Lecture 10. Plant-insect interactions (II)
antagonistic herbivory
overview

• **Brief introduction:** herbivory & arms race

• **Arms / Weapons:**
  – Diversity of plant defenses
  – Diversity of insect offence / counterdefense

• **Signaling interactions:**
  – Signals that plants received from herbivores
  – Signals that insects perceived from plants
Herbivory: who are the herbivorous insects?

- Collembola
- Phasmida
- Hemiptera
- Orthoptera
- Coleoptera
- Diptera
- Lepidoptera
Herbivory: host range

- Polyphagy
- Oligophagy (<3 plant families)
- Monophagy

- Generalist
- Specialist
Herbivory: an arms race

Insects attack plants → warfare → Plants defend against being eaten
The arms race: coevolution

stepwise reciprocal changes

Successful consumer → New defenses
New offenses ← Successful defender

Evolution of offense

Evolution of defense
The arms race: a typical example

1. Insect eats plant
2. Plants make toxin 1
3. Insect resists toxin 1
4. Plants make toxin 2
5. Insect resists toxin 2
6. Plants make toxin 3
7. Insect resists toxin 3
8. Plants make toxin 4
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Arms: diversity of plant defenses

- **Avoidance** --- escape from herbivores, no actual feeding.

- **Resistance** --- reduce fitness of insects after contact

- **Tolerance** --- to stand and take it simply by outgrowing the damage --- compensatory growth
Plant defenses: avoidance

- Escape in time
- Escape in space
- Chemical escape (repellent production, no attractant)
- Morphological escape

- *Heliconius* butterflies avoid laying eggs on plants already occupied by eggs
- Plants *Passiflora* create fake yellow eggs
Plant defenses: Resistance

• Morphological resistance
  – hairs, spines, hook, sticky glands, immobilizing insects or puncturing their body wall

• Chemical resistance
  – Various toxic compounds

• Mechanical resistance
  – squirt-gun
Mechanical resistance: Bursera’s squirt-gun defense

Becerra, J. X., 2003, PNAS 100 (22), 12804-12807
Morphological resistance: hairs and spines
Morphological resistance: thorns

- The pronounced thorns endowed upon the trunk of this tree even can fend off vertebrate herbivores, such as sloths and monkeys.
Chemical resistance: diversity & classification

- **Chronic (quantitative) defense**: Large/complex molecules reduce digestibility / nutrition (tannins, lignins, cellulose, silica, etc).
- **Acute (qualitative) defense**: Small / simple molecules target specific insect system.
  1. Toxic amino acids
  2. Toxic proteins
  3. Proteinase inhibitors (=PIs)
  4. Allelochemicals (=secondary comounds)
     - cyanide, glycosides, alkaloids, terpenoids, saponins, flavenoids, furanocoumarins, indoles, phytoecdysteroids
Chemical resistance: functions of allelochemicals

• by-product and wastes of normal metabolism? (Muller 1970)

• to deter herbivores (Ehrlich & Raven 1964)
Chemical resistance: evidence for defensive roles of allelochemicals

- Toxic effects
- Constitutively high in valuable tissues
- Induced by herbivory
- Costly

Zangerl & Berenbaum: webworm-parsnip chemical coevolution
Chemical resistance: two ways of escalation

Newer & more toxic

Mixture of two or more toxins 1+1>2

Larval performance diet containing xanthotoxin and angelicin separately and in mixture

Zangerl & Berenbaum: webworm-parsnip chemical coevolution
Chemical resistance: indirect defense

Parasitoids & Predators

Herbivores

Plants

Mutualism
Arms: Insect’s offense/counterdefenses

- Behavioral avoidance: selectively choose hostplants, feeding/oviposition choice
- Modify its own behavior, or biochemistry to overcome plant defense
  - Behavioral counterdefense (or offense)
  - Biochemical counterdefense
- Actively manipulate hostplants’s nutrition & defense
Insect’s counterdefenses:
Behavioral offense

- Vein cutting
- trenching
- Leaf rolling
- Mining
- Gardening
- Gregarious feeding
Behavioral offense: vein cutting

*Bursera*’s defense squirt-gun

Specialized *Blepharida*’s counterdefense vein cutting

Becerra, J. X., 2003, *PNAS* 100 (22), 12804-12807
Behavioral offense: trenching

avoid intoxication by trenching the laticifers upstream of their intended feeding site (Wittstock & Gershenzon, 2002)

Larvae of *Erinnyis alope* starting to feed after servering (trenching) a *Carica papaya*
Behavioral offense: leaf-rolling

Berenbaum & Zangerl: webworm-parsnip chemical co-evolution
Behavioral offense: gardening

- Leaf cutter ants (Azteca) use leaf material and flower to culture a fungal garden (facilitate food storage and toxin degradation), which is then used for food.
Behavioral offense: gregarious feeding
(group counterdefense)

- Sunn Pest: gregarious feeding on wheat
- Increases host plant susceptibility
- Pine beetle: calling for help if needed
Insect’s counterdefenses:
Biochemical counterdefense

