst trophic levels. The ability to assay arthropod responses to volatile

compounds and to detect them and manipulate is revealing the complexity of this fascinating volatile world.

Case study: Spider mites and predatory mites

Spider mites feed on over 900 plant species and reproduce rapidly. Plant induced volatiles are recognized by predatory mites. Within a spider mite population, a large amount of phenotypic variation contributes to this species' ability to adapt to a very broad host range.

Case study: Acacia and ants

Myrmecophytes are plants that live mutualistically with ants. As an example, acacia trees provide their ant hosts with hollowed out thorns as domatia (places to live), extrafloral nectar optimized for the plants nutritional needs, and protein rich Beltian bodies (food bodies). In return, the ants drive away herbivores and encroachment by other plants.

Alliance #2 – Plants and pollinators (87 – 116)

Flowers and pollinators have evolved physiological compatibilities. Flower pigments attract pollinators, flower shapes facilitate pollination, flower fragrances attract pollinators and floral nectar rewards pollinators. The garden snapdragon has well-developed genetic resources and is used for studies pollinator interactions. In petunia, closely related species attract different pollinators, and hybrid lines sending mixed messages can be produced. Figs and fig wasps have an obligate mutualism that is thought to have persisted for some 90 million years. The relationship between *Nicotiana attenuata* and its herbivore / pollinator *Manduca sexta* has been studied for many years and has revealed the delicate balance by which the plant manipulates the arthropod through production of toxins and attractants and availability of flowers.

Cheaters, thieves and deceivers (117 – 123)

Natural selection maximizes reproductive success and dishonesty can do just that, but do organisms that cheat, steal and deceive succeed on the long run? Stealing nectar leads to increased production of toxins in nectar, or sequestration of nectar in inaccessible locations. Crying wolf selects for arthropods that ignore herbivore-induced plant volatiles, weakening the fitness of the cheater. In the long term, mutualists that are honest with their partners are selected for, which has allowed these alliances to persist for millions of years.

The effects of climate change on herbivory (124)

Ongoing questions and studies (125)

Understanding the interactions between plants and arthropods will help us to control herbivore damage to crop plants in a sustainable manner, while protecting the alliances with the herbivores' natural enemies and pollinators.

Slide Concepts

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24 – 34	Induced defenses and herbivore countermeasures Perception of herbivory Signaling and response to herbivory Direct and indirect, local and systemic responses
35 – 51	Defensive chemicals and herbivore countermeasures Secondary metabolites Toxins, converted to toxins, anti-nutritive Some attract pollinators, predators or parasitoids Glucosinolates – the mustard oil bomb, and detoxification schemes
52 – 63	Case studies: Milkweeds and monarchs, Heliconian butterflies and passion flowers, aphids and whiteflies
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87 - 116	Alliance #2: Plants and pollinators Flowers and pollinators evolved physiological compatibilities Bee vision Flower fragrance Nectar rewards Antirrhinum and bumblebee Petunia hybrids Fig and fig wasps *Nicotiana attenuata* and *Manduca sexta*
117 - 123	Cheaters, thieves and deceivers Nectar robbers, Plants that cry wolf, deceivers, carnivorous plants Alliances are tenuous but in the long term honesty is selected for
124	Effects of climate change on herbivory
125	Ongoing studies