- Rapid excretion
- Sequestration of toxins
- Detoxification of toxins: cytochrome P450 monooxygenase (P450), esterase, glutathione-S-transferase (GST), etc.
- Target site insensitivity
Biochemical counterdefense: rapid excretion

Experiment:
Nicotine dose in artificial diet → 93% excreted within 2 hours!
Experiment:
Nicotine injected into hemolymph

*Manduca sexta*
Biochemical counterdefense: sequestration

- Unpalatable insects sequestrate allelochemicals for their own defense
- Many also develop warning color or/and gregarious feeding
Biochemical counterdefense: detoxification

Cotton bollworm P450 CYP6B8 can metabolize both allelochemicals and insecticides

Biochemical counterdefense: target site insensitivity

Na+,K+-ATPase is sensitive to ouabain (a cardiac glycoside). In Monarch butterflies a single-point mutation resulted in insensitive ATPase.

Other example: induction of proteases in herbivore gut, which are insensitive of proteinase inhibitors.
Insect’s counterdefenses: manipulate hostplants

- Manipulate plants’ growth & nutrition
  - Induction of plant galls: abnormal structures where gall makers (aphids, wasp, mites, etc.) feed inside

- Manipulate plants’ defenses
Manipulate hostplants: induction of plant galls

Sumac galls

Aphids in sumac galls

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Manipulate hostplants: repress toxin production

GOX = glucose oxidase

Musser et al., 2002, Nature
overview

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Plant-insect signaling interactions

• Are all plant defenses (or insect counterdefenses) expressed (or present) all the time? Why or why not?

• If yes, are they expressed at their highest level all the time? Why or why not?
Plant-insect signaling interactions: “spy” on each other and induction

![Graph showing induced and constitutive defense or counterdefense over time with a lag and decay phase.](image-url)
Plant-insect signaling interactions: constitutive vs. induced defense or counterdefense

**Constitutive**
- Present round-the-clock
- Predictable interactive partners (e.g., specialist herbivores)
- Pre-pay and fix the cost of defense / counterdefense no matter they are needed or not
- Permanent protection. No signal input required in either side.

**Induced**
- Present or up-regulated only when the interacting individuals encounter each other
- Unpredictable interactive partners (generalist herbivores)
- Defer the cost of defense/counterdefense until they are needed. But there is a lag time.
- Temporary protection. Signal input from the other side needed
Plant-insect signaling interactions: signals that plants receive from herbivores and other plants

- **Wounding**: feeding or mechanical damages
- **Herbivore-associated molecular patterns (HAMPs)**
  - Chemicals: Fatty acid-amino acid conjugate (FAC), caeliferins, 2-hydroxyoctadecatrienoic acid, bruchins, and benzyl cyanide
  - Enzymes: Glucose oxidase, β-glucosidase
  - Proteolytic fragments of plant protein or enzymes: e.g. inceptin (ICDINGVCVDA) from plant chloroplastic ATP synthase
- **Talking tree**: volatiles emitted from infested plants
Wounding and HAMPs trigger production of endogenous plant defense signals

- **Plant peptide hormones**
  - Systemin: mainly in the Solanaceae family
  - HypSys pepetides: mainly in the Solanaceae family
  - AtPep1: throughout the plant kingdom

- **Plant defense signaling hormones**
  - JA (jasmonic acid), Ethylene (ET), SA (salicylic acid): well-characterized
  - abscisic acid (ABA), auxin, gibberellic acid (GA), cytokinin (CK), and brassinosteroids (BR)
Signals that plants received from herbivores: Wounding

- Wounding often leads to accumulation of plant defense signal molecules such as **JA**, **salicylic acid (SA)**, and **ethylene (E)**, which are plant hormones.
- Plant defense hormones are systemic signals.
- JA lead to production of the end defense products such as allelochemicals and proteinase inhibitors (PIs).
Signals that plants received from herbivores: **HAMP**

- JA burst
- Ethylene burst

Elicitors modulate defense response

Direct defense: nicotine

Kessler & Baldwin 2002
Signals that plants received: volatiles emitted from infested plants

- Dolch & Tscharntke (2000)

Field experiment: *Alnus*

- Volatile organic compounds (VOCs): terpenes, green leafy volatiles
- Methyljasmonate (MeJA)
- Talking tree
Plant-insect signaling interactions: signals that insects received from plants

• Plant defense compounds (end products)
  – Allelochemicals
  – Proteinase inhibitors (PIs)

• Plant defense signaling hormones
  – JA
  – SA
  – Ethylene
Signals insects received from plants: allelochemicals and protease inhibitors

Li et al., 2002
Signals insects received from plants: plant defense signaling hormone

Li et al., 2002, Nature
Types of plant-insect interactions

- **Mutualism (+, +)**: flower plants/pollinators, plants/ants

- **Antagonistic herbivory (+, -)**: Insects eat plants and plants suffer tissue loss, low survival and reproduction.

- **Antagonistic insectivory (+, -)**: plants eat insects for nitrogen nutrients.

- **Commensalism (+, 0)**: